*Journal of Biogeography*

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Journal of Biogeography

RESEARCH ARTICLE

# Biogeography and Anthropogenic Development Shape Mesopredator Distributions in a Rapidly Developing Region

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**Received:** 12 November 2024 | **Revised:** 26 December 2025 | **Accepted:** 5 January 2026

**Keywords:** coyote | development | land cover | mesopredator | occupancy model | scale | trail camera

## ABSTRACT

**Aim:** To investigate effects of anthropogenic development at regional and landscape scales on the distributions of mid-trophic level mammalian predators (mesopredators) across the southeastern United States.

**Location:** The study area encompasses seven ecoregions across a large portion of the southeastern United States.

**Taxon:** Mammalian mesopredators.

**Methods:** We compiled trail camera data from 21 studies across the southeastern United States and used occupancy modelling to assess mesopredator distributions and account for heterogeneous detection probabilities. We examined drivers of occupancy at regional and landscape scales. At the regional scale, we assessed occupancy patterns across ecoregions differing in topography, productivity, and human population growth. At the landscape scale, we analysed the influence of land cover types (forest, developed, agriculture) and non-native coyote (*Canis latrans*) activity on occupancy.

**Results:** Regionally, mesopredator occurrence was highest in ecoregions characterised by low productivity and greater topographic variability. Common species (predicted occupancy $\geq 0.19$) showed positive associations with developed and agricultural land covers, while less common species (predicted occupancy $\leq 0.10$) showed negative associations or were too rare to model. Coyote activity had mixed effects, positively associated with some species while negatively associated with others.

**Main Conclusions:** Anthropogenic development affects mesopredator communities at both regional and landscape scales, favouring generalist species that are tolerant of human-modified landscapes.

## 1 | Introduction

Large-scale spatial patterns shape wildlife distributions, yet development and other anthropogenic disturbances significantly alter these patterns (Luck 2007; Whittaker et al. 2005). Land cover change (Foley et al. 2005) and the spread of competitively dominant, non-native species (Shochat et al. 2010) have impacted many terrestrial mammalian predators (Marneweck et al. 2021; Ripple et al. 2014). However, some mid-sized terrestrial predators (mesopredators) benefit from low levels of development, expanding into human-dominated regions via supplemental food resources (Newsome et al. 2015) and decreased predation risk due to apex predator extirpation (Prugh et al. 2009). Yet, other mesopredator species have experienced range contractions with increasing anthropogenic disturbance, primarily due to habitat loss from land use change (Jachowski et al. 2021; Torres-Romero and Giordano 2022). Dietary and habitat generalists are more likely to benefit from development, while specialists with narrow resource requirements are more vulnerable to habitat loss and altered resource availability (McKinney 2006). Mesopredators are functionally diverse, globally ubiquitous, and perform a wide variety of ecosystem services (Marneweck et al. 2021), highlighting the need to explore the drivers of mesopredator distributions in areas affected by development. The role of biogeographic drivers in shaping mesopredator distributions in developed (i.e., human-modified) landscapes remains unclear, especially at broad spatial scales where environmental and anthropogenic influences interact.

At a regional scale, such as the geographical range of a species, mesopredator distributions reflect underlying macroecological drivers of mammal communities (Smith et al. 2020). For example, greater topographic complexity is associated with greater mammal diversity than more topographically homogeneous regions (Badgley 2010). Similarly, increased productivity is associated with increased mammalian species richness, though North American mammal communities exhibit the inverse trend (Davies et al. 2011). Development can disrupt these macroecological drivers of regional species distributions (Luck 2007), yet whether established biogeographic patterns persist in rapidly developing regions, or are overridden by anthropogenic factors (Frishkoff et al. 2019) remains poorly understood for mesopredators.

Compared to regional scales, more is known about how anthropogenic development at local scales influences an individual's home range and habitat components (henceforth, landscape scale). Development is associated with changes in land cover, with natural land covers like forests and wetlands increasingly converted to residential, commercial, industrial and agricultural areas (Moll et al. 2019). Loss of habitat associated with development, along with corresponding changes in species interactions, can cause some mesopredators to avoid human-disturbed areas (Heim et al. 2019). However, other mesopredator species benefit from low-density developed land covers as these areas can provide supplemental resources, such as anthropogenic food sources and decreased predation risk due to the extirpation of apex predators (Prugh et al. 2009; Rega-Brodsky et al. 2023). Although the role of prey availability on predator distributions in terrestrial systems remains equivocal (King et al. 2025; Sutton et al. 2023), many mesopredators predate rodents, which often have disproportionately high biomass in developed areas (McCleery 2010). Thus, for some mesopredators, occurrence may be enhanced by low to moderate amounts of anthropogenic disturbance (Suraci et al. 2021).

At the landscape scale, development is associated with non-native species introductions that can alter mesopredator distributions (McKinney 2006), particularly when the introduced species is competitively dominant relative to other native species (Thompson et al. 2025). Globally, small and medium-sized canids are associated with colonising new ecosystems, often in response to anthropogenically-driven apex predator extirpation (e.g., Hody and Kays 2018; Krofel et al. 2017). In the absence of apex predators, competitively dominant non-native canids have widespread ecological impacts in areas they colonise, potentially influencing other mesopredator distributions (Young et al. 2011).

In this study, we investigate how development influences mesopredator distributions at regional and landscape scales. We assemble a dataset from trail cameras deployed throughout the southeastern United States (henceforth, the Southeast) to identify regional- and landscape-scale drivers of mesopredator distributions in a region that has experienced rapid development. Specifically, we address the following research goals: (1) assess regional variation in mesopredator occurrence across the Southeast and determine whether biogeographic patterns observed at continental scales persist in this rapidly developing region; (2) assess how regional biogeographic drivers and landscape-scale anthropogenic drivers jointly influence mesopredator occurrence; and (3) assess how landscape-level facets of development, land cover change, and the spread of a putatively dominant non-native canid, the coyote (*Canis latrans*), affect mesopredator occurrence. We predict that mesopredator occupancy will be greater in ecoregions with more topographic variation and lower productivity, consistent with North American biogeographic patterns (Badgley 2010; Davies et al. 2011). We also predict that generalist species will be more likely to occur in areas with moderate amounts of development and cropland because these areas provide resource supplementation and reduced predation risk for species capable of exploiting anthropogenic resources, while specialist species will avoid or show reduced occupancy in developed areas (Rega-Brodsky et al. 2023).

## 2 | Methods

### 2.1 | Southeastern Ecosystems

We define the Southeast as the coastal and inland region from eastern Texas to Virginia. Historically, it was dominated by open, frequently burned forests (Hanberry et al. 2020) with grasslands and wetlands more common in the southern part of the region, and mixed/hardwood forests in the more topographically diverse north and west. Indigenous peoples and early European settlers altered these landscapes through agriculture, silviculture and resource extraction, creating a patchwork of land use (Munoz et al. 2014; Lear et al. 2004). Over the past century, fire suppression, logging, and other extractive activities further modified forests, leading to widespread mesophication of Eastern forests (Woodbridge et al. 2022). Remaining portions of many native forests in the Southeast are estimated to cover less than 10% of their historic range (Noss et al. 1996).

In addition to altering land cover, humans further impacted southeastern ecosystems by facilitating the introduction of non-native coyotes. Coyotes are native to the southwestern U.S. but expanded eastward following anthropogenically driven apex predator extirpation and forest fragmentation starting in the early 1900s. The earliest recorded coyote colonisation in the Southeast occurred in the western portions of the region

(Louisiana, Arkansas) in the 1950s, with expansion continuing to the rest of the Southeast through the 1990s (Hody and Kays 2018). Unlike free-roaming domestic dogs (*Canis familiaris*), which are generally associated with humans (Parsons et al. 2016) and have been part of southeastern U.S. ecosystems for over 10,000 years (Perri et al. 2021), coyotes arrived recently and are widespread in undeveloped and developed areas (Breck et al. 2019). Thus, coyotes are more likely than dogs to impact other mesopredator species, though the direction and magnitude of their impact on mesopredator distributions remains unclear (Avrin et al. 2023; Egan et al. 2021).

In the early 21st century, greater awareness of the Southeast's biodiversity and its disproportionately high rates of occurrence of endemic North American mammals (Jenkins et al. 2015) prompted calls for improved resource use and protection. Still, the Southeast has received comparatively little protection for natural areas relative to other biodiverse areas in the U.S. (Jenkins et al. 2015). The lack of protection for natural areas has been compounded by rapid human population growth and development. Between 2010 and 2020, the southern region of the U.S., which includes the Southeast and bordering states, experienced the greatest human population increase of all U.S. regions (US Census Bureau 2021). This population growth has coincided with high rates of land cover change in the Southeast, and urban development in the region is expected to more than double over the next 50 years (Terando et al. 2014).

## 2.2 | Study Site and Species

Between 2012 and 2019, we deployed trail cameras in the southeastern states of Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee (Figure 1). We focused our study on 14 species that have typically comprised the mesopredator community of the Southeast: bobcat (*Lynx rufus*), domestic cat (*Felis catus*), coyote, domestic dog, grey fox (*Urocyon cinereoargenteus*), least weasel (*Mustela nivalis*), long-tailed weasel (*M. frenata*), mink (*Neogale vison*), Virginia opossum (*Didelphis virginianus*; henceforth opossum), North American river otter (*Lontra canadensis*; henceforth otter), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), eastern spotted skunk (*Spilogale putorius*), and striped skunk (*Mephitis mephitis*). We grouped each camera by its United States Environmental Protection Agency (US EPA) level III ecoregion classification (Griffith 2010), and cameras were deployed across seven ecoregions: Blue Ridge, Interior Plateau, Piedmont, Southeastern Plains, Southern Coastal Plain, Southern Florida Coastal Plain, and Southwestern Appalachians.

## 2.3 | Study Design

We assessed mesopredator occupancy in the Southeast by aggregating data from 21 trail camera studies conducted between 2012 and 2019 (see Appendix S1 Table S1.1 for individual

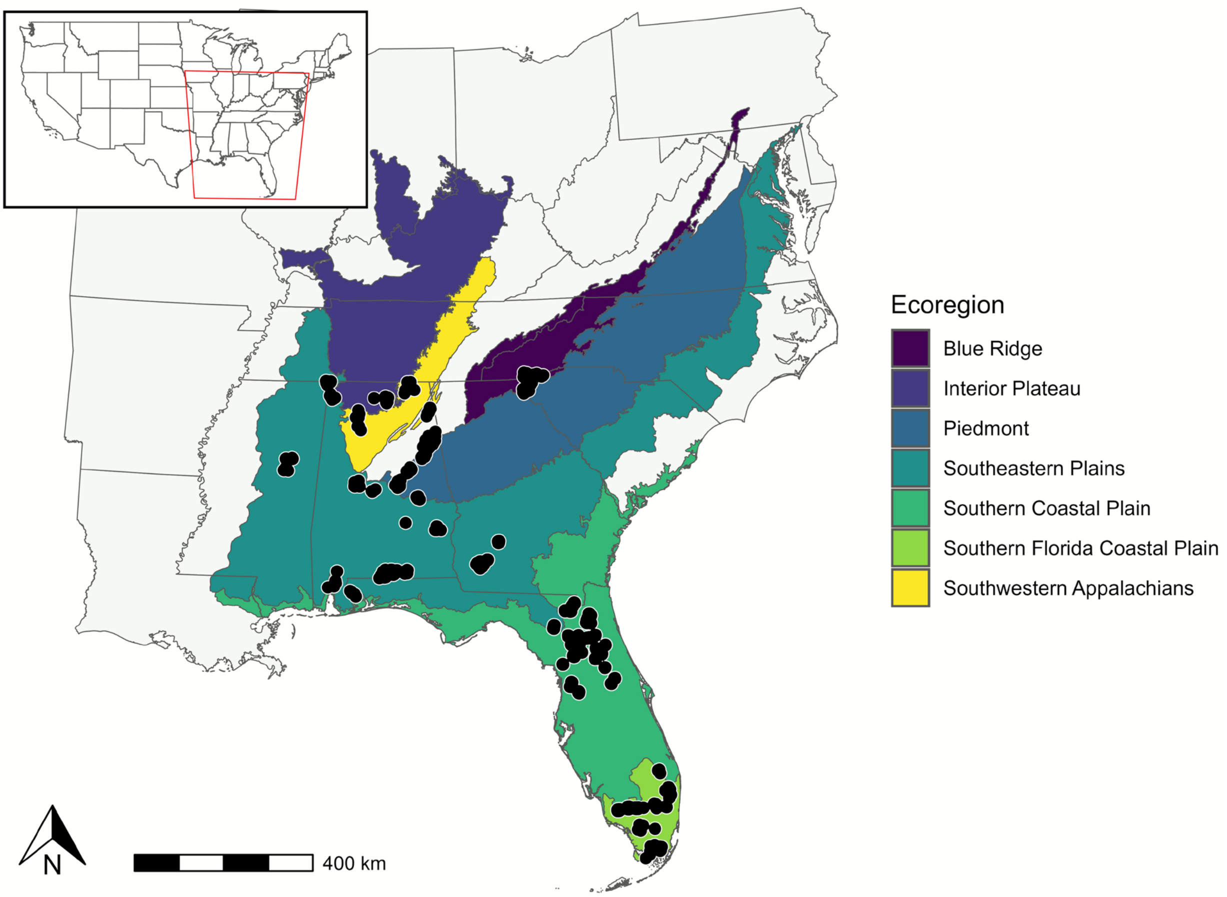


**FIGURE 1** | Map of the southeastern United States study region showing 27 camera landscapes (black polygons) and seven ecoregions used for investigating mesopredator occupancy.

study design details). All studies were designed with the goal of detecting terrestrial mammals including the mesopredators described above, as well as fox squirrel (*Sciurus niger*), feral pig (*Sus scrofa*), American black bear (*Ursus americanus*), and white-tailed deer (*Odocoileus virginianus*). In total, we set cameras at 3491 unique points, which we grouped into 27 camera landscapes. A camera landscape comprised a group of cameras in close spatial proximity and we therefore assumed shared landscape-level attributes. We created camera landscapes by first buffering the coordinates of each camera point by 15 km and assigning all cameras with overlapping buffers to the same camera landscape. We selected 15 km as a buffer because it is larger than a typical resident coyote's core space use (Hinton et al. 2015), and since the coyote was the most mobile species in our study, we considered each camera landscape to be spatially independent (see Appendix S1 Table S1.2 for details on each landscape).

## 2.4 | Occupancy Model

To assess mesopredator distributions and the factors that influenced them across the Southeast, we used a single-species, single-season Bayesian occupancy model framework (MacKenzie et al. 2006; Royle and Kéry 2007). We did not use a multi-species occupancy model because the hierarchical pooling used to integrate data from multiple species can mask or bias species-specific covariate effects (MacKenzie et al. 2018). Occupancy modelling accounted for differences between study designs and explicitly modelled factors affecting detection, which could influence occupancy estimates (Fletcher et al. 2019; Suraci et al. 2021). Detection parameters included whether cameras were baited, set to take a burst of photos, placed on human or game trails, and their deployment height (see Appendix S2 for details on detection covariates).

For occupancy parameters, we used three groups of variables: Region, Land Cover, and Coyote Activity. The Region group consisted of the seven ecoregions where the studies occurred. We included Region as a parameter to better understand the biogeographic impacts on distributions of mesopredators in the Southeast. Using the 2021 National Land Cover Database (NLCD; Dewitz 2021), we collapsed land covers into four categories: Developed, Forest, Wetland and Agriculture (Appendix S1 Table S1.3). For each camera landscape, we calculated the proportion of each land cover category as a predictor variable for mesopredator occupancy. These land cover data provided insight into landscape-scale attributes in the Southeast where forest and wetland land covers have been increasingly converted into developed and agricultural areas (Martinuzzi et al. 2015). Lastly, to capture a gradient of coyote influence, we derived an index of coyote activity (henceforth we use the capitalised 'Coyote' to refer only to the model parameter and use the lowercase 'coyote' for all other situations), which we calculated as the number of independent coyote detections (pictures of coyotes separated by a minimum of 15 min) per 100 trail camera nights in each landscape. We assessed the correlation ($r$) between all predictor variables and excluded one variable from any pair with $r \geq 0.7$ prior to fitting a model.

To fit our occupancy models, we first derived a binary (1 = detected, 0 = not detected) encounter history at every camera for each of our target species, using a daily sampling interval. To improve model convergence, we $z$-standardised all continuous detection and occupancy covariates to have a mean equal to 0 and standard deviation equal to 1. We initially included a random intercept effect for Camera Landscape to account for autocorrelation due to spatial clustering. However, we found that the random effect did not improve model fit and therefore removed it from our final occupancy model to better detect covariate impacts on occupancy. Thus, the final model for each species:

$$\Psi(\text{Region} + \text{Land Cover} + \text{Coyote})p(\text{Bait} + \text{Burst} + \text{Height} + \text{Trail})$$

where $\psi$ represents the occupancy portion of the model and $p$ represents the detection component of the model, with covariates listed in parentheses. We omitted the Coyote parameter from the model for coyote occupancy because both metrics were derived from the same dataset and were therefore highly correlated.

For each parameter in our models, we estimated the posterior distribution using Markov chain Monte Carlo (MCMC) sampling. We performed the MCMC sampling using R v4.4.1 (R Core Team 2024) with packages rStan (Stan Development Team 2022) and ubms (Kellner et al. 2022). We began with uninformative priors and generated five chains of 7000 iterations. The first 3500 iterations were considered burn-in and were discarded (Kellner et al. 2022). We assessed convergence by ensuring that each parameter's Rhat value was < 1.1 (Gelman and Hill 2006). We assessed model goodness-of-fit by visually inspecting binned residual plots based on Dunn-Smyth randomised-quantile residuals (Dunn and Smyth 1996; Kellner et al. 2022). For the occupancy component of each species' model, we computed Dunn–Smyth residuals for 1000 posterior draws. We partitioned observations into five equal-count bins using the posterior-mean predicted occupancy probability. For each draw, we computed the mean residual within each bin and for each bin, we summarised the posterior distribution of the mean residuals by the 2.5% and 97.5% quantiles, giving the 95% posterior credible interval. We also calculated the median of the distribution of mean residuals. Adequate model fit was indicated when the bin-mean credibility interval included zero, whereas intervals consistently excluding zero within a probability range indicated systematic misfit.

To aid in interpretation of results, we used the model output to predict each species' occupancy across the ranges of observed conditions for each parameter of interest while holding all other parameters constant at their means. We predicted occupancy for each land cover and Coyote parameter across a single ecoregion. For land cover predictions, we selected the Southern Coastal Plains as it exhibited the widest range of each land cover class. We used the Southeastern Plains ecoregion for predicting occupancy as a function of Coyote activity because this ecoregion exhibited the widest range of Coyote activity. When calculating the predicted occupancy conditioned on Coyote activity, we also held all land covers at their mean value within the Southeastern Plains ecoregion.

We further explored the underlying biogeographic factors affecting mesopredator distributions by modelling occupancy as a function of four biogeographic features known to influence mammal diversity: increases in human population and human population density (Luck 2007), topographic complexity (Badgley 2010), and productivity (Davies et al. 2011). We obtained human population data at the county level for each ecoregion from the US Census Bureau's (2021) decennial census and calculated human population growth rate between 2010 and 2020. For each ecoregion, we divided the difference in population between 2020 and 2010 by the ecoregion's area to derive change in population density. As a measure of topographic complexity, we calculated the standard deviation (sd) of elevation across each ecoregion using a digital elevation map (DEM) with a 1-arc-second resolution (Farr et al. 2007). As a measure of productivity, we obtained mean daily evapotranspiration (Davies et al. 2011) values for each ecoregion between 2012 and 2019 from the MODIS Global Terrestrial Evapotranspiration 8-Day Global 1-km dataset (Mu et al. 2014).

To identify which biogeographic factors best explained patterns of occupancy across ecoregions, we fit separate mixed-effects regression models for each predictor variable (population increase, density increase, topographic complexity, productivity), using predicted occupancy for each species as the response and including species as a random intercept effect. Since the response variable was a proportion, we used a beta regression, which is appropriate for response values bounded between 0 and 1. All predictor variables were mean-centered and scaled to allow unitless comparison. We also fit a null model with no fixed effects for comparison, as well as a global model that included all predictor variables as additive fixed effects. Models were ranked using Akaike's Information Criterion for small samples (AICc), and any model with $\Delta$AICc $<10$ of the top-ranked model was considered competitive, with substantial support for $\Delta$AICc $<2$ (Burnham and Anderson 2004). For each model with substantial support, we confirmed that model assumptions were met using the function ‘check_model’ from the package performance (Lüdecke et al. 2021). For all competitive models containing multiple fixed effects, we calculated adjusted variance inflation factors (VIFs) using the check_collinearity function in the performance package. The adjusted VIF accounts for predictors with multiple degrees of freedom by scaling generalised VIFs to be comparable to standard VIF values, and values $<2.0$ indicated that collinearity did not influence model fit (Fox and Monette 1992). We also calculated the marginal pseudo-$R^2$ value, the variance explained by only the fixed effects, using the ‘r.squaredGLMM’ function in package MuMIn (Barton 2020) for each top model.

## 3 | Results

We were only able to model occupancy for 11 of the 14 species we targeted for our study. The three species we were unable to model were all members of the family Mustelidae; we recorded a single observation of a long-tailed weasel and observed no least weasels or mink. We therefore report results for only the remaining 11 species for which there were sufficient data to model detection-corrected occupancy. For most species, the 95% posterior credible intervals for bin mean residuals included zero across the predicted occupancy range, indicating adequate model fit. Only the residuals for coyote, opossum, and raccoon showed departures in specific portions of the predicted occupancy range, with some bin means above or below zero (Appendix S3 Figure S3.1).

The amount of forest land cover was highly correlated with wetland land cover ($r = -0.79$), and we therefore removed the wetland predictor from all models as it was more closely correlated with other covariates than forest cover. Predicted occupancy ranged from 0.01 (95% Credibility Interval [CRI] = < 0.01–0.04) for red fox to 0.65 (95% CRI = 0.57–0.73) for bobcat. Coyote predicted occupancy was 0.44 (95% CRI = 0.36–0.52), followed by raccoon at 0.36 (95% CRI = 0.31–0.40), opossum at 0.24 (95% CRI = 0.21–0.28), domestic dog at 0.19 (95% CRI = 0.13–0.27), and domestic cat at 0.19 (95% CRI = 0.06–0.35). Species with lower occupancy included otter at 0.10 (95% CRI = 0.03–0.23), grey fox at 0.06 (95% CRI = 0.04–0.09), striped skunk at 0.02 (95% CRI = < 0.01–0.07), and spotted skunk at 0.02 (95% CRI = 0.01–0.03; Figure 2). Impacts of variations in study design on detection were species-specific (Appendix S1 Table S1.4).

### 3.1 | Land Cover

Across all 27 landscapes, the proportion of available land cover types varied considerably. Developed land cover ranged from 0.003–0.33 (mean = 0.09, sd = 0.06), agricultural land cover ranged from 0.00–0.48 (mean = 0.18, sd = 0.13), and forest land cover ranged from 0.007–0.81 (mean = 0.39, sd = 0.18). In the Southern Coastal Plains, the region we used to predict conditional occupancy across land cover gradients, the range for developed, agricultural, and forest land cover was 0.02–0.33 (mean = 0.18, sd = 0.13), 0.02–0.46 (mean = 0.18, sd = 0.13), and 0.02–0.45 (mean = 0.18, sd = 0.13), respectively (Appendix S1 Table S1.5).

Different land cover types influenced occupancy patterns across several mesopredator species in our model. Forest cover significantly increased occupancy for multiple species, including coyote ($\beta = 1.20$, 95% CRI = 0.50–1.91), grey fox ($\beta = 1.17$, 95% CRI = 0.54–1.92), opossum ($\beta = 1.37$, 95% CRI = 0.91–1.85), and raccoon ($\beta = 0.59$, 95% CRI = 0.15–1.04). Developed areas had the strongest positive effect on bobcat occupancy ($\beta = 2.88$, 95% CRI = 2.14–3.69) and positively influenced opossums ($\beta = 0.43$, 95% CRI = 0.27–0.59) and otters ($\beta = 1.50$, 95% CRI = 0.07–3.99). Agricultural land significantly increased occupancy for coyotes ($\beta = 1.77$, 95% CRI = 1.33–2.22) and raccoons ($\beta = 0.48$, 95% CRI = 0.15–0.81). Credibility intervals for all other mesopredator-land cover relationships contained 0, indicating no significant effect on occupancy using these results (Figure 3, Table 1).

### 3.2 | Region

Compared to the Piedmont, our reference ecoregion, occupancy was significantly higher in the Blue Ridge for several species, including coyote ($\beta = 2.47$, 95% CRI = 0.69–5.43), dog ($\beta = 2.13$, 95% CRI = 0.37–5.04), raccoon ($\beta = 1.29$, 95% CRI = 0.51–2.18), and spotted skunk ($\beta = 2.89$, 95% CRI = 1.37–4.38), though opossum

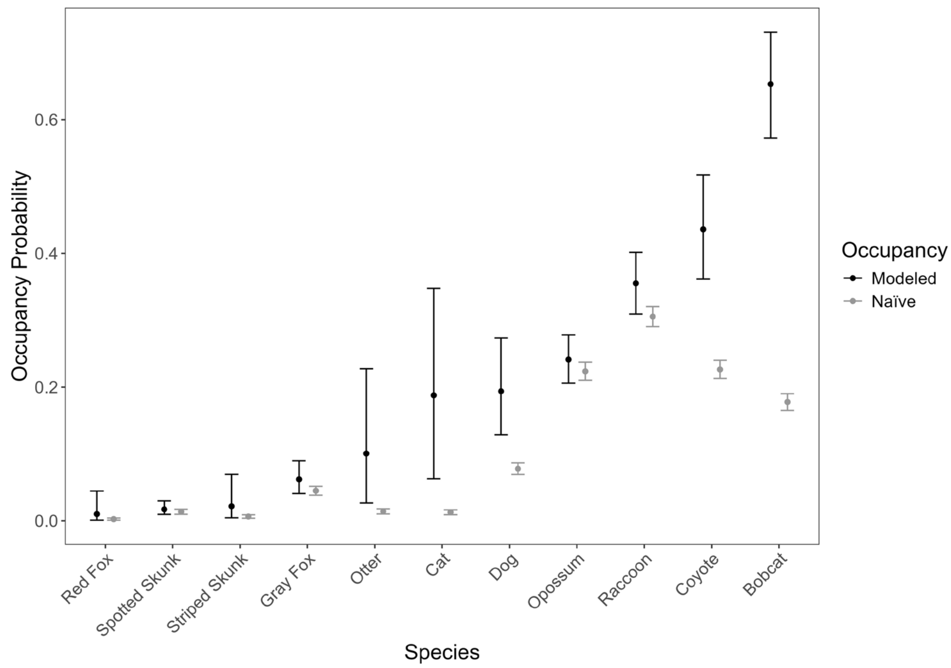


**FIGURE 2** | Naïve and modelled occupancy with 95% confidence intervals for 11 mesopredator species observed in the southeastern United States.

occupancy was significantly lower ($\beta = -0.86$, 95% CRI = −1.58 to −0.16). Coyote and opossum occupancy differed significantly from the Piedmont in the Interior Plateau (coyote: $\beta = 2.44$, 95% CRI = 0.21–5.61; opossum: $\beta = 2.56$, 95% CRI = 1.03–4.14), while opossum occupancy also differed in the Southwestern Appalachians ($\beta = 0.88$, 95% CRI = 0.14–1.62). The Southeastern Plains showed significant differences in occupancy for multiple species, with higher occupancy for opossum ($\beta = 2.47$, 95% CRI = 1.94–3.02) and raccoon ($\beta = 1.27$, 95% CRI = 0.50–2.35), but lower occupancy for coyote ($\beta = -1.09$, 95% CRI = −1.94 to −0.27) and spotted skunk ($\beta = -3.06$, 95% CRI = −6.52 to −0.70). Grey fox and spotted skunk showed significantly lower occupancy in the Southern Coastal Plain (grey fox: $\beta = -2.44$, 95% CRI = −3.66 to −1.19; spotted skunk: $\beta = -3.63$, 95% CRI = −6.25 to −1.41). The Southern Florida Coastal Plain exhibited significant differences for coyote ($\beta = 4.14$, 95% CRI = 1.62–6.75), opossum ($\beta = 5.60$, 95% CRI = 3.84–7.43), and raccoon ($\beta = 3.72$, 95% CRI = 2.02–5.56; Figure 4; Appendix S1 Table S1.6).

Between 2010 and 2020, the human population within our study extent grew by 9.6%, corresponding to a 9.01% increase in human population density. All ecoregions experienced human population growth, with the greatest population increase in the Southern Coastal Plains (11.58%) and Piedmont (11.46%), and the least population increase in the Southwestern Appalachians (5.72%). Population density increased most in the Southern Florida Coastal Plain (379.9 people/km$^2$) while the lowest increases in population density were in the Southeastern Plains (8.27 people/km$^2$) and Southwestern Appalachians (8.82 people/km$^2$). The Blue Ridge was the most topographically diverse (Elevation SD = 279.91 m), while the Southern Florida Coastal Plains showed almost no topographic variation (Elevation SD = 2.87 m). Productivity was greatest in the Southern Coastal Plains (Evapotranspiration = 2.47 mm/day) and lowest in the Interior Plateau (2.12 mm/day; Appendix S1 Table S1.7).

Only the global model was identified as a top model for explaining the underlying biogeographic pattern within ecoregions (Table 2), with the fixed effects explaining 23.3% of the variation in the data. All adjusted VIFs were < 2.0, indicating that collinearity did not influence model fit (Appendix S1 Table S1.8). Mesopredator occupancy increased significantly with increasing human population growth between 2010 and 2020 ($\beta = 0.39$, 95% CI = 0.13–0.65) and decreased significantly with evapotranspiration ($\beta = -0.81$, 95% CI = −1.11 to −0.51). Confidence intervals for absolute change in human population density between 2010 and 2020 ($\beta = 0.05$, 95% CI = −0.17–0.27) and topographic complexity ($\beta = -0.09$, 95% CI = −0.38–0.19) overlapped 0, indicating that they were not significant predictors of mesopredator occupancy within ecoregions.

## 3.3 | Coyote Activity

Coyote activity significantly influenced occupancy for five out of ten mesopredator species in our study (Figure 5). Bobcat showed the strongest positive response to coyote activity ($\beta = 1.34$, 95% CRI = 0.40–2.35), followed by otter ($\beta = 1.24$, 95% CRI = 0.35–2.77) and raccoon ($\beta = 0.32$, 95% CRI = 0.05–0.79). In contrast, both grey fox ($\beta = -0.38$, 95% CRI = −0.80 to −0.08) and opossum ($\beta = -0.12$, 95% CRI = −0.21 to −0.04) exhibited significant negative responses to coyote activity. Credibility intervals for domestic cat, domestic dog, red fox, spotted skunk, and striped skunk contained 0, indicating no significant relationship between these species' occupancy and coyote activity.

# 4 | Discussion

Mesopredator distributions across the Southeast exhibited clear patterns in responses to human activities. The most common

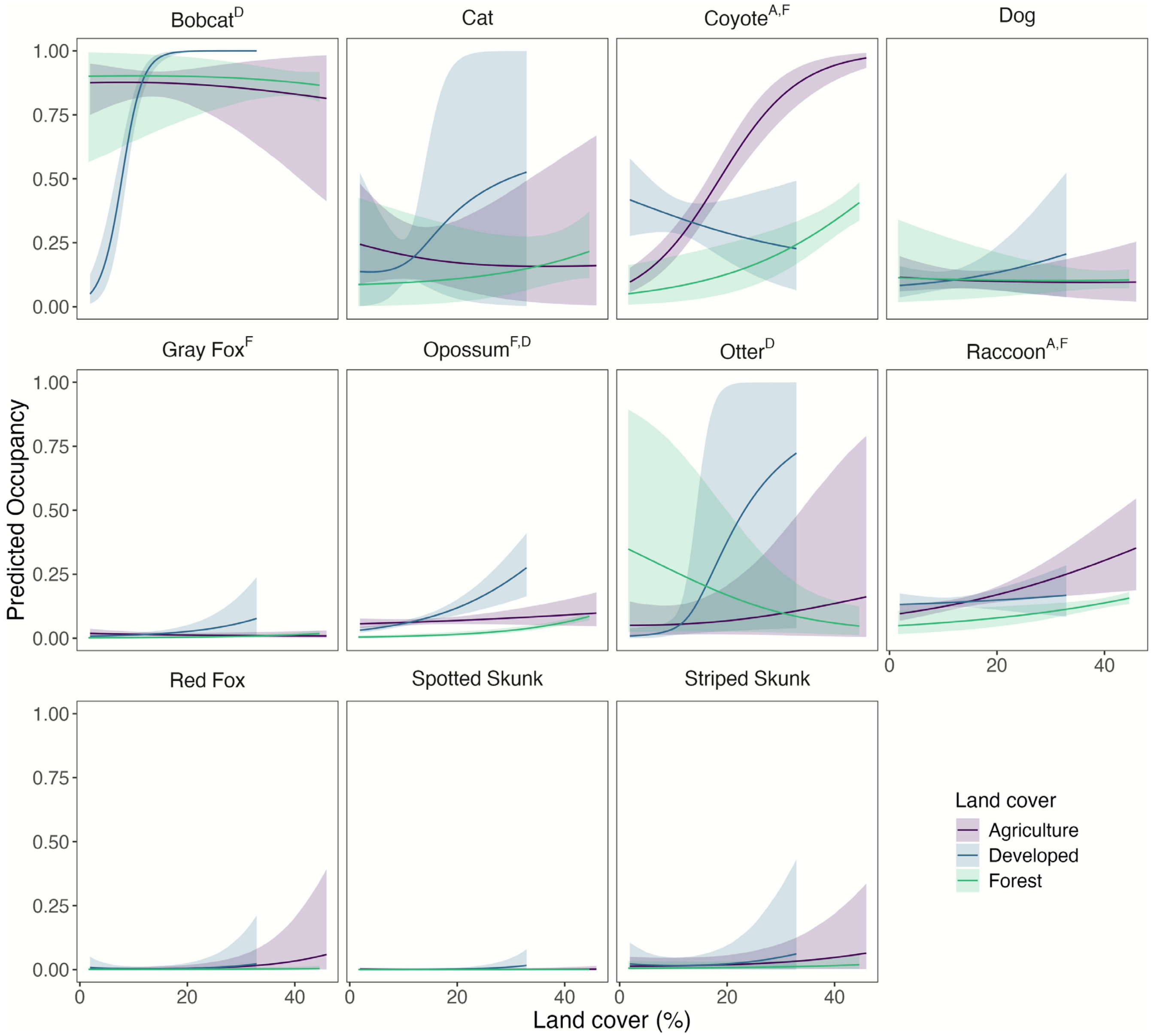


**FIGURE 3** | Impact of different land covers on predicted occupancy for 11 mesopredator species in the southeastern United States. Solid lines show occupancy estimates and shaded areas show 95% confidence intervals. Superscripts indicate significant relationships between species occupancy and land cover (A = Agriculture, D = Developed, F = Forest).

species (predicted occupancy ≥0.19: bobcat, coyote, raccoon, opossum, domestic dog and cat) showed positive associations with development. In contrast, less common species (predicted occupancy ≤0.10: otter, grey fox, striped skunk, spotted skunk, red fox, and mustelids which were too rare to model) showed negative associations or avoidance of developed areas. These patterns suggest development differentially affects mesopredators based on their resource requirements and tolerance to human activities.

The mesopredators we identified as common in the Southeast are also common across much of North America, reflecting their tolerance to disturbance and ability to exploit supplemental anthropogenic food resources, including increased prey availability due to increased rodent biomass. Several of these species have been shown to experience a release (i.e., relaxed population constraint) in disturbed areas where apex predator extirpation has reduced predation risk (Jachowski et al. 2020; Prugh et al. 2009). Furthermore, many of these species are associated with mesic habitats and may benefit from ongoing anthropogenically driven mesophication of eastern forests (Woodbridge et al. 2022). In contrast, species with more specialised ecological requirements (otter, grey fox, striped skunk, spotted skunk, red fox) were likely unable to take advantage of these supplemental resources or were negatively affected by the loss of other key resources, such as refugia or breeding habitat, due to development. For example, grey foxes may be unable to access supplemental resources in developed areas due to the lack of vegetative cover (Farías et al. 2012). Similarly, the loss of wetlands and access to waterways due to development negatively affected otter occurrence (Holland et al. 2019). Furthermore, our limited observations of once

**TABLE 1** | Standardised betas with 95% credibility intervals (CRI; in parentheses) for occupancy (Psi) covariates for 11 mesopredators found throughout the southeastern United States. Only parameters with CRIs that did not overlap 0 (i.e., informative parameters) are presented.

| | Psi | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Region | | | | | | Land Cover | | | |
| Species | Southeastern Plains | Blue Ridge | Southwestern Appalachians | Interior Plateau | Southern Coastal Plains | Southern Florida Coastal Plains | Developed | Forest | Agriculture | Coyote |
| Bobcat | — | — | — | — | — | — | 2.88 (2.14–3.69) | — | — | 1.34 (0.40–2.35) |
| Domestic cat | — | — | — | — | — | — | — | — | — | — |
| Coyote | −1.09 (−1.94 to −0.27) | 2.47 (0.69–5.43) | — | 2.44 (0.21–5.61) | — | 4.14 (1.62–6.75) | — | 1.20 (0.50–1.91) | 1.77 (1.33–2.22) | NA* |
| Domestic dog | — | 2.13 (0.37–5.04) | — | — | — | — | — | — | — | — |
| Grey Fox | — | — | — | — | −2.44 (−3.66 to −1.19) | — | — | 1.17 (0.54–1.92) | — | −0.38 (−0.80 to −0.08) |
| Opossum | 2.47 (1.94–3.02) | −0.86 (−1.58 to −0.16) | 0.88 (0.14–1.62) | 2.56 (1.03–4.14) | — | 5.60 (3.84–7.43) | 0.43 (0.27–0.59) | 1.37 (0.91–1.85) | — | −0.12 (−0.21 to −0.04) |
| Otter | — | — | — | — | — | — | 1.50 (0.07–3.99) | — | — | 1.24 (0.35–2.77) |
| Raccoon | 1.27 (0.50–2.35) | 1.29 (0.51–2.18) | — | — | — | 3.72 (2.02–5.56) | — | 0.59 (0.15–1.04) | 0.48 (0.15–0.81) | 0.32 (0.05–0.79) |
| Red Fox | — | — | — | — | — | — | — | — | — | — |
| Spotted Skunk | −3.06 (−6.52 to −0.70) | 2.89 (1.37–4.38) | — | — | −3.63 (−6.25 to −1.41) | — | — | — | — | — |
| Striped Skunk | — | — | — | — | — | — | — | — | — | — |

*Coyote covariate was derived from the same dataset as the response and was therefore omitted from the coyote model.

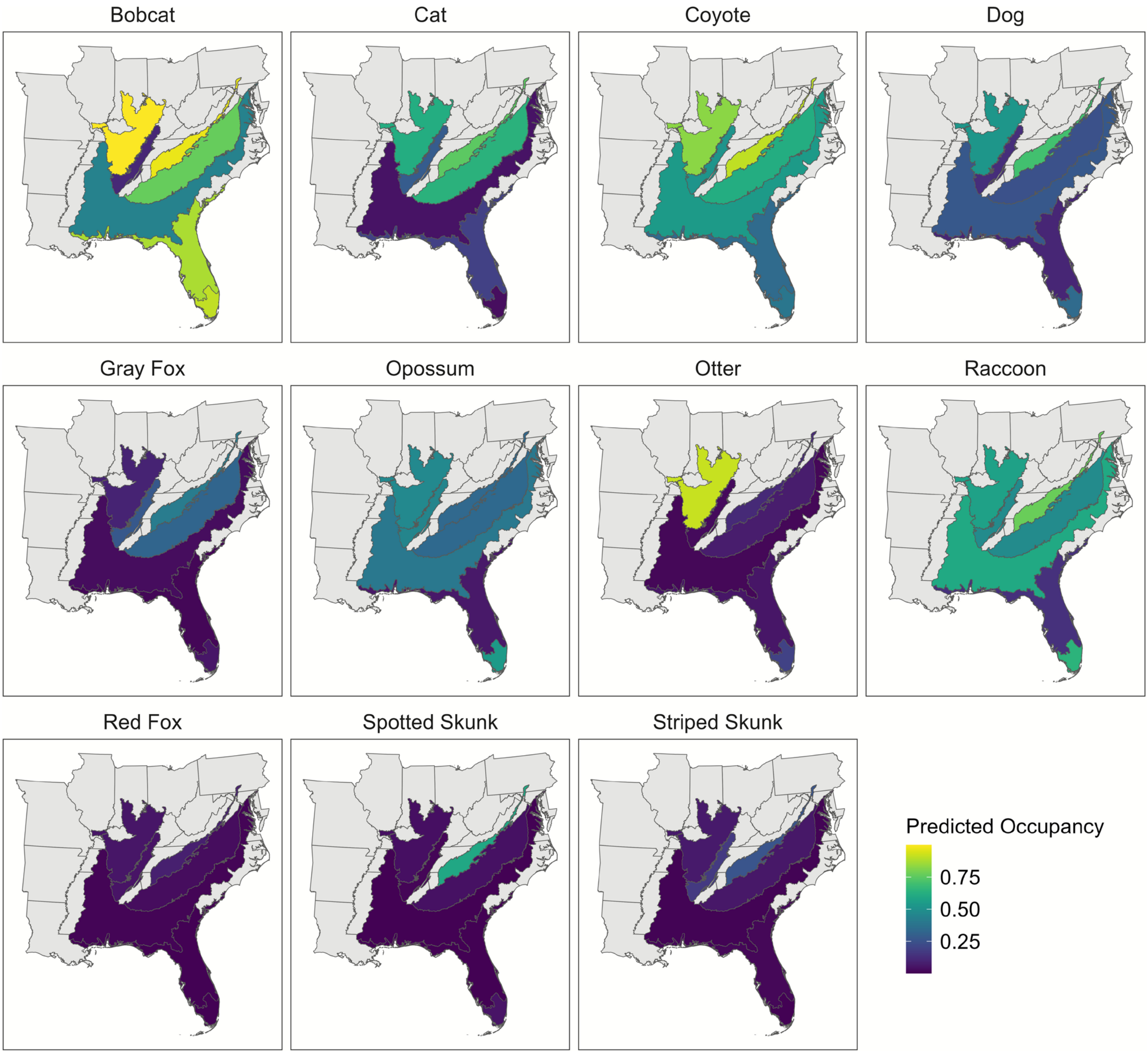


**FIGURE 4** | Predicted occupancy for 11 mesopredator species in seven ecoregions of the southeastern United States.

**TABLE 2** | Model selection for candidate beta regression models investigating the biogeographic drivers of mesopredator occupancy within ecoregions in the southeastern US. Models are ranked by Akaike Information Criterion for small sample size (AICc), where $k$ = number of parameters, $w$ = AICc weight, and Marginal $R^2$ = the amount of variation explained by only the fixed effects in the model. All models included species as a random intercept effect.

| Model | $k$ | AICc | ΔAICc | $w$ | Marginal $R^2$ |
|---|---|---|---|---|---|
| Human population growth rate + change in human population density + productivity + elevation variation (global) | 7 | −96.4 | — | 0.81 | 0.23 |
| Productivity | 4 | −93.5 | 2.94 | 0.19 | 0.18 |
| Elevation variation | 4 | −78.6 | 17.80 | 0 | 0.09 |
| 1 (null) | 3 | −70.3 | 26.10 | 0 | 0 |
| Change in human population density | 4 | −69.7 | 26.65 | 0 | 0.01 |
| Human population growth rate | 4 | −68.3 | 28.09 | 0 | < 0.01 |

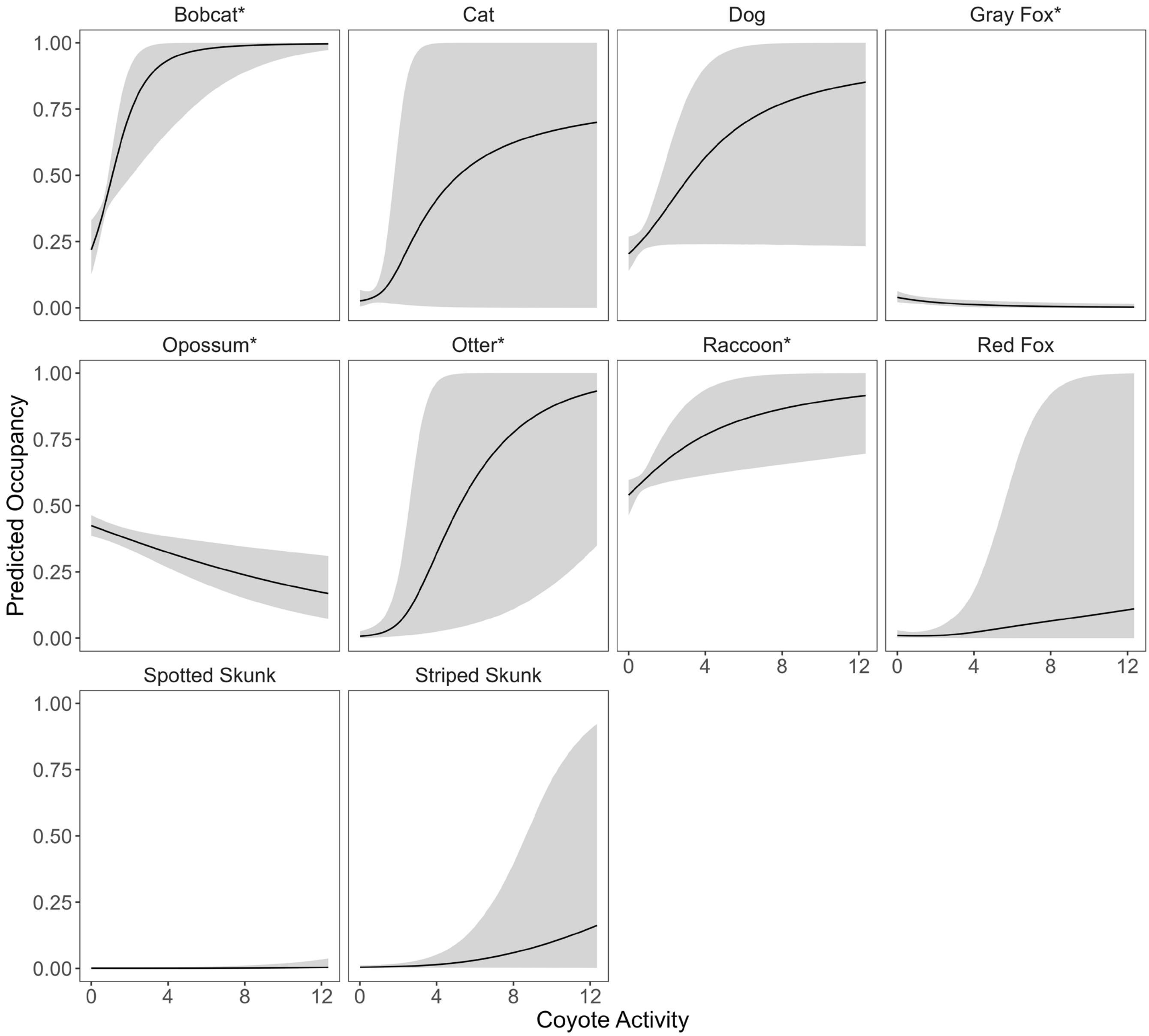


**FIGURE 5** | Impact of coyote activity on predicted occupancy for 10 mesopredator species in the southeastern United States. Solid lines show occupancy estimates and shaded areas show 95% confidence intervals. Significant relationships between species occupancy and coyote activity are indicated by *.

common mustelids and spotted skunks may reflect their sensitivity to increasing development occurring throughout the region (Gompper and Hackett 2005; Jachowski et al. 2021). Overall, these patterns underscore the discrepancy between common, generalist mesopredators, which can exploit human-altered landscapes, and rarer, specialist species, which tend to be negatively affected by development.

There were likely species-specific reasons for the rarity we observed for the less common mesopredators in our study. For grey foxes, low predicted occupancy (0.06) in the Southeast may be the result of increased antagonistic interactions with competitively dominant, and increasingly common, coyotes (Figure 5; Egan et al. 2021). Grey fox occupancy was positively associated with forest ecosystems and may therefore have been especially impacted by declining forest cover (Fritzell and Haroldson 1982). Furthermore, coyotes also exhibited higher occupancy in more forested landscapes, likely increasing antagonistic interactions between coyotes and grey foxes in remaining forest habitat (Egan et al. 2021). Striped skunk occupancy showed no response to any of the covariates we included, suggesting that striped skunk distributions were driven by population constraints not included in our model, such as disease (Gehrt et al. 2010). Grey fox and striped skunk distributions were unlikely to have been driven by prey availability as both species are dietary generalists (Fritzell and Haroldson 1982; Wade-Smith and Verts 1982) and are less sensitive to prey availability than more specialised predators (Bassing et al. 2025).

Red fox and otter were also comparatively rare in our data, possibly reflecting study designs that insufficiently sampled grasslands and wetlands (Larivière and Pasitschniak-Arts 1996; Larivière and Walton 1998). Low otter occupancy may also have been influenced by our removing wetland cover from the analysis due to a high inverse correlation with forest cover, which is supported by our finding that forest cover had a negative, albeit statistically non-significant, impact on otter occupancy (Figure 3). Most cameras were deployed in peri-urban and suburban areas, which may have under-sampled red foxes that are known to use urban areas. Other focal species included in our study were habitat generalists or specialists in land cover types that were well represented in our sample (e.g., grey fox and forest cover), so limited sampling of grassland, wetland, or highly developed areas likely did not affect their estimates in the same way. Incorporating additional landscape covariates, including other land cover types, prey availability, and predator abundance may provide greater insight into the underlying occupancy drivers of less common mesopredators.

Regionally, mesopredator occupancy for most species was highest in the two least productive ecoregions, the Blue Ridge and Interior Plateau, while the most productive ecoregion, the Southern Coastal Plain, was the most depauperate. This pattern matches the inverse relationship between productivity and biodiversity that has been observed in North America (Davies et al. 2011), demonstrating that this macroecological pattern persists even in rapidly developing regions. Additionally, mesopredator occupancy was greater in regions with more rapidly growing human populations, suggesting potential benefits from human expansion through increased food subsidies (Newsome et al. 2015) and reduced apex predator pressure (Berger 2007; Prugh et al. 2009). However, it is also possible that correlations between mesopredator occurrence and human population growth reflect humans having disproportionately moved into areas with already high existing mesopredator occurrence (Martinuzzi et al. 2013). This interpretation suggests the potential for increased human-wildlife conflict, particularly along the urban-wildland interface, and may favor more human-tolerant mesopredators at the expense of less tolerant species (McKinney 2006).

We found that bobcats were common in developed environments, aligning with other studies that have shown bobcats to successfully use urban and suburban environments (e.g., Riley et al. 2010; Young et al. 2019). Although bobcat occupancy estimates may be inflated due to their low detectability (see Appendix S2 for further discussion on detectability), there is evidence that bobcat populations are increasing across the Southeast (Roberts and Crimmins 2010). Our results suggest that these increases may be linked with bobcats' success in developed environments. Unsurprisingly, opossum occupancy was greater in developed areas, reflecting opossums' known urban adaptability and possible selection for urban areas (Markovchick-Nicholls et al. 2008). Differing from findings of prior researchers (Holland et al. 2019), we found otters were more likely to occur in developed environments. However, this pattern is reflected in similar species, such as the Eurasian otter (*Lutra lutra*) and Cape clawless otter (*Aonyx capensis*), which are both common in developed areas that retain sufficient forested and wetland cover (Hong and Joo 2021; Okes and O'Riain 2017). Positive associations between agricultural land and the presence of coyotes and raccoons suggest that both species readily use working landscapes, reflecting their generalist responses to prey and food subsidies (Ferreira et al. 2018). The absence of land cover effects for other mesopredators suggests that these species may be more influenced at this spatial scale by localized factors such as food availability (Newsome et al. 2015), predation risk (Prugh et al. 2009), or interspecific interactions (Parsons et al. 2019) rather than land cover.

Despite being one of the most common mesopredators in the Southeast, coyotes did not have a strong influence on most mesopredator species' occurrence. However, their positive impact on otter occupancy and negative effect on grey foxes suggest complex, species-specific interactions within the mesopredator community. The positive association between otter occupancy and coyote activity may reflect a facultative relationship whereby otters indirectly provide food resources for scavenging coyotes at latrine sites (Gerraty et al. 2024), potentially increasing coyote presence in areas where otters are common. Where they are native, coyotes influence the occurrence of other mesopredator species (Lonsinger et al. 2017), but there is equivocal evidence for their impact on other mesopredators in areas where coyotes have spread (Avrin et al. 2023; Egan et al. 2021; Gehrt and Prange 2007). It is also possible that coyote impacts on mesopredator communities occurred via interactions and scales that we did not measure, such as through changes in mesopredator behaviour (Jensen et al. 2023). Given that their colonisation of the Southeast was a relatively recent occurrence (Hody and Kays 2018), the ecological ramifications of non-native coyote colonisation of the Southeast remain an active research topic.

While our study provides an overview of mesopredator community composition and its drivers at the biogeographic scale, inconsistent model fit in parts of the predicted occupancy range for three common species (coyote, opossum, raccoon) suggests that unmodeled environmental factors or nonlinear relationships may influence occupancy for these species. However, the overall fit for these three species was acceptable across most of the predicted-occupancy range, indicating that our models broadly captured the biogeographic drivers of their distributions in the Southeast. At more local scales, our definition of a landscape (areas of continuously overlapping buffers around camera locations) may not have fully captured variation in vegetation communities, resource availability, or predation risk, all of which are known to affect fine-scale occurrence patterns. Similarly, aggregating land-cover types into broad categories likely oversimplified within-category heterogeneity that could drive occupancy patterns. Although many studies have evaluated local occupancy drivers for mesopredators (e.g., Holland et al. 2019; Morin et al. 2022; Rodriguez et al. 2021), we addressed knowledge gaps in distributional patterns at broader, regional to continental scales.

Mesopredators show complex responses to anthropogenic disturbance, as evidenced by both calls for increased research and conservation of certain species (Jachowski and Edelman 2021; Marneweck et al. 2021) while others exhibit population release (Prugh et al. 2009). These contrasting trends are reflected in the spatial variability of mesopredator presence at both biogeographic and landscape scales, indicating that humans alter the biogeographic drivers of mesopredator occupancy through changes in land cover and non-native species introduction. Moreover, species-specific differences in occupancy across regions and landscapes suggest that certain mesopredators disproportionately benefit from anthropogenic disturbance, which may have ramifications for long-term mesopredator community composition. Given the myriad ecological roles of different mesopredators, anthropogenic impacts on mesopredator communities may have wide-reaching effects on ecosystems.

## Author Contributions

**Alex D. Potash:** data curation, formal analysis, methodology, visualisation, writing – original draft preparation; **L. Mike Conner:** conceptualization, investigation, methodology, supervision, writing – review and editing; **Marcus Lashley:** investigation, supervision, writing – review and editing; **Michael Cherry:** investigation, writing – review and editing; **Andrew J. Edelman:** investigation, writing – review and editing; **Elina Garrison:** investigation, writing – review and editing; **Daniel U. Greene:** investigation, writing – review and editing; **William Gulsby:** investigation, writing – review and editing; **Matthew T. Hallett:** investigation, writing – review and editing; **David S. Jachowski:** investigation, writing – review and editing; **Paul Taillie:** investigation, writing – review and editing; **Robert A. McCleery:** conceptualization, data curation, investigation, methodology, project administration, supervision, writing – review and editing.

## Acknowledgements

We thank all funding sources and research institutions that contributed to this research, as well as the myriad students, technicians, and volunteers that helped collect these data. Richard Chandler, Robin Eng, and Colleen Olfenbuttel contributed data. We also thank the two anonymous reviewers for their thoughtful feedback, which greatly improved the quality of this manuscript. No permits were required for this research as data were collected using passive methods.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings of this study are available in Dryad at http://10.5061/dryad.sn02v6xfg. upon manuscript publication.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jbi70147-sup-0001-AppendixS1-TableS1-S1.docx. **Appendix S2:** jbi70147-sup-0002-AppendixS3-FigureS.docx. **Appendix S3:** jbi70147-sup-0003-AppendixS2.docx.