

ARTICLE

Methods, Tools, and Technologies

Exploring spatial nonstationarity for four mammal species reveals regional variation in environmental relationships

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Funding information

North Carolina Wildlife Resources Commission

Handling Editor: Debra P. C. Peters

Abstract

Broad-scale ecological research on species distributions commonly presumes that the correlative relationships discovered are stationary over space. This is an assumption of most species distribution models (SDMs) that combine observations of species occurrence with environmental characteristics to understand current ecological correlates and to predict distributions based on those relationships. However, ecological relationships may vary spatially because of changes in the environment (i.e., resource availability) or the organism itself (i.e., local adaptation). Discovering this within-species variation typically requires dense datasets over large geographic areas, which are now being provided by the recent proliferation of open-access biodiversity occurrence records. Using nearly 4000 sampling locations from an open-access, state-wide camera-trapping project, we explore the space-varying effects of covariates on the distribution of four mammal species at two scales: region-specific and fine resolution, with the latter estimated using spatially varying coefficients (SVC) models, to understand the scale of spatial variation in ecological relationships. Among the four species tested, the ecological relationships for two were best explained with the regional models, equivocal results for one species, while the SVC model had superior fit and predictive performance for the final species (white-tailed deer, *Odocoileus virginianus*). Spatial nonstationarity was more common in relationships with landscape composition characteristics, such as housing density, than in landscape configuration metrics, such as patch richness density. One of the most appealing results of an SVC approach is not only the improved predictions across large landscapes but also understanding how animals are responding to the environment differently at the management unit level. For example, we found that deer's spatially varying relationship with forest cover was best explained by an interactive effect of deer management units (i.e., differences in deer populations) and predator pressure. These findings lead to a new hypothesis about how deer may be differentially using forested environments across space and could be a promising area of future research. Given sufficient data, accounting for nonstationarity in SDMs can show large-scale ecological patterns

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while also detecting local level changes in animal ecology in areas small enough that management or protection can be readily implemented.

KEYWORDS

spatial nonstationarity, species distributions, species–environment relationships

INTRODUCTION

Broad-scale ecological research on species distributions commonly presumes that the correlative relationships discovered are stationary over space (Miller, 2012). However, as the spatial extent of a modeling increases, the likelihood of heterogeneity in the response and the resulting species–environment relationships varying across space also increases. That is, a fixed set of regression coefficients estimated in a species distribution model (SDM) may not represent the actual space-varying relationships between a response (e.g., animal abundance or occupancy) and environmental covariates (e.g., forest cover) (Figure 1). This is

termed “nonstationarity” and describes variation in the magnitude and/or direction of a correlative relationship across space or time (Rollinson et al., 2021).

Nonstationarity in ecological processes may be a result of external (i.e., environmental) and/or internal (i.e., local adaptation by the organism) factors. External factors may include functional responses to variation in resource availability, differences in predator–prey dynamics, or interspecific competition, whereas internal factors include intraspecific variation and local adaptations. Nonstationarity as a result of varied resource availability could arise when a given environmental feature is completely absent in some parts of the study area but present in other areas, potentially resulting in a varied statistical response because the environmental feature cannot be continually used by all populations in the study area. The relative coverage of an environmental feature could also create nonstationarity. For example, consider the common occurrence of some environmental feature being available only in isolated pockets in some regions but occurring in large, contiguous blocks in others; the statistical importance of this feature could be quite different between regions,

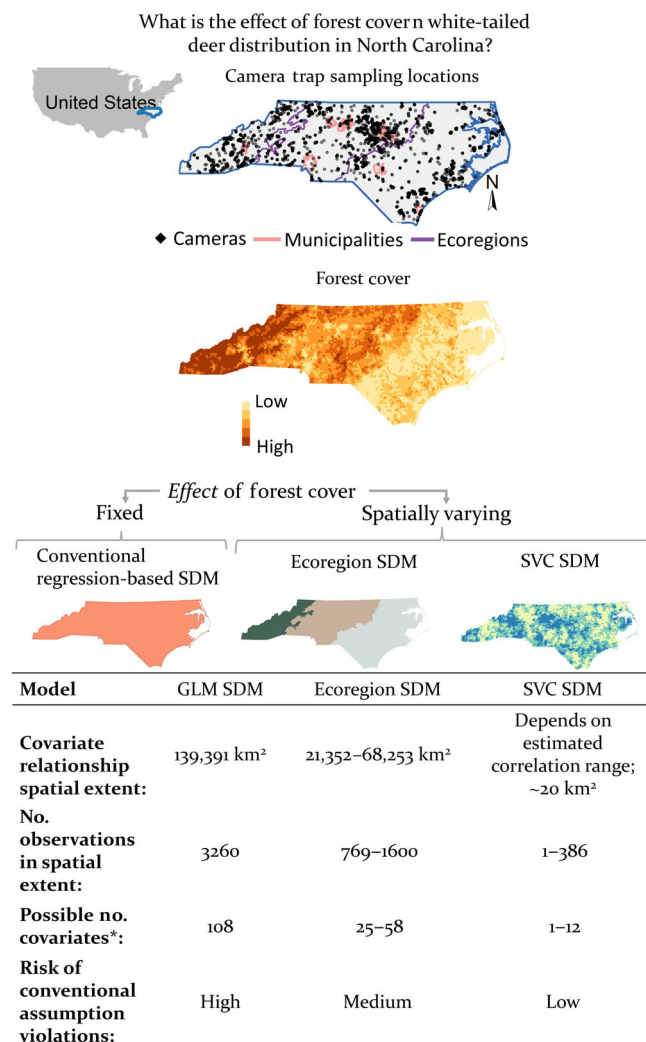


FIGURE 1 Conceptual diagram of nonstationary effects of forest cover on white-tailed deer (*Odocoileus virginianus*) distribution in North Carolina, USA. Conventional regression-based SDM refers to a species distribution model where coefficient effects are assumed to be stationary across space. Ecoregion SDM depicts region-level nonstationarity in the effect of forest cover on deer distribution. A Bayesian spatially varying coefficients model to account for fine-scale variation in covariate effects is represented by SVC SDM. Each scenario has a different spatial extent over which the covariate is assumed to be constant (covariate relationship spatial extent). Changing the scale of analysis also results in different numbers of observations from our empirical dataset that would be available to estimate this effect (number of observations in spatial extent) and thus differences in the possible number of covariates the given number of observations could theoretically estimate (possible number of covariates; * = based on the standard guide of 30 observations per explanatory variable). We also give a qualitative evaluation of the risk of assumption violation for each approach based on the spatial extent and the number of covariates. The inset of North Carolina in the top left represents actual camera-trapping locations ($n = 3678$; black dots) during 2015–2019; the three primary physiographic regions (i.e., ecoregions) in North Carolina are delineated along with municipalities human populations greater than 90,000.

especially where a species is more strongly drawn to the resource when its availability is restricted (Chase & Leibold, 2009; Elton, 1946). Other external factors include predator–prey interactions, where the importance of such interactions vary with space as community composition, relative abundances, and environmental conditions (e.g., connectivity and habitat-mediated predator–prey dynamics) differ across large space, ultimately resulting in varied behavior of the focal organism that leads to ecological nonstationarity (Berger et al., 2001; Gorini et al., 2012; Roemer et al., 2009). Interspecific competition is induced by competing species and the presence/absence of those competitors across large space (and/or a difference suite of competitors across large space); this may result in varied species–environment relationships because of behavioral differences induced by competitors and/or predators (Jones & Barmuta, 2000; Schoener, 1986). In summary, the external factors resulting in spatial nonstationarity may often be due to missing covariates and/or model misspecification, where the pattern is arising because important ecological information is missing. By contrast, internal factors leading to nonstationarity may be a function of phylogenetic differences across a species' range and would indicate a lack of niche conservatism, reflecting recent local adaptation (Wiens & Graham, 2005; Myers et al., 2020; Peterson, 2011).

Spatial nonstationarity is likely common in ecological systems (Bini et al., 2009) but has received little attention in wildlife research (Miller, 2012), in part because more data are typically required to understand space-varying effects compared to traditional approaches assuming stationarity. Fortunately, the accumulation of long-term biodiversity monitoring programs, new digital sensors, and growing citizen science efforts is providing spatially dense animal occurrence records at the continental or global scale (Kays, McShea, & Wikelski, 2020). Coupled with a movement toward open-access data in ecology (Reichman et al., 2011), the wealth of animal occurrence records has prompted a notable increase in the use of SDMs to relate animal observations to environmental conditions and predict how animals will respond to future changes. Several methods to account for nonstationarity in SDMs have been developed, including eigenvector spatial filtering (Griffith, 1996, 2008), generalized additive models (Wood, 2017), geographic weighted regression (GWR; Fotheringham et al., 2003), and Bayesian spatially varying coefficient (SVC) models (Banerjee et al., 2014; Gelfand et al., 2003), each with their own advantages and disadvantages.

Although previous research has warranted further exploration of space-varying effects (Fortin et al., 2008; Shi et al., 2006; Smith et al., 2019), and despite extensive use of GWR (Fotheringham et al., 2003), a number of important ecological aspects are unresolved. Namely, it is unclear which species tend to respond differently across space, which type of

ecological predictors the species are responding to differently (e.g., landscape composition vs. configuration), and whether the magnitude (i.e., strength) and resolution (i.e., fine vs. large scale) of the space-varying effects relate to the ecology of the species so that some general trends arise. Given the breadth of open questions in this area of research, we pursued two problems: the spatial resolution of nonstationarity and exploring the types of ecological predictors in which spatially varying relationships occurred (e.g., landscape composition or configuration metrics). Our primary objective was to (1) identify the spatial resolution at which spatial nonstationarity was occurring (e.g., regional or fine scale) and (2) test for evidence of nonstationarity in effects of landscape composition and configuration (e.g., patch size) on medium-to-large-sized mammals across the state of North Carolina, USA.

We expected that nonstationarity would exist, but it was unclear whether the nonconstant relationships would be best delineated by coarse-scale characteristics such as physiographic regions (i.e., ecoregions) or better described by fine-scale responses (e.g., population level). We expected that the spatially varying effects would differ among species and that they would reflect the ecology of each species. That is, for highly adaptable, generalist species such as white-tailed deer (*Odocoileus virginianus*), northern raccoon (*Procyon lotor*), or coyote (*Canis latrans*), we predicted nonstationarity and the resulting spatially varying relationships would be fine-scale, reflecting localized environmental conditions and the species' ability to use and exploit a wide variety of conditions. By contrast, we predicted that species with a restricted niche breadth or those known to avoid specific environmental conditions would have wide-reaching, consistent responses to environmental conditions (e.g., a specialist). While few true specialists exist in North Carolina, we chose to use bobcat (*Lynx rufus*) as a proxy for this species type because it was the one mammal species with sufficient camera detection data that also typically avoids specific environmental conditions (e.g., human development/urbanization) in North Carolina (but see Parsons et al., 2018).

METHODS

Study area

The study area was the state of North Carolina, USA (Figure 1). North Carolina has an estimated human population of 10.3 million, covers an area of 139,390 km², lies between 33° 50' N to 36° 35' N and 75° 28' W to 84° 19' W, and ranges between 0 and 2037 m in elevation. Land cover across the state is approximately 40% forest (deciduous, coniferous, and mixed), 20% row crop agriculture, 10% developed, and 10% water, with the remaining 20% being comprised of

wetlands, scrubland, or grasslands (Homer et al., 2015). The state consists of three primary physiographic regions: the Coastal Plain, Piedmont, and Appalachian Mountains (i.e., Level III Ecoregions) (North Carolina Wildlife Resources Commission, 2018; Omernik & Griffith, 2014). The Coastal Plain comprises about 45% of the state and is characterized primarily by agricultural land cover, wetlands, and mixed coniferous forests. The Piedmont lies between the Coastal Plain and Mountains and topographically consists of gentle rolling hills, gaining in elevation toward the mountains. The Piedmont contains the primary urban centers of the North Carolina and is mosaic of developed, forested, and row crop agriculture land covers. Containing the state's most rugged topography, the Appalachian Mountain region is predominantly forested but makes up just 10% of the state.

Data source: Citizen science camera trapping

We analyzed camera-trap data from the North Carolina Candid Critters (NCCC) project (Lasky et al., 2021) that occurred in North Carolina starting in October 2015 and ending December 2019, with camera deployments occurring year-round (Figure 1). Compared to past mammal monitoring efforts, the spatial extent and camera-trapping effort from the NCCC project were unprecedented. The Candid Critters project relied on volunteer citizen scientists to deploy cameras that followed a standardized protocol: Camera sites were unbaited, and cameras were mounted 40–50 cm above ground, active 24 h/day, and had a target deployment length of 21 days (Kays, Arbogast, et al., 2020; Pease et al., 2016). All cameras had trigger speeds <0.5 s and were equipped with infrared flash. Cameras were set to maximum trigger sensitivity, to have no rest period between triggers, and to record multiple photographs per trigger. Triggers within 60 s of each other were considered one detection and grouped into a sequence, and then, we used these sequences as independent records for subsequent analysis of detection rate (sequences per day). Cameras continued to re-trigger if the animal was still in the detection zone of the camera. Camera locations were either at the volunteer's discretion or using preselected locations determined by stratified random sampling of land cover types in North Carolina. Previous analyses determined that the camera locations were representative of the state's land cover (Kays et al., 2021). Citizen science volunteers used the eMammal software to upload pictures and identify all photographed wildlife species. Uploaded pictures were then vetted by project staff using the eMammal Expert Review Tool, where species identification was confirmed or corrected (McShea et al., 2016).

We removed deployments that lasted <7 days or >35 days, as this indicated camera malfunction or

deployments that did not adhere to protocol (Kays, Arbogast, et al., 2020). We also spatially thinned deployments from the same month of a given year or that were separated by ≤ 50 m, resulting in 3678 camera-trap deployments. Cameras were deployed on both public (~40%) and private lands (~60%), and deployments were set in all 100 North Carolina counties.

We imposed a 5×5 km regular hexagonal grid across North Carolina (resulting in 5497 grid cells) for all analyses. We chose this resolution because it is representative of the range of environmental conditions likely encountered during daily movements and seasonal home ranges of the four focal wildlife species (i.e., deer, raccoon, coyote, and bobcat); this resolution was based on estimated home ranges and scale of effects for each species (Clare et al., 2015; Constible et al., 2006; Kie et al., 2002; Woolf et al., 2002). We assigned all camera deployments to their respective grid cell and summarized all environmental covariates within each grid cell. For simplicity, we summed the number of species-specific daily detections and recorded the cumulative number of days all cameras were deployed within each cell.

Ecological correlates

We focused on covariates describing landscape composition and configuration known to influence mammal habitat use in North Carolina (Kays et al., 2017; Parsons et al., 2018) and beyond (Kie et al., 2002) (Table 1). Covariates describing land cover composition included forest cover and housing density, and configuration metrics included patch richness density (PRD) and contagion index (herein, focal covariates) and were derived from the 2011 30×30 m National Land Cover Data product (Homer et al., 2015) and the North Carolina housing density estimates, which were based on the 2010 TIGER census blocks (Bureau, 2010). Contagion index and PRD were calculated using the R package *landscapemetrics* (Hesselbarth et al., 2019). We considered several other landscape metrics to represent configuration but determined that PRD and contagion captured many characteristics known to affect mammal distribution and abundance (Cherry et al., 2017; Constible et al., 2006; Kie et al., 2002; Nielsen & Woolf, 2002; Saïd & Servanty, 2005; Walter et al., 2009). Specifically, the two chosen metrics had correlation coefficients ≥ 0.5 (positive or negative) with edge density, mean patch area, and Shannon's Diversity Index, suggesting that these two measures were capturing several important determinants of mammal distribution and abundance (Kie et al., 2002). The landscape composition and configuration covariates were summarized in 5×5 km hexagonal grid cells across North Carolina. Four additional camera-level covariates were used to describe camera-level variation (Table 1); we used the Microsoft US Building Footprints for North Carolina (Bing Team

TABLE 1 Ecological predictors used to model space-varying ecological effects across North Carolina, USA, during October 2015–December 2019.

Category	Covariate	Description
Landscape composition	Forest cover	Proportion of forest cover in 5×5 km grid cell
Landscape composition	Housing density	Mean housing density (in houses per kilometer) in 5×5 km grid cell
Landscape configuration	Contagion index	The degree of clumping among land cover types in 5×5 km grid cell, or the propensity for a raster pixel of a given land cover class to be neighboring a different land cover class
Landscape configuration	Patch richness density	No. land cover types per 100 ha in 5×5 km grid cell
Camera-level	Distance to road	Mean minimum distance to road from camera traps within a grid cell
Camera-level	Distance to building structure	Mean minimum distance to building structures from camera traps within a grid cell
Camera-level	Distance to water source	Mean minimum distance to water source from camera traps within a grid cell
Camera-level	Detection distance	Mean detection distance for cameras within a grid cell
Survey effort	Trap nights	Length (days) of camera-trap deployment used to represent effort of camera trapping

Maps, 2018) to calculate camera distance to building structures, distances to roads used the North Carolina Department of Transportation's linear features database (North Carolina Dept. of Transportation, 2021), and water source distance calculations used the Natural Earth waterways database (Natural Earth, 2009). We also included detection distance—a field-based measurement of the distance from the mounted camera a human can be detected—determined by walk tests performed by the volunteer deploying the camera. Lastly, we used the length of the camera deployment to represent the amount of camera-trapping effort. All covariates included in a model were checked to have correlation coefficients <0.6 and were mean-centered prior to analysis to aid computation and interpretation of parameter estimates (Baird & Bieber, 2016; Tabachnick et al., 2007).

Model descriptions

We used the same animal and environmental data to build SDMs with three different modeling approaches to compare their performance, and thus quantify the importance of accounting for nonstationarity. As our starting point, we used single-season, single-species occupancy models as the underlying regression-based SDM; the occupancy model is a regression-based SDM that accounts for imperfect detection hierarchically by separately modeling the ecological and observation processes (MacKenzie et al., 2017). Although more complicated models occupancy models are described (MacKenzie et al., 2017), we chose to use single-season, single-species models to keep the base model simple and allow for a methodological exploration of spatial nonstationarity in species detection/nondetection data.

We acknowledge the limitations of this approach and urge caution in interpreting the estimated occurrence probabilities for the use in wildlife conservation and management. The occupancy model assumed that a given covariate effect is constant across space (i.e., assumes stationarity), reflecting the hypothesis that a species is responding consistently across the area of interest. We added a spatial random effect to the occupancy model (and subsequent models) to account for autocorrelation and other remaining patterns of spatially structured residuals (see below for description of the spatial random effect). Herein, we will refer to this occupancy model as the “stationary” model. The following two models below are also occupancy models—they have identical baseline detection and ecological submodels as the stationary model—but are modified to test for spatial nonstationarity.

In the other two models, we allowed the effects of the landscape composition and configuration covariates to *vary over space* (Table 1). One model uses the three primary ecoregions (“ecoregion model”) of North Carolina to test for coarse-scale nonstationarity. That is, the model assumes that some effect of landscape composition or configuration is constant within the ecoregion, but the effect may be different across ecoregions. In all, beyond the parameters estimated in the stationary occupancy model, the ecoregion model estimates a total of 12 effects of landscape composition and configuration metrics (i.e., four covariates in three regions). The ecoregion model reflects the hypothesis that nonstationarity is occurring but at coarse natural boundaries (i.e., coarse resolution).

The third approach extended our stationary occupancy to the form of a SVC model (Gelfand et al., 2003), which allowed a given parameter effect (e.g., forest cover) to vary continuously over the region of interest (“SVC model”);

unlike the ecoregion model, this model does not impose boundaries where a given effect is thought to differ, but rather directly uses the response data to estimate where the variation in effect occurs. The SVC model reflects the hypothesis that nonstationarity exists and is occurring at a fine-scale resolution (e.g., population-level variation). The SVC model is a form of “local spatial modeling” that uses neighborhood response and predictor information to estimate ecological relationships at a fine scale (Lloyd, 2010). Ultimately, the three models evaluated whether a given species showed signs of nonstationarity in ecological relationships, and if so, at which resolution (i.e., regionally or finer), as evaluated by model fit and predictive performance.

We implemented the single-species, single-season occupancy model described by (MacKenzie et al., 2017) for each species. We start with a description of an occupancy model with covariates affecting the detection and state process (“occupancy model”):

$$\begin{aligned} Z_i &\sim \text{Bernoulli}(\psi_i) \\ \text{logit}(\psi_i) &= \mathbf{X}_i^T \boldsymbol{\beta} + \theta_i \\ y_i &\sim \text{Binomial}(n_i, \mu_i), \\ \mu_i &= Z_i \times p_i \\ \text{logit}(p_i) &= \mathbf{X}_i^T \boldsymbol{\alpha} \end{aligned} \quad (1)$$

where Z_i is an unobserved parameter indicating whether grid cell i is truly occupied (1 = occupied and 0 = unoccupied), ψ_i is the probability that a grid cell is occupied, \mathbf{X}_i is a vector of covariates (“landscape composition and configuration” categories in Table 1), $\boldsymbol{\beta}$ is the corresponding vector of fixed regression coefficients, θ_i represents an improper conditional autoregressive (CAR; Banerjee et al., 2014) random effect, y_i indicates the number of detections within grid cell i out of a total of n_i camera-trap nights per grid cell, p_i is the probability of detecting a species conditional on its occurrence state, and $\boldsymbol{\alpha}$ is an additional vector of regression coefficients describing effects on the detection process (“Camera-level” categories in Table 1). The CAR random effect creates spatial dependence among neighboring grid cells. Specifically, for responses $y = (y_1, \dots, y_N)$, the improper CAR is

$$p(y_i | y_{-i}, \tau) \sim N\left(\frac{1}{w_{i+}} \sum_{j \in N_i} w_{ij} y_j, w_{i+} \tau\right), \quad (2)$$

where y_{-i} represents all elements of y except y_i , the neighborhood N_i of grid cell i is the set of all j for which region j is a neighbor of region i , $w_{i+} = \sum_{j \in N_i} w_{ij}$, and the normal distribution is parameterized in terms of precision τ . Adding a CAR random effect to the linear predictor assumes that the response at grid cell i is a function of site covariates and the responses at neighboring grid cells.

To extend the stationary occupancy model to the ecoregion model, we indexed each regression coefficient of the ecological process in Equation (1) with an indicator of which physiographic region site i is located within

$$\text{logit}(\psi_i) = \mathbf{X}_i^T \boldsymbol{\beta}_{(e)} + \theta_i, \quad (3)$$

where e is the indicator of ecoregion taking on either coastal plains, mountains, or piedmont; this results in three independent estimated coefficients for each covariate in \mathbf{X} .

Finally, we fit a full spatially varying coefficients model (“SVC model”) that allows for the effect of a given covariate to vary over space. To implement this, we modified the linear predictor of the latent state Z_i in Equation (1)

$$\text{logit}(\psi_i) = \mathbf{X}_i^T \boldsymbol{\omega}_i, \quad (4)$$

where $\boldsymbol{\omega}_i$ is a vector of SVCs arising from a spatial Gaussian process (Gelfand et al., 2003). Each j th element in the $\boldsymbol{\omega}_i$ vector at location i is distributed as an improper CAR random effect as described in Equation (3).

For all SVCs, we calculated a “stationarity index” (SI) to compare the global coefficient of each landscape composition and configuration metric estimated using the occupancy model to the estimated SVCs. For each coefficient, we calculated the interquartile range in the SVC and divided it by two times the SE of the global regression coefficient for the same variable from the occupancy model. Thus, higher values indicate more spatial variation in the ecological relationship and values >1 suggest support for nonstationarity (Osborne et al., 2007).

We estimated parameters under Bayesian inference with Markov chain Monte Carlo sampled using the *nimble* package (de Valpine et al., 2017) within the R statistical computing environment (R Core Team, 2020). We generated three chains of 20,000 iterations after a burn-in of 10,000 iterations and thinned by 20 iterations to reduce file size. We used normally distributed, uninformative priors (mean = 0, SD = 5, and precision = 0.04) for regression coefficients in both the observation and ecological models. To evaluate model fit, we examined trace plots and looked at estimated Gelman–Rubin statistics to ensure proper convergence. We used widely applicable information criterion (WAIC) calculated within *nimble* to compare models (Scollnik, 2022). To evaluate predictive performance, we used the Brier Score, which is a proper score function described by the mean squared error of the probabilistic model predictions and the observed presence or absence in the data, and the well-known area under the receiving operator characteristic curve (AUC) (Faraggi & Reiser, 2002; Long et al., 2011; Pacifici et al., 2016; Zipkin et al., 2012).

Additional file and data manipulation were done using packages *data.table* (Dowle & Srinivasan, 2019), *here* (Müller, 2017), *sf* (Pebesma, 2018), and the *tidyverse* (Wickham et al., 2019). Data visualization was done using packages *ggplot2* (Wickham, 2016), *tmap* (Tennekes, 2018), and *RColorBrewer* (Neuwirth, 2014). Code and model descriptions are publicly available at <https://github.com/BrentPease1/nc-svc>.

Post hoc drivers of nonstationarity

We conducted additional post hoc analyses to investigate what might be driving nonstationarity in species–environmental relationships found to be spatially varying (based on the stationary indices described above) and to stimulate future research into this topic. For the relationship we documented to have a stationary index >1 , we developed four hypotheses for potential causes of this nonstationarity (Table 4) and then fit seven models to test these hypotheses (four primary hypothesis models, two interactive models, and one global model). The four primary hypotheses as drivers of nonstationarity included (1) spatial variation in resource availability, (2) spatial variation in predator pressure, (3) intraspecific variation in deer populations across North Carolina, and (4) missing environmental covariates. We hypothesized that the effect of predator pressure may also depend on resource availability and intraspecific deer variation, so we created two interactive models to describe this hypothesis. Finally, we fit a global model that included each primary hypothesis as an additive effect.

We used existing covariates described in Table 1 or developed new covariates for describing each hypothesis. For the resource availability hypothesis, we used the amount of forest cover within a given cell based on the five classes of forest cover in 2018 MODIS data (Sulla-Menashe & Friedl, 2018). The predator pressure hypothesis was represented by a combination of wildlife predation risk to deer and human predation risk, represented by hunting pressure within the state. We used the combined detection rate (ratio of detections to the number of camera deployment days) of American black bear (*Ursus americanus*), coyote, and bobcat to reflect wildlife predation risk to deer. We used surveys from the North Carolina Wildlife Resources Commission (annual mail surveys 2016–2019) to calculate mean deer hunter effort (i.e., number of hours spent hunting) in each grid cell to reflect human predation risk. The hunter information is summarized at the county level, so all grid cells within a given county were assigned the same hunter effort value. To test whether intraspecific variation of the species (e.g., behavioral differences across

North Carolina) was the driver of nonstationarity, we used five deer management units (DMUs) delineated by the North Carolina Wildlife Resources Commission as a categorical predictor. The North Carolina DMUs are based on biological differences across the state including peak conception date, average number of bucks harvested, latitude/longitude, and average weights of 1.5- and 2.5-year-old does (Howard et al., 2015; Serenari et al., 2019; Shaw et al., 2016). Given that we did not have genetic data to explicitly test intraspecific variation, we used the DMUs as a proxy because they reflect biological differences in deer populations.

To test each hypothesis, we fit frequentist-based linear models using the *lm* function from the base R software that had the SVCs of each ecological covariate with a stationary index >1 as the response, and then used the hypothesis-specific covariates as linear predictors. The models were compared using Akaike information criterion (AIC) to evaluate support among models, where the model was the lowest AIC was considered the most supported model.

RESULTS

Camera trapping

Volunteers deployed camera traps in all 100 counties of North Carolina with a greater concentration of deployments around more populated areas (Figure 1). Forty-nine percent of the deployments were in the Piedmont region, followed by 27% in the Coastal Plains, and 24% in the Mountain region. We recorded 37,408 detections of deer, raccoons, coyotes, and bobcats over 73,967 trap nights of effort at 3678 camera-trap locations. Deer were consistently the most detected species, making up 42% of the detections (30,703 detections; naïve occupancy = 0.82), followed by raccoon (4739 detections or 13% of detections; naïve occupancy = 0.34), coyote (1653 detections or 4%; naïve occupancy = 0.21), and bobcat (313 detections or 0.8%; naïve occupancy = 0.05).

Model comparisons

Evidence of nonstationarity varied among the species tested (Tables 2 and 3). White-tailed deer was the only species with top support for the SVC model (Table 2). The SVC model was also within two WAIC points of the top model for bobcat (Table 2). There was little support for the SVC model for coyote or raccoon; instead, the ecoregion model had the most support for both species (Table 2). Irrespective of model fit, the SVC models consistently had the highest AUC and lowest

TABLE 2 Model comparison of parsimony (WAIC) and predictive performance (Brier Score, AUC) for single-season occupancy analysis of bobcat, coyote, raccoon, and white-tailed deer in North Carolina, USA, during October 2015–December 2019.

Species	Model	Δ WAIC	AUC	Δ AUC	BRIER	Δ BRIER
Bobcat	Occupancy	0	0.77	0.02	0.16	0
	SVC ^a	1.57	0.79	0	0.17	0.01
	Ecoregion	17.37	0.74	0.05	0.19	0.03
Coyote	Ecoregion	0	0.63	0.04	0.31	0.01
	SVC	5.62	0.67	0	0.3	0
	Occupancy	6.09	0.62	0.05	0.3	0
Raccoon	Ecoregion	0	0.64	0.01	0.25	0.01
	SVC	9.63	0.65	0	0.24	0
	Occupancy	18.02	0.65	0	0.24	0
Deer	SVC	0	0.83	0	0.08	0
	Ecoregion	10.4	0.83	0	0.08	0
	Occupancy	16.82	0.8	0.03	0.09	0.01

Note: The three models used were as follows: site-occupancy model with a spatial random effect; ecoregion, occupancy with a spatial random effect and ecoregional random effects on landscape composition and configuration metrics; SVC, spatially varying coefficients model. We report on the change in (delta) the widely applicable information criterion (WAIC) from the best fitting model (0 indicates best fitting model), area under the curve (AUC; higher values are better, perfect score = 1), and Brier Score (BRIER; lower values are better, perfect score = 0). Bold values indicate the best score for each category, and models are sorted based on best lowest WAIC.

^aIndicates model ≤ 2 WAIC points of top model.

TABLE 3 Stationarity indices for bobcat, coyote, raccoon, and white-tailed deer in North Carolina, USA, during October 2015–December 2019.

Species	Landscape configuration		Landscape composition	
	Contagion	Patch richness	Forest cover	Development
Bobcat	0.34	0.49	0.44	0.27
Coyote	0.69	0.48	0.62	0.50
Raccoon	0.62	0.38	0.33	1.36
Deer	0.85	0.47	2.13	0.91

Note: For each variable, we calculated the interquartile range in the spatially varying coefficient and divided it by two times the SE of the global regression coefficient for the same variable from the Generalized Linear Model. Thus, higher values indicate more spatial variation in the ecological relationship and values >1 suggest support for nonstationarity.

TABLE 4 Hypothesis of potential drivers of nonstationarity in the relationship between white-tailed deer and forest cover.

Hypothesis	Covariates	Δ AIC	No. parameters	R^2
Predator \times biology	Deer management units; wildlife predator detection rates; deer hunter harvest effort	0	16	0.65
Global	All	558	13	0.60
Deer biology	Deer management units	1094	6	0.57
Predator \times resource	Wildlife predator detection rates; deer hunter harvest effort; forest availability	3786	7	0.30
Predator pressure	Wildlife predator detection rates; deer hunter harvest effort	3796	4	0.30
Resource availability	Forest availability	5589	7	0.02
Missing covariate	Forest types (coniferous, deciduous, and mixed)	5654	3	0.03

Abbreviation: AIC, Akaike information criterion.

Brier Score for all species (Table 2), indicating superior predictive performance by accounting for local-level variation.

The range and magnitude of estimated occupancy probabilities for each species were relatively consistent across all models (Figure 2); estimated occupancy probabilities were most uncertain under the SVC model for all species, though deer had comparable uncertainties to the stationary and ecoregion models (Figure 2). Averaging across all models, mean occupancy was 0.88 (SD = 0.13), 0.79 (SD = 0.14), 0.67 (SD = 0.15), and 0.36 (SD = 0.18) for deer, raccoon, coyote, and bobcat, respectively. Similarly, we documented consistent grid cell-level detection probabilities across all models for each species (Appendix S1: Figure S1); at the grid cell level, we poorly detected most species (detection probabilities $p \leq 0.1$), except deer (average $p = 0.23$) (Appendix S1: Figure S1).

The estimated landscape coefficients from the stationary model had similar strength and direction as the ecoregion model, but some relationships varied across ecoregions (Appendix S1: Tables S1 and S2). Although the added flexibility of the ecoregion models improved fit for some species, the smaller, regional sample size relative to the stationary model also resulted in increased uncertainty in the posterior distributions of the landscape covariates (Appendix S1: Tables S1 and S2). Site coefficient estimates were nearly identical across all models although we did not expect this vary because these components remained constant for all species and models (Appendix S1: Figure S2).

Ecological relationships

All species tended to have stronger and more precise relationships with landscape composition (i.e., cover of forest and developed areas) than landscape configuration (i.e., contagion index and PRD), resulting in distribution estimates more reflective of the land cover of North Carolina rather than configuration metrics (Figure 3; Appendix S1: Figure S3 and Tables S1 and S2). Further, in both the ecoregion and SVC model, we documented spatial variation in the way some species responded to forest cover and housing density (Table 3; Appendix S1: Table S1). Specifically, deer had the most spatially varying relationship with forest cover ($SI = 2.13$; $SI > 1$ indicates evidence of nonstationarity), ranging from strongly negative ($\hat{\beta} \leq -2$) to strongly positive ($\hat{\beta} \geq 3$) across the state (Table 3; Figure 4; Appendix S1: Figure S4). Interestingly, for deer, the strongest relationships with landscape composition metrics tended to be at transition zones between the major ecoregions in the state (Figure 4). Although the SVC model was within two WAIC points of the top model for bobcat, all SIs were < 1 (Table 3; Appendix S1: Figures S5 and S6). However, across all species and predictors, the lowest overall SI was bobcat's negative relationship with human development, making it the most constant ecological relationship across space (Table 3; Appendix S1: Figures S5 and S6). Additionally, bobcat had the lowest contagion index SI, suggesting their need for large, contiguous blocks of

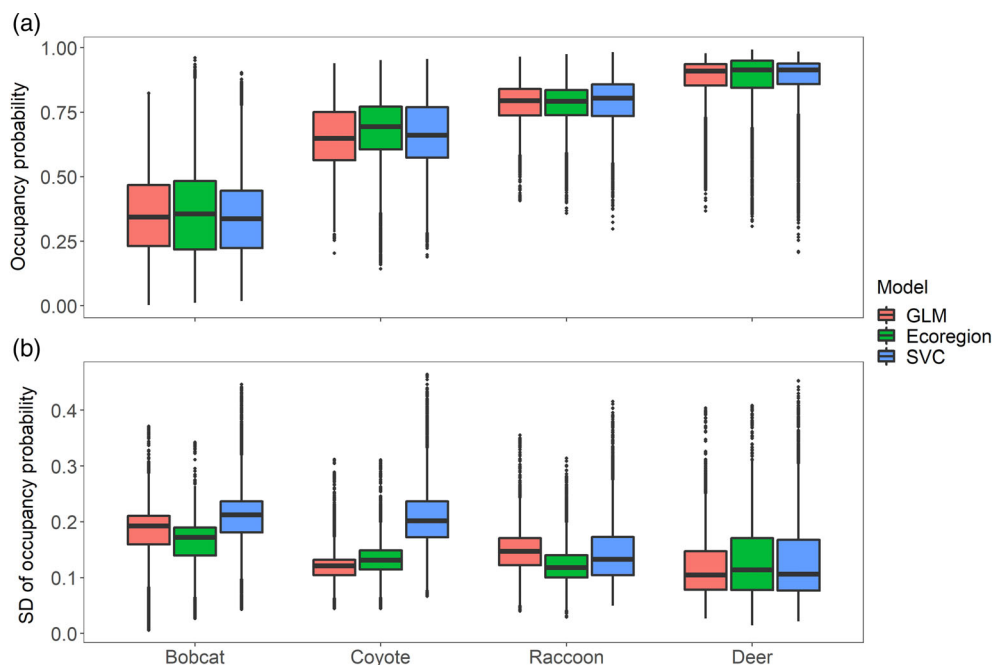


FIGURE 2 (a) Distribution of all estimated occupancy probabilities ($n = 5497$ for each model) for bobcat, coyote, raccoon, and white-tailed deer in North Carolina, USA, during October 2015–December 2019 along with the (b) distribution of uncertainty (SD) in those estimates.

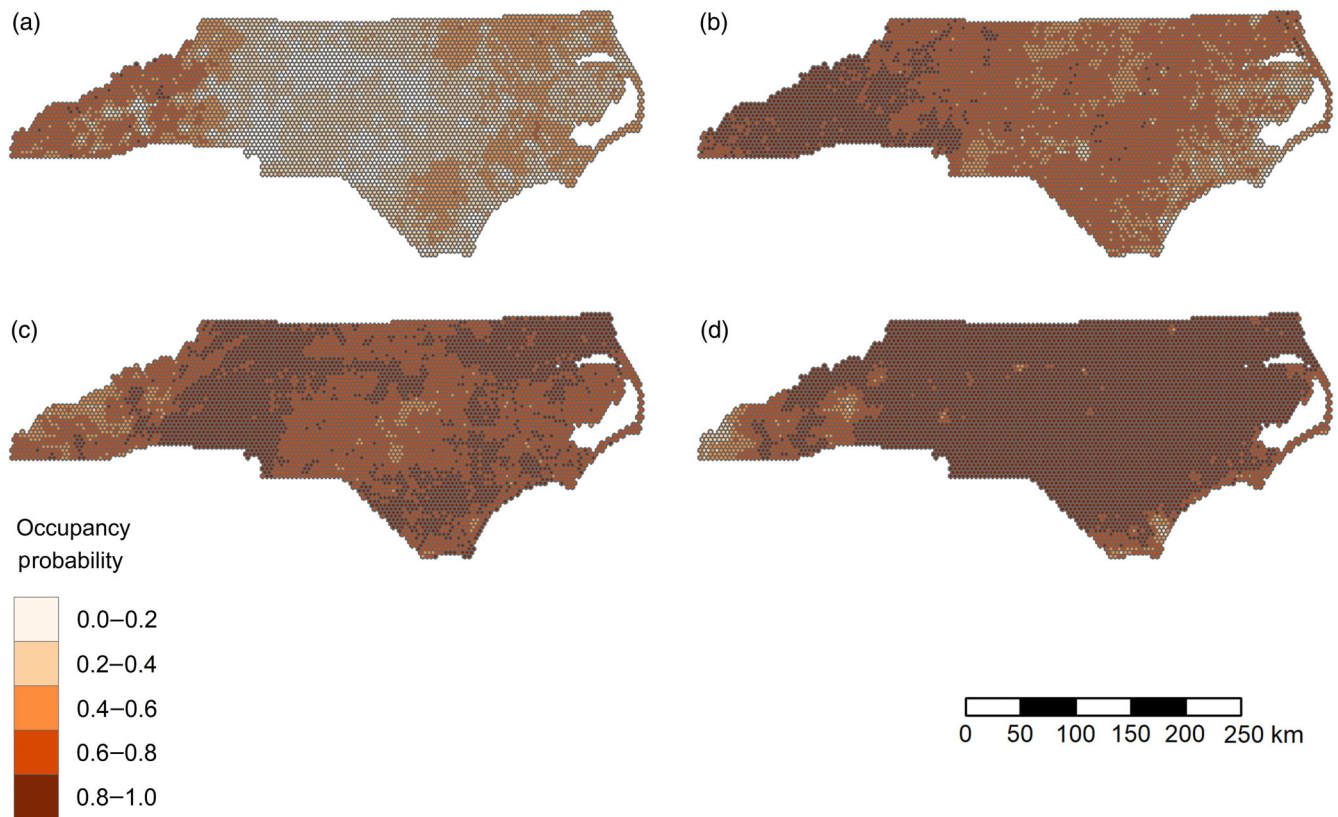


FIGURE 3 Estimated occupancy probability from the species-specific top model (Table 2) for (a) bobcat, (b) coyote, (c) raccoon, and (d) deer during October 2015–December 2019 in North Carolina, USA.

undeveloped land cover was ubiquitous across their distribution in North Carolina (Table 3).

We documented strong and precise relationships with most of the proximity-based, camera-level covariates, although this varied across species. For bobcat, there was a strong, positive relationship with distance to buildings (i.e., greater distance and greater site use by bobcats), but little effect of proximity to roads or water sources (Appendix S1: Figure S2). By contrast, raccoon, coyote, and deer all had strong, negative relationships with distance to building (Appendix S1: Figure S2). Raccoon additionally had a strong, negative effect of distance to road, whereas deer and coyote responded positively (Appendix S1: Figure S2). Coyote also had a precise, positive effect of distance to water source, while deer and raccoon had negative relationships with these features (Appendix S1: Figure S2).

Potential drivers of nonstationarity

Although we found evidence of nonstationarity, it was difficult to evaluate the underlying ecological drivers, so we conducted additional post hoc analyses to investigate what might be driving nonstationarity in the

relationship between deer and forest cover, and to stimulate future research into this topic. We developed five hypotheses for potential causes of the nonstationarity (Table 4) and selected additional covariates to add to the model. The four primary hypotheses included spatial variation in resource availability or predator pressure, intraspecific variation in deer populations across North Carolina, and missing environmental covariates. We hypothesized that the effect of predator pressure may depend on resource availability and intraspecific deer variation, so we created models to describe this interaction. We used the amount of forest cover within a given cell based on the five classes of forest cover in 2018 MODIS data to reflect the resource availability hypothesis (Sulla-Menashe & Friedl, 2018). We used the combined detection rate (ratio of detections to the number of camera deployment days) of American black bear (*Ursus americanus*), coyote, and bobcat to reflect wildlife predation risk to deer. We also included mean deer hunter effort (i.e., number of hours spent hunting) in each grid cell based on surveys from the North Carolina Wildlife Resources Commission (annual mail surveys 2016–2019) to reflect human predation risk. The hunter information is summarized at the county level, so all grid cells within a given county were assigned the same hunter effort value.

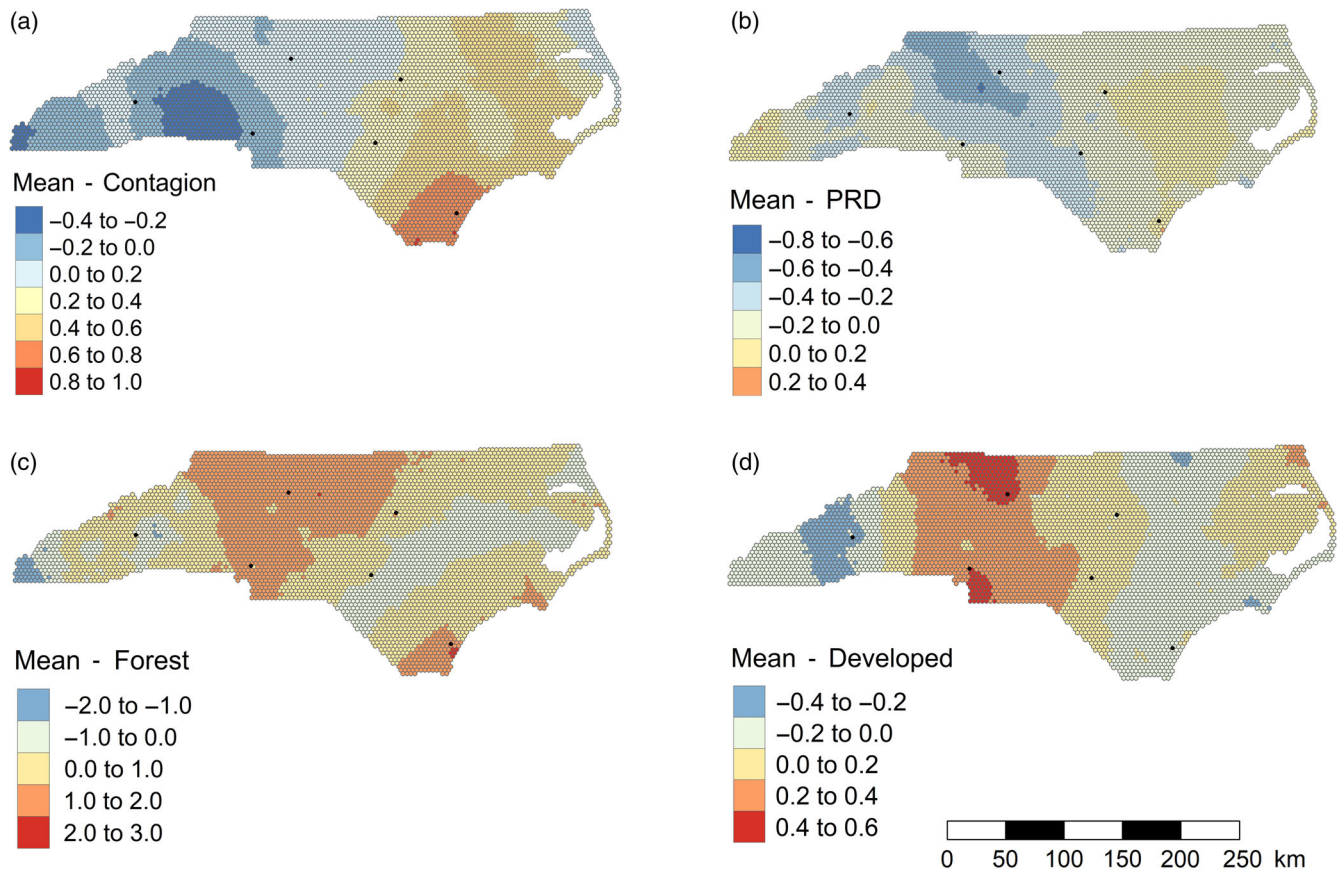


FIGURE 4 Spatially varying coefficient estimates (and stationary indices, $SI > 1$ indicates nonstationarity) of (a) contagion index ($SI = 0.85$), (b) patch richness density ($SI = 0.47$), (c) forest cover ($SI = 2.13$), and (d) developed ($SI = 0.91$) for white-tailed deer during October 2015–December 2019 in North Carolina, USA. Black dots are for spatial reference and represent cities with populations with 100,000 people or more.

To test whether intraspecific variation was the driver of nonstationarity, we used five DMUs delineated by the North Carolina Wildlife Resources Commission as a categorical predictor. The North Carolina DMUs are based on biological differences across the state including peak conception date, average number of bucks harvested, latitude/longitude, and average weights of 1.5- and 2.5-year-old does (Howard et al., 2015; Serenari et al., 2019; Shaw et al., 2016). Given that we did not have genetic data to explicitly test intraspecific variation, we used the DMUs as a proxy because they reflect biological differences in deer populations. To test each hypothesis, we fit linear models with the SVC of forest cover as the response, and using the hypothesis-specific covariates as predictors, and then compared with AIC to evaluate support.

The greatest support was for the hypothesis that the interactive effect of predator pressure and intraspecific deer variation explained the spatial variation in the effects of forest cover on deer occupancy (Table 4; Figure 5). For example, in the western DMU, deer exhibited a negative relationship with forest cover under low predator pressure scenarios, whereas high predator pressure conditions resulted in a positive effect of forest cover (Figure 5).

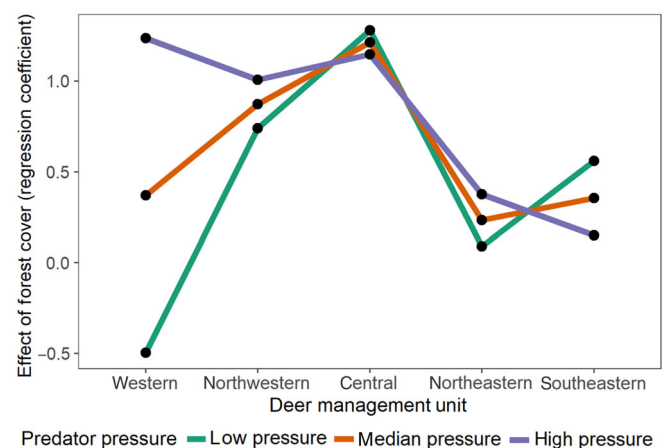


FIGURE 5 The interactive effect of predator pressure and deer biology best explain nonstationary effects of forest cover on white-tailed deer. The y-axis is the estimated spatially varying effect of forest cover on white-tailed deer (Figure 4c) from models described in Table 2. The x-axis lists the North Carolina deer management units and serve as proxies for biological differences in deer populations across the state. Predator pressure includes effects of wild (American black bear, coyote, and bobcat) and human predators, as estimated by deer hunting pressure across the state.

DISCUSSION

Although it is widely recognized that ecological relationships can vary across the range of a species, most SDMs presume spatial stationarity. Here, we showed how accounting for nonstationarity provided new insights into the types of ecological predictors that had varying species–environment relationships for four mammal species and the resolution at which it was occurring. We also described how the widely used occupancy model (MacKenzie et al., 2017) can be extended to allow for SVCs. Most importantly, given the range in resolution and strength at which nonstationarity occurred, exploring the possible drivers of nonstationarity and how the spatially varying relationships reflect the ecology of the species set a direction for future research.

Spatially varying relationships between wildlife and the environment reflect biological differences within species that could be driven by interactions of external and internal factors. Nonstationarity may indicate a species' ability to exploit a range of environmental conditions by locally adapting, but the magnitude of variability is usually governed by the species' niche (Chase & Leibold, 2009). That is, the degree to which species–environment relationships exhibit nonstationarity is likely a function of the species' niche breadth, or total niche width, which describes the total variation in resources that can be exploited by a species (Roughgarden, 1972). Further, populations of species with greater local adaptations (or other behavioral specializations) are more likely to result in patterns of spatial nonstationarity in species–environment relationships, especially when analyzed over large areas (Sargeant, 2007). This does not necessarily exclude the possibility of spatial nonstationarity in species with high niche conservatism because even if there is high tendency for species to retain ancestral ecological characteristics and if the species has a relatively wide niche width, then it is reasonable to expect varied responses to the different environmental conditions they encounter across the range of the species (Wiens et al., 2010).

One potential limitation of our work is the lack of a comparative analysis among all approaches to explore spatial nonstationarity. As previously mentioned, several methods exist and each individual approach may have advantages over the next. Fortunately, previous work compared GWR, the most widely used method for local spatial modeling, with SVC and found several improvements when using the latter, leading us to forego the GWR approach (Finley, 2011). One alternative approach to the standard GWR may be the so-called multiscale GWR (MGWR) that may more closely mimic the SVC model but a direct comparison is still lacking (Fotheringham et al., 2017). Patterns of nonstationarity may also be explored with GAMs, and some research suggests

that nonlinear relationships in the data may be mistaken for spatial nonstationarity (Austin, 2007); future work should first explore nonlinear effects prior to spatial nonstationarity. The results did not align consistently with our hypotheses and predictions. For example, we predicted that raccoon and coyote would exhibit *fine-scale* spatial nonstationarity but instead documented *coarse-scale* variation. Similarly, we predicted that bobcat exhibit would stationary responses to environmental conditions, but instead we documented support for fine-scale spatial nonstationarity. By contrast, our results for white-tailed deer did align with our predictions, where we predicted *fine-scale* nonstationarity for deer. Below we discuss these results further for each species.

In our state-wide analyses, an SVC model outperformed conventional occupancy SDMs and regional partitions for deer, which agrees with several studies that have formally accounted for nonstationarity either through geographically weighted regression (Fotheringham et al., 2003) or SVC models (Gelfand et al., 2003). Past research studying spatial nonstationarity has typically focused on ecological metrics such as species richness, diversity, or turnover, but our research shows that this also occurs at, and below, the species level, reinforcing the idea that spatial nonstationarity is likely a common phenomenon in ecology (Foody, 2004; Fortin et al., 2008; Jarzyna et al., 2014; Osborne et al., 2007; Shi et al., 2006; Smith et al., 2019; Windle et al., 2009).

Deer was the only species with the SVC model receiving the most support, driven primarily by the high variability in their relationship with forest cover across the state. We followed these findings with a post hoc analysis to explore what might be the drivers of this nonstationarity and found the most support for an interactive effect of external (predator pressure) and internal (population differences) factors. In the western-most part of the state where forest cover is most contiguous and relatively little human development exists, deer exhibited a negative relationship with forest cover under low predator pressure but a positive relationship under high predator pressure. However, in the central part of the state where there is the greatest human population densities and hunter effort, deer consistently had strong, positive relationships with forest cover—regardless of predator pressure levels. These findings support the idea that predation risk influences deer decisions, but do not alone explain all variation in the use of forested environments across space. Individually, the DMU hypothesis received far greater support than the predation risk hypothesis ($R^2 = 0.57$ and 0.30 , respectively). Specifically, the central and northwestern management units were quite different than the other regions and had the strongest, positive relationship with forest cover, which corresponds with the hypothesis of forest as a predator avoidance tactic.

Although the top model for bobcat was the stationary occupancy model, the SVC model was within two WAIC points suggesting nearly equal support for spatially varying ecological relationships (Anderson & Burnham, 2004). On one hand, the data suggest that bobcat are responding similarly at the state level, and given the environmental conditions across the state, this may align well with documented species–environment relationships of bobcat. By contrast, the SVC model had support, but no stationary index was >1 . The lowest SI—across all species and covariates—was for the relationship between bobcat and housing density, suggesting that bobcat consistently avoid human development, regardless of the location within the state. This is a well-known relationship in North Carolina, and our results corroborate previous work in the state (Parsons et al., 2019). However, when considering the continental range of bobcats, there is evidence that bobcats thrive in some urban areas (e.g., Texas; Young et al., 2019). That the most stationary species–environment relationship in our state-wide study is clearly nonstationary at the continental level highlights the importance of accounting for stationarity in large-scale SDMs, using SVCs, or other approaches, to map variation in ecological relationships (Clare et al., 2015; Lombardi et al., 2017; Tigas et al., 2002).

Coyote and raccoon both had top support for the ecoregion model, indicating that ecological relationships vary in ways that match regional ecology. Coyote responded similarly to forest cover in the coastal and mountain region, but similarly to development in the mountains and piedmont regions. With forest cover, coyotes had a strong, positive response in the piedmont region; this may be due to fragmented green spaces providing the necessary resources to exist in developed areas (Parsons et al., 2018, 2019). Similarly, coyotes showed avoidance of developed spaces in the coastal region where relatively less forest cover exists, suggesting these forests help them reach higher occurrence probabilities in human-developed areas. Raccoon, in contrast, tended to use developed areas across their range with the strongest relationship was strongest in the piedmont region, which also has the most urban areas within the state. However, unlike the other regions, raccoon had a negative response to PRD in the piedmont, suggesting a positive relationship with contiguous land cover in highly developed areas.

One trade-off of using local spatial models, like our ecoregion or SVC approaches, to account for nonstationarity is that the sample size for each model is smaller, and thus, models should be able to reliably estimate fewer explanatory variables. That is, a conventional global regression analysis will generally be able to accommodate many more predictors (Green, 1991) because they use all observations in one model, whereas local models

only consider a subset of nearby observations and thus typically will be able to estimate fewer predictor effects. The result of this trade-off is apparent when comparing the magnitude and uncertainty estimates of predictor variables across spatial and nonspatial models, where we observed an increase in uncertainty and moderate changes in magnitude as we incorporated spatial random effects and allowed the focal coefficients to vary over space. The increase in uncertainty, particularly for the spatial ecoregion and SVC models, in part reflects fewer observations available to inform estimates and, when combined with changes in magnitude, provides evidence that the independence assumption of the conventional occupancy model was not being met. This phenomenon is typically referred to as the *bias-variance trade-off* and is a well-known property of increased model complexity (i.e., including spatial random effects; Bolker et al., 2009). Previous work in ecological nonstationarity demonstrated this as well, where Meehan et al. (2019) had greater uncertainty in information-poor areas when using an SVC model compared to traditional analyses, and Osborne and Suárez-Seoane (2002) had larger variance estimates when partitioning data for large-scale SDMs. Additionally, Jarzyna et al. (2014) found differences in coefficient magnitude when comparing spatial and nonspatial models, and Byrne et al. (2019) found changes in direction and strength of effect across ecoregions. The challenges with this approach may become less of a concern with larger, denser biodiversity databases. Currently, there is no guidance on the data requirements of the SVC approach, but encourage future research to focus on data requirements for reliable estimate of this approach.

CONCLUSIONS

The interest in moving toward open-access, publicly available animal occurrence repositories, such as the Global Biodiversity Information Facility, will likely continue to increase, where we see widespread adoption of these databases as primary resources to inform ecological conservation and management (Kays, McShea, & Wikelski, 2020). These databases are essential to continue understanding spatial variation in ecological relationships through local spatial modeling. One of the most appealing results of local spatial modeling is not only the improved predictions to future conditions across landscapes (e.g., regions and countries), but the high resolution of responses to predictors at the management unit level. For example, we documented an interesting relationship that deer management zones in North Carolina—zones based explicitly on population differences across the state—were also exhibiting different ecological relationships across the

state. The powerful combination of predicting large-scale patterns while also emphasizing areas small enough that management or protection highlights the usefulness of this approach in ecology. Thus, we suggest those interested in building SDMs should consider the use of SVCs when the spatial extent of the area of interest exceeds population-level inference and sufficient occurrence records exist.

ACKNOWLEDGMENTS

We thank the volunteers of the North Carolina Candid Critters project for their support in deploying, retrieving, and reviewing photographs. Special thanks to the North Carolina Wildlife Resources Commission for their support of this project and helpful discussions along the way. We are also thankful for valuable conversation and manuscript review from Christopher Moorman. This manuscript was substantially improved following comments from Adam B. Smith and three anonymous reviewers.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Pease, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6478204>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Pease, Brent S., Krishna Pacifici, and Roland Kays. 2022. "Exploring Spatial Nonstationarity for Four Mammal Species Reveals Regional Variation in Environmental Relationships." *Ecosphere* 13(8): e4166. <https://doi.org/10.1002/ecs2.4166>