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The impact of urbanization on genetic connectivity of 10 mammal species in New Jersey

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Abstract

Rapid human modification of landscapes around the world has made understanding how humans affect the genetic connectivity of wildlife populations urgent. The consistency of anthropogenic impact on genetic connectivity across taxa is unclear, in part because it is rare to have data representing functional connectivity for multiple taxa on the same landscape. We use microsatellite data for 10 mammalian species in New Jersey, USA, to assess cross-taxonomic patterns in the impact of urbanization on genetic connectivity. In doing so, we also evaluate the efficacy of species-specific and species-agnostic approaches for representing landscape resistance in landscape genetics analyses. We found relative consistency in the relationship between genetic connectivity and a resistance surface built using a species-agnostic index of human modification. High levels of human modification impeded genetic connectivity in 7/10 species. However, despite this relative consistency, for 7/10 species the highest performing resistance surfaces reflected a suite of variables individually tailored to each species' ecology, rather than species-agnostic representations of human infrastructure. Other land cover covariates, like forest, shrub, and herbaceous cover, consistently facilitated genetic connectivity. These results show that while human modification of the environment is important in explaining patterns of genetic connectivity across taxa, there is enough variation in how species respond to the suite of factors that define a landscape that functional connectivity is not always well represented by human modification alone.

KEYWORDS
connectivity, landscape genetics, mammal, modeling, urbanization, wildlife

INTRODUCTION

The extent of urbanization and human modification of the earth's surface is growing rapidly (Theobald et al., 2020), making understanding the impact of urbanization central to biodiversity conservation. Despite the large changes that humans have made to the landscape, these impacts are not felt evenly across taxonomic groups. Prior studies have shown that the genetic connectivity of specific taxonomic groups, like mammals, may be especially affected by

urbanization (Schmidt et al., 2020). Furthermore, mammals with certain life history traits (e.g., body size) might be more negatively affected by urbanization than others (Habrich et al., 2021; Richardson et al., 2021). In the rapidly growing urban ecology literature, researchers have postulated that this variation exists because urbanization and human infrastructure like roads may have disparate impacts on mobility and survival across taxa (e.g., Richardson et al., 2021).

While an impressive array of data syntheses (Habrich et al., 2021; Schmidt et al., 2020) and meta-analyses (Miles et al., 2019) have evaluated the impact of urbanization on genetic structure, few studies have done so across species with divergent life history traits inhabiting the same landscape, which has been identified as a promising path for research (Miles et al., 2019). Notable exceptions include work by Richardson et al. (2021), which compared genetic structuring and gene flow within white-footed mice (*Peromyscus leucopus*) and big brown bats (*Eptesicus fuscus*) across an urbanization gradient. This study found that the less mobile mouse showed much stronger genetic structuring and less gene flow with urbanization, while genetic structuring in the vagile big brown bat was very weak and not obviously affected by the urban environment.

We capitalized on a dataset collected by the state of New Jersey (USA) to study the impact of human landscape modification on genetic connectivity of 10 mammal species with different life histories. These species occupy home ranges from 0.0081 km^2 (gray squirrel—*Sciurus carolinensis*) to 28.4 km^2 (bobcat—*Lynx rufus*), differ by up to 137-fold in mass, and exhibit varied dietary strategies (Jones et al., 2009), among other life history differences. New Jersey has a long history of intense urbanization, and as of 2015, nearly 27% of the state was considered "urbanized" (NJDEP, Division of Science and Research, 2020), making this an appropriate landscape in which to study the impacts of urbanization on wildlife (Figure 1). This dataset provided us not only with a way to test how mammals with different life history traits were affected by human landscape modification, but also the chance to test two different approaches to model that relationship within a landscape genetics framework. Multiple techniques have been developed to describe and quantify the resistance of landscapes to animal movement and gene flow (reviewed in Zeller et al., 2012). Resistance is the degree to which landscape features impede movement through behavioral aversion, physiological costs, mortality, and other processes (McRae, 2006; Zeller et al., 2012). Within this literature, some researchers develop "species-specific" representations of landscape resistance and others develop "species-agnostic" resistance surfaces (summarized in Belote et al., 2022). Species-specific surfaces represent resistance for one species, often combining vegetation, topographic, or other spatial layers related to the species' habitat and movement requirements and parameterizing it with empirical data from that species (e.g., Cushman et al., 2006; Zeller et al., 2023). Species-agnostic approaches model resistance with spatial layers characterizing human development that may be applicable across taxa (e.g., Krosby et al., 2015) and may be especially useful when species-specific data are not available. While the benefits and costs of specificity and generalizability in resistance modeling likely trade off (Krosby et al., 2015), few studies have compared the utility of these two approaches by testing their ability to predict functional connectivity in multiple species. Furthermore, relatively few multispecies genetic datasets have been assembled to evaluate vertebrate functional connectivity on landscape scales, with most testing 2–4 species (see Biello et al., 2023; Frantz et al., 2012; Marrotte et al., 2017; Mech & Hallett, 2001; Robertson et al., 2018; Thatte et al., 2020; Wultsch et al., 2016).

The objectives of this study were twofold. First, we aimed to evaluate the impact of urbanization in New Jersey on genetic connectivity in 10 different mammal species with different life history traits. Second, we aimed to use this novel dataset to evaluate the appropriateness of species-specific and species-agnostic resistance surfaces for representing genetic connectivity in these diverse taxa. We hypothesized that the relationship between genetic distance and human modification of the environment would be species-specific, with genetic connectivity in human-averse carnivores, like bobcat, showing a stronger negative response to human modification than species that are known to frequent urban and suburban environments, like raccoons (*Procyon lotor*). We expected that species-specific resistance surfaces would be more informative representations of landscape resistance than species-agnostic surfaces in general, but that species-agnostic resistance surfaces would also perform highly for human-averse taxa.

MATERIALS AND METHODS

Study area

This study was conducted in New Jersey, a coastal state in the eastern United States (Figure 1). New Jersey borders the metropolises of Philadelphia and New York City and had a population density of 12,981.89 people per square mile in 2024 (New Jersey Department of Labor and Workforce Development, New Jersey State Data Center 2024), the highest density of any state in the United States. In addition to the 27% of the state that is considered urban, 36% of the state is water or wetlands, 26% of the state is

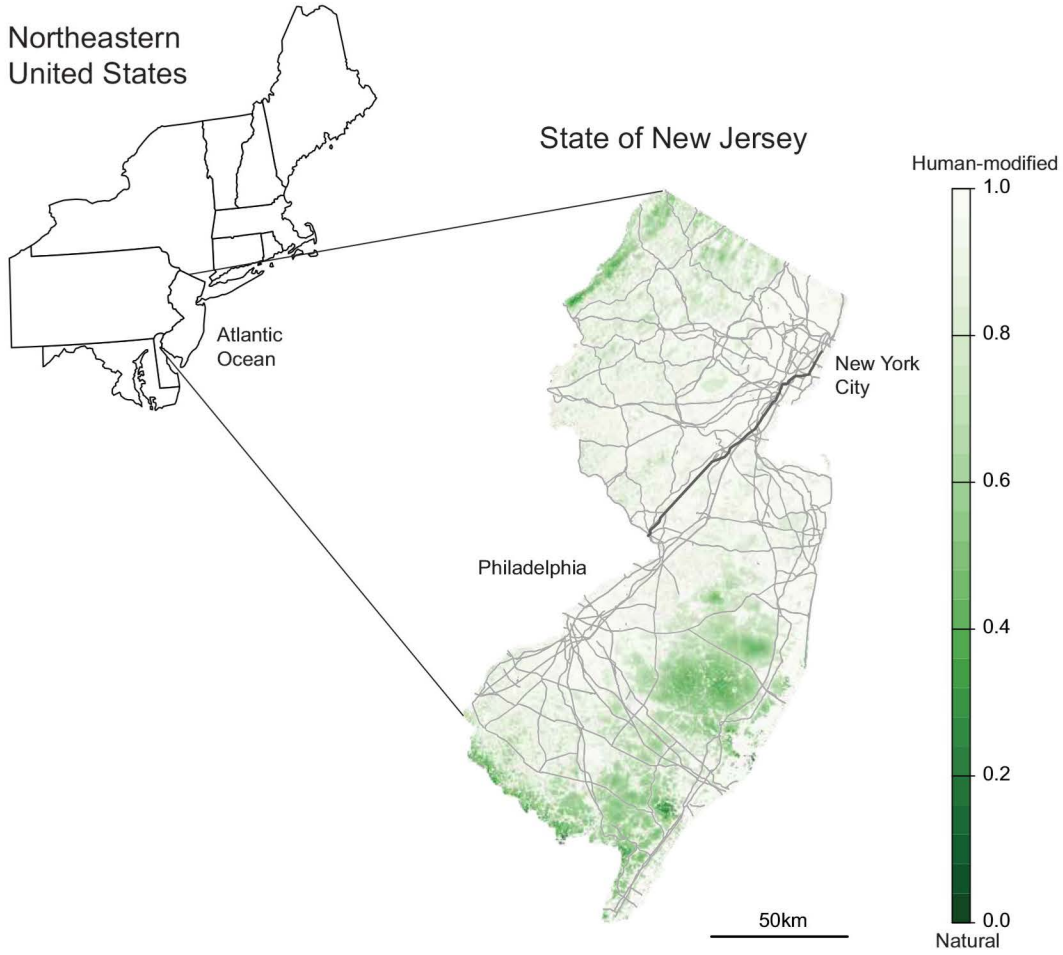

FIGURE 1 Map of study area relative to the Northeastern United States. The colored shading represents the degree of human modification across the state of New Jersey with green colors indicating low levels of modification and light gray colors represent high levels of development. Dark gray lines indicate major roads in the state (Tiger Roads classes S1100 and S1200). The thick gray line is Highway 1, which we use to divide the northern and southern portions of the state for barrier hypothesis models.

forested, and 10% is agricultural (NJDEP, Division of Science and Research, 2020). There are numerous barrier islands along the Atlantic coast of eastern New Jersey, and the Delaware River flanks its western border.

Sample collection and preparation

Our final analysis included 1164 samples from 10 species across New Jersey (Appendix S1: Figure S1): bobcat (*Lynx rufus*; $n = 145$), coyote (*Canis latrans*; $n = 66$), eastern cottontail (*Sylvilagus floridanus*; $n = 127$), Eastern gray squirrel (*Sciurus carolinensis*; $n = 138$), groundhog (*Marmota monax*; $n = 78$), opossum (*Didelphis virginiana*; $n = 106$), raccoon (*Procyon lotor*; $n = 136$), North American river otter (*Lontra canadensis*; $n = 152$), red fox (*Vulpes vulpes*; $n = 99$), and white-tailed deer (*Odocoileus virginianus*; $n = 117$). Our sources included samples from recreational harvest, harvest under threatened and endangered species (T/E) depredation permits, rehabilitation centers, scat surveys, and individuals killed by traffic. Most were tissue samples, although a few raccoon, bobcat, and red fox samples came from scat or hair. We used samples collected year-round from 2018 to 2022, as well as a few additional samples for otter, red fox, and opossum collected in 2017. We obtained GPS coordinates of the collection site for all samples, except for harvested deer and otter. Given this limitation and the large number of deer in our dataset, our final dataset does not include 140 harvested deer. Harvested river otters were placed at the center of the waterbody in which they were trapped. A large number of red fox samples came from T/E depredation harvest on barrier islands, and we tested the impact of heavy sample collection on barrier islands on conclusions (Appendix S1). As a result of this supplemental analysis, we report results for mainland red fox in the main text.

DNA extraction methods differed by sample type. We extracted DNA from tissue using the QIAGEN DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. We extracted DNA from scat using the QIAGEN QIAmp stool mini kit, also following the manufacturer's instructions. For hair samples, we used the QIAGEN DNeasy Blood and Tissue kit but conducted the extraction with an overnight incubation in lysis buffer and proteinase K on a rocker at 60°C and eluted samples in 90 μL of AE buffer. Each species was genotyped at 10–12 microsatellite loci (Table 1) at the National Genomics Center for Fish and Wildlife Conservation. We performed PCR in 10 μL reaction volumes with the following components: 1.0 μL stock DNA extract, 1× reaction buffer (Thermo Fisher Scientific), 2.5 mM $MgCl_2$, 200 μM of each dNTP, 1 μM reverse primer, 1 μM dye-labeled forward primer, 1.5 mg/mL BSA, and 1 U *Taq* polymerase (Thermo Fisher Scientific). We used a PCR thermal profile of 94°C/5 min, (94°C/1 min, 55°C/1 min, 72°C/30 s) × 36 cycles. DNA from hair and scat samples was amplified using the multitube approach to screen for allele dropout, stutter artifacts, and false alleles (Dewoody et al., 2006). We visualized all products in a LI-COR DNA analyzer (LI-COR Biotechnology, NE, USA). Only samples that amplified at 70% or more of locations were included in analyses. All data were evaluated using DROPOUT 2.3 (McKelvey & Schwartz, 2005) and GENALEX v. 6.5 (Peakall & Smouse, 2006) to detect and correct genotyping error.

TABLE 1 Final sample size and microsatellite loci used in genetic analyses for each species.

Species	*N*	# loci	Microsatellites	References
Bobcat (*Lynx rufus*)	145	10	Fca559, Fca96, Lc106, Lc109, Lc111, Lc118, Fca132, Fca57, Fca43, PcoA208	Carmichael et al. (2000), Menotti-Raymond et al. (2004), Kurushima et al. (2006)
Coyote (*Canis latrans*)	66	11	FH2137, FH2088, FH2010, FH2079, FH2096, FH2054, PEZ17, FH2001, FH2161, cxx250, FH2004	Ostrander et al. (1993), Francisco et al. (1996), Neff et al. (1999)
Eastern cottontail (*Sylvilagus floridanus*)	127	10	Sol03, Sol44, 7L1D3, Sol08, Sat16, 5L1A8, Sat5, Sol30, Sol33, Sat12	Rico et al. (1994), Mougel et al. (1997), Surridge et al. (1997), Korstanje et al. (2003)
Gray squirrel (*Sciurus carolinensis*)	138	10	GR09, GR10, GR16, GR17, GR22, GR48, GR51; Scv31, Scv12, Scv13	Hale et al. (2001), Fike et al. (2013)
Groundhog (*Marmota monax*)	78	11	Bibl36, GS14, Bibl4, Bibl25, ST10, MS56, GS25, MS53, Bibl18, GS22, MS45	Stevens et al. (1997), Goossens et al. (1998), Hanslik and Kruckenhauser (2000), McEachern et al. (2011)
Opossum (*Didelphis virginiana*)	106	11	Op03, Op38, Op16, Op46, Op30, Op39, Op31, Op41, Op36, Op48, Op02	Fike et al. (2009)
Raccoon (*Procyon lotor*)	136	11	Plot06, Plot10, Plot07, Plot11, Plot01, Plot02, PLOM15, PLO371, PLOM20, PLOM17, Pfl11	Kays et al. (2000), Cullingham et al. (2006), Fike et al. (2007)
Red fox (mainland) (*Vulpes vulpes*)	99	10	CPH8, FH2004, CPH12, FH2010, PEZ17, FH2054, CXX250, FH2088, AHT130, C20253	Ostrander et al. (1993), Fredholm and Winterø (1995), Holmes et al. (1995), Francisco et al. (1996), Neff et al. (1999)
River otter (*Lontra canadensis*)	152	12	Lut782, Lut604, Lut435, Lut457, Mvis075, Tt1, Gg7, RIO07, Gg14, RIO11, Lut701, RIO17	Dallas and Piertney (1998), Davis and Strobeck (1998), Fleming et al. (1999), Beheler et al. (2004)
White-tailed deer (*Odocoileus virginianus*)	117	10	BM888, FCB193, RT7, Cervid1, T7P, BM4107, BM4208, RT9, C89D, BM1225	Buchanan and Crawford (1993), Bishop et al. (1994), DeWoody et al. (1995), Wilson et al. (1997), Jones et al. (2002)

Species-specific resistance surfaces

We identified 14 covariates expected to influence the dispersal and movement of species in New Jersey (Table 2). We selected land cover products that represented each covariate at a 30 m resolution and reprojected layers to epsg:4326 for analyses. All categorical variables were smoothed within a 90-m moving window in the R package *spatialEco* (Evans & Murphy, 2023). While studies have shown that landscape resistance models can be optimized by testing the impact of variables represented at different spatial scales (e.g., Cushman & Landguth, 2010), computational limits made testing multiple scales across this many species infeasible and not in keeping with our objectives.

We used a pseudo-optimization approach to select the optimal functional form relating genetic distance to resistance for each covariate and for each species (Zeller et al., 2023). All rasters were rescaled to values from 1 to 100 and transformed using seven transformations (positive linear, negative linear, positive concave monomolecular, negative concave monomolecular, positive convex monomolecular, negative concave monomolecular, inverse ricker) (Peterman, 2018). These transformations allowed us to explore the degree to which different landscape features could facilitate genetic connectivity in some species and impede genetic connectivity in others. We used the R package *gdistance* v1.3-6 (van Etten, 2017) to correct each raster for geometric distortion and calculate least cost paths among all pairs of individuals within each species.

We built univariate maximum likelihood population effects (MLPE) models (Clarke et al., 2002) in the R package *nlme* (v3.1; Pinheiro et al., 2025) with the population correlation structure from package *corMLPE* (v0.0.3: https://github.com/nspope/corMLPE) to identify the "optimal" transformation for each covariate for each species. These models included cost distances for a single covariate and Euclidean distance to correct for spatial autocorrelation (Row et al., 2017), both of which were centered and scaled. Pairwise genetic distances between individuals were calculated as Nei's genetic distance with the R package *adgenet* (v2.1.7; Jombart, 2008). A preliminary analysis showed that results using principal components analysis (PCA) genetic distance were very similar to those obtained using Nei's genetic distance, and we chose to present data for one metric for the sake of simplicity. Pairwise Euclidean distances between individuals were calculated with *gdistance*. We used Akaike information criterion (AIC) to compare the performance of resistance transformations for each covariate. If none of the transformations outperformed a model with Euclidean distance alone, the covariate was considered uninformative and excluded from further models for that species.

We used a Pearson's correlation to evaluate raster correlations among top-performing transformations within each species. When correlations exceeded 0.6, we used

TABLE 2 All covariates used to build species-specific resistance surfaces.

Variable type	Variable	Source
Development	Traffic volume	NELCC Traffic Volume Product
	Urban	Theobald HM (30 m)
Hydrology	Distance to water	Calculated as distance to Theobald water mask (30 m)
	Water bodies	Theobald HM water mask (30 m) smoothed
Topography	Elevation	Global SRTM GL1 (30 m)
	Slope	Calculated from elevation (above)
Vegetation type and structure	Agriculture	Landfire (30 m)—EVT codes 7970:7979 smoothed
	Forest—canopy cover (%)	Landfire (30 m)—EVC
	Forest—distance to edge	Landfire (30 m)—EVT—calculate distance to all pixels classified as having "Tree" as the predominant landform
	Herbaceous veg cover (%)	Landfire (30 m)—EVC
	Riparian	National Wetlands Inventory—"Riverine" classification smoothed
	Shrub cover (%)	Landfire (30 m)—EVC
	Shrub height	Landfire (30 m)—EVH
	Wetlands	National Wetlands Inventory—"Freshwater Forested/Shrub," "Freshwater Emergent," or "Other" smoothed

Source: NASA Shuttle Radar Topography Mission (SRTM) (2013), McGarigal et al. (2017), LANDFIRE (2020), Doherty et al. (2022), U.S. Fish and Wildlife Service (2023).

AIC to select and retain the most informative raster for downstream analyses. We calculated AIC weights for remaining variables within each species and retained all surfaces that received at least 0.0001 weight (Table 3). We multiplied remaining rasters by AIC weight and summed rasters to create a single resistance surface for each species. Given that dispersing individuals perceive and respond to the landscape as a whole, recent studies have argued that a single composite resistance raster is the most appropriate representation of landscape resistance (Peterman & Pope, 2021).

Species "agnostic" resistance surface

We used the 30 m version of the Human Modification (HM) dataset (Doherty et al., 2022) as one of the potential covariates in species-specific resistance surfaces (see above), as well as a univariate species-agnostic index of human development. The HM is a cumulative measure of human development on the landscape (scaled 0–1), integrating information about urbanization, transportation, agriculture, energy infrastructure, mining activities, logging, pollution, and other forms of human modification into one spatially explicit data product (Theobald et al., 2020). Prior to modeling, we modified this layer by burning in waterbodies, roads, and railroads (resistance value = 1) on top of the surface (Theobald personal communication). Waterbodies were represented by the watermask used to generate the HM surface (Theobald et al., 2020), and roads and railroads were represented by the TIGER 2019 dataset (S1100, S1200, and railways) and the NLCD impervious descriptor layer (secondary, tertiary, thinned, non-road non-energy impervious). While the resistance weight

TABLE 3 Summary of model results.

Species	Variables in species-specific resistance surface	K-fold performance					Best model performance—full dataset
		SS	HM	Barrier	IBD	NULL	
Bobcat	Freshwater wetlands, slope, agriculture, distance to water, human modification, herbaceous cover, traffic volume, riverine wetlands, shrub height	5	5				Species-specific
Coyote	Forest cover, elevation, slope, agriculture	10					Species-specific
Eastern cottontail	Freshwater wetlands, forest cover	10					Species-specific
Gray squirrel	Agriculture, freshwater wetlands, elevation, riverine wetlands, herbaceous cover, human modification, traffic volume, slope, distance to forest, shrub height, distance to water, water presence	8	1	1			Species-specific
Groundhog	Forest cover, distance to forest, agriculture	10					Species-specific
Opossum	Forest cover, herbaceous cover, distance to forest, agriculture, elevation, slope	6		1	2	1	No best model
Otter	Water presence, riverine wetlands, forest cover, elevation, traffic volume, distance to water, slope, distance to forest, shrub height, freshwater wetlands, herbaceous cover, agriculture		1	9			Barrier
Raccoon	Water presence, distance to water, herbaceous cover, distance to forest, riverine wetlands, slope, elevation, agriculture	10					Species-specific
Red fox (mainland)	Riverine wetlands, herbaceous cover, agriculture, forest cover, distance to water, elevation, water presence, freshwater wetlands	10					Species-specific
White—tailed deer	Slope	10					Species-specific

Note: The first column lists variables in species-specific resistance surfaces. The middle columns report the number of times (max 10) that a model class performed best for each species. The final column reports the model class that performed best with all data.
Abbreviations: HM, human modification resistance; IBD, isolation by distance; SS, species-specific resistance.

assigned to water is debated in species-agnostic resistance modeling, this has been tested elsewhere (Marrec et al., 2020) and was beyond the scope of our study. All diagonals for roads in the NLCD impervious descriptor layer were filled using a Python implementation of the algorithm presented in Rothley (2005) to prevent "corner-crossing" errors in resistance cost distance calculations. We used the "pseudo-optimization" process described above to identify the functional form of resistance that best related the HM to genetic distance for each species.

Comparison of resistance modeling approaches

We built five MLPE models to test the power of two resistance surface modeling approaches (species-agnostic and species-specific) and three alternative hypotheses (panmixia, isolation by distance, and isolation by barrier) to explain patterns of genetic distance within each species. The barrier hypothesis predicted that Highway 1, which is an area of intense urbanization between Philadelphia and New York, would impede gene flow between northern and southern wildlife populations. While we chose Highway 1 as the feature to distinguish north from south (Figure 1), there are numerous highways running east to west in this area of New Jersey, including US 130, 206, the New Jersey Turnpike (I-95), and Interstate 195. The barrier hypothesis was tested for all species, excluding bobcat, which does not currently occur in the southern portion of the state (Cerreta et al., 2023). All models, excluding the null model for panmixia, had a term for Euclidian distance to correct for spatial autocorrelation (Row et al., 2017). Models were built in nlme with the corMLPE correlation structure as described above. We used k-fold cross validation to assess the stability of model performance by dividing the data into 10 folds and identifying the top-performing model when 10% of the data was withheld for all 10 possible datasets. We also ran a final model including all data and checked model residuals visually for normality and equality of variance.

RESULTS

Several covariates for vegetation and human development explained variation in genetic connectivity consistently across species (Figure 2; Appendix S1: Table S1). When HM values increased to high levels, genetic connectivity decreased (7 species; bobcat, fox, otter, deer, groundhog, cottontail, squirrel). Correspondingly, as forest cover increased, genetic connectivity increased (6 species; coyote, fox, otter, opossum, groundhog, cottontail) and this variable received more than 0.01 AIC weight for

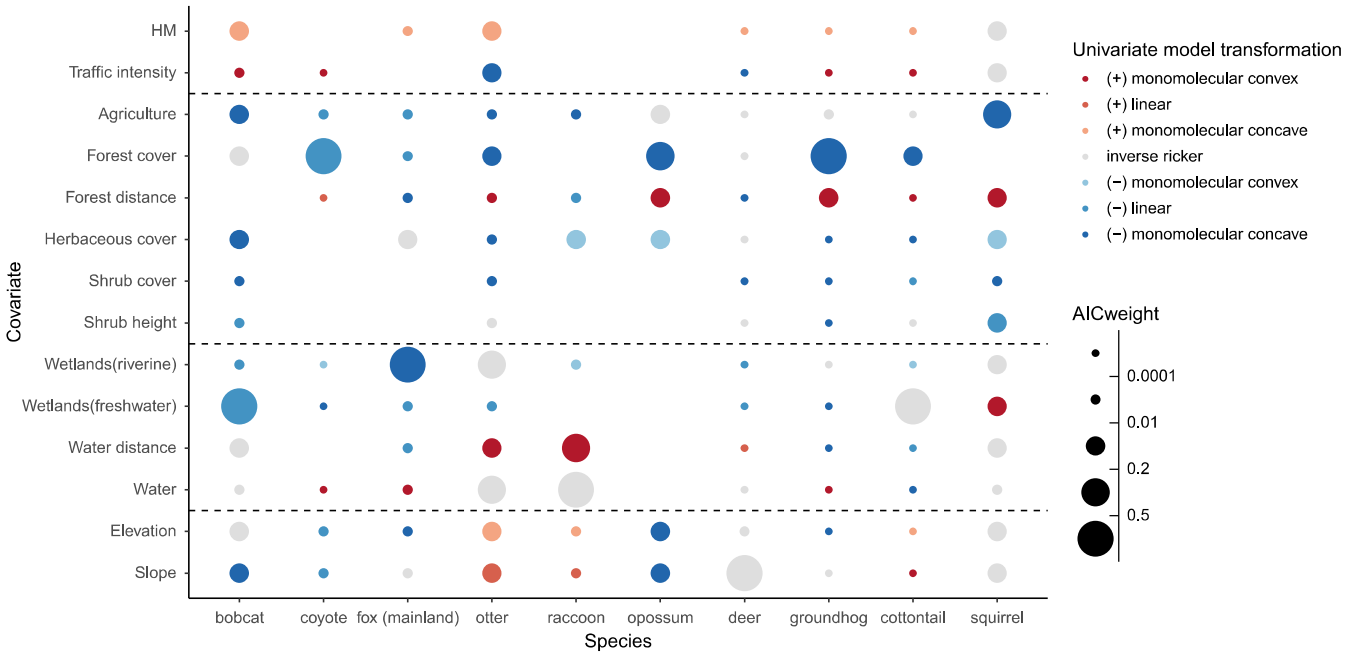

FIGURE 2 Heat map showing best performing univariate model (including transformation) for each variable for each species. The size of the dot represents the relative importance of each variable (Akaike information criterion [AIC] weight). The dot's color represents the functional form of the relationship between landscape variables and genetic connectivity, with red colors representing factors that impede connectivity and blue values representing factors that facilitate connectivity. The dashed lines group covariates thematically for ease of comparison. HM, human modification.

all species except mainland red fox. Other vegetation covariates also facilitated genetic connectivity including herbaceous cover (7 species; bobcat, otter, raccoon, opossum, groundhog, cottontail, squirrel), shrub cover (6 species; bobcat, otter, deer, groundhog, cottontail, squirrel), and agriculture (6 species; bobcat, coyote, fox, otter, raccoon, squirrel). The performance of other vegetation covariates was more variable across species. For example, the presence of freshwater wetlands facilitated genetic connectivity for many taxa (6 species; bobcat, coyote, fox, otter, deer, groundhog) but impeded gene flow in squirrels. Topographical variables had especially disparate impacts across species (Figure 2).

Most species-specific models were built from resistance surfaces incorporating multiple variables in different transformations (Table 3; Appendix S1: Table S1 and Figure S2). The notable exception was the species-specific resistance surface for white-tailed deer, which was based entirely on slope. In multiple instances, top-performing variables were highly correlated with each other (e.g., HM and forest cover, shrub cover and shrub height for specific transformations), and the covariate with the worst AIC score was not included in the final species-specific resistance layer. In 7 of 10 species (fox, coyote, raccoon, deer, groundhog, cottontail, and squirrel), the species-specific resistance surface best explained genetic distance (Table 3) in both analyses with the full dataset and the majority of k-fold cross-validation model runs. Species-specific resistance surfaces were highly similar for some pairs of species ($r = 0.96$ for groundhog and coyote) but highly dissimilar for other pairs of species ($r = -0.33$ for squirrel and eastern cottontail) (Appendix S1: Table S2). For bobcat, the species-specific resistance surface and the species-agnostic resistance each performed best in 5/10 model runs under k-fold cross-validation (Table 3). For otter, the "barrier hypothesis" model performed best. There was no top-performing model of genetic distance in opossum, with the null model performing similarly to alternatives.

DISCUSSION

We were able to look at functional genetic connectivity for 10 mammal species across different taxa and life history traits in the state of New Jersey, USA. The breadth of species and the history of development in this area allowed us to quantify the sensitivity of different species to urbanization. Across most species, HM and several land cover covariates explained patterns of genetic connectivity consistently. In general, human modification of the environment impeded gene flow, while land cover covariates such as forest, shrub, and herbaceous cover facilitated gene flow. Even agriculture facilitated gene flow in several species. Interestingly for HM, our model selection approach showed that the same transformation (positive monomolecular concave) best described the relationship by which human modification increased landscape resistance in 6/10 taxa. That is, resistance to gene flow increased sharply at high HM values.

Despite conducting this work in New Jersey, a heavily urbanized landscape, and studying numerous species associated with urban environments, we did not find evidence that human landscape modification facilitated gene flow for any of our 10 species. In fact, we found that high values of human modification impeded gene flow even in "human tolerant" species like red fox and groundhog. However, resistance values remained low for low and intermediate values of HM. This may indicate that the species in this study are inherently tolerant of urbanization to an extent or that, given the longevity of urbanization patterns in New Jersey, they have adapted to tolerate all but the most extreme levels of urbanization. To explore this relationship, more multispecies studies in areas with differing levels of urbanization would be needed. For example, a study of four carnivores in central India found that human infrastructure negatively impacted genetic connectivity for all species (Thatte et al., 2020). In our study, HM did not predict genetic distance in opossum, coyote, and raccoon. In squirrels, medium HM values were associated with the lowest levels of landscape resistance, but intense urbanization did not facilitate connectivity.

Overall, our results showed that species-specific models of landscape resistance typically outperformed species-agnostic models of landscape resistance, but that species-agnostic surfaces were informative in predicting connectivity across many species. Indeed, for several species, the degree of correlation between species-specific resistance layers and HM was moderate to high (>0.4; bobcat, opossum, groundhog, cottontail), suggesting that they are capturing similar landscape phenomena, at least in the highly urban landscape of New Jersey. Other land cover covariates may also be useful univariate cross-taxonomic representations of landscape resistance. For example, forest cover was one of the most heavily weighted variables in resistance surfaces for multiple species. However, despite the consistent importance of some covariates in explaining patterns of genetic connectivity across taxa, "optimal" species-specific surfaces varied dramatically: correlations among species-specific surfaces ranged from −0.33 to 0.96, reflecting variation in species' experiences of the landscape. This variability parallels findings showing that "umbrella" species approaches, in

which connectivity for one species is used to represent connectivity for multiple species in the ecosystem, may not work well for the full breadth of an ecological community (Brennan et al., 2020). Interestingly, our species-specific resistance surfaces were most similar for several pairs of taxa known to have a predator–prey relationship (bobcat–cottontail: 0.67; coyote–groundhog: 0.96; coyote–opossum: 0.91) (Appendix S1: Table S2).

Neither resistance modeling approach best explained genetic differentiation within opossum and otters. In opossum, all models, including isolation by distance, performed similarly to the null intercept only model. This is consistent with what would be expected in a panmictic population. Indeed, two studies in Indiana found no evidence of genetic clustering in this species (Beatty et al., 2012; Hennessy et al., 2015), although another found clustering on larger spatial scales in the Great Lakes Region of the United States (Walsh & Tucker, 2018). Prior studies have suggested that this may be because opossums are undergoing a range expansion in the Northeastern and Midwestern United States, and some maps suggest that opossum arrived in New Jersey between 1500 and 1912 (Gardner & Sunquist, 2003). Otters also showed distinctive patterns of genetic differentiation in our study, with most model support going to the barrier hypothesis, which postulated a genetic break between populations in the north and south of the state. While it is tempting to view this as a response to dense urbanization in the middle of the state, there are alternative explanations. While HM impeded genetic connectivity in this species, traffic intensity facilitated genetic connectivity in otters, potentially due to culverts or bridges associated with larger, busier roadways and larger waterways—this could be formally tested if a high-resolution dataset of these structures were available. Additionally, these results are puzzling because the Delaware River is a major potential North–South corridor for otter movement in the west. Instead, it is possible that urbanization along the Delaware River and NJ coast, combined with the distribution of North–South waterways in the central part of the state, impeded otter movement.

Genetic datasets can be integrated with other data streams to demonstrate the varying impacts of urbanization across space and time. Continental and global-scale camera trap studies are documenting the widespread impact of urbanization on species' activity and occupancy (Burton et al., 2024; Haight et al., 2023; Suraci et al., 2021). However, these results also show interesting patterns of taxonomic, trait-level, and context dependence. For example, that occupancy and intensity of site use in the same species may respond differently to the presence of human infrastructure versus human activity on the landscape (Nickel et al., 2020; Suraci et al., 2021). Longer term genetic consequences of human modification on the landscape may or may not parallel findings in studies on occupancy and activity. Interestingly, camera-trapping studies have suggested that raccoons and white-tailed deer increase site occupancy and intensity of use with increased human infrastructure (Suraci et al., 2021); however, in our study, HM had a modest negative impact on white-tailed deer genetic connectivity and no impact on genetic connectivity in raccoons. This suggests that the effects of urbanization on genetic connectivity may not parallel the impacts measured for species' behavior.

Human infrastructure is likely to expand its footprint, making understanding how human-modified environments affect biological systems an ongoing area of conservation concern. A growing body of work suggests that while the impacts of urbanization are profound, they also are variable across taxa. Our work shows both cross-taxonomic consistency and species-specific variability in the response of 10 common mammals to urbanization in New Jersey. These findings offer empirical support to the idea that caution is warranted in "umbrella species" approaches to connectivity planning. Additionally, for applications where the conservation cost of potentially mischaracterizing connectivity by relying on species-agnostic approaches to connectivity modeling is high, the additional cost and effort to develop and test species-specific resistance surfaces may be warranted.

AUTHOR CONTRIBUTIONS

Conceptualization: Helen E. Chmura, Katherine A. Zeller, Michael K. Schwartz. *Formal analysis*: Helen E. Chmura. *Funding*: Gretchen Fowles. *Investigation*: Helen E. Chmura, Gretchen Fowles, Kristine L. Pilgrim, Jolene M. Strand. *Methodology*: Helen E. Chmura, Gretchen Fowles, Kristine L. Pilgrim, Michael K. Schwartz, David M. Theobald, Katherine A. Zeller. *Project administration*: Gretchen Fowles, Kristine L. Pilgrim. *Resources*: David M. Theobald. *Writing—original draft*: Helen E. Chmura. *Writing—review and editing*: Helen E. Chmura, GF, Kristine L. Pilgrim, Michael K. Schwartz, David M. Theobald, Katherine A. Zeller.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Chmura, 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.29921855.v1 for all species excluding bobcat. Data for bobcat, a state threatened species, are sensitive and not available publicly. Bobcat data are owned by the State of New Jersey and available to qualified researchers by contacting the New Jersey Department of Environmental Protection Fish and Wildlife Endangered and Nongame Species Program (Gretchen.Fowles@dep.nj.gov) and referencing this publication. Requestors may be required to complete a data-sharing agreement.

ETHICS STATEMENT

Sample collection was overseen by New Jersey DEP Fish and Wildlife (an agency mandated by state law to review and perform all monitoring and permitting).

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SUPPORTING INFORMATION

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

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