Anthropogenic Environments Shape Wildlife Communities and Human-Wildlife Coexistence Across Urbanizing Landscapes

by

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ABSTRACT

With a growing majority of humans living within cities and towns, urbanization is one of the most persistent drivers of change in global land use and challenges to sustainability and biodiversity conservation. The development of cities and towns can substantially shape local and regional environments in which wildlife communities persist. Although urbanization can negatively affect wildlife communities – through processes such as habitat fragmentation and non-native species introduction – cities can also provide resources to wildlife, such as through food, water, and space, creating potential opportunities for conservation. However, managing wildlife communities persisting in urbanizing landscapes requires better understanding of how urbanized landscapes influence the ability of wildlife to coexist with one another and with people at local and regional scales. In this dissertation, I addressed these research needs by evaluating the environmental and human factors driving dynamic wildlife community distributions and people's attitudes towards wildlife. In my first two chapters, I used wildlife camera data collected from across the Phoenix Metropolitan Area, AZ to examine seasonal patterns of wildlife space use, species richness, and interspecific interactions across levels of urbanization with varying landscape characteristics, including plant productivity and spatial land use heterogeneity. Here I found that urbanization was a primary driver of wildlife community characteristics within the region, but that seasonal resource availability and landscape heterogeneity could have mediating influences that require further exploration. In my third chapter, I partnered with wildlife researchers across North America to examine how relationships between urbanization and community composition vary among cities with distinct social-ecological characteristics, finding that effects of local urbanization were more negative in warmer, less vegetated, and more urbanized cities. In my fourth and final chapter, I explored the potential for human-wildlife coexistence by examining how various ideological, environmental, and sociodemographic factors influenced Phoenix area residents' level of comfort living near different wildlife groups. Although I found that residents' attitudes were primarily shaped by their relatively static wildlife values, comfort living near wildlife also depended on the characteristics of the neighboring environment, of the residents, and of the wildlife involved, indicating the potential for facilitating conditions for human-wildlife coexistence. Altogether, the findings of this dissertation suggest that the management of wildlife and their interactions with people within cities would benefit from more proactive and holistic consideration of the interacting environmental, wildlife, and human characteristics that influence the persistence of biodiversity within an increasingly urbanized world.

DEDICATION

To All of the Critters

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1.1 Introduction

The ways that urbanization and other forms of human landscape modification shape ecological communities vary greatly over both space and time. Changes in landscape composition across gradients of urbanization, including increased impervious surface cover and housing density (McDonnell and Pickett, 1990; Moll et al., 2019), reduce habitat and native species richness (Aronson *et al.*, 2014; Beninde *et al.*, 2015; Fidino *et al.*, 2020; Magle *et al.*, 2012; McKinney, 2008; Norton *et al.*, 2016; Shochat *et al.*, 2010). However, species richness can also peak at intermediate levels of urbanization in some systems (Blair, 1996; Blair and Launer, 1997; Germaine and Wakeling, 2001; McKinney, 2008; Parsons *et al.*, 2018), consistent with patterns predicted by the intermediate disturbance hypothesis (Connell, 1978; McIntyre, 2014) and the heterogeneity-species diversity hypothesis (Ben-Hur and Kadmon, 2020; Farwell *et al.*, 2020; Stein *et al.*, 2014; Turner, 1989). Such biodiversity patterns can also vary over time, potentially driven by both short- and long-term changes in environmental conditions (de Albuquerque *et al.*, 2021; Lerman *et al.*, 2020; Warren *et al.*, 2019).

The ecological mechanisms driving spatial and temporal variation of wildlife communities across urbanization gradients remain unclear (Ramalho and Hobbs, 2012), in large part because human activities alter resource phenology as well as landscape composition and configuration in ways that can have simultaneously positive and negative impacts on biodiversity (Fahrig *et al.*, 2011; Martin *et al.*, 2019; Regolin *et al.*, 2020). For instance, anthropogenic landscape heterogeneity and augmented resource availability in cities may increase species richness, thus compensating for the predominantly negative effects of anthropogenic habitat loss (Martin *et al.*, 2021). These co-occurring effects could support higher biodiversity in moderately urbanized environments by increasing temporal turnover of communities (Gallo *et al.*, 2017; Magle *et al.*, 2010). Understanding the mechanisms underlying the interacting effects of human landscape modification and temporal resource heterogeneity is critical for developing strategies to actively manage wildlife communities over time (Andrade *et al.*, 2020; Ramalho and Hobbs, 2012; Shochat *et al.*, 2007).

Temporal dynamics of wildlife communities are influenced by processes of seasonal wildlife space use, including patch colonization and persistence (Bissonette and Storch, 2007). These processes are likely to be particularly pronounced in deserts and other dryland ecosystems characterized by wide seasonal fluctuations in precipitation and primary productivity (Prăvălie, 2016; Safriel and Adeel, 2005), which drive shifts in space use by a wide variety of wildlife species. For instance, certain wildlife species in the Sonoran Desert region of the Southwestern US increasingly utilize areas of higher vegetation productivity and water availability during the early-summer dry season, when those resources are typically most limiting (Gedir *et al.*, 2020; Marshal *et al.*, 2006). Accounting for these temporal patterns is fundamental to effectively managing wildlife across gradients of human development (Andrew and Fox, 2020; Gallo *et al.*, 2017; Ramalho and Hobbs, 2012), but to date, most research on temporal patterns of wildlife has occurred in relatively natural systems.

The management of wildlife communities and their co-occurrence with people across urbanized landscapes requires further understanding of how shifts in community composition may result from how functionally-diverse species utilize space over time (Andrade *et al.*, 2020; Bateman *et al.*, 2015b; de Albuquerque *et al.*, 2021; Leveau *et al.*, 2018). Human landscape modification shapes spatiotemporal patterns of ecological resources on which wildlife depend (Avolio *et al.*, 2021; McIntyre, 2014), particularly by masking natural climate-driven environmental variation (Faeth *et al.*, 2011; Shochat *et al.*, 2007). Wildlife in arid environments may take advantage of year-round and relatively high plant productivity supported by irrigation and vegetation management practices within moderately and highly urbanized areas, especially during periods when natural plant productivity is relatively low (Bateman *et al.*, 2015b; Buyantuyev and Wu, 2012; Faeth *et al.*, 2005). For example, perennial anthropogenic resource provisioning may result in seasonally consistent usage of suburban environments by coyotes (*Canis latrans*) and javelina (*Pecari tajacu*; Bellantoni and Krausman, 1993; DeStefano and DeGraaf, 2003; Grinder and Krausman, 2001; Ticer *et al.*, 1998).

The species traits that enable wildlife to utilize anthropogenic landscapes are likely key factors underlying seasonal changes in wildlife communities in cities. Human activities can augment or attenuate wildlife occurrence, depending on species characteristics such as geographic origin (native vs. introduced; Shochat *et al.*, 2010; Aronson *et al.*, 2014), diet and trophic level (Faeth *et al.*, 2005; Santini *et al.*, 2019; Warren *et al.*, 2006), and reproductive strategy (Marzluff, 2001). Specifically, certain species may be more capable of utilizing more urbanized spaces due to traits associated with their abilities to both colonize fragmented habitat patches (e.g., body size) and persist within those patches by utilize seasonally stable anthropogenic resources (e.g., omnivory; Bateman and Fleming, 2012). For instance, medium-sized carnivore species with more generalist diets tend to more successfully take advantage of more urbanized, fragmented environments, as compared to larger carnivores with more specific diets and extensive landscape area needs (Bateman and Fleming, 2012; DeStefano and DeGraaf, 2003; Suraci *et al.*, 2021). The few species that are able to adapt to fragmented habitats tend to become more abundant in urban and suburban areas than they were in exurban, rural, and wildland areas, reducing species evenness and increasing biotic homogenization (McKinney and Lockwood, 1999). Although species traits influence community assembly (Andrade *et al.*, 2020; Aronson *et al.*, 2016), the relative roles of traits and environmental conditions in shaping seasonal community process in cities remains unclear.

In this study, we examined how the seasonal dynamics and composition of a community of mammals and ground-dwelling birds related to landscape characteristics (urbanization, landscape heterogeneity, seasonal plant productivity) within the metropolitan area of Phoenix, Arizona (Metro Phoenix), a rapidly urbanizing desert system noted for patterns of resource availability strongly linked to seasonal water limitations and anthropogenic water provisioning (Buyantuyev and Wu, 2009, 2012). Our first objective was to quantify dynamic wildlife site use (occupancy, persistence, and colonization) as a function of landscape characteristics and species traits (size and diet) across three seasons. We hypothesized that probabilities of site use would be negatively associated with urbanization and positively associated with landscape heterogeneity (patch type diversity) and plant productivity, indicating increased usage of moderately urbanized sites with greater resource availability (de Albuquerque *et al.*, 2021; McIntyre, 2014). We further predicted that species traits would mediate responses to landscape characteristics, with dietary generalists being more likely to use more heterogeneous and moderately urbanized areas, and with larger-bodied species being less likely to use more highly urbanized sites (Bateman and Fleming, 2012; Rega-Brodsky *et al.*, 2023). Our second objective was to examine relationships among species richness and landscape characteristics and how they vary among seasons. We hypothesized that trends in species richness would reflect patterns of seasonal site use predicted above, increasing with greater vegetation greenness and landscape heterogeneity but declining with increased urbanization across all season, with richness potentially peaking at sites with low-to-moderate urbanization (Martin *et al.*, 2021; Stein *et al.*, 2014) or exhibiting a more linear negative relationship (Aronson *et al.*, 2014; Magle *et al.*, 2021; Lerman *et al.*, 2020; Norton *et al.*, 2016).

1.2 Methods

1.2.1 Study Area and Site Selection

We assessed spatial distributions of wildlife community composition across the metropolitan area of Phoenix, Arizona. Metro Phoenix is the 10th largest and one of the fastest-growing metropolitan areas in the United States (Bureau, 2021). Metro Phoenix is located within the arid Sonoran Desert, where wildland and exurban environments are characterized by species such including creosote bush (*Larrea tridentata*), bursage (*Ambrosia* spp.), brittlebush (*Encelia farinosa*), velvet mesquite (*Prosopis velutina*), palo verde (*Parkinsonia* spp.), and saguaro (*Carnegiea gigantea*). Urban and suburban vegetation communities vary considerably, shaped by the decision-making of the area's residents and land managers and supported via extensive irrigation practices (Larson *et al.*, 2009). Rainfall within the region is generally low (<200 mm per year) and bimodally distributed across two seasons, with precipitation driven by monsoonal moisture in the hot late summer (June-September) and by frontal storms from the west in cooler winter months (Buyantuyev and Wu, 2012). This bimodal precipitation pattern is typically associated with a peak in natural herbaceous vegetation productivity toward the end of the warm and wet monsoon season and a peak in woody vegetation productivity during late spring and early summer, though the complex relationships among vegetation phenology and precipitation are poorly understood in urbanizing dryland systems (Buyantuyev and Wu, 2009, 2012).

We surveyed ground-dwelling wildlife species continuously for approximately one year (March 2019 to April 2020) by deploying motion-activated trail cameras situated across a gradient of urbanization. We co-located our survey sites with existing ecological survey sites of the Central Arizona-Phoenix Long-Term Ecological Research (CAP LTER) program (Allen *et al.*, 2018; Bateman *et al.*, 2018; Childers *et al.*, 2018), selecting sites via a stratified random sampling process based on broad levels of urbanization. Based on the most current fine-resolution (1 meter resolution) land cover data available at the time of site selection (Li, 2015), we calculated the proportion of impervious cover types (i.e., buildings and roads) within a 1000 meter radius buffer and grouped sites into five urbanization strata based on that proportion: Stratum 1 (0 to 0.01%); Stratum 2 (0.01 to 17.00%); Stratum 3 (17.01 to 36.00%); Stratum 4 (36.01 to 53.00%); and Stratum 5 (>53.00%). Potential sites surrounded by >10% agricultural land cover types containing > 10% agricultural land cover or above 545 m elevation were excluded to further maintain consistency in land use and topography among sites at each level of urbanization. We then randomly selected 10 sites within each stratum, for a total of 50 sampling sites. To account for spatial independence among sampling locations, all sites were situated at least 2 km apart.

At each sampling site, we installed one wildlife camera (Bushnell Trophy Trail Camera Essential E3, n = 30; and Cuddeback Silver Series Black Flash, n = 20), following the experimental protocol of the Urban Wildlife Information Network (Magle et al., 2019). Cameras were placed in areas believed to maximize the probability of detecting wildlife moving through the area, typically adjacent to washes, fences, and trails. Each camera was programmed to record a series of two images for each trigger of its infrared sensor, with a minimum 30 second rest period between each trigger. Camera collected photos continuously for one year and were visited regularly (every 3-8 weeks) to ensure the proper operation of the cameras and to retrieve image data. We identified mammals and ground-dwelling birds in wildlife camera photos to the species or genus level, in accordance with a list of mammal and ground-dwelling bird species believed to occur within the study (Arizona Game and Fish Department, 2012; iNaturalist.org, 2018; IUCN, 2016). All photo identification was conducted by trained personnel.

1.2.2 Species Detection Data

Based on our hypotheses, we organized species detections into three distinct 96-day seasons: Warm-Dry (April 15th – July 19th), Warm-Wet (July 20th – October 23rd), and Cool-Wet (December 1st – March 5th). We selected these particular dates to represent these seasons due to the unique seasonal patterns of temperature and bimodal precipitation that characterize the Sonoran Desert region where the hottest months of each year can be distinctly divided into a dry period with little to no precipitation and a wet period (Buyantuyev and Wu, 2012; Thornton *et al.*, 2020). To aid in the estimation of detection probability of rare species, we further grouped daily detections of each species into six 16-day sampling occasions for each season and summarized site-level sampling effort as the number of days in which each camera was operational across seasons.

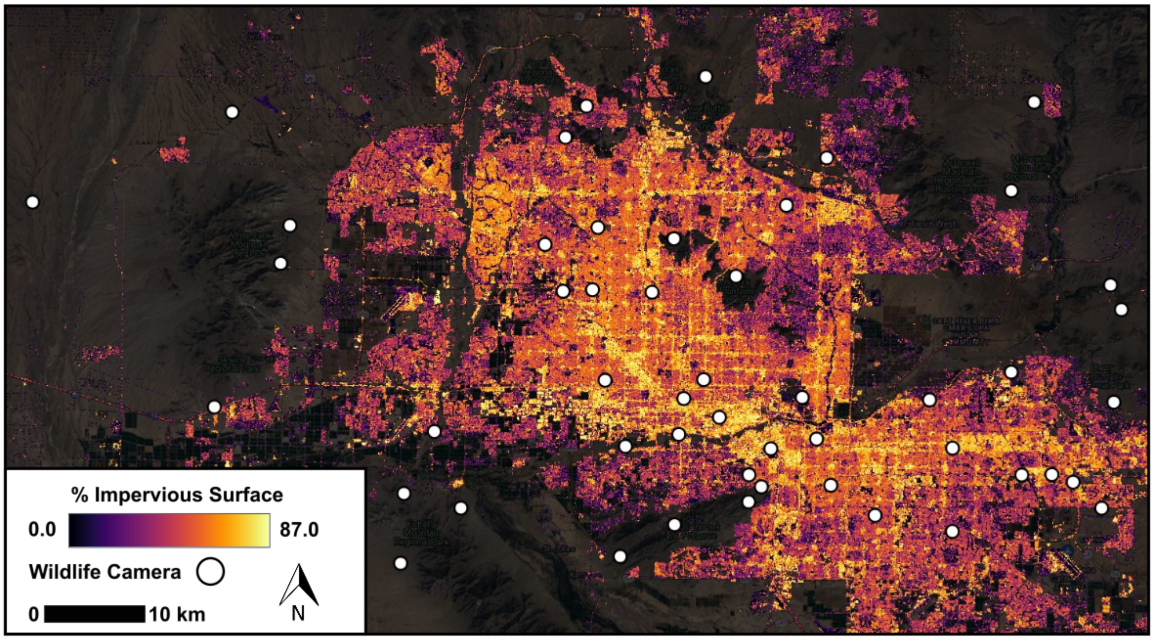

Figure 1.1: Distribution of wildlife camera sites across a gradient of urbanization (% impervious surface cover) within the Phoenix Metropolitan Area, Arizona, USA

1.2.3 Environmental Characterization

We quantified a suite of environmental landscape characteristics potentially associated with the gradient of urbanization and its effects on the presence and diversity of wildlife species across multiple seasons. To address how species use environmental factors across varying spatial scales (Mayor *et al.*, 2009; McGarigal *et al.*, 2016), we evaluated each landscape characteristic within three differently sized buffers: fine (100 m), medium (1 km), and broad (5 km). At each of these spatial scales, we used the *raster* package in R version 4.0.1 (R Core Team, 2020) to estimate the *urbanization* covariate as the mean impervious surface cover percentage from the 2019 National Land Cover Database (NLCD; Dewitz, 2021). At each scale, we produced an additional metric of *quadratic urbanization* for which high values represented both low and high urbanization by standardizing then squaring values of urbanization.

We used Google Earth Engine (Gorelick *et al.*, 2017) and 30 m Landsat 8 surface reflectance to calculate median values of Normalized Difference in Vegetation Index (NDVI) within each sampling season. We represented values of vegetation *greenness* as the mean NDVI value within each buffer size. At the 1 km scale, urbanization was not highly correlated with vegetation greenness during the warm-dry (Pearson's r = -0.33) or warm-wet seasons (r = -0.15), but it was negatively associated with greenness during the cool-wet season (r = -0.72). We grouped values of greenness by season and standardized values around each season-specific mean. Due to high collinearity between urbanization and greenness during the cool-wet season, we did not estimated effects of greenness in any season-specific models that also assessed urbanization relationships – i.e., we excluded greenness as a covariate in the species richness meta-analysis model described below.

We then evaluated compositional and configurational patch heterogeneity at different levels of urbanization by quantifying a series of landscape metrics. We used 30-m land cover data from the 2019 NLCD and the *landscapemetrics* R package (Hesselbarth et al., 2019) to measure landscape-level patch richness, patch diversity, patch density, edge density, and contagion within the 100 m, 1 km, and 5 km buffers (McGarigal *et al.*, 2012). All landscape metrics we calculated were very highly correlated with one another ($r > 0.6$) at each spatial scale. Patch diversity and patch density were the metrics of landscape heterogeneity most negatively correlated with quadratic urbanization across scales (Appendix A.1), indicating that these metrics peak at moderate levels of urbanization. Based on this assessment, we chose to represent landscape heterogentiy using the compositional metric of *patch diversity*, which we represented using the Shannon Diversity Index of land cover patch types in the area surrounding each site.

1.2.4 Species Traits

We assessed two key species functional traits – body size and diet diversity – hypothesized to influence variation in patch dynamics among species and across urbanization gradients, using data from the EltonTraits database (Wilman *et al.*, 2016). We represented the *body size* of each species using its mean body mass, which we log-transformed. To contrast dietary-specialized species from more highly omnivorous, dietary-generalist species, we calculated each species' level of *dietary diversity* by calculating a Shannon Index based on the proportions of all 10 food item categories, following the methods of Santini et al. (2019).

1.2.5 Modeling Multi-Season Community Dynamics

We estimated the multi-season, site-level occupancy states of all observed species using dynamic community occupancy models (DCMs; Dorazio *et al.*, 2006; Kéry and

Royle, 2021b). Because the home range size of large mammal species included in this analysis likely exceeded the 1 km buffer between cameras, all resulting estimates of species occupancy (presence) should be interpreted as that species 'use' of that site, rather than true occupancy (Magle *et al.*, 2021). We formulated our DCM such that the likelihoods of species presence in each season were estimated as a function of their probabilities of detection, initial occupancy, colonization, and persistence (Kéry and Royle, 2021b). Below we describe the hierarchical structure of this model, including how we adapted existing models to examine among-site and among-species variation in each process.

The first part of the model estimated species occupancy in the first sampled season. For j in 1,..,J sampled sites, we let $z_{s,1,j}$ be a Bernoulli random variable with a value of 1 when species s is present at a site in the first sampling season and 0 when the species is absent. For simplicity, we drop the subscript j from much of the remaining model explanation. We let $\psi_{s,1}$ be the probability of occupying a site in the first season, such that

$$z_{s,1,j} \sim Bernoulli(\psi_{s,1}) \tag{1.1}$$

The second part of the model estimated the probabilities of species remaining at already-occupied sites (persistence, ϕ) and arriving at unoccupied sites (colonization, γ), and then used both probabilities to derive the dynamic occupancy states of each species. For t in 2,...,T sampling seasons, we let each species' presence at a site $z_{s,t,j}$ be a Bernoulli variable with the cumulative probabilities of the species persisting at sites where it was present in the previous season and colonizing sites where it was previously absent, such that

$$z_{s,t,j} \sim Bernoulli(\psi_{s,1} \times \phi_{s,t} + (1 - \psi_{s,1}) \times \gamma_{s,t}) \tag{1.2}$$

where local species richness at each site during each season $\alpha_{t,j}$ was represented as the across-species of sum of all latent occupancy states ($\alpha_{t,j} = \Sigma z_{s,t,j}$) (Kéry and Royle, 2016; Magle et al., 2021).

The third part of the model accounted for imperfect detection. We let $y_{s,t,j}$be a binomial random variable that is the number of survey occasions in which species s was observed at site j in season t; where $k_{t,j}$ is the total number of survey occasions in which a camera trap was functional; and $\rho_{s,t}$ is the probability that a species is detected in each season, given its presence, such that

$$\begin{aligned} y_{s,t,j} &\sim Binomial(\rho_{s,t} \times z_{s,t,j} \times k_{t,j}) \\ \rho_{s,t} &\sim Normal(\hat{\rho_s}, \sigma_{\hat{\rho_s}}) \end{aligned} \tag{1.3}$$

where the species- and season-specific detection parameter $\rho_{s,t}$ varied around each species' season-average detection parameter $\hat{\rho_s}$ via the standard deviation term $\sigma_{\hat{\rho_s}}$. We further allowed initial occupancy, persistence, colonization, and detection to vary across sites as a function of environmental covariates via the logit link, such that

$$\begin{aligned} logit(\psi_{s,1}) = \beta_{\psi,Intercept,s} \\ + \beta_{\psi,Urbanization,s} \times Urbanization + \beta_{\psi,QuadraticUrbanization,s} \times Urbanization^2 \\ + \beta_{\psi,PatchDiversity,s} \times PatchDiversity + \beta_{\psi,Greenness,s} \times Greenness \end{aligned} \tag{1.4}$$

$$\begin{aligned} logit(\phi_{s,1}) = \beta_{\phi,Intercept,s} \\ + \beta_{\phi,Urbanization,s} \times Urbanization + \beta_{\phi,QuadraticUrbanization,s} \times Urbanization^2 \\ + \beta_{\phi,PatchDiversity,s} \times PatchDiversity + \beta_{\phi,Greenness,s} \times Greenness \end{aligned} \tag{1.5}$$

$$
\begin{aligned}
logit(\gamma_{s,1}) = \beta_{\gamma,Intercept,s} & \\
+ \beta_{\gamma,Urbanization,s} \times Urbanization + \beta_{\gamma,QuadraticUrbanization,s} \times Urbanization^2 & \\
+ \beta_{\gamma,PatchDiversity,s} \times PatchDiversity + \beta_{\gamma,Greenness,s} \times Greenness & \quad (1.6)
\end{aligned}
$$

where the terms *Urbanization*, *Patch Diversity*, *Greenness*, and *Effort* correspond to standardized values of each environmental covariate across sites – and across seasons, in the case of *Greenness.*

We parameterized all intercept and slope terms in the model such that species-level parameters were drawn from community-level (species-averaged) parameters. We used a near-identical hierarchical parameterization for all intercept and slope terms within Eq. 1 through 4. As such, we explain only the prior specification for the initial occupancy intercept, which was

$$
\begin{aligned}
\beta_{\psi,Intercept,c} &\sim Normal(0, 1.5) \\
\beta_{\psi,Intercept,s} &\sim Normal(\beta_{\psi,Intercept,c}, \sigma_{\psi,Intercept,c}) \\
\sigma_{\psi,Intercept,c} &\sim Inv-Gamma(0.1, 0.1)
\end{aligned}
\quad (1.7)
$$

Where $\beta_{\psi,Intercept,c}$ is the logit-scale average intercept across species and $\beta_{\psi,Intercept,s}$ is the species-specific logit-scale average intercept that varied around $\beta_{\psi,Intercept,c}$ via the standard deviation term $\sigma_{\psi,Intercept,c}$.

As the sole exception to the parameterization described above, we allowed certain species-specific parameters to vary from the community parameters, partially as a function of species traits. In the model, among-species covariates were assumed to partially influence the degrees to which each species-level parameter (occupancy, persistence, colonization, and the relationships of each with environmental covariates) varies from its respective community-average parameter.

1.2.6 Model Fitting

We implemented all DCMs in a Bayesian framework using R programming language version 4.0.1 (R Core Team, 2020) and JAGS 4.3.0 (Plummer, 2003). Following a 10,000 step adaptation and a 370,000 step burn-in, we sampled the posterior of each model 90,000 times across three chains. We thinned each chain by 3 to reduce complexity in monitoring model parameters, resulting in a total of 30,000 posterior samples. We calculated the conditional predictive ordinate (CPO) for each data point at each Markov chain Monte Carlo (MCMC) step. To assess the relative fit and compare overall performance of all DCMs (see Covariate Selection Process below), we used the summary statistic $-\Sigma_{k,t} log(CPO_{k,t}$ for data point k and MCMC step t (hereafter referred to as the *CPO summary statistic*), where lower values indicated better relative performance (Hooten and Hobbs, 2015). We verified convergence for all modeled parameters by examining the Gelman-Rubins diagnostics ($\hat{R} < 1.1$; Gelman *et al.*, 2014).

1.2.7 Covariate Selection Process

We evaluated our hypotheses using global DCM containing each environmental covariate at an optimal spatial scale, in order to improve the predictive power of our model. We optimized the spatial scales of covariates by fitting a series of univariate models, each including a single covariate (urbanization with the quadratic term; patch diversity; greenness) at each individual spatial scale (100-m, 1-km, 5-km). For each covariate, we then compared the relative fit of univariate models fit at different scales using the CPO summary statistic. For each covariate, we then considered the scale used in the best-fit univariate model to be its ‘optimal’ spatial scale. After verifying relatively low collinearity ($r < 0.6$) among the scale-optimized covariates, we combined them into the full global DCM outlined in the equations above.

Finally, we fit a second global DCM in which we removed the quadratic urbanization parameters (see Eq. 1.4 to 1.6). We compared the relative fit of these two global models, to further assess the shape of relationships among urbanization and occupancy, persistence, and colonization. Although we primarily focused on the discussion of parameter estimates and analyses of species richness based on the best-supported (lower CPO) of the two DCMs, we additionally noted where results from the less-supported DCM differed.

1.2.8 Species Richness Meta-analysis

We modeled relationships between species richness estimates from the best-supported DCM and environmental covariates using a Bayesian meta-analysis approach. Using the same model fitting parameters as above (with the exception of increasing the sampling of the posterior to 90,000 estimates, to ensure model convergence), we fit a log-link generalized linear model (GLM) with season t as a random effect (intercept and slope), allowing site-level species richness (α_t) to vary as a function of the environmental covariates included in the best-fit dynamic community occupancy model, but excluding vegetation greenness due to its high collinearity with urbanization during the cool-wet season specifically, such that

$$\begin{aligned} ln(\alpha_t) = \beta_{Richness,Intercept,t} + \beta_{Richness,Urbanization,t} \times Urbanization \\ + \beta_{Richness,QuadraticUrbanization,t} \times Urbanization^2 \\ + \beta_{Richness,PatchDiversity,t} \times PatchDiversity + \epsilon_t \end{aligned} \tag{1.8}$$

$$\alpha_t \sim Normal(\bar{\alpha_s}, \sigma_{\bar{\alpha}}) \tag{1.9}$$

where ϵ_t represented the standard residual error term within a log-linear model, which allowed each data point (species richness estimate) to vary from the modeled relationship. All intercept and slope parameters were given vague normal priors (e.g.,$\alpha_t \sim Normal(0, 10)$). To propagate the uncertainty of site-level richness estimates from the dynamic community occupancy model into this meta-analysis, we parameterized normal priors for local richness based on $\bar{\alpha_t}$and $\sigma_{\bar{\alpha}}$, which respectively correspond to the mean and standard deviation of site-specific richness across all 30,000 posterior estimates from the best-supported global DCM.

1.2.9 Interpreting Modeled Effects

For both models above, we evaluated the hypothesized influences of predictor variables by examining the posterior distributions of each random slope parameter (i.e., standardized effect coefficients β and Δ). For each predicted effect, we treated the proportion of the posterior estimates sharing a sign (positive or negative) with the mean of the estimates (f-statistic) as a representation of the probability of detecting a substantial relationship between the predictor and response variables. For instance, if 95% of the posterior distribution of a slope parameter had a positive value, then we considered that probability of detecting a positive relationship to be 95%, though the magnitude of positive relationships may vary among posterior estimates. To increase the clarity of how we discussed relationships where the 95% Bayesian Credible Interval for a slope parameter overlapped zero, but the probability of detecting a relationship was substantial (>85%), we refer to these relationships as having a 'moderate' probability. Finally, we assessed seasonal differences in urbanization relationships in the species richness meta-analysis model, where season was treated as a random effect (slope and intercept), by comparing the 95% CRIs of the season-specific slopes $\beta_{Urbanization}$ and $\beta_{QuadraticUrbanization}$. We considered urbanization relationships to be the same among seasons when the CRI of each slope parameter for one season overlapped with the mean estimates from the others.

To further clarify the language, when discussing results from models that contained a quadratic urbanization term, we described trends in response variables (occupancy, persistence, colonization, and species richness) across the gradient of urbanization using the slope parameters for quadratic urbanization ($\beta_{QuadraticUrbanization}$) and non-quadratic urbanization ($\beta_{Urbanization}$). By predicting response variable values across levels of urbanization using both slope parameters, we then referred to an urbanization relationship as substantially 'quadratic' if there was both a visible peak in the predicted mean value (i.e., the maximum value was located at a non-zero level of urbanization) and moderately likelihood (i.e. >85% probability) of detecting relationships with both slope parameters. If both these conditions were not met, then we did not regard that urbanization relationship as being quadratic.

1.3 Results

Sampling across 50 wildlife camera sites resulted in detections of 22 native wildlife species over a total of 26,620 camera trap-days across the warm-dry (4,477 trap-days), warm-wet (4,477 trap-days), and cool-wet seasons (4,356 trap-days). Cumulative daily species detections across sites varied between 5,644 (Desert Cottontail Rabbit, *Sylvilagus audubonii*) and 1 (Mountain Lion, *Puma concolor*). Based on our scale optimization process, we ultimately fit the global DCM using the covariates of urbanization, patch diversity, and vegetation greenness measured at the respective scales of 1 km, 5 km, and 1 km, as these were the scales at which univariate model fit was greatest (Appendix A.2). The global model including the quadratic urbanization term demonstrated greater relative performance (CPO summary statistic = 2585.6) than the global model without it (CPO summary statistic = 2599.6), indicating that some variation in parameters in multi-season wildlife site use (occupancy, persistence, and colonization) was partially substantially explained by a quadratic model of urbanization, though the substantiality of those relationships required further assessment. As such, we primarily present parameter estimates and analyses of species richness derived from the global DCM with the quadratic term below, though we highlight where resulting parameters contrast with those from the global DCM that excluded the quadratic term (Appendix A.3).

1.3.1 Community Patch Dynamics

As predicted, variation in landscape characteristics among sites affected wildlife occupancy, persistence, and colonization at the community-level. The likelihood of wildlife initially occupying a site (i.e., the community-average occupancy, the mean among species) was negatively associated with urbanization (Table 1.1, $\beta_{\psi,Urbanization}$ and $\beta_{\psi,QuadraticUrbanization}$; Figure 1.2a). Wildlife were also less likely to initially occupy sites with greater patch diversity ($\beta_{\psi,PatchDiversity}$; Figure 1.2b) and lower vegetation greenness (Table 1.1, $\beta_{\psi,Greenness}$; Figure 1.2c). Colonization also demonstrated a negative quadratic relationship with urbanization (Table 1.1, probabilities of $\beta_{\gamma,Urbanization}$ and $\beta_{\gamma,QuadraticUrbanization}$ >85%; Figure 1.2g), with the beta coefficients predicting that wildlife were most likely to colonize sites at approximately 16.5% impervious surface cover (when patch diversity and vegetation were held constant at their mean). Within the global model including quadratic urbanization, wildlife were less likely to colonize sites with greater patch diversity (Table 1.1, $\beta_{\gamma,PatchDiversity}$; Figure 1.2h), though there was not a substantial likelihood of detecting this relationship (<85% probability) when quadratic urbanization was excluded from the model (Appendix A.3). Wildlife detection probability did not vary substantially according to the by-occasion sampling effort (mean $\alpha_{Effort} = 0.09$, 95% CRI -0.22 to 0.37;

74.4% probability).

Relationships between landscape characteristics and dynamic site use varied within the community according to the relative diversity of species' diets within the global model that considered quadratic urbanization effects (Figure 1.3). As predicted, diet diversity demonstrated positive relationships with urbanization's effects on occupancy (mean $\Delta_{\psi,UrbanizationDiet} = 0.44$, 87.1% probability; mean $\Delta_{\psi,QuadraticUrbanizationDiet} = 0.67$, 98.2% probability) – i.e., diet specialist occupancy was generally greater at sites with low impervious surface cover, relative to diet generalists (Figure 3a). Contrary to predictions, effects of urbanization on persistence were negatively associated with diet diversity (mean $\Delta_{\phi,UrbanizationDiet} = -0.43$, 89.2% probability; $\Delta_{\phi,QuadraticUrbanizationDiet} = -0.85$, 96.2% probability), indicating that diet generalists were less likely to remain at sites with higher impervious surface cover during the warm-wet and warm-dry seasons (Figure 1.3b). Species with more diverse diets were less likely to colonize lower urbanization sites (mean $\Delta_{\gamma,UrbanizationDiet} = 1.83$, probability = 99.0%; Figure 1.3c). As expected, sites with lower patch diversity were more likely to be used by diet specialists (mean $\Delta_{\psi,PatchDiversityDiet} = 0.21$, 90.5% probability; Figure 1.3d).

Seasonal site use also varied among species of different body size (Figure 1.4). Within the global DCM with quadratic urbanization, larger-bodied species were moderately likely to utilize fewer sites overall during the initial warm-dry season (mean $\Delta_{\psi,Size} = -0.78$, 88.0% probability; Figure 1.4a) but more likely to persist at sites that they did already use (mean $\Delta_{\phi,Size} = 0.78$, 95.9% probability; Figure 1.4b). Moderately urbanized sites were more likely to be colonized by smaller species (mean $\Delta_{\gamma,UrbanizationSize} = 0.93$, 88.7% probability; mean $\Delta_{\gamma,QuadraticUrbanizationSize} = -0.85$, 96.2% probability; Figure 1.4c). Finally, smaller-bodied species were more likely to colonize sites with lower patch diversity (mean $\Delta_{\gamma,PatchDiversitySize} = 0.48$, probability = 92.8%; Figure 4f) and lower vegetation greenness (mean $\Delta_{\gamma,GreennessSize} = 0.50$, probability = 96.1%; Figure 1.4i).

1.3.2 Species Richness

Season-specific estimates of local species richness demonstrated relationships with landscape characteristics (Table 1.2; Figure 1.5). Exponentiated season-specific intercepts from the log-normal meta-analysis model estimated that average richness across sites was similar during the warm-dry (mean = 3.20, 95% CRI 1.75 to 5.50), warm-wet (mean = 3.01, 95% CRI 1.62 to 5.44), and cool-wet seasons (mean 3.55, 95% CRI 2.08 to 6.24). Species richness was negatively associated with urbanization during all three seasons, though the overlap in the 95% CRIs of estimated urbanization-richness relationships (Table 1.2, $\beta_{Urbanization}$ and $\beta_{QuadraticUrbanization}$) indicated that richness did not vary among seasons or demonstrate peaks at moderate levels of urbanization (Figure 1.5). We failed to detect relationships between species richness and patch diversity ($\beta_{PatchDiversity}$) in any season.

Table 1.1: Relationships of environmental predictor variables with wildlife community-level (among-species average) site use response variables, based on the dynamic (multi-season) community occupancy model that included the potential effect of quadratic urbanization. ** = high (<95%) probability of detecting relationship, * = moderate (<85%) probability of detecting relationship

Response Variable	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
Occupancy, ψ	Urbanization	-1.92	-2.75, -1.19	100.0%**
	Quadratic Urbanization	-0.53	-1.26, 0.06	96.1%**
	Patch Diversity	-0.38	-0.69, -0.08	99.4%**
	Greenness	0.23	-0.17, 0.61	87.8%*
Persistence, ϕ	Urbanization	-0.29	-1.02, 0.42	80.0%
	Quadratic Urbanization	-0.45	-1.44, 0.53	82.1%
	Patch Diversity	-0.08	-0.63, 0.47	63.7%
	Greenness	0.16	-0.66, 1.32	58.7%
Colonization, γ	Urbanization	-2.62	-4.28, -1.35	100.0%**
	Quadratic Urbanization	-2.35	-4.89, -0.58	99.7%**
	Patch Diversity	-0.58	-1.21, -0.05	98.4%**
	Greenness	0.11	-0.53, 0.74	64.4%

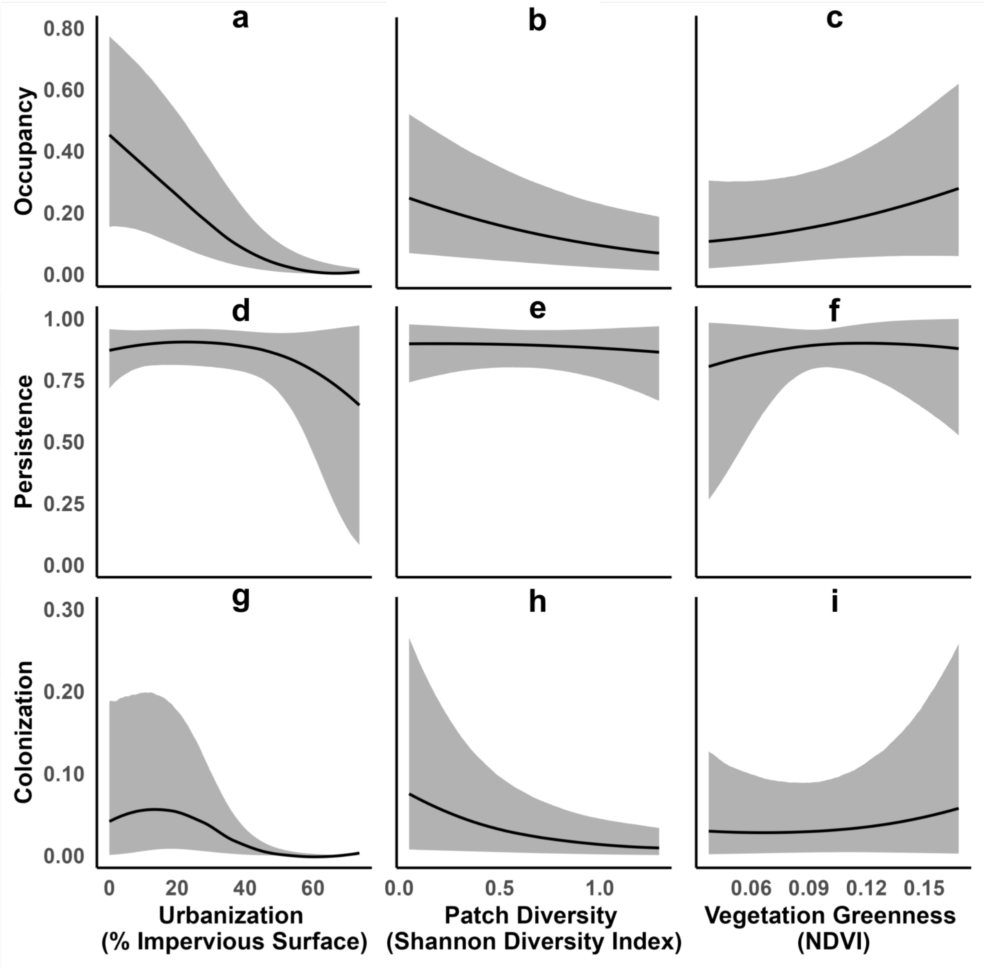

Figure 1.2: Community-level (among-species average) relationships between environmental covariates (urbanization, patch diversity, vegetation greenness) and community patch dynamic parameters: initial site use (a/b/c); persistence (d/e/f), colonization (g/h/i). Values of each response variable were predicted across hypothetical values of each environmental covariate (with all other covariates were constant at their mean value) using slope parameters from a dynamic (multi-season) community occupancy model (Table 1.4). Lines and their corresponding shaded regions correspond to the median and 95% Bayesian credible interval (CRI) of 30,000 posterior parameter estimates.

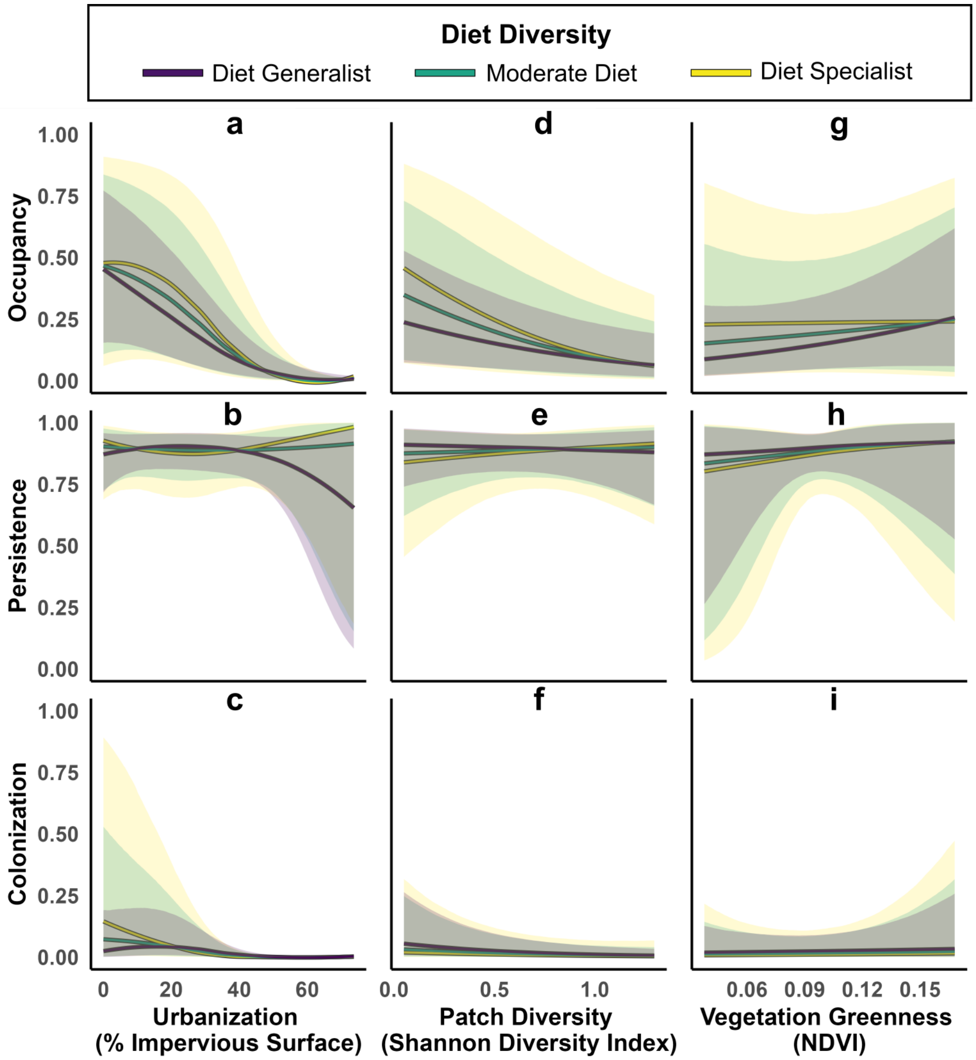

Figure 1.3: Among-species variation in dynamic wildlife site use (occupancy, persistence, colonization) across local environmental gradients, as predicted for three idealized species with contrasting diet diversity (Shannon diversity index), but the same body size (log-transformed body mass). Based on environmental covariate and species trait effect parameters from a dynamic community occupancy model (β estimates in Table 1.2 and Δ_{Diet} parameters in the text), we predicted individual species-level effect parameters for three levels of diet diversity (with body size held constant at its mean) and three body sizes (with diet diversity held constant at its mean value). We then used those trait-dependent, species-level urbanization effect parameters to predict values of each response variable across a range of urbanization values, with all other environmental covariate held constant at their mean values. Lines and their corresponding shaded regions represent the median and 95% Bayesian credible interval (CRI) of 30,000 posterior parameter estimates for each separate species.

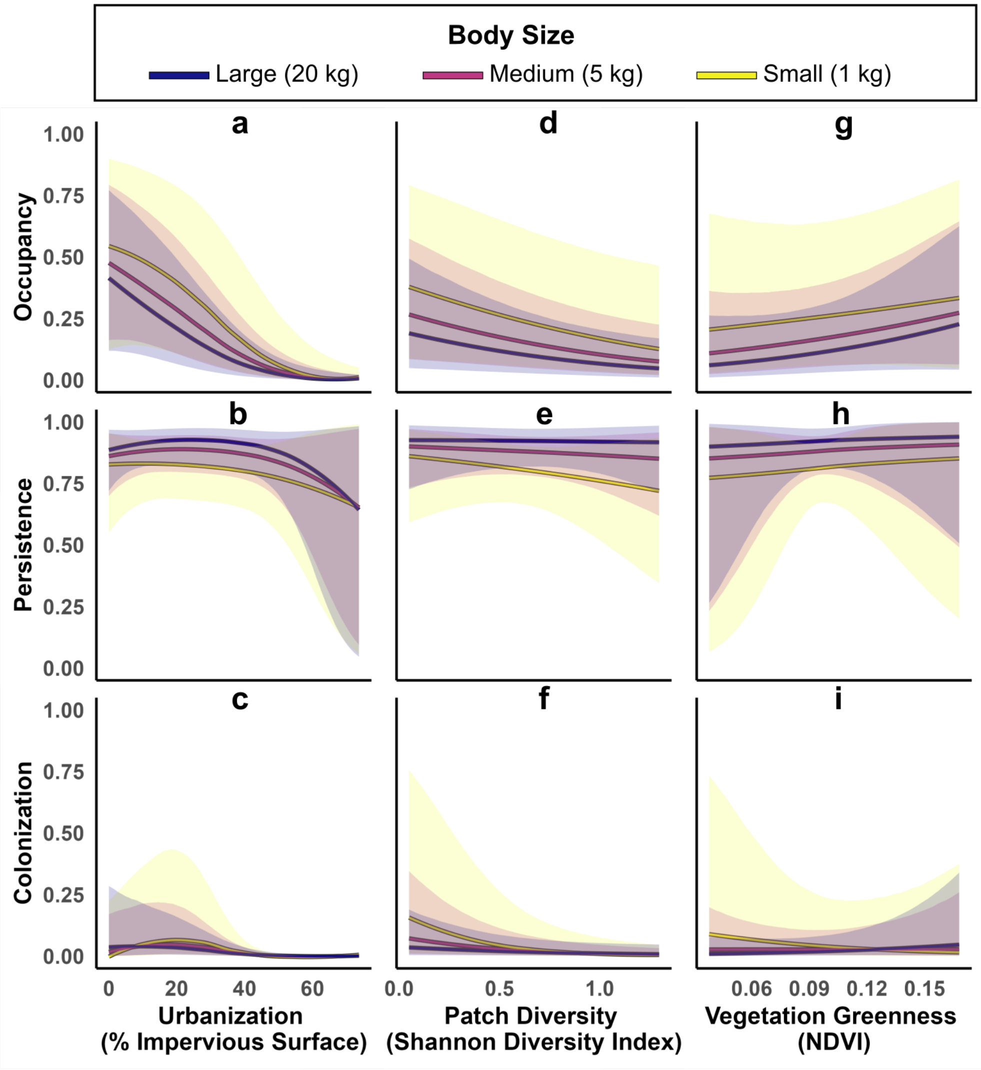

Figure 1.4: Among-species variation in dynamic wildlife site use (occupancy, persistence, colonization) across local environmental gradients, as predicted for three idealized species with varying body sizes (log-transformed body mass), but the same diet diversity (Shannon diversity index). Based on environmental covariate and species trait effect parameters from a dynamic community occupancy model (β parameters in Table 1.2 and Δ_{Size} parameters in the text), we predicted individual species-level effect parameters for three levels of diet diversity (with body size held constant at its mean) and three body sizes (with diet diversity held constant at its mean value). We then used those trait-dependent, species-level urbanization effect parameters to predict values of each response variable across a range of urbanization values, with all other environmental covariate held constant at their mean values. Lines and their corresponding shaded regions represent the median and 95% Bayesian credible interval (CRI) of 30,000 posterior parameter estimates for each separate species.

Table 1.2: Summary results of Bayesian meta-analysis of relationships between species richness and environmental characteristics in multiple seasons. ** = high (<95%) probability of detecting relationship, * = moderate (<85%) probability of detecting relationship

Season	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
Warm-Dry	Urbanization	-1.00	-1.38, -0.64	100.0%**
	Quadratic Urbanization	-0.07	-0.58, 0.45	61.8%
	Patch Diversity	0.01	-0.38, 0.42	51.3%
	Residual Error	1.04	0.81, 1.34	NA
Warm-Wet	Urbanization	-1.15	-1.59, -0.73	100.0%**
	Quadratic Urbanization	-0.18	-0.70, 0.32	74.9%
	Patch Diversity	-0.05	-0.46, 0.35	59.8%
	Residual Error	1.17	0.91, 1.34	NA
Cool-Wet	Urbanization	-1.09	-1.45, -0.73	100.0%**
	Quadratic Urbanization	-0.31	-0.80, 0.16	90.7%*
	Patch Diversity	-0.03	-0.41, 0.33	55.5%
	Residual Error	1.01	0.78, 1.31	NA

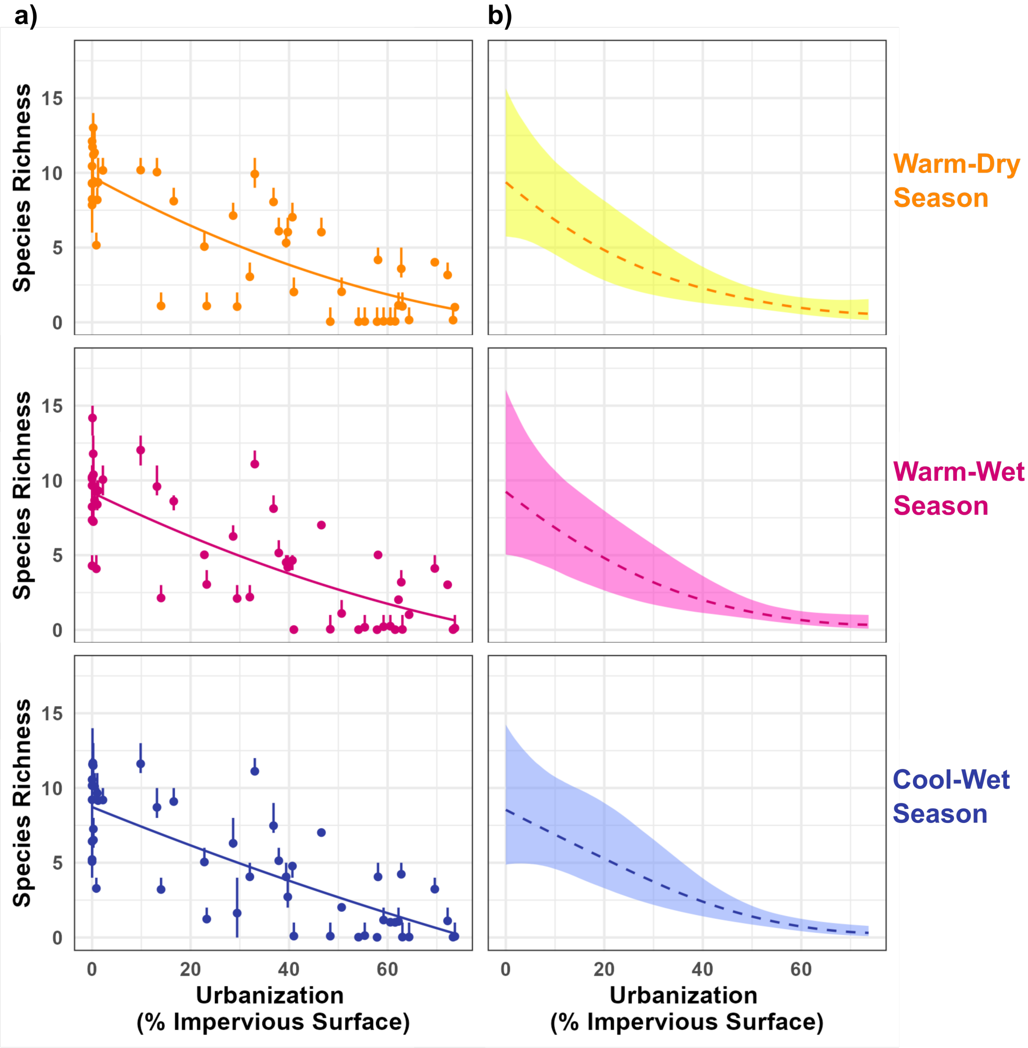

Figure 1.5: Multi-season trends in species richness across a gradient of urbanization, measured as percent impervious surface cover. Panel (a) depicts values of site-level species richness (total number of species at each site) estimated using a dynamic (multi-season) community occupancy model, with points and bars correspond to the mean and 95% Bayesian credible interval (CRI) of species richness at each camera site, drawn from 30,000 posterior estimates. Solid lines in both panels depict quadratic regression trendlines fit to mean species richness estimates using the *stat_smooth* function in the *ggplot* R package. Panel (b) depicts values of richness predicted across a hypothetical range of urbanization values when all other landscape variables (patch diversity and vegetation) were held constant at their mean values, based on the modeled effects resulting from the Bayesian meta-analysis (see Table 5). We represented median and 95% Bayesian credible interval (CRI) of the predicted values using the dashed trendlines and their corresponding shaded regions, respectively.

1.4 Discussion

Consistent with the effects of human landscape modification on biodiversity widely documented across other systems (Aronson *et al.*, 2014; Beninde *et al.*, 2015; McKinney, 2008; Norton *et al.*, 2016; Suraci *et al.*, 2021), urbanization and landscape heterogeneity demonstrated broadly negative relationships with seasonal wildlife site use and richness within our study. However, species richness did not peak at intermediate levels of urbanization or change across seasons. Species traits additionally influenced the community responses to urbanization, with smaller-bodied species and those with less diverse diets more likely to use less fragmented areas across seasons (Rega-Brodsky *et al.*, 2023; Suraci *et al.*, 2021). Overall, these results emphasize that the relatively slowly changing characteristics of the built environment and of species are both fundamental drivers of wildlife community patterns across urbanized landscapes, even within systems featuring highly seasonal resource gradients.

1.4.1 Seasonal Wildlife Dynamics

The impacts of human activities on resource availability may contribute to community-level responses to urbanization that vary over different spatial and temporal scales. Wildlife utilize human-dominated landscapes in ways that reduce negative impacts of human disturbance while maximizing benefits from shifting resource availability (Lewis *et al.*, 2021; Martin *et al.*, 2021), including naturally and anthropogenically driven distributions of food, water, and shelter (Bateman *et al.*, 2015b; Brown *et al.*, 2022; Buyantuyev and Wu, 2009; Chamberlain *et al.*, 2020). For example, our results indicated that wildlife occupancy was greater at sites with more vegetation greenness, consistent with predictions that vegetation can positively affect wildlife abundance by buffering against negative impacts of development (Farwell *et al.*, 2020; Martin *et al.*, 2021).

However, links between wildlife communities and seasonal changes in resource availability are often more difficult to establish. For instance, vegetation did not noticeably alter patterns of site use or species richness across seasons, in contrast with previous studies demonstrating positive relationships of wildlife abundance and diversity to seasonal environmental characteristics including vegetation and precipitation (de Albuquerque *et al.*, 2021). Considering the generally low rates of colonization found in this study, the lack of a response to seasonal resource availability may be partially attributed to the human land management practices that fragment the landscapes surrounding seasonally-limiting water and vegetation (Bateman *et al.*, 2015a; Chamberlain *et al.*, 2020). Such practices have been found to result in anthropogenic resource supplementation that is concentrated within urban and suburban areas that are relatively inaccessible to wildlife use due to barriers to wildlife movement (DeStefano and DeGraaf, 2003; Forman, 2014b; Larson *et al.*, 2022b). Better quantifying the availability of anthropogenic resources to wildlife necessitates further consideration of the factors influencing the ability wildlife communities to access resources across urbanizing landscapes, including the community's diversity of functional characteristics.

1.4.2 Species Traits

Species functional traits are important predictors of seasonal community responses to human landscape modification, as wildlife vary in their abilities to tolerate anthropogenic disturbance and to take advantage of resources provided by human-dominated environments (Lewis *et al.*, 2021; McKinney, 2002; Shochat *et al.*, 2007; Suraci *et al.*, 2021). Although our findings demonstrated a generally negative relationship between wildlife site use and landscape heterogeneity, as measured by patch type diversity, smaller-bodied species and species with more specialized diets were even more likely to use the areas with lower patch diversity. This result was like consistent with smaller, less-mobile species experiencing more negative edge effects (Fahrig, 2017, 2003), as multiple metrics of spatial landscape heterogeneity (e.g., patch diversity, edge density, mean patch area) are often strongly associated with habitat fragmentation (Forman, 2014b; Wu *et al.*, 2011). As such, functional traits may be especially critical for understanding how capable native wildlife are of persisting within moderately urbanized (e.g., suburban) environments that are characterized by highly fragmented patterns of land use and resource availability (Forman, 2014b; DeStefano and DeGraaf, 2003).

These species traits that mediate responses to landscape modification can also vary within species, across seasons (e.g., movement rates, mating season, diet), and across broader biogeographical contexts (e.g., variation in coyote home range and body size or gray fox diet across North America; Chamberlain and Leopold, 2005; Gese *et al.*, 2012; Larson *et al.*, 2015; Poessel *et al.*, 2016; Rega-Brodsky *et al.*, 2023; Way *et al.*, 2006), potentially altering the functional diversity of wildlife communities across gradients of urbanization (Rega-Brodsky *et al.*, 2023). Although the assessment of intra-specific variation in traits and how it could further shape seasonal wildlife community dynamics was beyond the scope of this study, our results indicate that further exploration of trait-mediated wildlife dynamics and their relationships to community composition across broader spatial and temporal scales is certainly warranted.

1.4.3 Biodiversity Patterns Across Broader Scales

Relationships among the temporally dynamic characteristics of human-modified environments and biodiversity patterns require further study across more expansive spatial scales, including long-term study of wildlife communities across networks of diverse cities with a variety of bioclimatic conditions (Magle *et al.*, 2019). Local relationships between urbanization and community composition vary widely among metropolitan regions with different seasonal bioclimatic patterns (e.g., plant productivity, precipitation), different sociocultural characteristics (e.g. human movements, wealth distributions, vegetation management practices), and different species pools (Aronson *et al.*, 2014; Beninde *et al.*, 2015; Catterall, 2009; Chamberlain *et al.*, 2020; Magle *et al.*, 2021; Newbold *et al.*, 2020; Norton *et al.*, 2016). The negative effects of urbanization on species richness within our arid study system were consistent with patterns observed across many cities; however, our results did not provide evidence that species richness peaked in moderately urbanized areas, as found among wildlife communities in relatively mesic systems with more abundant natural vegetation (Blair, 1996; McKinney, 2008; Parsons *et al.*, 2018). Although previous studies have indicated that seasonal vegetation can be positively associated with wildlife diversity (de Albuquerque *et al.*, 2021), the positive effects of plant productivity on wildlife presence within our study did not appear to strongly mitigate the effects of human disturbance and increase species richness in moderately urbanized areas (Martin *et al.*, 2021; McIntyre, 2014).

To better detect seasonal trends in wildlife communities, future research must also be conducted across more expansive temporal scales, as effects of seasonal environmental conditions on wildlife communities are linked with broader trends in urbanization and climate change (de Albuquerque *et al.*, 2021; Newbold *et al.*, 2020; Warren *et al.*, 2019). Especially within rapidly-urbanizing regions, such as our study area of Metro Phoenix, substantial increases in development can occur across seasons (Ramalho and Hobbs, 2012), potentially reducing temporal resource heterogeneity more than expected under the assumption of a less urbanized landscape (Faeth *et al.*, 2011; Groffman *et al.*, 2017; Norton *et al.*, 2016). For studies based in a single year of seasonal data, such as our own, rapid urbanization potentially confounds results by decreasing richness across seasons, though evaluating such confounding effects requires data of human footprint at finer temporal resolutions than presently exists. As such, longer-term studies of wildlife communities and the trade-offs they face between resource availability and anthropogenic landscape change could contribute to a better understanding of seasonal drivers of wildlife activity and diversity.

1.4.4 Management Implications

Investigating the ecological mechanisms that underlie dynamics of wildlife communities across gradients of landscape change is vital for quantifying the impacts of landscape management and other human behaviors on community assembly and stability (Andrade *et al.*, 2020; Aronson *et al.*, 2016; Avolio *et al.*, 2021). Through our examination of how both landscape characteristics and species traits shape seasonal wildlife community dynamics, we demonstrated that explicit incorporation of traits into assessments of wildlife responses to human landscape modification can help develop a more mechanistic understanding of biodiversity's persistence within human-dominated environments (Rega-Brodsky *et al.*, 2023). As such, our findings suggest that conservation and management efforts aimed at entire wildlife communities may consider additional use of trait-specific approaches that target the habitat needs of the species most sensitive to effects of urbanization, such as larger carnivores (Cypher *et al.*, 2010). Furthermore, understanding how wildlife utilize anthropogenic resources across seasons is fundamental to predicting spatiotemporal patterns of co-occurrence among wildlife and people, which can people's attitudes toward nature (Andrade *et al.*, 2019; Kay *et al.*, 2022; Lerman *et al.*, 2020; Soulsbury and White, 2019). Since the success of conservation efforts within metropolitan regions is shaped by the complex relationships among human and wildlife behaviors (Avolio *et al.*, 2021; Carter and Linnell, 2023; Dietsch *et al.*, 2019), those behaviors provide critical context for the study of community dynamics and the promotion of human-wildlife coexistence across urbanizing landscapes.

Chapter 2

SPECIES INTERACTIONS AMONG CARNIVORES ACROSS LEVELS OF URBANIZATION AND SEASONS WITHIN A DESERT ECOSYSTEM

2.1 Introduction

Interactions among species can drive the distributions of animals and composition of their communities. Although local and regional abiotic characteristics serve as primary filters during community assembly (Poff, 1997), the occurrence of individual species is also influenced by the presence of other species (MacArthur, 1958; Vellend, 2010). Especially among mammalian carnivores, the ability of a species to occupy an area can be limited by interspecific competition, resulting from resource competition, intraguild predation, and competitive exclusion (Bateman and Fleming, 2012; Crooks *et al.*, 2010; Schoener, 1983). For example, the absence of top predators (e.g. coyotes, *Canis latrans*) in some systems can lead to increased abundance of intermediate predator species, with the ultimate effect of reducing prey species abundance and diversity (mesopredator release hypothesis; Brashares *et al.*, 2013; Crooks and Soulé, 1999; Soulé *et al.*, 1988). By altering the distributions and diversity of species at multiple trophic levels, direct and indirect interspecific interactions thus create feedbacks that further restructure the community (Heim *et al.*, 2019; HilleRisLambers *et al.*, 2012; Wilmers *et al.*, 2002). Although interspecific interactions among species are key drivers of community structure, it is less clear how species interactions vary through time and space, especially in relation to human activities and landscape change.

Urbanization is a pervasive form of landscape change that can restructure species interactions by altering the distributions of species across multiple spatial and temporal scales in multiple ways. Reduced habitat for species resulting from urbanization can restrict species movements and potentially increase the potential for interspecific interactions Forman (2014b); Lewis *et al.* (2017); Parsons *et al.* (2019). In addition, urbanization can alter daily activity patterns of wildlife, where animals become more nocturnal and increase overlap in activity patterns (Lewis *et al.*, 2015), potentially increasing competition (Chitwood *et al.*, 2020; Gaynor *et al.*, 2018; Gehrt and Prange, 2007). In contrast, at some scales, interspecific interactions can be similar between wildland and urbanized areas (Lewis *et al.*, 2015, 2017; Wang *et al.*, 2015; Gámez and Harris, 2021) or even be reduced at higher levels of urbanization (Riley *et al.*, 2010; Parsons *et al.*, 2019; Riley, 2006; Smith *et al.*, 2018). These confounding effects of urbanization on competition and predation may be due to how availability of limiting resources (food, water, shelter) shapes animal distributions (Bateman *et al.*, 2015b; Brown *et al.*, 2022; de Albuquerque *et al.*, 2021; Warren *et al.*, 2006).

Variations in limiting resources across the landscape may drive seasonal differences in interspecific interactions across urbanization gradients. Within natural landscapes, seasonal differences in the amount and diversity of resources, especially water and vegetation, drive seasonal variation in wildlife populations (Bissonette and Storch, 2007). However, people in cities may provide year-round food, water, and other resources through planting and irrigation of vegetation and the direct and indirect feeding of animals (Aronson *et al.*, 2016; DeStefano and DeGraaf, 2003; Faeth *et al.*, 2005; Warren *et al.*, 2006). Wildlife use of these anthropogenic resources may be particularly pronounced during seasons when resources are most limited within the surrounding wildland landscape, such as periods of low precipitation and primary productivity within desert ecosystems (Buyantuyev and Wu, 2012; de Albuquerque *et al.*, 2021; Faeth *et al.*, 2005; Safriel and Adeel, 2005). Thus, interspecific competition may potentially increase in urbanized areas during seasons when resources are limiting in natural environments. However, studies of wildlife interactions across urbanized landscapes have largely been restricted to single seasons (Crooks *et al.*, 2010; Lewis *et al.*, 2015; Parsons *et al.*, 2019). Relatively little is known about how the potential for competition changes across the gradient of urbanization and in relation to seasonal resource availability.

In this study, we evaluated how urbanization and seasonal changes in resource availability within a desert ecosystem affected the potential for interspecific interactions among carnivores and between carnivores and their prey. Our first objective was to evaluate the spatial heterogeneity of interspecific interactions, focusing on four carnivore species widely detected across the gradient of urbanization – coyote, gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), and raccoon (*Procyon lotor*; Figure 2.1). While we hypothesized that increased presence and activity of coyotes would reduce the site use of the three mesocarnivore species, we expected these antagonistic interactions to be reduced during seasons in which resource availability (i.e., plant productivity and prey activity) increased. We further predicted that, in areas of greater urbanization, carnivores would increasingly co-occur due to the concentration of animal use within smaller, more isolated habitat fragments (Lewis *et al.*, 2015; Parsons *et al.*, 2019). We alternatively predicted that urbanization might reduce opportunities for co-occurrence and potential competitive interactions, as certain species (e.g., bobcats, coyotes) can exhibit more negative response to urbanization than others (e.g., raccoons, gray foxes), resulting in release from interspecific competition (Crooks and Soulé, 1999; Gámez and Harris, 2021). Our second objective was to evaluate how species interacted temporally by comparing the daily activity patterns between species, including competitors, predators, and prey. Here we hypothesized that shifts in activity patterns across the gradient of urbanization and among seasons would result in varying degrees of temporal overlap among species, with typically crepuscular species (e.g. coyote; gray fox; black-tailed jackrabbit, *Lepus californicus*; javelina, *Pecari tajacu*) exhibiting greater nocturnality and interspecific daily activity overlap in more urbanized areas.

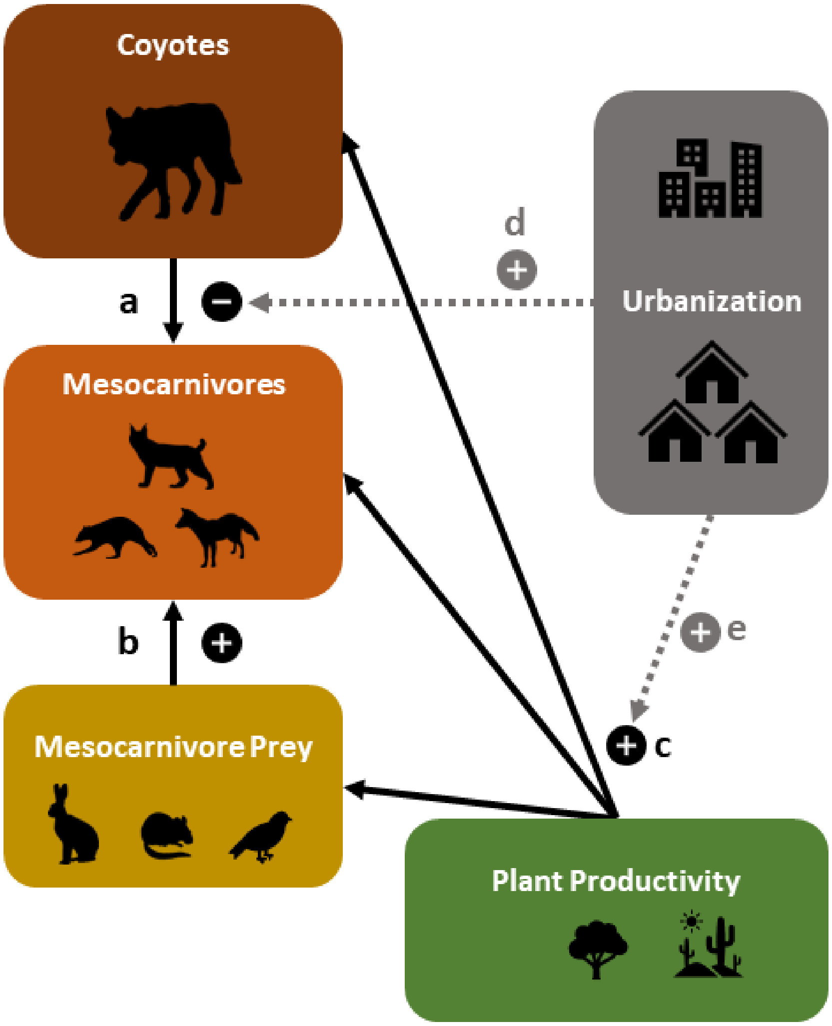

Figure 2.1: Predicted relationships among carnivore species occurrence (site use and frequency of use), prey species activity, and seasonal resource availability modeled at low and high levels of urbanization. Solid arrows represent predicted interspecific effects of coyote **(a)** and prey **(b)** occurrence on the occurrence of mesocarnivores (gray fox, bobcats, and raccoons), as well as the increases wildlife site use and co-occurrence during seasons of elevated plant productivity **(c)**. Plus/minus signs indicate the predicted directionalities of each effect (e.g., mesocarnivore detection was predicted to be lower where coyotes were present). Dashed arrows indicate the predicted mediating effects of urbanization on mesocarnivore occurrence, including hypothesized positive effects of urbanization on interspecific co-occurrence **(d)** and increased co-occurrence within more highly urbanized areas during seasons of lower plant productivity **(e)**.

2.2 Methods

2.2.1 Study Area

We assessed distributions of interspecific interactions across the metropolitan area of Phoenix, Arizona. Metro Phoenix is the 10th largest and one of the fastest-growing metropolitan areas in the United States (Bureau, 2021). Metro Phoenix is located within the arid Sonoran Desert, where natural desert environments are characterized by creosote bush (*Larrea tridentata*), bursage (*Ambrosia dumosa*), velvet mesquite (*Prosopis velutina*), palo verde (*Parkinsonia* spp.), and saguaro (*Carnegiea gigantea*). Rainfall within the region is generally distributed bimodally across the year, with both precipitation driven by monsoonal moisture in the hot late summer (June-September) and precipitation in cooler winter months, generally resulting in peak natural vegetation productivity during early spring.

2.2.2 Site Selection and Field Data Collection

We continuously surveyed ground-dwelling mammal and bird species for approximately one year (March 2019 to April 2020) by deploying motion-activated trail cameras across 50 sites associated with the long-term ecological survey framework of the Central Arizona-Phoenix Long-Term Ecological Research (CAP LTER) program (Figure 2.2a). Starting with existing sets of CAP LTER survey locations (Allen et al., 2018; Bateman et al., 2018; Childers et al., 2018), we selected sampling sites via a stratified random sampling process aimed at representing broad-scale variation in urbanization. We calculated the proportion of impervious land cover types (buildings and roads; Li, 2015) within 1000 meters of each potential site and placed sites into one of five strata: Stratum 1 ($< 0.01\%$ imperviousness), Stratum 2 ($0.01 - 17\%$), Stratum 3 ($17 - 36\%$), Stratum 4 ($36 - 53\%$), and Stratum 5 (> 53). Sites surrounded by more than 10% agricultural land cover or above 545 m elevation were excluded to maintain consistency of characteristics (vegetation types, topography, precipitation, etc.) among sites. We then randomly selected 10 sites within each stratum, for a total of 50 sampling sites. To account for spatial independence among sampling locations, all sites were placed at least 2 km apart.

At each sampling site, we installed one wildlife camera, following the experimental protocol of the Urban Wildlife Information Network ((UWIN; Magle *et al.*, 2019). Two models of camera were utilized for this study: the Bushnell Trophy Trail Camera Essential E3 (n = 30) and the Cuddeback Silver Series Black Flash (n = 20). Cameras were placed in areas believed to maximize the probability of detecting wildlife moving through the area, such as along washes trails, and movement corridors. Each camera was programmed to record a series of two images for each trigger, with a minimum 30 second rest period between each trigger. Cameras collected data for one year and were visited regularly (every 3-8 weeks) to ensure the proper operation of the cameras and to retrieve image data. We identified mammals and ground-dwelling birds in wildlife camera photos to the species or genus level, in accordance with a list of mammal and ground-dwelling bird. All image identification was conducted by trained personnel. Based on our hypotheses and on seasonal patterns of temperature and precipitation within the region, we grouped species detections into three distinct 96-day seasons: warm-dry (April 15th-July 19th), warm-wet (July 20th-October 23rd), and cool-wet (December 1st-March 5th).

2.2.3 Environmental Characterization

The distributions of and interactions among carnivore species can additionally vary based on environmental heterogeneity across the landscape (Lewis *et al.*, 2015; Parsons *et al.*, 2019). To control for effects of environmental heterogeneity and isolate the effects of interspecific competition within our analyses, we quantified two key landscape characteristics: urbanization and vegetation. We quantified each site's *imperviousness* as the mean percentage of impervious surface cover within a 1000 meter radius buffer, based on the 2019 National Land Cover Database (Wickham *et al.*, 2021). We further reclassified sites into two ordinal urbanization levels by sorting sites by their imperviousness, classifying sites with the highest imperviousness (>38%) as *high urbanization* (n = 27), and the remaining sites with being classified as *low urbanization* (<38% imperviousness; n = 23; Figure 2.2a). High urbanization sites were characterized by high-density residential, industrial, commercial land uses, as well as medium-density suburban residential areas intermixed with vegetation (Radeloff *et al.*, 2005). Low urbanization sites were located on minimally-developed public and private lands consisting of large areas of contiguous desert habitat, with the most urbanized sites in this group being positioned at the wildland-urban interface, in natural areas immediately adjacent to human development (Radeloff *et al.*, 2005).

We measured the covariate *plant productivity* by using Google Earth Engine (Gorelick *et al.*, 2017) and 30 m Landsat 8 surface reflectance to estimating the median value of Normalized Difference in Vegetation Index (NDVI) within each season, and then calculating the mean NDVI within 1000 m of each site. We used plant productivity as a proxy measure of spatiotemporal variation in resource availability at low and high urbanization levels (Figure 2.2b), as previous studies in this system have shown that variations in plant productivity and cover are positively associated with bird and herpetofauna abundance and with the provisioning of anthropogenic water resources across metro Phoenix (Bateman *et al.*, 2015b; de Albuquerque *et al.*, 2021).

We further characterized conditions at each site based on the seasonal-wide activity of wildlife species and species groups. We quantified indices of relative activity

(RA) for each mammal and ground-dwelling bird species at each site in each season as the number of independent detections of that species divided by the total number of days in which the camera was operational for that site and season (George and Crooks, 2006; Goad *et al.*, 2014). We considered detections to be independent when a particular species was observed more than 30 minutes apart at that specific site. RA indices included the seasonally variable relative activity of coyotes (RA_{Coyote}), as the dominant carnivore species across both low and high urbanization levels (Figure B.1a). We also summed the RA values of all potential mesocarnivore prey species - including lagomorphs (cottontail rabbit, black-tailed jackrabbit), small mammals (e.g., ground squirrels, woodrats, kangaroo rats), and birds (e.g., roadrunners, quail, doves; Table B.1) – into a single index of relative mesocarnivore prey activity for each season (RA_{Prey}; Figure B.1b).

Imperviousness was strongly associated with variation in seasonal environmental conditions at both levels of urbanization. Among high urbanization sites, imperviousness was highly correlated with plant productivity in the warm-dry (r = -0.71), warm-wet (r = -0.70), and cool-wet seasons (r = -0.77). Among low urbanization sites, imperviousness was most strongly collinear with plant productivity during cool-wet season (r = -0.60), relative to the warm-dry (r = -0.30) or warm-wet seasons (-0.14). Variation in RA_{Coyote} among high urbanization was moderately associated with imperviousness in the warm-dry (r = -0.43), warm-wet (r = -0.55), and cool-wet seasons (r = -0.51), but RA_{Coyote} at less urban sites was not correlated with imperviousness in any season (r = -0.11 for warm-dry, r = -0.25 for warm-wet, and r = -0.18 for cool-wet). Similarly, RA_{Prey}; in all three seasons was moderately collinear with imperviousness at high urbanization sites (r = -0.36 for warm-dry, r = -0.30 for warm-wet, and r = -0.27 for cool-wet), but not at low urbanization sites (r = -0.01 for warm-dry, r = 0.06 for warm-wet, and r = -0.19 for cool-wet). Due to these high levels of collinearity, we excluded imperviousness from all analyses conducted at both low and high levels of urbanization (see below).

2.2.4 Modeling Seasonal Mesocarnivore Site Use and Detection

Competitive interactions among species can occur when the occurrence and activity of a dominant species at broad and fine temporal scales (season, days, etc.) either excludes the presence of a subordinate species or causes behavioral shifts in how frequently a subordinate species uses that site (Crooks *et al.*, 2010; McIntyre, 2014). We assessed these potential interactions at both broad and fine scales by estimating patterns of spatial co-occurrence among four native carnivore species that were widely detected across the urbanization gradient – coyotes, bobcats, gray foxes, and raccoons. These four species were predicted to demonstrate a competitive hierarchy in which the largest carnivore species (coyote) influences the occurrence and behaviors of mesocarnivores: bobcat, gray fox, and raccoon (Chitwood *et al.*, 2020; Crooks and Soulé, 1999; Fedriani *et al.*, 2000; Gehrt and Prange, 2007; McKinney and Smith, 2007).

We examined potential interspecific interactions using two distinct sets of occupancy models at both low and high levels of urbanization, each of which we describe in detail in the subsections below. First, we evaluated relationships between broad-scale (seasonal) coyote presence on the site use and relative activity of each mesocarnivore by fitting a set of two-species conditional occupancy models (Kéry and Royle, 2021a; Richmond *et al.*, 2010). Second, we estimated how the fine-scale relative activity of coyotes within each season impacted the relative habitat use by mesocarnivores using a series of single-species occupancy models, while also controlling for spatiotemporal variation in plant productivity, and prey activity (Richmond *et al.*, 2010; Royle and Nichols, 2003). We fit all models using R 4.0.1 (R Core Team, 2020) and the package *wiqid* (Meredith, 2022). For each occupancy model, we summarized species detections at each site by sixteen-day occasions (1 = detected; 0 = not detected) within each sampling season.

Effects of Competitor Presence

To assess competitive effects of broad-scale coyote presence on mesocarnivore species, we fit conditional two-species occupancy models for each individual season and urbanization level (low and high; Richmond et al., 2010). Conditional occupancy models consider how the presence (occupancy probability, ψ) of a dominant species (A) influences a subordinate (B) species' presence, as well as the likelihood of being detected across survey occasions (detection probability, p). For each mesocarnivore species, we fit four separate conditional models that made different assumptions about how the presence of the coyotes affected the presence and probability of detecting the subordinate species (Table B.2). The first model was a no-interaction model that assumed that the probability of mesocarnivore occupancy (ψ^B) and detection (p^B) were independent of the presence of coyote (ψ^A) is equal to its presence in the absence of coyote (ψ^{Ba}; i.e., no interaction is present). The second model assumed that mesocarnivore presence at sites where coyotes were present was different than it was at sites where coyotes were presumed absent ($\psi^{BA} \neq \psi^{Ba}$), but that the frequency with which the mesocarnivore used sites did not depend on coyotes ($p^B = r^{BA} = r^{Ba}$, where r^{BA} and r^{Ba} respectively represent the detection probabilities of the subordinate species conditional on whether the dominant species was detected and not detected at that site). Conversely, the third model assumed that the presence of the dominant species at a site affected the detection of the subordinate species ($p^B \neq r^{B\cdot}$, i.e. subordinate species detection probability was different at sites used and not used by the dominant species). The fourth and final model further assumed that both the presence and detection of the subordinate species varied among sites where coyote were present versus absent ($\psi^{BA} \neq \psi^{Ba}$ and $p^{B} \neq r^{B\cdot}$). We used the Akaike Information Criterion adjusted for low sample size (AIC$_\mathrm{c}$) to evaluate the relative performance of each of the above models within each season and urbanization level, with the lowest AIC$_\mathrm{c}$ value representing the top model (Burnham and Anderson, 2002). For the top model for each mesocarnivore, we further considered differences between parameters of interest (e.g. between ψ^{BA} and ψ^{Ba}) to be statistically significant where their 95% confidence intervals (CIs) did not overlap with one another. Similarly, we considered covariate effects to be significant when the 95% CI of their standardized beta estimate did not overlap 0.

Effects of Competitor Activity and Environmental Heterogeneity

To assess fine-scale competitive effects of coyotes on mesocarnivore behaviors, we fit a series of single-species occupancy models examining how each species' relative site use varies according to the relative activity of coyotes and prey species across each season and urbanization level (MacKenzie *et al.*, 2018). We used the Royle-Nichols method to estimate relative habitat use (λ) while accommodating for abundance-induced heterogeneity in detection probability (Royle and Nichols, 2003). We allowed relative habitat use to vary as a function of combinations of seasonally dynamic site-level covariates, including relative activity of mesocarnivore prey species (RA_{Prey}), relative activity of coyotes (RA_{Coyote}) and plant productivity. For each mesocarnivore species, season, and urbanization level, we fit a global model containing all the above covariates for each species, season, as well as a series of candidate submodels containing all possible combinations of the three covariates (Table B.3). We compared the relative quality of these models using AIC$_\mathrm{c}$, designating the models with the lowest AIC$_\mathrm{c}$ for each species, season, and urbanization level as the top models. Finally, we compared estimates of relative habitat use, detection probability, and covariate effect sizes among top models.

2.2.5 Modeling Daily Activity Patterns

We evaluated overlap in daily activity patterns among species by using independent (¿ 30 minutes apart) timestamped observations of species to estimate daily activity patterns within all three seasons. We used kernel density statistics and the package *overlap* (Meredith and Ridout, 2015) in R version 4.0.1 (R Core Team, 2020) to estimate the daily activity patterns at urban, suburban, and wildland sites. We selected bandwidth, overlap estimators, and number of bootstraps in accordance with recommendations (Ridout and Linkie, 2009). We compared interspecific similarities in activity patterns across both urbanization levels (high and low) and across seasons using the overlap estimator Δ^1 when the minimum sample size was <50 independent observations; otherwise, we used Δ^4. We excluded species from overlap analyses during individual seasons and at specific urbanization levels if their number of independent detections was fewer than 20, due to unreliability of activity pattern estimates at small sample sizes. We considered the activity patterns of two species to overlap significantly when the upper bound of the 95% confidence interval of their overlap coefficient was >0.90 (Lewis *et al.*, 2021).

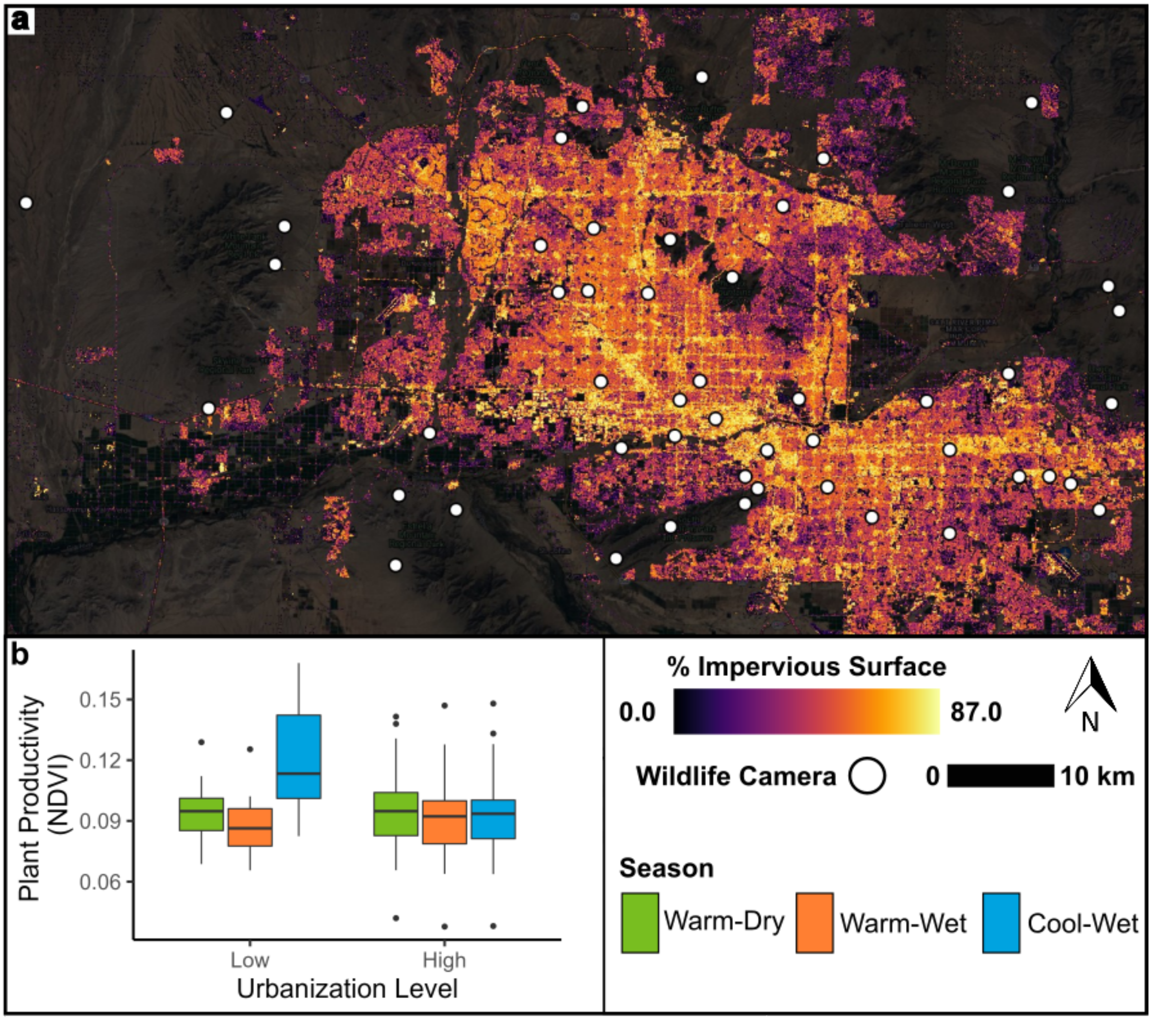

Figure 2.2: (a) Distribution of wildlife camera sites across a gradient of urbanization (percent impervious surface cover) in the Phoenix Metropolitan Area, Arizona, USA. **(b)** Seasonal variation in plant productivity (Normalized Difference in Vegetation Index; NDVI) at low urbanization (<38% impervious surface) and high urbanization sites (>38% impervious surface).

2.3 Results

2.3.1 *Effects of Competitor Presence on Mesocarnivores*

Co-occurrence among coyotes and mesocarnivores species varied across urbanization levels and seasons (Table 2.1; Table B.4). Counter to the predicted effects of coyote competition, we found no evidence that the occupancy or detection of any of the three mesocarnivore species was associated with coyote presence during the cool-wet season (i.e., the top model was the null-interaction model, which did not include interaction terms). During the warm-dry and warm-wet seasons, coyotes were detected across all low urbanization sites (i.e., $\psi^{A} = 1.00$); thus, due to lack of variability in coyote occupancy, we did not evaluate models at this level of urbanization across seasons.

Consistent with predictions that urbanization would increase the likelihood of carnivore co-occurrence, the presence of coyotes at higher urbanization sites was positively associated with the occupancy and detection of mesocarnivores species (Table 2.1; Table B.4), particularly during the two seasons with lower plant productivity (warm-dry and warm-wet seasons; Figure 2.1b). Although generally high site occupancy of coyotes likely contributed to high parameter uncertainty across all two-species conditional occupancy models, differences in support ($\mathrm{AIC_c}$) among models indicated potential relationships between coyote presence and mesocarnivore presence and detection. The top two-species conditional occupancy models for gray fox at high urbanization sites during the warm-wet season, which exhibited similar support ($\Delta\mathrm{AIC_c} = 0.002$), were the two models including the occupancy and detection interaction terms, indicating gray fox occupancy and detection were higher at sites where coyotes were present ($\psi^{BA} = 0.44$, 95%, SE = 0.67; $r^{B} = 0.32$, SE = 0.63) than at sites where they were absent ($\psi^{Ba} = 0.00$, SE = 1.00; $p^{B} = 0.00$, SE = 1.00). During the warm-dry season, raccoons were more likely to be detected at high urbanization sites where coyotes were present (r^B = 0.58, SE = 0.65) compared to where coyotes were absent (p^B = 0.08, SE = 0.71). Raccoon occupancy across high urbanization sites was also positively associated with coyote presence during the warm-wet season (ψ^{BA} = 0.54, SE = 0.67; ψ^{Ba} = 0.08, SE = 0.76). Counter to predictions, the two raccoon models with similar support ($\Delta\text{AIC}_\text{c}$ = 0.001) during the cool-wet season at high urbanization sites indicated that raccoon occupancy and detection were greater in the presence of coyotes (ψ^{BA} = 0.37, SE = 0.66; r^B = 0.34, SE = 0.62) than in their absence (ψ^{Ba} = 0.00, SE = 1.00; p^B = 0.00, SE = 1.00).

2.3.2 Effects of Competitor Activity and Resources on Mesocarnivore Habitat Use

Top models of relative habitat use for the three mesocarnivore species indicated that their habitat use was associated with variation in coyote activity, prey activity, and plant productivity across seasons and urbanization levels (Table 2.2). Consistent with predicted increases in co-occurrence during seasons of lower plant productivity, gray fox habitat use at high urbanization sites was positively associated and prey species activity during the warm-dry season (β_{mean} = 2.64, 95% CI = 0.03 to 5.26) and during the warm-wet season (β_{mean} = 0.71, 95% CI = -5.07 x 10^{-3} to 1.43). The top model for gray foxes at higher urbanization sites during the warm-dry season also indicated that gray fox habitat use was negatively associated with the relative activity of coyotes, but reliable estimates of this effect could not be produced (β_{mean} = -147.44, 95% CI = -3.48 x 10^3 to 3.19 x 10^3). Counter to predictions, relative habitat use by bobcats at low urbanization sites was positively associated with coyote activity during the warm-wet season (β_{mean} = 0.36, 95% CI = -0.05 to 0.77). We found no evidence that bobcat habitat use varied among sites during other seasons and urbanization levels, as no models of bobcat habitat use converged at high urbanization sites during the warm-wet season, due to the absence of bobcat detections. Counter to predictions, at high urbanization sites, raccoon habitat use was positively associated with the activity of mesocarnivore prey species during both the warm-wet season ($\beta_{mean} = 0.60$, 95% CI = 0.05 to 1.15), and the cool-wet season ($\beta_{mean} = 1.09$, 95% CI = 0.50 to 1.68).

2.3.3 Daily Activity Patterns

The daily activity patterns of some carnivores overlapped more at higher levels of urbanization across all seasons (Table 2.3; Figure 2.3). Consistent with predictions that urbanization would increase interspecific overlap, especially among species that are crepuscular in wildlands (e.g., coyote), activity patterns of both gray foxes and raccoons overlapped more with coyote activity patterns at high urbanization sites, compared to low urbanization sites. As was expected for species that are generally more nocturnal, overlap between the activity patterns of gray foxes and raccoons were similar across levels of urbanization. Although bobcat activity overlapped with coyotes, gray foxes, and raccoons at low levels of urbanization (i.e., the 95% CI of the overlap statistic overlapped with a value of 0.90), effects of urbanization on overlap with bobcats could not be estimated due to low bobcat detections at high urbanization sites (n = 3). Contrary to predictions, overlap in activity among species at low and high urbanization sites generally remained consistent across individual seasons, though lower numbers of seasonal detections (<20 observations) resulted in an inability to evaluate seasonal overlap for many species Tables B.6, B.7, B.8).

Across all seasons, overlap estimates between the activity patterns of commonly observed carnivores and their potential prey species – specifically cottontail rabbits and jackrabbits – also varied across urbanization levels (Table 2.4; Figure 2.4). Aligned with predictions, gray fox overlap with cottontail rabbit and jackrabbit activity and raccoon overlap with jackrabbits was greater across high urbanization sites. Counter to predictions, coyote overlap with both cottontail rabbits and jackrabbits was lower at more highly urbanized sites, compared to lower urbanization sites. Bobcat activity overlapped with jackrabbits at low urbanization sites, but the effect of urbanization could not be assessed due to low bobcat detections. Activity patterns of neither coyotes, gray foxes, nor raccoons overlapped substantially with activity of rock squirrels, Gambel's quail, or roadrunners.

Table 2.1: Model selection table for two-species models of mesocarnivore occupancy conditioned on the presence of coyotes at high and low urbanization sites in three seasons. Values depict the Akaike Information Criterion adjusted for small sample size (AIC_c) for each model with number of parameters K, with ‘*’ highlighting the value of the best quality (lowest AIC_c) model(s) for each season and level of urbanization. ’NA’ values indicate failure of a model to converge due to lack of species detections (in the case of bobcats) or unevenness in the presence of the dominant species A (coyotes).

			Warm-Dry		**Warm-Wet**		**Cool-Wet**	
Subordinate Species	**Model Name**	**K**	**Low Urb.**	**High Urb.**	**Low Urb.**	**High Urb.**	**Low Urb.**	**High Urb.**
Gray Fox	null-interaction	4	197.01*	148.65*	285.84*	169.30	269.50*	192.21*
	OccA-OccB	5	NA	149.54	NA	165.20*	271.82	193.24
	OccA-DetB	5	NA	149.54	NA	165.20*	271.82	195.32
	OccA-OccB + OccA-DetB	6	NA	NA	NA	NA	NA	196.79
Bobcat	null-interaction	4	272.80*	134.13	327.41*	NA	305.57	146.34*
	OccA-OccB	5	NA	135.71	NA	NA	307.47	148.36
	OccA-DetB	5	NA	137.71	NA	NA	307.47	148.36
	OccA-OccB + OccA-DetB	6	NA	NA	NA	NA	NA	NA
Raccoon	null-interaction	4	153.63*	170.92	226.06*	192.61	195.98*	186.87
	OccA-OccB	5	NA	174.14	NA	190.60*	198.86	184.24*
	OccA-DetB	5	NA	167.80*	NA	192.84	198.86	184.24
	OccA-OccB + OccA-DetB	6	NA	170.42	NA	194.16	202.20	NA

Table 2.2: Model selection table for models of mesocarnivore relative habitat use at low and high urbanization sites, as a function of plant productivity and the relative activity levels of both coyotes and prey species. Values depict the Akaike Information Criterion adjusted for small sample size (AIC_c) for each model with number of parameters K, with '*' indicating the value of the best quality (lowest AIC_c) model for each season and level of urbanization. 'NA' values indicate failure of a model to converge due to lack of species detections.

			Warm-Dry		**Warm-Wet**		**Cool-Wet**	
Subordinate Species	**Model Name**	**K**	**Low Urb.**	**High Urb.**	**Low Urb.**	**High Urb.**	**Low Urb.**	**High Urb.**
Gray Fox	null	2	101.29*	34.57	128.81*	53.09	136.39	61.41*
	veg	3	103.58	35.91	129.94	55.72	134.89*	63.98
	coyote	3	102.51	34.65	131.30	55.21	137.92	62.97
	prey	3	102.90	37.20	131.16	52.16*	138.03	62.70
	coyote+prey	4	104.76	33.83*	133.93	55.08	140.35	65.22
	veg+coyote	4	104.89	34.88	132.69	57.94	135.92	64.94
	veg+prey	4	105.45	38.59	132.62	55.03	135.29	65.27
	veg+coyote+prey	5	107.41	37.13	135.48	58.33	137.69	67.55
Bobcat	null	2	173.08*	20.26*	166.71	NA	175.68	16.33*
	veg	3	175.60	22.36	168.68	NA	173.59*	17.73
	coyote	3	175.36	22.91	166.46*	NA	176.97	17.40
	prey	3	174.59	22.36	168.77	NA	177.54	18.24
	coyote+prey	4	176.62	23.97 1	69.24	NA	179.61	NA
	veg+coyote	4	178.10	25.17	169.12	NA	175.55	20.11
	veg+prey	4	177.36	NA	171.01	NA	176.29	NA
	veg+coyote+prey	5	179.66	NA	172.16	NA	178.57	NA
Raccoon	null	2	58.28	56.23*	71.23	76.51	67.08*	56.03
	veg	3	56.92*	57.84	66.06*	77.25	69.61	57.05
	coyote	3	59.31	58.04	73.77	75.54	68.99	58.34
	prey	3	60.46	58.09	72.91	75.39*	69.49	48.19*
	coyote+prey	4	60.69	60.98	75.42	77.54	71.77	49.55
	veg+coyote	4	58.34	60.71	67.71	78.46	71.71	59.89
	veg+prey	4	59.57	60.69	67.49	77.88	72.21	50.72
	veg+coyote+prey	5	60.82	63.99	70.12	80.82	74.75	52.83

Table 2.3: Results for overlap in wildlife activity patterns between carnivore species at low and high levels of urbanization across all seasons, including the sample sizes for both wildlife species (n_A and n_B), mean estimate of activity pattern overlap (overlap estimate), and 95% confidence intervals for the overlap estimate, for four mammalian carnivore species in the Phoenix Metropolitan Area, Arizona, USA. 'NA' indicates where reliable overlap estimates could not be produced due to a low minimum sample size (<20 independent observations).

Species A	**Species B**	**Urbanization Level**	n_A	n_B	**Overlap Estimate**	**95% CI**	
						Lower	Upper
Coyote	Gray fox	Low	2996	293	0.82	0.78	0.86
		High	435	283	0.84	0.77	0.90
Coyote	Bobcat	Low	2996	298	0.89	0.85	0.91
		High	435	3	NA	NA	NA
Coyote	Raccoon	Low	2996	71	0.83	0.77	0.89
		High	435	52	0.88	0.81	0.93
Gray fox	Bobcat	Low	293	298	0.90	0.84	0.94
		High	283	3	NA	NA	NA
Gray fox	Raccoon	Low	293	71	0.89	0.81	0.94
		High	283	52	0.84	0.69	0.93
Bobcat	Raccoon	Low	298	71	0.91	0.83	0.96
		High	3	52	NA	NA	NA

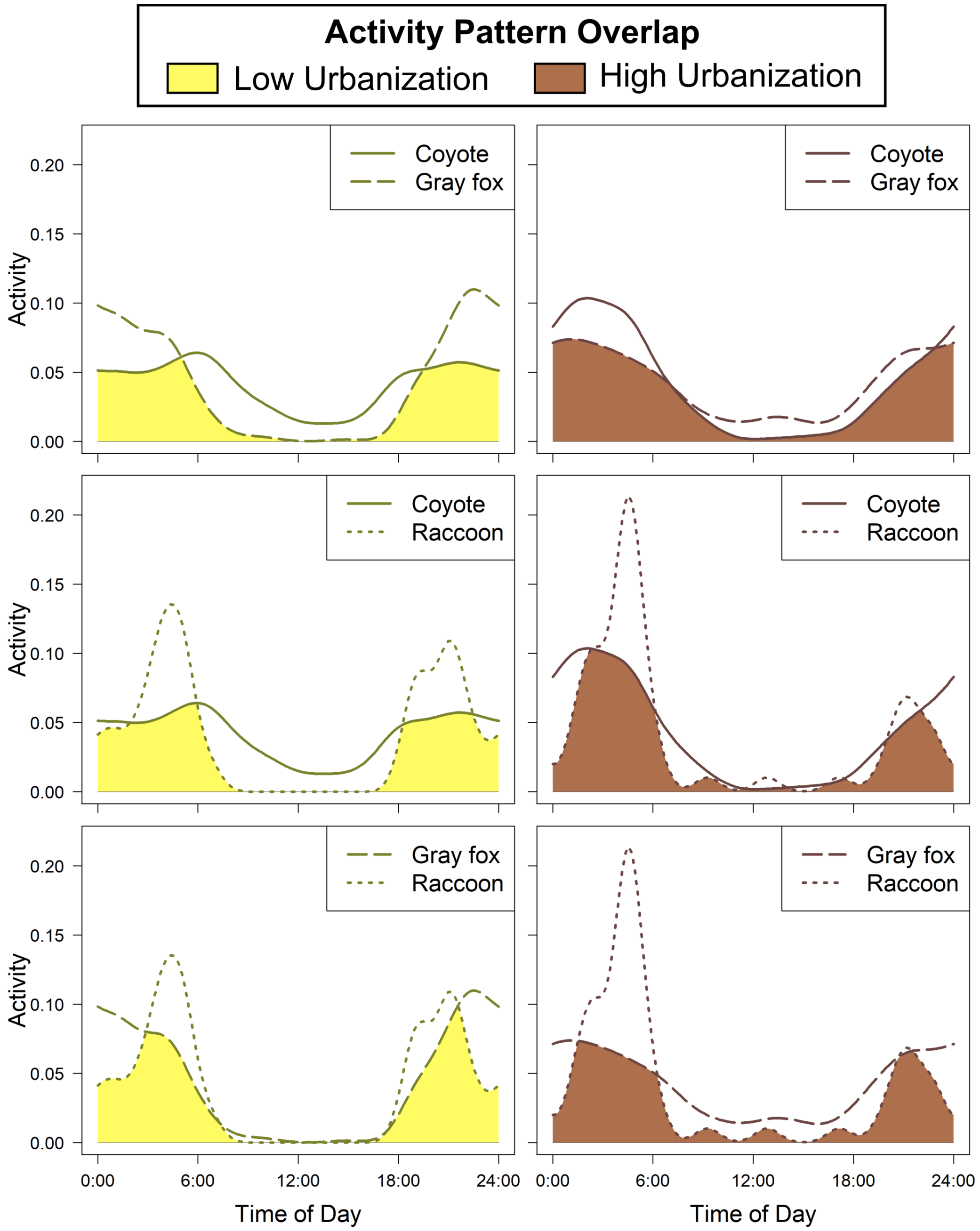

Figure 2.3: Overlap in activity patterns between pairs of three carnivore species (coyotes, gray foxes, and raccoons) commonly co-occurring at both low and higher urbanization sites within the Phoenix Metropolitan Area, Arizona, USA, based on their detections across three seasons between April 2019 and March 2020.

Table 2.4: Results for overlap in wildlife activity patterns between four carnivore species (bobcats, coyotes, gray foxes, and raccoons) and five prey species (cottontail rabbits, jackrabbits, rock squirrels, gambel's quail, and roadrunners) commonly observed at low and high levels of urbanization across all seasons, including the sample sizes for both wildlife species (n_A and n_B), mean estimate of activity pattern overlap (overlap estimate), and 95% confidence intervals for the overlap estimate, for four mammalian carnivore species in the Phoenix Metropolitan Area, Arizona, USA. 'NA' indicates where reliable overlap estimates could not be produced due to a low minimum sample size (<20 independent observations).

Species A	**Species B**	**Urbanization Level**	n_A	n_B	**Overlap Estimate**	**95% CI**	
						Lower	Upper
Bobcat	Cottontail Rabbit	Low	298	4760	0.82	0.79	0.86
		High	3	2678	NA	NA	NA
	Jackrabbit	Low	298	3293	0.89	0.86	0.91
		High	3	308 NA	NA	NA	
	Rock Squirrel	Low	298	199	0.31	0.26	0.36
		High	3	491	NA	NA	NA
	Gambel's Quail	Low	298	2784	0.47	0.42	0.51
		High	3	344	NA	NA	NA
	Roadrunner	Low	298	616	0.44	0.39	0.48
		High	3	86	NA	NA	NA
Coyote	Cottontail Rabbit	Low	2996	4760	0.89	0.87	0.91
		High	435	2678	0.85	0.81	0.88
	Jackrabbit	Low	2996	3293	0.96	0.95	0.98
		High	435	308	0.88	0.83	0.93
	Rock Squirrel	Low	2996	199	0.32	0.28	0.36
		High	435	491	0.21	0.17	0.24
	Gambel's Quail	Low	2996	2784	0.51	0.49	0.53
		High	435	344	0.34	0.31	0.38
	Roadrunner	Low	2996	616	0.47	0.44	0.49
		High	435	86	0.29	0.23	0.35
Gray Fox	Cottontail Rabbit	Low	293	4760	0.75	0.71	0.78
		High	283	2678	0.87	0.84	0.91
	Jackrabbit	Low	293	3293	0.82	0.79	0.86
		High	283	308	0.90	0.83	0.95
	Rock Squirrel	Low	293	199	0.21	0.17	0.26
		High	283	491	0.31	0.27	0.35
	Gambel's Quail	Low	293	2784	0.36	0.32	0.40
		High	283	344	0.44	0.39	0.49
	Roadrunner	Low	293	616	0.33	0.29	0.37
		High	283	86	0.39	0.32	0.46
Raccoon	Cottontail Rabbit	Low	71	4760	0.78	0.72	0.84
		High	52	2678	0.83	0.75	0.88
	Jackrabbit	Low	71	3293	0.83	0.77	0.88
		High	52	308	0.87	0.76	0.93
	Rock Squirrel	Low	71	199	0.29	0.22	0.37
		High	52	491	0.27	0.20	0.35
	Gambel's Quail	Low	71	2784	0.45	0.37	0.53
		High	52	344	0.42	0.32	0.52
	Roadrunner	Low	71	616	0.42	0.34	0.50
		High	52	86	0.36	0.26	0.46

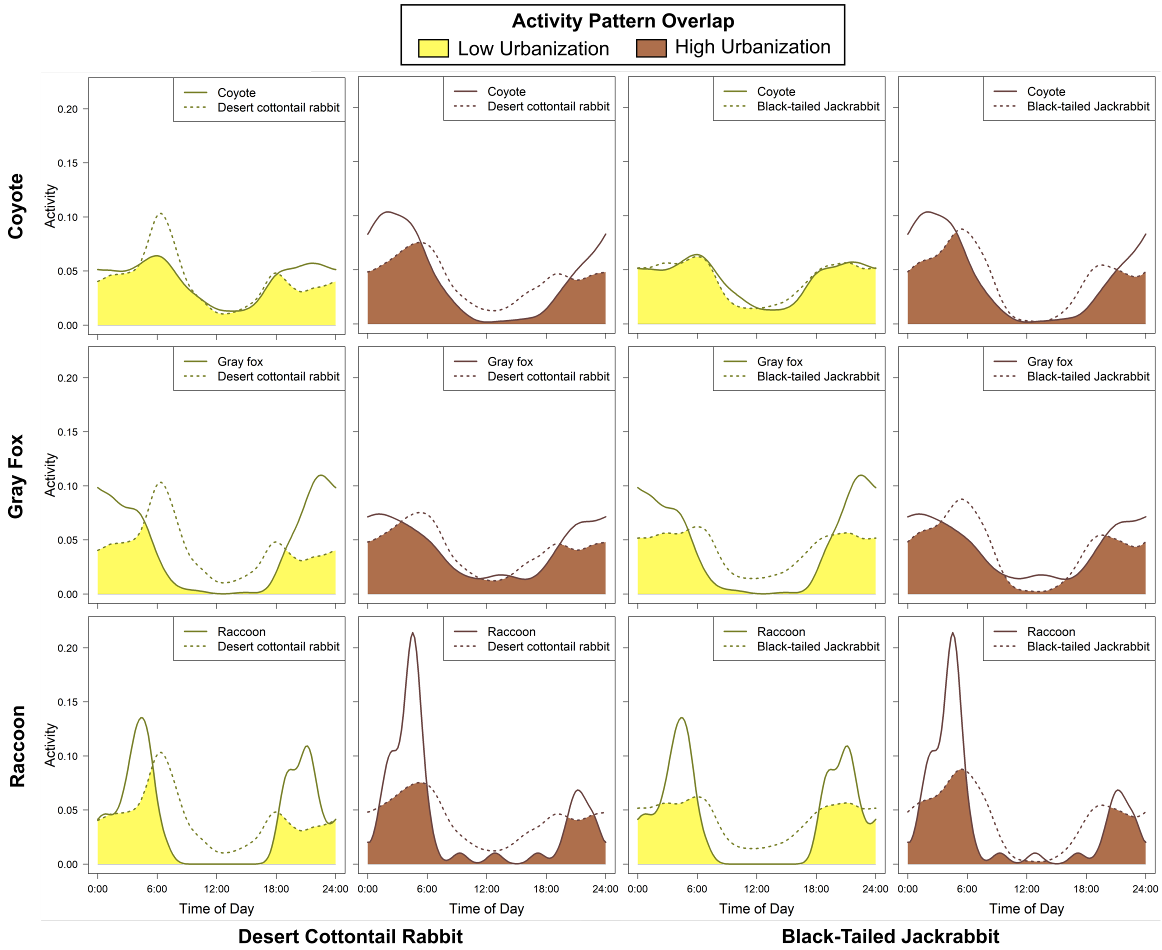

Figure 2.4: Overlap in activity patterns between three carnivore species (coyotes, gray foxes, and raccoons) and two mesocarnivore prey species (desert cottontail rabbits and jackrabbits) commonly co-occurring at both low and higher urbanization sites within the Phoenix Metropolitan Area, Arizona, USA, based on their detections across three seasons between April 2019 and March 2020.

2.4 Discussion

Within our study, seasonal co-occurrence and daily activity pattern overlap among coyotes, mesocarnivores, and prey species were generally greater at higher levels of urbanization across seasons. As such, our findings were consistent with urbanization and human activity intensifying potentially interspecific interactions (Lewis *et al.*, 2017, 2021, 2015; Parsons *et al.*, 2019; Smith *et al.*, 2018) rather than reducing them, as was alternatively hypothesized (Crooks and Soulé, 1999; Gámez and Harris, 2021). As predicted, the potential for interspecific interactions at more urbanized sites was greater during seasons of lower plant productivity in more natural areas for certain species (e.g., between foxes, coyotes, and prey during the warm-dry season). However, shifts in interactions between some species across seasons and urbanization levels contradicted predictions, such as raccoons and coyotes demonstrating increased co-occurrence at high urbanization sites during the cool-wet season. As such, differences in interspecific interactions may not be as strongly linked to seasonally varying resource availability, highlighting how additional consideration of temporal change is key to evaluating hypothesized changes in wildlife community structure across highly dynamic, human-modified landscapes (Aronson *et al.*, 2016; Faeth *et al.*, 2005; Ramalho and Hobbs, 2012).

Urbanization can alter the spatial distributions of species in ways that change the potential for interspecific interactions. In particular, urbanization and its associated human activities tend to concentrate animal movements by fragmenting habitats and aggregating the distributions of resources (Forman, 2014b; McIntyre, 2014; Riley *et al.*, 2010), including water (Bateman *et al.*, 2015b), anthropogenic food (Brown *et al.*, 2022; Warren *et al.*, 2006), and vegetation that provides refugia from competition, predation, and human disturbance (Lewis *et al.*, 2021). Aligning with these general patterns and with the findings of previous studies (Lewis *et al.*, 2021, 2015; Parsons *et al.*, 2019; Smith *et al.*, 2018), our results showing that gray foxes and raccoons were more likely to co-occur with coyotes within more highly urbanized areas support the hypothesis of increased interspecific interactions due to urbanization and human activity. In contrast, we failed to detect substantial competitive interactions among most carnivore species in less urbanized areas, reflecting how broader areas of undeveloped landscapes can enable carnivores to avoid competition through spatial, temporal, and dietary niche partitioning (Crooks *et al.*, 2010; Shochat *et al.*, 2010; Smith *et al.*, 2018).

The potential for competitive interactions across gradients of urbanization can also vary across seasons, though the degree to which those temporal dynamics are linked with natural fluctuations in resource availability remains unclear (de Albuquerque *et al.*, 2021; Faeth *et al.*, 2005, 2011). For instance, seasonal shifts in interactions among certain carnivore species – such as increased gray fox use of urbanized areas with greater coyote activity during the warm-dry and warm-wet seasons – were consistent with increases in wildlife co-occurrence within more urbanized areas that were predicted during seasons of low natural plant productivity (Buyantuyev and Wu, 2012)(Buyantuyev and Wu, 2012; Shochat *et al.*, 2010). However, potential interactions between other carnivores (i.e., coyotes and raccoons, coyotes and bobcats) did not clearly vary between periods of low and high natural plant productivity, in contrast with previous research within this system indicating that seasonal vegetation can drive changes in wildlife abundance and site use across urbanization levels for other species, such as birds and reptiles (Bateman *et al.*, 2015b; de Albuquerque *et al.*, 2021).

Inconsistencies in seasonal wildlife responses to urbanization may be partially attributed to how climatically-driven resource patterns vary among years. For instance, our study system's resource dynamics are characterized by high within-season variability in plant phenology mediated by urbanization and interannual differences in the magnitude and timing of winter and summer precipitation (Buyantuyev and Wu, 2012, 2009). In our study period, plant productivity during warm-dry season was greater than that in the warm-wet monsoon season, likely reflecting higher-than-average precipitation during the preceding winter having extended the spring growing season and lower monsoonal moisture having failed to trigger substantial plant growth during the fall months (de Albuquerque *et al.*, 2021; Thornton *et al.*, 2020). Although these patterns of precipitation and vegetation were not entirely unexpected (Buyantuyev and Wu, 2012; Wheeler *et al.*, 2021), their departure from the multi-year normal may have confounded hypothesized relationships between wildlife behavior and plant productivity. As such, further consideration of how the seasonality of resource availability varies across years could enable future studies to better evaluate links between resource availability and interspecific interactions.

By concentrating wildlife activity within smaller areas of habitat, urbanization can further affect overlap in daily activity patterns among potentially competing carnivores and their prey species. For example, the activity of gray foxes and raccoons demonstrated greater overlap with coyotes across more urbanized sites, reflecting how these three species can become increasingly nocturnal under the influences of anthropogenic disturbance (Gaynor *et al.*, 2018; Lewis *et al.*, 2021). Greater activity overlap among carnivores at higher urbanization also coincided with increased overlap of gray foxes and raccoons with key prey species (i.e., cottontail rabbits and jackrabbits), suggesting the potential for increased resource competition through higher dietary niche overlap (Smith *et al.*, 2018). However, overall overlap in activity among coyotes, gray foxes, and raccoons was generally high across both urbanization levels, consistent with previous carnivore studies indicating a broad lack of temporal niche partitioning among these species (Chitwood *et al.*, 2020; Gámez and Harris, 2021; Gehrt and Prange, 2007; Hadidian *et al.*, 2010; Parsons *et al.*, 2022; Wang *et al.*, 2015). This high degree of activity overlap implies the need for wildlife management approaches that further consider how the potential outcomes of species interactions, including dietary shifts and pathogen transmission (Crooks *et al.*, 2010; Riley *et al.*, 2010; Warren *et al.*, 2006), may vary according to human activity.

Urbanization can both create or reduce opportunities for carnivore species to co-occur and directly alter each other's distributions and behaviors through competitive effects such as territorial exclusion and intraguild predation (Crooks *et al.*, 2010; McIntyre, 2014; Ritchie and Johnson, 2009; Ryan and Partan, 2014). However, the effects of urbanization on interspecific competition vary among taxa, among ecosystems, and over time (Faeth *et al.*, 2005) with the strongest antagonistic species interactions generally occurring among more ecologically similar species (Crooks *et al.*, 2010). For example, coyotes engage in resource competition and can displace other smaller canids, such as gray foxes (Crooks and Soulé, 1999; Fedriani *et al.*, 2000; Larson *et al.*, 2015; Rich *et al.*, 2018), though there is little evidence that coyotes have substantial antagonistic effects on other mesocarnivores, such as raccoons (Gámez and Harris, 2021; Gehrt and Prange, 2007; Hadidian *et al.*, 2010). Finally, studies of broad-scale carnivore co-occurrence may help to quantify the potential for interspecific interactions, but understanding the actual outcomes of inter- and intra-guild competition and predation requires finer-scale investigations of species interactions across gradients of urbanization, including studies of diet and animal movement (Lewis *et al.*, 2017; McKinney and Smith, 2007; Smith *et al.*, 2018).

2.4.1 Conclusion

As species interactions are a key component to the stability of community structure over both space and time, changes in interactions due to human landscape modification have major implications for wildlife management of biodiversity across urbanizing landscapes (Faeth *et al.*, 2005; Magle *et al.*, 2012). Due in part to the logistical difficulties of quantifying carnivore community structure (Bateman and Fleming, 2012; Crooks *et al.*, 2010; McIntyre, 2014), interspecific interactions are a driver of wildlife populations that has not been widely considered within the single-species and biodiversity-focused planning and wildlife management efforts typically implemented across urbanized landscapes (Cypher *et al.*, 2010; Hess *et al.*, 2014; Nilon *et al.*, 2017). Our results indicating that interspecific interactions could increase in more urbanized environments further imply that urbanization could alter the interactions of carnivores with a variety of other species important to wildlife management within metropolitan settings, including introduced species, domestic animals, and species of conservation concern (Cypher *et al.*, 2010; Gehrt *et al.*, 2013; Shochat *et al.*, 2010; Warren *et al.*, 2006). Urbanization has the potential to mediate how carnivores impact on species of management interest, highlighting how needs for human-wildlife conflict mitigation can vary across gradients of human landscape modification (Bateman and Fleming, 2012; Curtis and Hadidian, 2010; Reidinger and Miller, 2013). Finally, carnivore interactions with people and other species of human interest (e.g., pets and livestock) may alter people's willingness to tolerate and accept carnivore presence by shaping their positive and negative experiences with wildlife (Bhatia, 2021; Carter and Linnell, 2016; Soulsbury and White, 2019), indicating that further consideration of species interactions could enhance the potential for human-carnivore coexistence across urbanizing landscapes.

Chapter 3

URBANIZATION, CLIMATE, AND SPECIES TRAITS SHAPE MAMMAL COMMUNITIES FROM LOCAL TO CONTINENTAL SCALES

3.1 Introduction

Biotic and abiotic factors impacted by human activities shape ecological communities across scales. Broad-scale bioclimatic gradients and human land use patterns drive global and regional biodiversity (Gaston, 2000; Seto *et al.*, 2012; Newbold *et al.*, 2020), while finer-scale patterns of resource availability, ecological disturbance, and species traits influence local community composition through habitat use, species interactions, and population processes (White and Harrod, 1997; Leibold *et al.*, 2004; Aronson *et al.*, 2016; Andrade *et al.*, 2020). Habitat modification by humans alters environmental conditions at each of these scales, leading to widespread losses of native biodiversity and changes in community composition, including the total number of species (i.e., species richness) and related metrics that account for species evenness (i.e., species diversity indices; Seto *et al.*, 2012; Mazor *et al.*, 2018). Despite the critical influences that broader-scale environmental factors can have on the mechanisms by which local human activities shape community composition (Aronson *et al.*, 2014; Beninde *et al.*, 2015; McGill *et al.*, 2015; Norton *et al.*, 2016; Lerman *et al.*, 2021), it is largely unknown to what extent such cross-scale interactions can help predict future impacts of intensifying human development on certain wildlife taxa central to biodiversity conservation, such as mammals (Fidino *et al.*, 2020; Magle *et al.*, 2021; Rega-Brodsky *et al.*, 2022).

Human-driven landscape changes can influence the distribution and diversity of species across multiple scales and along urbanization gradients, ranging from undeveloped to urban (McDonnell and Pickett, 1990; Magle *et al.*, 2019). Greater levels of urbanization negatively affect wildlife communities across scales (Shochat *et al.*, 2010; Faeth *et al.*, 2011; Aronson *et al.*, 2014; Beninde *et al.*, 2015; Fidino *et al.*, 2020; Magle *et al.*, 2021), with community composition varying within and among cities according to each city's broad biophysical characteristics (Aronson *et al.*, 2016; Norton *et al.*, 2016; Avolio *et al.*, 2021). Regionally, urban species pools can be associated with variation in climate, city size, and land cover (Gaston, 2000; Norton *et al.*, 2016; Magle *et al.*, 2019). For instance, warmer, mesic ecoregions and more recently urbanized regions often exhibit greater biodiversity (Seto *et al.*, 2012; Ferenc *et al.*, 2014; IPBES, 2019). Locally, communities may respond differently to urbanization due to regional differences in urban footprint (Fidino *et al.*, 2020; Uchida *et al.*, 2021), vegetation (Aronson *et al.*, 2014; Beninde *et al.*, 2015), and age of development (Crooks and Soulé, 1999; Aronson *et al.*, 2014). These multi-scale landscape changes can individually influence biodiversity patterns (Newbold *et al.*, 2020), but their combined effects on communities are poorly understood (Mazor *et al.*, 2018; Magle *et al.*, 2019).

Species' functional traits may also influence relationships between human development and community composition. Life history traits like body size, home range, and diet can mediate species' tolerance of urbanization (McKinney, 2002; Santini *et al.*, 2019; Rega-Brodsky *et al.*, 2023). Wider-ranging, larger-bodied, and more carnivorous mammals, for example, are often most negatively affected by human development or persecution (Riley *et al.*, 2010; Bateman and Fleming, 2012; Suraci *et al.*, 2021). The few urbanization-tolerant species that remain can become abundant in human-dominated landscapes, resulting in lower species evenness and diversity (McKinney and Lockwood, 1999; Marzluff, 2001; Turrini and Knop, 2015; Boron *et al.*, 2019). Community composition within cities is thus a consequence of species traits and multi-scale landscape factors (Aronson *et al.*, 2016). However, it is unclear how these factors interact across scales to drive biodiversity patterns (Catterall, 2009; Rega-Brodsky *et al.*, 2022).

Here we tested whether local- and regional-scale environmental factors and species traits influenced mammal presence, community composition, and relationships of both with anthropogenic landscape changes. We conducted this study across 20 North American cities within the Urban Wildlife Information Network (UWIN; Figure 3.1; Table C.1), a long-term, multi-region study with the purpose of systematically monitoring biodiversity across cities of varying size, histories, and ecoregional contexts (Magle *et al.*, 2019). We used data from a continent-wide camera trap array and a multi-city, multi-species occupancy model to address three research objectives (Sutherland *et al.*, 2016). First, we evaluated how local mammal species occupancy, richness, and diversity related to three types of human landscape modification within cities – urbanization, natural patch density (fragmentation), and agriculture – during the summer season. Second, we assessed how among-city continental variation in environmental conditions (vegetation greenness, temperature, regional urbanization, and city age) influenced regional species richness and local trends in species occupancy and community composition across urbanization gradients. Finally, we examined how variation in life history traits (diet and body size) among species mediated relationships among species distributions, community structure, and urbanization.

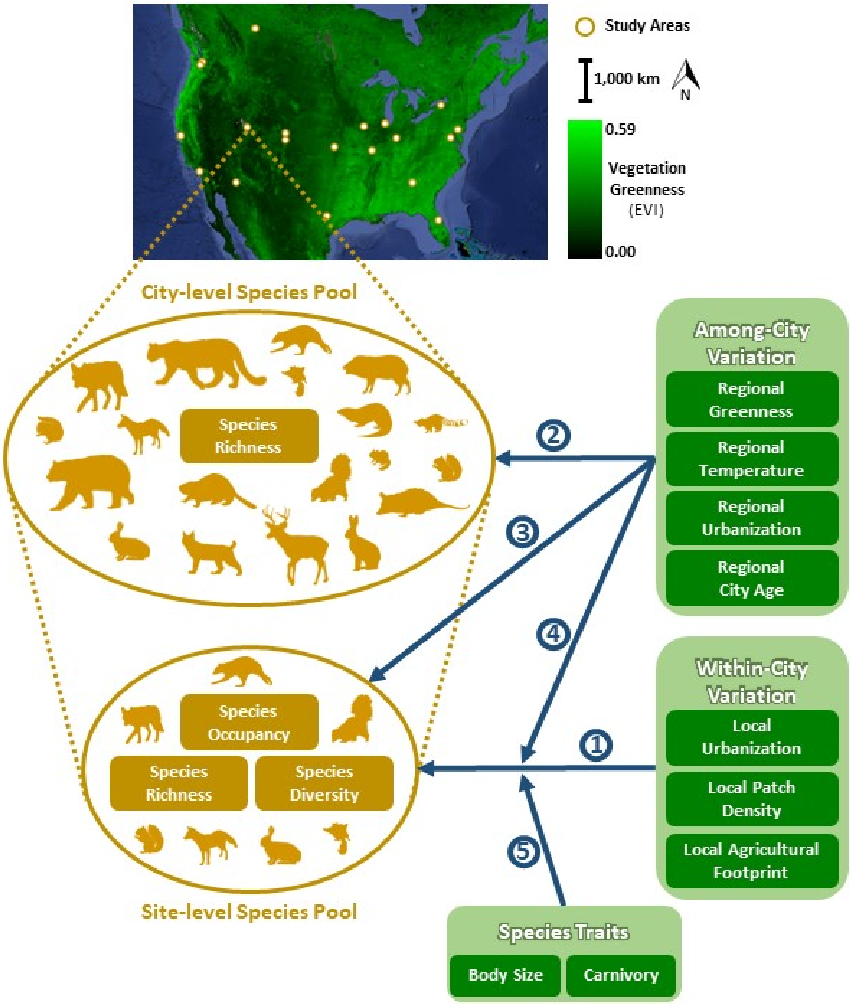

Figure 3.1: Map of study cities across North America and conceptual diagram of the study's modeling approach. We depict the location of 20 cities participating in the long-term monitoring of wildlife species, as part of the Urban Wildlife Information Network, across a continental gradient of vegetation greenness (Enhanced Vegetation Index; EVI). Arrows represent five types of effects, distinct pathways by which multi-scale environmental characteristics and species traits may interact with one another to affect wildlife communities at local (site-level) and regional (city-level) scales: (1) variation in environmental predictors within cities (e.g., local urbanization) influencing site-level species pools (e.g., average species occupancy, alpha diversity); (2) environmental variation among cities (e.g., EVI) driving differences in regional species pools (e.g., gamma diversity); (3) among-city variation directly affecting local species pools; (4) among-city predictors interacting with within-city predictors across scales, influencing how the latter shapes local communities; and (5) species traits shaping local species pools by mediating among-species differences in within-city responses to environmental predictors.

3.2 Methods

3.2.1 Site Selection and Experimental Design

We used camera trap data collected in the summer months to assess mammal species occupancy, richness, and diversity across 20 cities in the United States and Canada (Figure 3.1; Table C.1). Data was collected using a camera trapping protocol established by the Urban Wildlife Information Network for the long-term monitoring of ground-dwelling wildlife species (Magle *et al.*, 2019). Within each city, passive infrared triggered wildlife cameras were located along likely wildlife travel corridors (e.g., parks, preserves, riparian corridors, trails, alleys, canals) across a gradient of urbanization (defined as % impervious surface cover), and positioned a minimum of 1 km apart from one another to increase the independence of each sampling site.

3.2.2 Data Collection

We identified mammals in camera trap photos to the species or genus level. All photo identification was conducted by trained personnel, including university students and faculty, community member volunteers, and wildlife professionals in governmental and non-governmental organizations. Primarily due to limitations in the ability to identify species solely on wildlife camera photographs, observations of seven sets of closely-related congeneric species (Antelope Ground Squirrel, Chipmunks, Cottontail Rabbits, Flying Squirrels, Gray Squirrels, Jackrabbits, Weasels) were grouped for estimation of species presence, detection, and community composition. Although certain small mammals were also widely detected and identified across all cities (e.g., squirrel species), mid-to-large sized mammal species were likely over-represented and many smaller-bodied species were under-represented or not detected at all within our sampling, a potential source of bias typical of camera trapping as a method for sampling wildlife communities (Meek *et al.*, 2014).

We analyzed data for 37 mammal species and species groups (we hereafter refer to both as 'species', for simplicity) that were observed at least once across all cities during a 35-day summer sampling period (June 29th - August 2nd; Table C.2). Each UWIN partner began and ended data collection at different times between 2016-2020, with certain cities having only single full or partial year's worth of data available at the time of this analysis (e.g. Manhattan, Kansas stopped collecting data in 2016).Thus, we chose a single year's summer sampling period per city for inclusion in this analysis, focusing on the specific sampling year that maximized the number of sites within each city (Table C.1). We specifically selected the summer season for analysis as we predicted that this would be the season of greatest mammal activity across North American biomes, increasing our ability to detect potential effects of regional bioclimatic variables on responses to urbanization. Due to data availability, focusing our analysis on a single season additionally enabled us to utilize data from cities spanning a wider range of environmental characteristics and wildlife communities. The combined dataset included observations from 725 camera traps sites that were sampled for a minimum and maximum of 12 and 35 days, respectively. Over the 2016 through 2020 period, no regional species colonization events are known to have occurred, allowing us to assume the closure of regional species pools across years. We limit any discussion of species-level results to the 29 species with more than 10 daily detections (0.05% of the total camera trap-days). As described in our statistical modeling framework below, we treated 'city' as a random effect in the estimation of species occupancy and community composition, allowing for greater parameter uncertainty in cities with lower sample sizes and capturing the combined statistical influences of other potentially influential but ultimately excluded among-city variables.

3.2.3 Variables

Within-City Covariates

We estimated a within-city *urbanization* covariate as the mean percentage of impervious surface cover within 1 km of each site, based on the combination of data from the 2016 National Land Cover Database Imperviousness dataset (for all US cities) and road and building footprint data (for the City of Edmonton; of Edmonton's Open Data Portal, 2018, 2019; Wickham *et al.*, 2021). Within the R programming language version 4.0.1 (R Core Team, 2020), we then calculated a series of potential within-city variables of landscape composition and configuration around each camera site using the 2015 North American Land Cover Monitoring System (NALCMS) 30-meter dataset (Homer *et al.*, 2017; for Environmental Cooperation, 2020), and the R package *landscapemetrics* (Hesselbarth *et al.*, 2019). We used two of these variables as additional within-city covariates for species occupancy, richness, and diversity: agricultural footprint and patch density. We calculated *agricultural footprint* as the proportion of the 1 km buffered area surrounding each site classified as 'Cropland'. We quantified *patch density* as the number of natural patches – defined as contiguous areas of non-urban, non-agricultural land cover classes – within the 1 km buffer. Differences in patch densities represented local variation in habitat patchiness and fragmentation that are observably greater in areas of moderate urbanization (Figure C.3). To reduce the influence of differences in sample size (number of wildlife cameras) among cities, values of all within-city covariates were standardized by city prior to model implementation, following best-practice recommendations for multi-level modeling (Aguinis *et al.*, 2013; Milliren *et al.*, 2018). Lastly, we tested for potential cross-scale interactions between local effects of human development and the regional environmental context by allowing within-city species occupancy and each species' relationship between occupancy and urbanization to partially vary according to species traits and to a set of covariates that varied among cities (explained in detail below).

Among-City Covariates

We quantified an array of metrics for their potential use as among-city covariates of regional species richness and differences in within-city urbanization-occupancy trends, including average bioclimatic values, land cover proportions, and landscape heterogeneity metrics within a 10 km buffer surrounding all sites in each city (Figure C.4). We included four of these variables as among-city covariates in our model based on their alignment with regional environmental characteristics hypothesized to drive regional species diversity and influence urbanization-community relationships. We measured vegetation greenness using the enhanced vegetation index (EVI), calculated in Google Earth Engine based on Landsat 5 TM 32-Day composite imagery from 1984-2012 (Gorelick *et al.*, 2017). We considered EVI to be associated with metrics of precipitation, aridity, natural patch density, and latitude, based on an arbitrary Pearson's coefficient > 0.5 cut-off (Figure C.4). Mean annual temperature (MAT) was derived from 1-km downscaled climate data for the 1981-2010 normal period produced by ClimateNA (Wang *et al.*, 2016), and was associated with mean summer temperature, potential evapotranspiration, aridity, and latitude (Figure C.4). The proportional amount of urban land cover type across the entire city – what we refer to as regional urbanization (URB) – was associated with regional agricultural and natural land cover types, as well as the aggregation of urban land cover patches (Figure C.4). We measured city age (AGE) using the years since the approximate date of earliest Euroamerican colonization or settlement of each city's metropolitan area, following the methods of Aronson et al. (2014). Although we chose to model the effects of these four city-level characteristics based on their hypothesized influences on among-city differences in local and regional mammal communities, such variation in communities among cities may further result from attributes of cities not included in this analysis (e.g., human population density, precipitation).

Species Trait Covariates

We assessed among-species variation in species occupancy and urbanization effects based on species trait data for all 37 species sourced from the EltonTraits and PanTHERIA databases (Jones *et al.*, 2009; Wilman *et al.*, 2016). We selected two traits to serve as species-level covariates that are hypothesized to mediate species presence across urbanization gradients by influencing space use and habitat requirements (McKinney, 2002; Santini *et al.*, 2019; Suraci *et al.*, 2021; Rega-Brodsky *et al.*, 2023): body mass and carnivory (Supplementary Data 1). We log-transformed *body mass*, which was positively collinear with home range size (r = 0.57), and we calculated *carnivory* as the total percentage of the species' diet consisting of vertebrate prey. For the seven species that represent assemblages of multiple taxonomic species (Antelope Ground Squirrels, Cottontail Rabbits, Flying Squirrels, Jackrabbits, Gray Squirrels, Chipmunks, Weasels), we calculated mean trait values among the known species in each assemblage.

3.2.4 Multi-City Community Occupancy Model

We estimated site- and city-level occupancy of all observed mammal species using a multi-city, multi-species occupancy model. Because the home range size of large mammal species included in this analysis likely exceeded the 1 km buffer between cameras, all resulting estimates of species occupancy or presence should be interpreted as 'relative use' rather than true occupancy (Magle *et al.*, 2021). Based on the multi-region community occupancy model structures described by Sutherland et al. (2016)

and Tenan et al. (2017), our model estimates the probability that 1) a species is present within the species pool of a given city, 2) a species is present at a site within a city, given their presence in a city's species pool, and 3) a species is detected at a site given its presence.

City-Level Species Presence

To model the occurrence of each of s in 1,. . . ,S species in each of r in 1,. . . ,R cities, we treat $\omega_{s,r}$ as a Bernoulli random variable that denotes whether species s is within the species pool of city r; and we let Ω_r (the completeness of each regional species pool) be the probability that all S species are within the species pool of city r, such that

$$\omega_{s,r} \sim Bernoulli(\Omega_r) \tag{3.1}$$

Site-Level Species Presence

Given this specification, if a species is not within a city's species pool, then $\psi_{s,j,r} \times \omega_{s,r} = 0$ and species s cannot be present at any of the j sites of city r. We used partial-pooling among cities and species to estimate $\psi_{s,j,r}$, which we also made a function of among-city covariates $(m_{EVI}, m_{MAT}, m_{URB}, m_{AGE})$, within-city covariates $(m_{Urbanization}, m_{PatchDensity}, m_{AgriculturalFootprint})$, and the interactions between the two (e.g., $m_{EVI} \times m_{Urbanization}$) via the logit link, such that

$$
\begin{aligned}
logit(\psi_{s,j,r}) = \phi_{0,s,r} &+ \phi_{Urbanization,s,r} \times m_{Urbanization,j,r} \\
&+ \phi_{PatchDensity,s,r} \times m_{PatchDensity,j,r} \\
&+ \phi_{AgriculturalFootprint,s,r} \times m_{AgriculturalFootprint,j,r} \\
&+ \phi_{EVI,s,r} \times m_{EVI,r} + \phi_{MAT,s,r} \times m_{MAT,r} \\
&+ \phi_{URB,s,r} \times m_{URB,r} + \phi_{AGE,s,r} \times m_{AGE,r} \\
&+ \phi_{EVIxUrbanization,s,r} \times m_{EVI,r} \times m_{Urbanization,j,r} \\
&+ \phi_{MATxUrbanization,s,r} \times m_{MAT,r} \times m_{Urbanization,j,r} \\
&+ \phi_{URBxUrbanization,s,r} \times m_{URB,r} \times m_{Urbanization,j,r} \\
&+ \phi_{AGExUrbanization,s,r} \times m_{AGE,r} \times m_{Urbanization,j,r} \\
&+ \epsilon_{Year,t}
\end{aligned}
\tag{3.2}
$$

Where each $\phi_{s,r}$ represents each species' city-specific logit-scale occupancy intercept and slope parameters and $\epsilon_{Year,t}$ estimates variation in occupancy associated with the individual sampling year t =1,…5 (2016-2020). We further let each species' occupancy and relationship with within-city urbanization to vary from community-level (i.e., among-species average) hyperparameters β based on species-level traits. In the model, among-species covariates were assumed to partially influence the degrees to which each species' occupancy within a city $\phi_{0,s,r}$ and among-city average relationship with urbanization $\delta_{Urbanization,s}$ both vary from their respective community-average mean parameters β_0 and $\beta_{Urbanization}$.

$$\begin{aligned}\phi_{0,s,r} \sim Normal(&\beta_0 + \beta_{OccupancyMass} \times m_{Mass,s} \\ &+ \beta_{OccupancyCarnivory} \times m_{Carnivory,s}, \sigma_{\beta_0})\end{aligned} \tag{3.3}$$

$$\begin{aligned}\delta_{Urbanization,s} \sim Normal(&\beta_{Urbanization} + \beta_{UrbanizationMass} \times m_{Mass,s} \\ &+ \beta_{UrbanizationCarnivory} \times m_{Carnivory,s}, \sigma_{\beta_{Urbanization}})\end{aligned} \tag{3.4}$$

Where $\beta_{OccupancyMass}$, $\beta_{OccupancyCarnivory}$, $\beta_{UrbanizationMass}$, and $\beta_{UrbanizationCarnivory}$ are community-level slope terms representing the effects of species traits on occupancy probabilities and relationships with urbanization. We used a near-identical hierarchical parameterization for all intercept, slope, and error terms within equations 3.2 to 3.4. As such, we explain only the model intercept prior specification, which was

$$\begin{aligned}\beta_0 &\sim Normal(0, 1.5) \\ \delta_{0,s} &\sim Normal(\beta_0, \sigma_{\beta_0}) \\ \sigma_{\beta_0} &\sim Inv - Gamma(0.1, 0.1) \\ \phi_{0,s,r} &\sim Normal(\delta_{0,s}, \sigma_{\delta_{0,s}}) \\ \sigma_{\delta_{0,s}} &\sim Inv - Gamma(0.1, 0.1)\end{aligned} \tag{3.5}$$

Where β_0 is the global logit-scale average intercept across all cities and species, $\delta_{0,s}$ is the species-specific, city-averaged logit-scale intercept that varied around β_0 via the standard deviation term σ_{β_0}, and $\phi_{0,s,r}$ is the species- and city-specific logit-scale intercept that varied around $\delta_{0,s}$ via the standard deviation term $\sigma_{\delta_{0,s}}$.

Site-Level Species Detection

The third and final level of the model accounted for imperfect detection. Let $y_{s,j,r}$ be a binomial random variable that is the number of days species s was observed at site j in city r, $k_{s,j,r}$ be the total number of days a camera trap was functional, and $\rho_{s,j,r}$ be the probability a species is detected given their presence, such that

$$\begin{aligned} y_{s,j,r} &\sim Binomial(\rho_{s,j,r} \times z_{s,j,r}, k_{s,j,r}) \\ logit(\rho_{s,j,r}) &= \eta_{0,s,r} \end{aligned} \tag{3.6}$$

Where $\eta_{0,s,r}$ was is the species and city-specific logit-scale parameter for detection probability. We specified priors for detection intercept parameters following a hierarchical parameterization identical to that of occupancy parameters shown in equation 3.5.

Model Fitting

We implemented our multi-city, community occupancy model in a Bayesian framework using R programming language version 4.0.1 (R Core Team, 2020) and JAGS 4.3.0 (Plummer, 2003). Following a 10,000 step adaptation and a 120,000 step burn-in, we sampled the posterior of each model 180,000 times across three chains. We thinned each chain by 3 to reduce complexity in monitoring model parameters, resulting in a total of 60,000 posterior samples. We verified convergence by examining the Gelman-Rubins diagnostics ($\hat{R} < 1.1$) and by visually inspecting traceplots for all modeled parameters (Gelman *et al.*, 2014).

Deriving Species Richness and Diversity

We used the model to predict two site-specific Hill numbers (^{q}D) that correspond to two common biodiversity metrics: (1) species richness (q = 0; the absolute sum of species present) and (2) species diversity (q = 1; an exponentiated Shannon entropy index)(Chao et al., 2014; Tenan et al., 2017). Parameter estimates from 10,000 posterior samples were randomly extracted from the model and used to predict occupancy probabilities ($\psi_{s,j,r}$) and latent occupancy states ($z_{s,j,r}$) for each species at each site. Species richness (^{0}D) was derived as the sum of all species occupancy states at that site(Kéry and Royle, 2016; Magle et al., 2021). Following the methods of Broms et al. (2015) and Tenan et al. (2017), we used occupancy estimates as stand-ins for abundance in the calculation species diversity(Broms et al., 2015; Tenan et al., 2017). We chose the metric of species diversity (^{1}D) as a representation of the effective number of species in a manner that accounts for the relative abundance of species at each site, with greater values of species diversity indicating both higher species richness and evenness.

3.2.5 Community Composition Meta-analysis

Treating the species richness and diversity estimates derived from the multi-city community occupancy model above as metrics of local community composition, we then modeled community composition in relation to within-city and among-city covariates using a Bayesian meta-analysis approach. We used two log-link generalized linear models (GLMs) to allow species richness (^{0}D) and species diversity (^{1}D) to individually vary as a function of the same set of covariates from the multi-city community occupancy model (e.g., within-city covariate $m_{Urbanization}$, among-city covariate m_{EVI}, and the combined interaction between the two $m_{EVI} \times m_{Urbanization}$), such that

$$\begin{aligned}
ln({}^{q}D_{j,r}) = \alpha_{0,j} &+ \alpha_{Urbanization,s,r} \times m_{Urbanization,j,r} \\
&+ \alpha_{PatchDensity,s,r} \times m_{PatchDensity,j,r} \\
&+ \alpha_{AgriculturalFootprint,s,r} \times m_{AgriculturalFootprint,j,r} \\
&+ \alpha_{EVI,s,r} \times m_{EVI,r} + \alpha_{MAT,s,r} \times m_{MAT,r} \\
&+ \alpha_{URB,s,r} \times m_{URB,r} + \alpha_{AGE,s,r} \times m_{AGE,r} \\
&+ \alpha_{EVIxUrbanization,s,r} \times m_{EVI,r} \times m_{Urbanization,j,r} \\
&+ \alpha_{MATxUrbanization,s,r} \times m_{MAT,r} \times m_{Urbanization,j,r} \\
&+ \alpha_{URBxUrbanization,s,r} \times m_{URB,r} \times m_{Urbanization,j,r} \\
&+ \alpha_{AGExUrbanization,s,r} \times m_{AGE,r} \times m_{Urbanization,j,r} \\
&+ \epsilon_{j,r}
\end{aligned} \tag{3.7}$$

$${}^{q}D_{j,r} \sim Normal(\bar{D}, \sigma_D) \tag{3.8}$$

Where $\alpha_{0,j}$ is the log-scale intercept of each community composition metric, remaining α terms are slope parameters representing the effects of each covariate or combination of covariates, and $\epsilon_{j,r}$ is an additional error term that allowed each data point to vary from the modeled relationship (i.e., the standard residual error term within a log-linear model). All intercept and slope parameters were given vague normal priors (e.g., $\alpha_{0,r} \sim Normal(0, 10)$). We parameterized normal priors for ${}^{q}D$ based on $\bar{D}$ and σ_D, which respectively correspond to the mean and standard deviation of 10,000 site-specific composition estimates. As such, this model propagates the uncertainty of species richness and diversity estimates from the occupancy model into this secondary analysis.

3.2.6 Evaluating Modeled Covariate Relationships

We evaluated the hypothesized influences of model covariates in the multi-city community occupancy and diversity models by examining the posterior distributions of each covariate's random slope parameters. For each covariate effect parameter, we used the proportion of the posterior estimates sharing a sign (positive or negative) with the mean of the estimates (f-statistic) to represent the probability of a substantial occupancy-covariate relationship being present. For instance, if 90% of the posterior distribution of a slope parameter had a negative value, then we considered there to be a 90% probability of detecting a negative relationship, though the magnitude of that negative relationship may vary. We additionally assessed the likelihood of covariate relationships using the Bayesian credible interval (CRI) and whether or not they overlap zero. In multilevel models such as ours, estimates of lower-level random parameters (e.g., our species-specific parameters) tend to be drawn toward the mean value of the upper-level parameters from which they are derived (e.g., our community-mean parameters), resulting in the shrinkage of lower-level parameters(Greenland, 2000). When necessary to account for the effect of parameter shrinkage within our models, we utilized multiple confidence levels in our terminology when referencing the likelihood of detecting informative covariate slope parameters, referring to relationships with >85% probability as "likely" and relationships with >95% probability as "highly likely" (Arnold, 2010; Suraci *et al.*, 2021).

3.3 Results

Sampling across 725 wildlife camera sites in 20 cities resulted in 37 mammal species detected over a total of 20,206 camera trap-days, with the number of trap-days in each region ranging between 336 (Austin, Texas) and 2,531 (Chicago, Illinois; Table C.1). Daily species detections varied between 2,900 (Raccoon, *Procyon lotor*) and 2 (Hooded Skunk, *Mephitis macroura*; Mountain Beaver, *Aplodontia rufa*; Richardson's Ground Squirrel, *Urocitellus richardsonii*; and Weasels, *Mustela* spp.). Eight species were detected fewer than 0.05% of the total camera trap-days (10 daily detections) and were excluded from species-level analyses (Table C.2).

3.3.1 Within Cities

Mammal species occupancy was associated with variations in human landscape modification within cities (Table 3.1, Effect Type 1; Figure C.1a-c). Across all sites, community-average occupancy probability (i.e., the among-species mean, community-level occupancy hyperparameter) strongly decreased with increasing local urbanization (mean impervious surface percentage around each site), with the city-average modeled relationship (Table 3.1) predicting occupancy probabilities of 0.16 (95% CRI 0.08 to 0.29) at sites with no impervious surface cover and 0.02 (95% CRI 0.01 to 0.06) at sites with the maximum of 87.4% impervious surface cover, corresponding to an overall 84% decrease in site use across the gradient (Figure C.1a). There was a positive relationship between local patch density (the number of natural, non-urban, non-agricultural land cover patches around each site) and community-average occupancy among all cities (Table 3.1), relationships upon which occupancy probabilities were expected to range between 0.07 (95% CRI 0.04 to 0.11) and 0.11 (95% CRI 0.05 to 0.23) at sites with minimum and maximum patch densities (Figure C.1b).

Community-average occupancy also demonstrated a moderate negative relationship with local agricultural footprint (Table 3.1), with occupancy probability predicted to decrease from 0.09 (95% CRI 0.05 to 0.14) at sites surrounded by no agricultural land cover to 0.04 (95% CRI 0.01 to 0.09) at sites with the maximum of 84.3% agricultural land cover (Figure C.1c).

Metrics of local community composition – specifically species richness (total number of species) and diversity (the exponentiated Shannon entropy index; number of species weighted by species evenness; see Online Methods for additional details) – also exhibited associations with gradients of landscape modification (Table 3.2, Effect Type 1). Across all sites, local urbanization demonstrated negative relationships with richness and diversity (Table 3.2; Figure C.1d-f). The average sites with the most impervious surface cover were predict to have values of richness (median = 3.23; 95% CRI 2.93 to 3.54) and diversity (median = 5.74; 95% CRI 5.50 to 6.00) that were 43% and 34% lower, respectively, than the richness (median = 5.74; 95% CRI 5.37 to 6.13) and diversity (median = 8.79; 95% CRI 8.53 to 9.06) at sites with no impervious surface cover (Figure C.1d,g). Local patch density was likely not associated with either richness or diversity (Table 3.2; Figure C.1e,h). Conversely, local agricultural footprint demonstrated negative relationships with both richness and diversity (Table 3.2), which predicted a 26% overall decrease in diversity across the gradient of agricultural land cover, from a median diversity of 7.80 (95% CRI 7.66 to 7.95) at sites with surrounded by no agricultural lands to 5.69 (95% CRI 5.30 to 6.12) at sites with the maximum amount of agricultural land cover (Figure C.1f,i). Variation in diversity – as a metric positively associated with species evenness – partially resulted from how effects of human landscape changes varied within the community, because the occupancy of several species exhibited stronger negative relationships with urbanization than others (Table C.3).

3.3.2 Among Cities

Among-city environmental variables were more strongly associated with local patterns of species occupancy and their relationships with urbanization than they were with regional (city-level) species richness. We failed to detect any relationships between a city's regional species richness (i.e., the overall probability of regional species presence) and regional environmental variables (Table 3.1, Effect Type 2; Figure C.2), including vegetation greenness (Enhanced Vegetation Index; EVI), temperature (mean annual temperature), regional urbanization (% of the city consisting of urban land cover types), or city age (years since colonization). However, species were more common across all sites (i.e., community-average occupancy was higher) in cities with greater vegetation greenness, lower regional urbanization, and colder temperatures (Table 3.1, Effect Type 3). Within-city relationships between local urbanization and community-average occupancy were moderately more negative in warmer cities and in cities with lower vegetation greenness (Figure 3.2a,b), but likely did not vary among cities of different ages or with different levels of regional urbanization (Figure 3.2c,d; Table 3.1, Effect Type 4). For instance, the negative effect of local urbanization on occupancy within the relatively low temperature and highly vegetated city of Tacoma, Washington was predicted to be 0.65 times weaker than that within the similarly vegetated but warmer St. Louis, Missouri, and 0.50 times weaker than that within the less vegetated but similarly cold Fort Collins, Colorado. Several species also exhibited interactions between urbanization and regional environmental variables that we failed to detect for other species, potentially contributing to among-city variation in local patterns of species evenness and diversity. For example, interaction effects for cottontail rabbits (Sylvilagus sp.) indicated that the species responded more negatively to urbanization within warmer cities (β_{mean} = -0.27, 95% CRI -

0.62 to 0.09, 93.5% of posterior distribution negative) and within cities with lower vegetation greenness (β_{mean} = 0.21, 95% CRI -0.08 to 0.50, f = 92.4% of posterior distribution positive).

Among-city differences in regional environmental variables also altered local community composition metrics (Table 3.2, Effect Type 3) and their within-city relationships with urbanization (Table 3.2, Effect Type 4; Figure 3.2e-l). In cities with greener vegetation, site-level richness and diversity tended to be greater and more positively associated with urbanization (Figure 3.2e,i). For example, the negative effects of local urbanization on richness and diversity within the least vegetated city (Phoenix, Arizona) were predicted to be, respectively, 1.45 and 3.60 times stronger those in the most vegetated city with similar temperature (Sanford, Florida). Conversely, warmer cities tended to have lower values of local richness and diversity across all their sites, as well as more negative associations between urbanization and both richness and diversity (Figure 3.2f,j). For instance, local urbanization within the warm city of Metropolitan Los Angeles, California, was expected to have negative relationships with richness and diversity that were 3.97 and 1.29 times stronger than those within Salt Lake City, Utah, one of the coldest cities with similar vegetation greenness. Cities with greater regional urbanization (i.e., more intensively urbanized landscapes) had lower site-level richness and diversity, both of which also had more negative relationships with local urbanization than in less urbanized cities (Figure 3.2g,k). Finally, site-level richness tended to be higher in older cities, whereas site-level diversity was lower(Figure 3.2h,l).

3.3.3 Among Species

Species traits (i.e., body size and carnivory) influenced each mammal species' occupancy and their responses to urbanization within cities (Figure 3.3; Figure C.3).

Although larger-bodied species were as common as (i.e., had similar species-level occupancy to) smaller-bodied species overall (Figure C.3a; β_{mean} = -0.07; 95% CRI -0.66 to 0.51; 59.8% of posterior positive), body mass exhibited a negative relationship to the urbanization effect (Figure 3.3a; β_{mean} = -0.36; 95% CRI -0.65 to -0.06; 99.0% of posterior distribution negative), indicating that larger species responded more negatively to urbanization. More carnivorous species were generally rarer across sites (Figure C.3b; β_{mean} = -0.53; 95% CRI -1.08 to 0.03; 96.9% of posterior distribution negative), but carnivory did not influence species' responses to urbanization (Figure 3.3b; β_{mean} = 0.03; 95% CRI -0.24 to 0.29; 58.5% of posterior distribution positive).

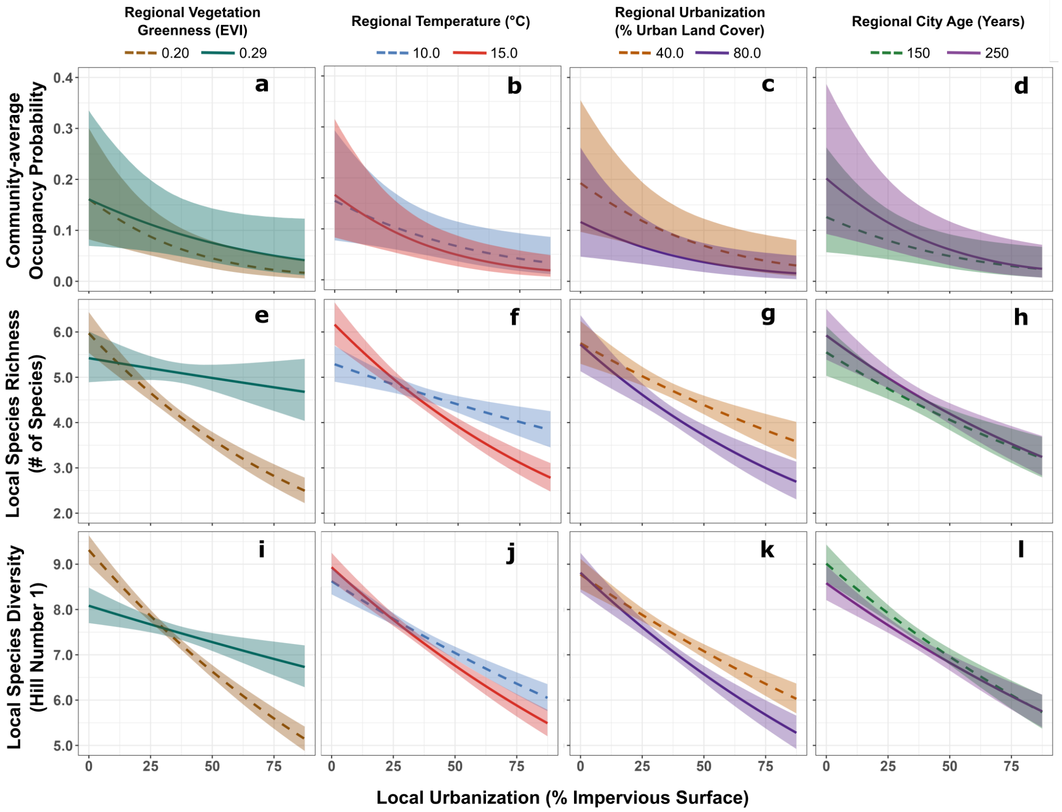

Figure 3.2: Influences of regional variation in vegetation greenness, temperature, urbanization, and city age on mammal community trends across gradients of local urbanization within 20 North American cities. **a,b,c,d**, community-average occupancy probability. **e,f,g,h**, species richness. **i,j,k,l**, species diversity. The response variables community-average occupancy, local species richness, and local species diversity refer, respectively to the average probability of site use among the mammal community, the total number of species at each site (Hill Number 0) and the number of species at each site weighted by species evenness (Hill Number 1; the exponentiated Shannon index). We visualize the modeled effects of within-city and among-city variables on occupancy (Table 3.1, Effect Type 1, 3, and 4) and on richness and diversity (Table 3.2, Effect Types 1, 3, and 4) by predicting values of each response variable across hypothetical ranges of local urbanization under two contrasting levels of each among-city variable, with all other within-city and among-city variables held constant at their mean values. We then depict the median and 95% Bayesian credible interval (CRI) of these predicted values using the trendlines and their corresponding shaded regions.

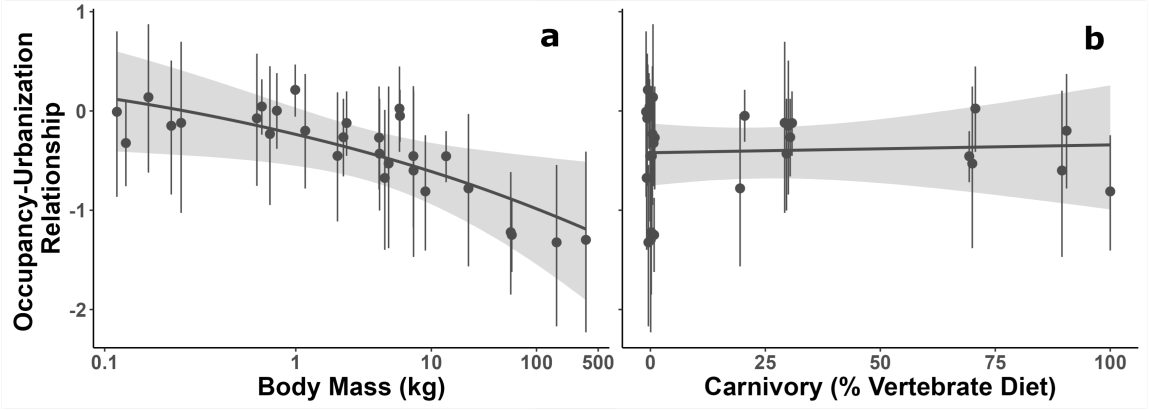

Figure 3.3: Influences of two species traits on within-city relationships between urbanization and mammal occupancy in North America. **a**, body mass, represented by the log-transformed mean body mass of each species (in kg). **b**, carnivory, calculated as the percentage of vertebrate prey in each species' diet. Each point and bar respectively represent the mean and 95% Bayesian credible interval (CRI) of estimated responses to urbanization for 29 commonly detected mammal species (excluding eight species detected in fewer than 10 days total). Trendline and shaded region depict the median and 95% CRI of response variables predicted across a hypothetical range of trait values. Results primarily demonstrate that larger-bodied species had more negative relationships with urbanization.

Table 3.1: Effects of local and regional environmental predictors on local community-average occupancy and regional species richness. We estimated standardized effects using a Bayesian multi-city community occupancy modeling approach across 725 sites in 20 North American cities, depicting the modeled effect of each set of predictor variables on each response variable by calculating means (β_{mean}) and 95% Bayesian credible intervals (CRI) across each effect parameter's posterior distribution. We measured the response variable local community-average occupancy as the average probability of site use among the mammal community and quantified regional species richness using the probability of the average species being present within each city (the proportion of a city's potential regional species pool that was present). We grouped effects into one of five types based on the spatial scale(s) at which they were assumed to operate, as depicted in Figure 3.1. Modeled effects included cross-scale interactions (Figure 3.1, Effect Type 4), the combined effects of regional environmental predictors and local urbanization on local community characteristics (i.e., average species occupancy; Figure 3.2a-c). Because of the inclusion of interaction terms, local urbanization effects (Figure 3.1, Effect Type 1) indicate the effects predicted at the average level of all other interacting variables (regional environmental predictors and species traits). We additionally represent the probability that a substantial relationship was detected between each predictor and response variable using the *f-statistic*, the percentage of each effect parameter's Bayesian posterior distribution that shared a sign (positive or negative) with the mean of the distribution.

Response Variable	**Predictor Variable(s)**	**Effect Type**	β_{mean}	**95% CRI (lower, upper)**	**f-statistic**
Local Community-average Occupancy	Local Urbanization	1	-0.41	-0.68, -0.17	100.0%
	Local Patch Density	1	0.08	-0.06, 0.21	87.1%
	Local Agricultural Footprint	1	-0.15	-0.31, 0.00	97.5%
	Regional Greenness	3	0.24	-0.09, 0.57	92.4%
	Regional Temperature	3	-0.19	-0.51, 0.12	89.3%

Response Variable	**Predictor Variable(s)**	**Effect Type**	β_{mean}	**95% CRI (lower, upper)**	**f-statistic**
	Regional Urbanization	3	-0.29	-0.57, -0.02	98.1%
	Regional City Age	3	0.19	-0.20, 0.56	84.5%
	Regional Greenness X Local Urbanization (Interaction)	4	0.12	-0.08, 0.31	88.4%
	Regional Temperature X Local Urbanization (Interaction)	4	-0.13	-0.38, 0.11	86.4%
	Regional Urbanization X Local Urbanization (Interaction)	4	-0.01	-0.17, 0.15	54.7%
	Regional City Age X Local Urbanization (Interaction)	4	-0.06	-0.26, 0.15	73.2%
Regional Species Richness	Regional Greenness	2	-0.08	-0.28, 0.12	78.1%
	Regional Temperature	2	-0.01	-0.19, 0.18	52.1%
	Regional Urbanization	2	-0.01	-0.19, 0.16	56.6%
	Regional City Age	2	-0.06	-0.27, 0.14	71.5%

Table 3.2: Effects of local and regional environmental predictors on local community composition. We estimated standardized effects using a Bayesian meta-analysis based on local species richness and diversity values derived from a multi-city community occupancy model across 725 sites in 20 North American cities, depicting the modeled effect of each set of predictor variables on each response variable by calculating means (β_{mean}) and 95% Bayesian credible intervals (CRI) across each effect parameter's posterior distribution. The response variable local species richness indicated the total number of species at each site (Hill Number 0), and local species diversity represented the effective number of species at each site accounting for species evenness (Hill Number 1; the exponentiated Shannon index), where sites with the greatest diversity were characterized by both high richness and evenness. Effects were grouped into one of five types based on the spatial scale(s) at which they were assumed to operate, as depicted in Fig. 3.1. Modeled effects included cross-scale interactions (Fig. 3.1, Effect Type 4), the combined effects of regional environmental predictors and local urbanization on local community composition (i.e., species richness and diversity; Fig. 3.2d-i). Because of the inclusion of interaction terms, local urbanization effects (Fig. 3.1, Effect Type 1) indicate the effects predicted at the average level of all other interacting variables (regional environmental predictors). We represented the probability that a substantial relationship was detected between each predictor and response variable using the *f-statistic*, the percentage of each effect parameter's Bayesian posterior distribution that shares a sign (positive or negative) with the mean of the distribution

Response Variable	**Predictor Variable(s)**	**Effect Type**	β_{mean}	**95% CRI (lower, upper)**	**Effect Probability**
Local Species Richness	Local Urbanization	1	-0.11	-0.14, -0.08	100.0%**
	Local Patch Density	1	0.01	-0.02, 0.04	71.8%
	Local Agricultural Footprint	1	-0.02	-0.05, 0.01	88.2%
	Regional Greenness	3	0.12	0.09, 0.16	100.00%
	Regional Temperature	3	-0.04	-0.07, 0.01	99.2%

Response Variable	**Predictor Variable(s)**	**Effect Type**	β_{mean}	**95% CRI (lower, upper)**	**Effect Probability**
Local Species Diversity	Regional Urbanization	3	-0.05	-0.08, -0.03	100.0%
	Regional City Age	3	0.02	-0.01, 0.06	91.6%
	Regional Greenness X Local Urbanization	4	0.09	0.06, 0.12	100.0%
	Regional Temperature X Local Urbanization	4	-0.04	-0.07, -0.06	100.00%
	Regional Urbanization X Local Urbanization	4	-0.03	-0.05, 0.00	96.6%
	Regional City Age X Local Urbanization	4	-0.01	-0.04, 0.03	63.6%
	Local Urbanization	1	-0.08	-0.10, -0.07	100.0%
	Local Patch Density	1	0.00	-0.02, 0.01	76.4%
	Local Agricultural Footprint	1	-0.05	-0.07, -0.04	100.0%
	Vegetation Greenness	3	0.02	0.00, 0.03	98.5%
	Mean Annual Temperature	3	-0.02	-0.03, 0.00	99.2%
	Regional Urbanization	3	-0.02	-0.04, -0.01	100.0%

Response Variable	**Predictor Variable(s)**	**Effect Type**	β_{mean}	**95% CRI (lower, upper)**	**Effect Probability**
	Regional City Age	3	-0.02	-0.03, 0.00	97.5%
	Regional Greenness X Local Urbanization	4	0.05	0.03, 0.07	100.0%
	Regional Temperature X Local Urbanization	4	-0.02	-0.04, -0.01	99.9%
	Regional Urbanization X Local Urbanization	4	-0.01	-0.02, 0.00	97.2%
	Regional City Age X Local Urbanization	4	0.01	-0.01, 0.02	75.2%

3.4 Discussion

Predicting how human development impacts biodiversity requires examining how communities have assembled under the influence of both fine-and broad-scale environmental factors and species traits. Here we tested for such patterns with a novel multi-city modeling approach and biodiversity data spanning North American biomes. As we hypothesized, local mammal communities varied substantially across gradients of human landscape change (Faeth *et al.*, 2011; Norton *et al.*, 2016; Fidino *et al.*, 2020; Magle *et al.*, 2021), and the broad environmental characteristics of cities shaped differences in how local communities related to urbanization (Aronson *et al.*, 2014; Beninde *et al.*, 2015; Norton *et al.*, 2016), with urbanization demonstrating stronger negative influences on communities within warmer, less vegetated cities. Furthermore, effects of urbanization on species presence were mediated by key life history traits (Suraci *et al.*, 2021). Overall, these results emphasize how urbanization's effects on biodiversity are locally and regionally driven, dependent on how environmental conditions and species traits interact with one another to influence community assembly processes across spatial scales (Aronson *et al.*, 2016).

To maintain diverse ecological communities in an urbanizing world, it is important to consider how different types of human activities can affect local community composition across spatially heterogeneous landscapes. Urbanization is widely regarded as a foremost threat to biodiversity, as species presence, richness, and diversity typically have strong negative associations with habitat losses due to urban development (Marzluff, 2001; Shochat *et al.*, 2010; Norton *et al.*, 2016). Across levels of urbanization, additional anthropogenic landscape changes such as agricultural land use and habitat fragmentation can either mitigate or exacerbate the effects of development on community composition (Wu *et al.*, 2011; Forman, 2014a; Moll *et al.*, 2019;

Padilla and Sutherland, 2019). These additional components of the human footprint may affect species richness, evenness, or both. High amounts of agricultural land may be more strongly associated with lower species diversity than with lower species richness, as the habitat heterogeneity created by moderate landscape cultivation can support coexistence among greater numbers of species (Boron *et al.*, 2019). Similarly, natural patch and edge density, proxy measures of habitat fragmentation and landscape heterogeneity that tend to vary most in moderately urbanized areas (Wu *et al.*, 2011; Forman, 2014a), may be either positively or negatively associated with richness (Fahrig, 2020; Regolin *et al.*, 2020; Martin *et al.*, 2021). More fragmented landscapes can also favor edge-tolerant, generalist species, reducing evenness and further complicating relationships between landscape heterogeneity and community composition (Marzluff, 2001; Fahrig, 2003; Shochat *et al.*, 2010). Finally, the effects of human activity on wildlife communities extend beyond changes to landscape structure, as the spatial distributions of wildlife communities can be directly influenced by variation in human presence (e.g., recreational activity) and other behaviors (e.g., wildlife feeding, yard management) across landscapes (Andrade *et al.*, 2020; Avolio *et al.*, 2021; Lerman *et al.*, 2021; Lewis *et al.*, 2021). Future research could further characterize these diverse relationships among landscape heterogeneity, human activity, and community composition by considering how those relationships may vary according to the regional characteristics of urban systems.

The broader bioclimatic characteristics of cities may have greater influence on local wildlife communities than they do on regional patterns of biodiversity. Contrary to our predictions, differences in regional mammal species pools among cities were not associated with continent-wide bioclimatic gradients of vegetation greenness and temperature, but those regional characteristics did influence the degree to which mammal populations and communities varied across local urbanization gradients. For instance, compared to species in cooler cities (e.g., Salt Lake City, Utah), species in warmer cities (e.g., Los Angeles, California) exhibited stronger negative relationships with urbanization, which further reduced local species richness and diversity at higher levels of urbanization. These apparent temperature-driven differences in urbanization effects may result, in part, from associations between temperature and other ecological characteristics that make cities from different ecoregions distinct, such as vegetation type, structure, and evapotranspiration. Urban heat island effects (i.e., increased temperatures in highly urbanized areas, compared to wildlands) may additionally be greater in warmer cities (Hall *et al.*, 2016). Particularly for endothermic species like mammals, combined increases in temperature and urbanization can negatively impact health and survival (Ouyang *et al.*, 2018; Hantak *et al.*, 2021). Conversely, cities with greener vegetation (which also tend to have higher mean annual precipitation; e.g., Sanford, Florida) were more likely than less vegetated, drier cities (e.g., Phoenix, Arizona) to support a richer, more diverse mammal community at greater levels of urbanization. Negative urbanization impacts may be mitigated in greener, wetter cities because species there have greater access to limited resources like food, water, and refugia from predators associated with greater vegetation and precipitation (Bateman *et al.*, 2015b; Fidino *et al.*, 2020). Overall, these results highlight how the ability to effectively mitigate the local impacts of urbanization on biodiversity across diverse biomes may be inextricably linked with interacting regional bioclimatic patterns.

Wildlife community responses to urbanization may further depend upon the unique sociocultural processes that characterize different cities. For example, local species diversity tended to be greater across sites within more recently developed and less urbanized cities within our study (e.g., Salt Lake City, Utah; Iowa City, Iowa), suggesting that the growth of cities has incurred local extinction debts that are still being realized in the form of gradual losses in local biodiversity(Crooks and Soulé, 1999; Aronson et al., 2014; Norton et al., 2016; Fidino et al., 2020). Despite potential mechanistic connections between overall age of a city and local species extinction and colonization processes(Norton et al., 2016), city age has uncertain relationships with biodiversity(Aronson et al., 2014), potentially due to cities growing more rapidly during different historical periods. Regardless of their overall ages, cities that have been more intensively built – either outward (via urban sprawl) and upward (via urban densification) – tend to be those in which human landscape changes most strongly impact biodiversity(Aronson et al., 2014; Fidino et al., 2020). These biophysical landscape characteristics that drive differences in biodiversity relationships among cities are additionally influenced by heterogeneous socioeconomic processes, including those associated with past and present distributions of wealth and social inequities(Schell et al., 2020; Magle et al., 2021). Understanding what makes a city more supportive of biodiversity persistence requires further recognition of how the complex human decision-making processes variably structure urbanizing landscapes and wildlife community patterns(Aronson et al., 2016; Nilon et al., 2017; Apfelbeck et al., 2020; Rega-Brodsky et al., 2022), bridging human histories with the natural histories of wildlife.

Species' functional traits can also influence how landscape change shapes wildlife communities. In particular, larger-bodied mammal species responded more negatively to urbanization, as was expected (McKinney, 2002; Suraci *et al.*, 2021). Although the greater mobility of larger species can enable them to better access anthropogenic resources across fragmented landscapes (Riley *et al.*, 2010; Gese *et al.*, 2012), those species are also generally more sensitive to urbanization-driven habitat losses due their greater space needs, lower reproductive rates, and increased persecution by humans (Crooks and Soulé, 1999; Kelt and Van Vuren, 1999; McKinney, 2002; Bateman and Fleming, 2012; Suraci *et al.*, 2021). While obligate carnivores (e.g., bobcats, mountain lions) are often regarded as being intolerant of urban environments (Riley *et al.*, 2010; Suraci *et al.*, 2021), more strictly carnivorous diets are not necessarily associated with more negative responses to urbanization. This may be because more carnivorous species are most frequently represented by generalist predators (e.g., coyotes, foxes, raccoons), whose flexible, omnivorous diets enable them to exploit anthropogenic resources in urban environments(Bateman and Fleming, 2012). As such, herbivores with more specialized diets may also be particularly sensitive to urbanization and other species traits such as dietary flexibility and diversity could provide more effective predictors of human impacts in future studies (Bateman and Fleming, 2012; Rega-Brodsky *et al.*, 2023). It is also important to acknowledge that assessments of functional traits and taxonomic diversity depend upon how wildlife communities were sampled across landscapes, where the use of multiple survey methods (e.g., camera trap, hair traps, live traps) may help future studies to reduce potential biases, such as the under-sampling of smaller-bodied species (De Bondi *et al.*, 2010; Meek *et al.*, 2014). Nevertheless, species functional traits play critical roles in community assembly across urbanization gradients by driving individual species distributions (Aronson *et al.*, 2016), with our results indicating that it is warranted to further examine how variation in species responses to human landscape change are linked with a wider diversity of species traits, and how such patterns vary within and among cities (Rega-Brodsky *et al.*, 2022).

Although we found that the effects of anthropogenic landscape change can vary among species with diverse traits and in relation to environmental conditions at multiple spatial scales, the temporal dimensions of these relationships require further exploration. Our study was focused on the North American summer season, in part because this was the season in which we expected regional bioclimatic variables and local impacts of urbanization to influence mammal communities most strongly across cities. However, intra-annual variations in species- and community-level responses to urbanization warrant additional consideration, as seasonal differences in climate and resource availability can lead to shifts in fine-scale wildlife habitat use and community composition across urbanization gradients (de Albuquerque *et al.*, 2021). For instance, during winter seasons, urban environments within colder cities may become more suitable for certain species, due to year-round anthropogenic resource provisioning and urban heat island effects counteracting the climate-driven extremes of the surrounding natural environments, providing food and thermal refugia that increase species survival (Kanda *et al.*, 2009). Furthermore, the usage of human-dominated environments by wildlife communities can vary significantly across years, driven changes in human land use/land cover and fluctuations in resource availability and human activity (Bates *et al.*, 2021; de Albuquerque *et al.*, 2021; Lewis *et al.*, 2021; Suraci *et al.*, 2021; Wilmers *et al.*, 2021; Anderson *et al.*, 2023). Although we controlled for confounding effects of interannual variation in wildlife community drivers in our analyses, evaluating temporal dynamics was beyond the scope of this study. Important next steps include examination and understanding of how wildlife communities vary in relation to changing landscapes and climates through time (Ramalho and Hobbs, 2012).

To conserve biodiversity in a rapidly-changing world, we must consider how wildlife communities respond to human-caused landscape change across local and regional scales. We specifically found that species richness and diversity at local scales can demonstrate varying responses to urbanization that depend on broad-scale climatic factors, reflecting the potential for synergistic effects between multiple drivers of global biodiversity loss (Mazor *et al.*, 2018; Newbold *et al.*, 2020; Rega-Brodsky *et al.*, 2022). For example, mammal species and communities in warmer, less vegetated cities appeared to be more negatively affected by urbanization, which could have implications for how biodiversity is impacted by a warming climate (Huang *et al.*, 2019; Santos *et al.*, 2021; Pörtner *et al.*, 2022). However, there are other key differences in warmer and greener cities that can drive these patterns (e.g., biome characteristics, vegetation communities, water availability, size of the regional species pool), and future studies could further explore potential mechanisms underlying these cross-scale relationships (Mazor *et al.*, 2018; Rega-Brodsky *et al.*, 2022). Likewise, when comparing the different results of past urban ecological studies, it is imperative to consider the broader context of the regional environment that includes, but is not limited to, climate and vegetation (Fidino *et al.*, 2020).

Interactions between urbanization and broad-scale environmental gradients suggest it is important to prioritize biodiversity loss mitigation measures differently among cities with distinct biophysical characteristics and regional species pools (Norton *et al.*, 2016; Iwaniec *et al.*, 2021; Santos *et al.*, 2021; Pörtner *et al.*, 2022). For instance, in warmer cities, it might be more important to provision thermal refuges and water resources for wildlife, with particular consideration given to the needs of species most sensitive to the combined impacts of urbanization and climate (Fischer *et al.*, 2015; Apfelbeck *et al.*, 2020). Effectively protecting biodiversity from the impacts of landscape change necessitates that ecological understanding of human-modified habitats be more thoroughly integrated into landscape design processes(Nassauer and Opdam, 2008; Parris *et al.*, 2018; Apfelbeck *et al.*, 2020). Toward this end, identifying key areas in which region-specific conservation priorities align with existing human-centered urban sustainability goals and management practices should be a priority for future research (Nilon *et al.*, 2017). Finally, we emphasize that research networks spanning multiple cities and continents can identify interconnected biodiversity threats and offer new recommendations to mitigate the impacts of global change (Magle *et al.*, 2019; Iwaniec *et al.*, 2021; Rega-Brodsky *et al.*, 2022). Leveraging such broad transdisciplinary networks can lead to the development of climate-conscious urban conservation strategies that enable declining species and communities to better persist in an increasingly human-dominated world.

Chapter 4

SOCIAL-ECOLOGICAL DRIVERS OF METROPOLITAN RESIDENTS′ COMFORT LIVING NEAR WILDLIFE

4.1 Introduction

With a growing majority of humanity living within cities and towns, metropolitan areas have emerged as critical environments for investigating and managing human interactions with nature. The expansion of human development into natural environments has placed humans and wildlife into increasing degrees of co-occurrence and contact, particularly in suburban and exurban neighborhoods where the activities of people and wildlife tend to overlap most frequently (DeStefano and DeGraaf, 2003; McKinney, 2008; Magle *et al.*, 2016). The outcomes of these human-wildlife encounters and other nature experiences are highly variable across urbanizing landscapes, where spatially heterogeneous social and environmental processes strongly shape people's environmental attitudes (Soga *et al.*, 2016; Soulsbury and White, 2019), including their support for biodiversity conservation and their comfort living among different wildlife species. People's varying wildlife attitudes help predict the positive and negative impacts of wildlife interactions (Kansky *et al.*, 2016; Larson *et al.*, 2023), as well as people's behavioral changes toward wildlife (Manfredo, 2008a). As such, understanding wildlife attitudes, and how those attitudes are shaped by both human and environmental dynamics, is important for predicting the potential for human-wildlife conflict and co-existence within urbanizing environments (Parris *et al.*, 2018; Apfelbeck *et al.*, 2020; Bhatia, 2021).

Although research exploring human-wildlife interactions has rapidly expanded in recent years, studies of coexistence have been limited by the emphasis placed on conflicts with certain problematic species (e.g., carnivores), over positive interactions with diverse wildlife communities, in addition to lacking attention to the interactions occurring within heterogeneous urbanized contexts (Hudenko *et al.*, 2010; Reidinger and Miller, 2013; Soulsbury and White, 2015). Beyond conflicts, interactions can positively affect the well-being of both human and wildlife, with the characteristics and behaviors of people and wildlife species shaping people's perceptions of and attitudes towards wildlife (Díaz *et al.*, 2018; Avolio *et al.*, 2021; Bhatia, 2021). Since variation in attitudes may be particularly pronounced across socially and ecologically heterogenous urbanized landscape (Soulsbury and White, 2019), research is needed to quantify variation in and drivers of metropolitan residents' attitudes toward particular wildlife groups, which can signal the potential for coexistence based on varying levels of tolerance, acceptance, and appreciation.

In this study, we examined an array of social-ecological influences on metropolitan residents' comfort living near three groups of native mammalian wildlife – coyotes (*Canis latrans*), foxes (including gray fox, *Urocyon cinereoargenteus* and kit fox, *Vulpes macrotis*), and rabbits (including desert cottontail rabbit, *Sylvilagus audubonii*, and black-tailed jackrabbit, *Lepus californicus*). Specifically in diverse neighborhoods of the Phoenix Metropolitan Area, Arizona, USA (Larson *et al.*, 2022a), we combine social survey data and location-based environmental features to answer the question: how do ideological, environmental, and sociodemographic factors differently affect residents' varied comfort levels living with three wildlife? We generally expected that comfort around each wildlife group would be most strongly associated with ideological factors, including individuals' wildlife value orientations and attachment to the local desert environment (Manfredo, 2008b,c). We further expected that comfort would be mediated by environmental and sociodemographic factors that influence either the frequency with which residents are likely to interact with these three wildlife groups or the ways in which residents perceive the risks associated with wildlife.

4.2 Literature Review

While attitudes affect human-wildlife coexistence, the ultimate interactions between people and wildlife are shaped by a combination of personal, environmental, and social factors, along with the characteristics of specific wildlife. As detailed below, the relative influence of exposure to nature on attitudes toward diverse urban wildlife is poorly understood.

4.2.1 Conceptualizing Coexistence

The concept of coexistence has recently emerged in the literature as a more holistic means of framing human-wildlife interactions in terms of both its positive and negative aspects (Bhatia, 2021; Pooley *et al.*, 2021). Reflecting a trend away from a focus on conflict as the primary aspect of coexistence, Pooley et al. define human-wildlife coexistence as "a sustainable though dynamic state in which humans and wildlife co-adapt to sharing landscapes, where human interactions with wildlife are effectively governed to ensure wildlife populations persist in socially legitimate ways that ensure tolerable risk levels." (2021, pg. 784). Conceptualizations of coexistence vary from this general definition depending on how the research context relates to the concepts of conflict, tolerance, acceptance, and stewardship (Glikman *et al.*, 2021). However, various perspectives of human-wildlife coexistence similarly acknowledge the presence of, or potential for, both negative coexistence (e.g., tolerance or acceptance of conflict) and positive coexistence (e.g., appreciation and stewardship; Bhatia, 2021; Hill, 2021) .

Research has shown that factors supporting coexistence depend partly upon the characteristics of the wildlife that shape those interactions (Hudenko *et al.*, 2010). Discomfort around wildlife perceived as more hazardous to people (e.g. large carnivores, venomous animals) can signify the potential for conflict and the need to reduce risks to tolerable levels (Bateman *et al.*, 2021; Carter and Linnell, 2016; Hadidian, 2015; Hill, 2021; Reidinger and Miller, 2013). Furthermore, levels of risk tolerance and acceptance vary substantially among people, with differences serving as fundamental sources of human-human conflict over how best to manage coexistence (Peterson *et al.*, 2010; Lute and Gore, 2019; Hill, 2021). Much of the current literature on human-wildlife coexistence has focused on large mammalian carnivores in more rural environments (Soulsbury and White, 2019; Larson *et al.*, 2023). Research has centered on fear as the primary emotive response (Jacobs and Vaske, 2019) and on cognitive beliefs about risks and impacts on people (Soulsbury and White, 2015; Bhatia, 2021). However, relatively few studies have directly addressed how attitudes toward wildlife depend upon the actual co-occurrence of humans and different wildlife species (i.e., their shared use of a space at a given point in time), the levels of which are expected to vary greatly across spatially heterogeneous urban environments (Soulsbury and White, 2019).

Conversely, comfort around wildlife regarded as less harmful to people can indicate the potential for positive forms of human-wildlife coexistence (adoration, appreciation, and stewardship), rather than risk tolerance (Bhatia, 2021; Larson *et al.*, 2023). Yet studies directly measuring such positive outcomes of human-wildlife interactions have been limited, especially within relatively urbanized settings where positive encounters with wildlife may have the greatest benefit for residents lacking frequent nature experiences (Soulsbury and White, 2015; Soga *et al.*, 2016). Within urbanized environments, fewer large mammal species and residents' lack of dependence on livelihoods directly impacted by wildlife (e.g., subsistence agriculture, livestock ranching) may result in fewer negative interactions and concerns from interacting with wildlife across more urbanized landscapes (Bateman and Fleming, 2012). Consequently, interactions with wildlife within metropolitan regions may have the potential to be more positive than in more rural settings, potentially producing greater benefits to residents' mental and spiritual well-being (Methorst *et al.*, 2020; Larson *et al.*, 2023). As such, previous research has suggested that managing for coexistence with diverse wildlife communities will require the simultaneous consideration of multiple types of coexistence (Glikman *et al.*, 2021), especially within urbanized contexts.

4.2.2 Ideological Factors in Coexistence

Previous research has shown that an individual's wildlife attitudes – defined as positive or negative judgments toward wildlife – are primarily shaped by subjective cognitive and affective judgments, including people's environmental value orientations or ecological worldviews (Dunlap *et al.*, 2000). In particular, attitudes toward wildlife are typically reflective of an individual's wildlife value orientations, which include people's basic beliefs (also known as worldviews) regarding how people should interact with wildlife (Fulton *et al.*, 1996; Manfredo, 2008c). Mutualistic dimensions of wildlife value orientations incorporate individuals' beliefs relating to the value of wildlife protection and coexistence, signaling the potential for positive attitudes toward wildlife presence and persistence and reflecting appreciation-oriented concepts of human-wildlife coexistence (Teel and Manfredo, 2010; Glikman *et al.*, 2021). In contrast, utilitarian dimensions of wildlife value orientations involve beliefs in human domination over and benefits from wildlife, reflecting anthropocentric worldviews that may drive distinct attitudes toward human-wildlife coexistence (Teel and Manfredo, 2010; Kaltenborn and Linnell, 2022). Although these domination-oriented wildlife values have been traditionally widespread across North America, their prevalence has also gradually decreased in recent decades, aligned with broader sociocultural shifts toward biocentric mutualism often linked with increasingly urban livelihoods (Manfredo *et al.*, 2016, 2020; Dietsch *et al.*, 2019).

Perceptions of human-wildlife interactions and attitudes toward wildlife are further a function of individuals' affective judgements about those wildlife and their environment, including place identity and emotional dispositions toward different types of animals (Jacobs and Vaske, 2019; Williams and Vaske, 2003; Manfredo, 2008b). Understanding people's place identities, or emotional attachments, is fundamental to interpreting how their attitudes toward their environments form (Williams and Vaske, 2003). Previous research has shown that wildlife themselves can help create and reinforce emotional attachments to place, particularly when wildlife-based experiences align with individuals' pro-wildlife dispositions (Anderson and Fulton, 2008; Folmer *et al.*, 2013). The place-dependent outcomes of human-nature interactions can subsequently affect human attitudes and behaviors, with both functional and emotional place attachments being positively linked with support for civic conservation actions and concern for recreational impacts on wildlife (Payton *et al.*, 2005; Eder and Arnberger, 2012). However, such studies of associations among place attachment and wildlife attitudes are limited, with very few considering how urbanization may alter place identity and its related environmental attitudes (Andrade *et al.*, 2019; Warren *et al.*, 2019).

4.2.3 Environmental Factors in Coexistence

The characteristics of a person's surrounding natural environment can influence their comfort living around wildlife, particularly by shaping the degree to which that person is exposed to nature and the likelihood with which they have personal experience with wildlife (Soulsbury and White, 2019). The direct and indirect effects of environmental characteristics on wildlife attitudes can vary considerably, depending on how they influence the frequency of human-wildlife interactions, the positive or negative nature of the interactions, and the type of wildlife species involved (Kansky and Knight, 2014). For instance, increased encounters with wildlife that present moderate-to-low risks to human well-being (e.g., coyotes, foxes, and other mid-sized carnivores) may make residents more familiar with the hazards associated with those species (Soulsbury and White, 2019; Nardi *et al.*, 2020), thereby reducing perceived risks and encouraging co-existence (Slovic, 1987; Zaradic *et al.*, 2009). However, positive effects of wildlife exposure on attitudes may be most readily observed for species that are seen as benign and desirable (e.g., rabbits and other small herbivores), but not detected for wildlife that pose more direct threats to human well-being (e.g., venomous snakes and larger carnivores; Bateman and Fleming, 2012; Dickman, 2010; Kansky and Knight, 2014; Reidinger and Miller, 2013). For instance, attitudes toward coyotes, as a widespread, medium-sized carnivore found across North American cities, can vary greatly as a result of people's experiences, which range from positive encounters that elicit appreciation coyotes and encounters with negative outcomes such as loss of pets and rare attacks on people (Gehrt and Riley, 2010; Alexander and Quinn, 2011; Poessel *et al.*, 2017). The role of environmental characteristics in shaping attitudes toward human-wildlife coexistence within urban environments, especially relative to attitudinal and sociodemographic factors, remains unclear.

4.2.4 Sociodemographic Factors in Coexistence

Lastly, attitudes toward wildlife are partially dependent upon an individual's personal and social characteristics, especially those associated with emotional responses to wildlife and vulnerability to environmental risks (Kansky and Knight, 2014; Pooley, 2021). For one, the safety of pets and other domestic animals (e.g., livestock) is a commonly cited risk associated with wildlife, with an individual's ownership of pets having the potential to decrease tolerance of carnivores (Hudenko *et al.*, 2010; Poessel *et al.*, 2013). However, pet ownership has more often been found to be associated with positive attitudes toward wildlife tolerance and stewardship (Shuttlewood *et al.*, 2016; Greenspan *et al.*, 2021), reflecting people's biophilic dispositions toward both wild and domestic animals (Kellert, 1985; Larson *et al.*, 2023).

Furthermore, difference in attitudes associated with wildlife and other sources of environmental risk are often aligned with individual's personal identities, particularly gender (Davidson and Freudenburg, 1996). For instance, previous research has indicated that people identifying as female may express greater safety concerns due to the presence of dangerous wildlife species (Zinn and Pierce, 2002). Conversely, women have also indicated positive attitudes toward wildlife more consistent with mutualistic and protectionist ideologies (Kellert and Berry, 1987), further indicating that gender identity is a key sociodemographic factor to consider in the examination of attitudes related to human-wildlife coexistence.

The formation of varying attitudes toward wildlife may be mediated by additional personal and social characteristics and identities that are associated with people's environmental worldviews and attitudes (e.g. ethnicity, class; Andrade et al., 2019; Grove and Burch, 1997; Larson et al., 2016). Subsequently, differences in ecological worldviews among ethnic or social groups have been documented as having varying relations with environmental risks (Larson et al., 2011, 2016). For instance, mutualistic worldviews rooted in Hispanic cultural traditions have been found to be fundamental factors in understanding opposition to lethal wildlife control in Tucson, Arizona, USA (Dietsch et al., 2012, 2019; Chase et al., 2016).

Income and education, as measures of affluence and knowledge, respectively, are widely recognized as driving access to experiences with wildlife and natural environments (Nilon, 2014; Andrade *et al.*, 2019). Greater access to positive nature experiences is subsequently associated with decreasing peoples' perceived exposure to environmental risks and increasing benefits from nature (Van Velsor and Nilon, 2006; Andrade *et al.*, 2019; Larson *et al.*, 2023). The cultural contexts within which people interact with wildlife and for attitudes toward human wildlife coexistence are further shaped by factors such as race, ethnicity, gender, and age (Van Velsor and Nilon, 2006; Nilon, 2014; Pooley, 2021). Examination of attitudes toward wildlife needs to account for social-demographic variation in how interactions with wildlife are perceived.

4.2.5 Hypotheses

Based on current understanding of factors contributing to human-wildlife coexistence, we hypothesized that attitudes toward different wildlife species groups would be variably associated with ideological, environmental, and social factors. Specifically, we predicted that residents living in places where wildlife are more likely to be present are expected to be associated with either (a) increased familiarity with those species, and therefore, increased comfort; or (b) increased perceived risk from wildlife due to proximity and, therefore, reduced comfort. Furthermore, we expected that these potential associations between attitudes and environmental factors would be strongest for those wildlife that are generally perceived as more hazardous to people or domestic animals (i.e. coyotes and foxes). Conversely, we predicted that attitudes toward less hazardous wildlife (i.e. rabbits) would be most clearly associated with attitudinal factors and certain sociodemographic factors, such as pet ownership.

4.3 Methods

4.3.1 Study System

The Phoenix-Mesa-Scottsdale metropolitan area (i.e., metro Phoenix) is located within the Sonoran Desert of the southwestern USA. Situated in central Arizona, metro Phoenix is the fourth most rapidly growing metropolitan area in the USA, with a current population of roughly 4.8 million. A significant portion (32%) of the population is Hispanic/Latino (32%; Bureau, 2021). Historical patterns of urbanization within metro Phoenix have had widespread impacts on both social and ecological processes contributing to human-wildlife coexistence. Specifically, the sprawling outward growth of cities has surrounded and isolated remnants of desert within a matrix of human development and agriculture, putting certain residents in closer proximity to the desert parks and preserves (Andrade *et al.*, 2019). For instance, previous research in the region has shown that how close residents live to these desert parks tend to be wealthier, have more positive attitudes toward the desert, and experience higher wildlife diversity and greater ecosystem services (Andrade *et al.*, 2019; Brown, 2020; Warren *et al.*, 2019).

The region's hot, semi-arid desert environment features natural vegetation communities that are predominantly composed of shrubland species, including palo verde (*Parkinsonia* spp.), mesquite (*Prosopis* spp.), creosote bush (*Larrea tridentata*), brittlebush (*Encelia farinosa*), and saguaro (*Carnegiea gigantea*). In contrast, the urban and suburban areas of the region are relatively lush, with higher levels of vegetation productivity and cover traditionally maintained by an extensive irrigation canal system (Buyantuyev and Wu, 2009; Larson *et al.*, 2009). The region also hosts relatively high regional diversity of mammals, birds, reptiles, and amphibians within urban, suburban, and natural environments (Banville *et al.*, 2017; Bateman *et al.*, 2015b;

Jenkins *et al.*, 2015), with the neighborhoods of metro Phoenix utilized by a variety of iconic desert wildlife species, such as coyotes, desert cottontail rabbit, javelina (*Pecari tajacu*), jackrabbits (*Lepus* sp.), gray fox, kit fox, roadrunners (*Geococcyx californianus*), rattlesnakes (*Crotalus* spp.) and Gambel's quail (*Callipepla gambelii*). Patterns of development and local vegetation and habitat management within and near neighborhoods affect the spatially distribution of wildlife species across residential landscapes, as well as the frequency with which those species interact with people and the need to manage human-wildlife coexistence (Bateman *et al.*, 2021).

4.3.2 Study Species

We focused this study on three mammal species – rabbits, foxes, and coyotes – whose varying size and behavior produce different levels of potential danger to residents, their domestic animals, and their livelihoods. Two species of rabbits are known to commonly occur in natural and urbanized areas of metro Phoenix: the desert cottontail rabbit and the black-tailed jackrabbit. Although human interactions of rabbits in North America generally range between positive and benign (Long *et al.*, 2020), negative attitudes toward co-existence rabbits can result from their damage to crops and residential landscaping and potential spread of zoonotic diseases (Abu Baker *et al.*, 2015; Simes *et al.*, 2015). Although two species of foxes occur in metro Phoenix, only the gray fox is frequently observed in suburban and urban neighborhoods, while the kit fox typically occurs in undeveloped, flat desert areas. Interactions with and perceptions of foxes are generally expected to be more negative than those rabbits, as foxes can present real and perceived threats to the safety of domestic animals, including small pets and chickens, even though threats to humans are minimal (Hudenko *et al.*, 2010; Soulsbury and White, 2015; Nardi *et al.*, 2020). The coyote is widely distributed throughout the study area but is encountered most frequently in the region's desert parks and their surrounding neighborhoods. Due to their larger size and opportunistic behaviors, coyotes are regarded as presenting a greater danger to domestic animals than foxes, while also potentially threatening the safety of people (Soulsbury and White, 2015; Poessel *et al.*, 2017; Nardi *et al.*, 2020).

4.3.3 Sampling Design and Implementation

In 2021, we surveyed residents of twelve neighborhoods within this study area as part of the Phoenix Area Social Survey (Larson *et al.*, 2022a), which is a long-term study of the Central-Arizona Long-Term Ecological Research (CAP LTER) program (Figure 1). The twelve neighborhoods, delineated by Census Block Groups, were purposively selected to capture variation in sociodemographic characteristics (e.g. income level, ethnicity) and represent a range of local environments (e.g. levels of urbanization, proximity to natural areas). The survey was sent to 1,549 addresses between May and July 2021, with 496 addresses representing households surveyed in a previous (2017) iteration of the survey. An additional 1,053 addresses from the 12 neighborhoods were randomly provided by the Marking Systems Group, which comes from the U.S. Postal Service's Delivery Sequence Files.

University of Northern Iowa's Center for Social and Behavior Research administered the survey via a six-wave mailing, including an advance letter with a link to the online version of the survey, three full questionnaire packets with self-addressed return envelopes, and two reminder postcards sent in-between and after mailings (Larson *et al.*, 2022a). A \$5 cash pre-incentive was included in the first questionnaire packet, regardless of response, and respondents were sent an additional \$25 post-response incentive. The cover letters and postcards informed individuals in Spanish that they could request a Spanish version of the survey via a phone number and email. The third mailed questionnaire included both an English and Spanish version for all households with Hispanic surnames (n = 245). Out of the 1375 successfully delivered surveys, a total of 509 eligible residents participated in the survey, with an overall response rate of 35.6%.

4.3.4 Sample Demographics

Survey respondents and neighborhoods varied in terms of the sociodemographic characteristics of interest in this study (Table 1). For all sociodemographic questions in the survey, respondents were provided with a refuse/prefer not to answer option. Most survey respondents identified their gender as female (62.9%), followed by male (36.7%) and non-binary (0.4%). 63% of respondents reported that they owned either a cat or dog at home. We measured income on an 11-point interval scale by asking respondents to select the median combined income of all household members from a provided list of $20,000 increments, from $20,000 and under (1) to more than $200,000 (11). Similarly, we evaluated level of education by asking respondents to select the highest level of school they have had the chance to complete, which we then quantified on a 7-point interval scale ranging from the completion of grades 1-8 to the attainment of a graduate or professional degree. Measured as such, the median respondent had a household income of approximately $100,000 and at least a community college or vocational school education, with 62% of respondents having completed a bachelor's degree or higher. The average respondent age was 54 years old, which we measured by subtracting the respondent-provided birth year from the year in which the survey was conducted (2021). Regarding race/ethnicity, 68% of respondents identified as White/Anglo, 20% as Hispanic/Latino, 6% as Black/African American, 5% as Asian or Asian American, 1% as Native American or American Indian, and 3% as "other", with multiple responses being provided as an option (Larson *et al.*, 2022a).

4.3.5 Data and Variables

Dependent variables: comfort living near wildlife

We measured our dependent variables representing residents' attitudes toward wildlife on five-point ordinal scale. Specifically, the survey read: "Below is a list of wildlife [coyotes, foxes, rabbits] that live in the greater Phoenix area. Please tell us how comfortable or uncomfortable you would feel seeing the following wildlife in and around where you live." The verbatim response options included: very uncomfortable (1), somewhat uncomfortable (2), neither uncomfortable nor comfortable (3), somewhat comfortable (4) and very comfortable (5). For consistency in terminology, we refer to these reported comfort levels as "comfort living near" each type of wildlife. The explanatory variables in our models include survey data (i.e., for ideological and sociodemographic variables) and geospatial data reflecting environmental variables.

Ideological Explanatory Variables

Our models included two value-based ideological variables to reflect 1) wildlife value orientations (i.e., emphasizing utilitarian benefits and domination versus protection and mutualism) and 2) desert identity (i.e., as a measure of place attachment). First, we measured wildlife value orientations using nine survey items adapted from previous research (Fulton *et al.*, 1996; Manfredo, 2009) that assess different dimensions of basic beliefs about people's relationships with wildlife (Table 4.2). Respondents were asked to rate their level of agreement with a series of statements, with responses ranging from strongly disagree (1) to strongly agree (5) with neutral (3) in the middle. The first three survey items measured value orientations related to respondents' residential wildlife experiences (i.e. their appreciation of wildlife in their local environments; Fulton *et al.*, 1996). The remaining six items, modified from Manfredo et al. (2009), assessed respondents' beliefs regarding human domination of wildlife (i.e. utilitarian uses such as hunting, and lethal population control) and mutualistic beliefs (i.e. values promoting wildlife protection and positive coexistence). We combined these wildlife value orientation scales by inverting responses to the three domination items (items 4-6 in Table 4.2) – so that higher numbers reflected pro-wildlife values – and then averaging all nine items, creating a reliable composite scale of pro-wildlife value orientation (Cronbach's alpha = 0.77).

Environmental Explanatory Variables

We assessed the local environmental conditions experienced by each survey respondent based on environmental variables associated with wildlife presence and residents' access to nature-based experiences, specifically urbanization, vegetation, and distance to desert parks. We measured *urbanization* as the mean percent impervious surface coverage within 1 km of each respondent using data from the 2019 National Land Cover Database (Dewitz, 2021). We quantified *vegetation* using the mean value of Normalized Difference in Vegetation Index (NDVI) within 1 km of each resident, based on 2018 MODIS imagery (de Albuquerque, 2020). We used a 1-km buffer around each respondent since it is a comparable scale to a 10-minute walkshed for people (Larson *et al.*, 2022a; Rigolon, 2016), as well as a typical scale used in analyses of wildlife distributions (McGarigal *et al.*, 2016). Finally, we measured the *distance to desert parks* as the log-transformed Euclidean distance to the nearest park or preserve with predominant natural desert vegetation, which we derived from park boundary data from the Trust for Public Lands (Brown *et al.*, 2021).

Sociodemographic Explanatory Variables

Finally, we used data collected in the 2021 PASS to quantify sociodemographic variables selected for their anticipated roles in mediating the outcomes of human-environment interactions. Specifically, we predicted that the variables *pet ownership* and *gender* may have risk-related effects on comfort living with all three species, since previous research has indicated that pet owners tend to have increased tolerance of wildlife and that men may express lesser safety concerns associated with wildlife (Zinn and Pierce, 2002; Shuttlewood *et al.*, 2016). We coded pet ownership as a binary variable, classifying pet ownerships as 1 and people without pets as 0. For purposes of analysis, we also considered respondent self-reported gender as a binary variable, coded as 0 for male and 1 for female or non-binary, with the latter groups having been combined for the purpose of statistical analysis due to their historically similar socialization as relatively marginalized gender identities.

Additionally, we included the demographic variables of income, education, age, and ethnicity largely as control variables in the analysis. For the ethnicity, we coded a variable for *Latino identity* to reflect whether (1) or not (0) respondents identified as either "Mexican, Mexican-American, Chicano, Hispanic, or Latino". For age, education, and income, the variables included the continuous and ordinal measures described above.

4.3.6 Statistical Analyses

We evaluated the influence of ideological, environmental, and sociodemographic variables on comfort around each wildlife species using generalized linear mixed models (GLMM), which we fit in the R programming language 4.0.1 using the *glmmTMB* package (Brooks *et al.*, 2017; R Core Team, 2020). First, we tested for correlations between each pair of explanatory variables, confirming a lack of bivariate collinearity ($r < 0.5$), and then standardized all continuous explanatory variables and. Secondly, we fit three multivariate GLMMs for each species that included subsets of explanatory variables (i.e., ideological only, environmental only, sociodemographic only) as fixed effects and the neighborhood as a random effect (intercept). Inclusion of the neighborhood random intercept enabled us to account for among-neighborhood variation in attitudes associated with other potential explanatory factors not already incorporated into the model, such as varying number of responses per neighborhood. Thirdly, we fit a global model for each species, with each including all explanatory variables as fixed effects (Eq. 4.1; Figure 4.1). We then used the Akaike Information Criterion (AIC) to compared the relative support of each partial model to that of the global model for each species, with the lowest model AIC indicating the best model with the highest relative quality (Burnham and Anderson, 2002). Finally, we used the R package 'performance' (Lüdecke *et al.*, 2021) and the Variable Importance Factor (VIF) to verify low multi-collinearity ($VIF < 5$) among explanatory variables included within the global models (Table D.1).

$$\begin{multline} Comfort \sim WVO + DesertIdentity \\ + Urbanization + Vegetation + DistanceToDesertParks \\ + Income + Education + Age \\ + PetOwnership + Gender + LatinoIdentity \\ + (1|Neighborhood) \tag{4.1} \end{multline}$$

Table 4.1: Summary statistics of sociodemographic characteristics of metropolitan residents surveyed across twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USA

Explanatory Variable	Mean	SD	Range	Valid N
Gender (female or non-binary)	64.70%		0-100 (% respondents)	499
Pet ownership	62.58%		0-100 (% respondents)	489
Income	5.87	3.34	1-11	483
Education	5.31	1.59	1-7	497
Age	54.28	17.38	18-100	491
Latino Identity	20.40%		0-100 (% respondents)	495

Table 4.2: Summary statistics of sociodemographic characteristics of metropolitan residents surveyed across twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USASummary statistics of wildlife value orientations reported by metropolitan residents surveyed across twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USA. The statements for each survey item reflect verbatim wording on the survey, adapted from Fulton et al. 1996 and Manfredo et al. 2009.’*’ indicates values that were reverse-coded prior to averaging all nine scale items into the single index of ‘Pro-Wildlife Value Orientation’.

Explanatory Variable	Mean	SD	Valid N
Pro-Wildlife Value Orientation (Cronbach’s alpha = 0.77)	3.92	1.11	497
I notice the birds and wildlife around me most days.	4.26	1.03	498
The wildlife I see in and around where I live are important to me.	4.07	1.09	499
Having wildlife around my home is important to me.	4.01	1.12	499
It is acceptable for people to kill wildlife if they think it poses a threat.*	2.68	1.32	498
Wildlife are on earth primarily for people to use.*	1.82	1.00	498
The needs of humans should take priority over protecting wildlife.*	2.48	1.27	496
I want to protect wildlife.	4.26	0.88	493
I care about wildlife as much as I do other people.	3.43	1.27	495
We should strive for a world where humans and wildlife can live side by side.	4.23	0.99	497

Table 4.3: Summary statistics of desert identity reported by metropolitan residents surveyed across twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USA. The statements for each scale item reflect verbatim wording on the survey, adapted from the standardized statements of Williams and Vaske (2003).

Explanatory Variable	Mean	SD	Valid N
Desert identity index (Cronbach's alpha = 0.96)	3.59	1.07	502
I feel the desert parks in the Valley are a part of me.	3.82	1.06	504
The desert parks in the Valley are very special to me.	3.50	1.12	503
I identify strongly with desert parks in the Valley.	3.53	1.17	502
I am very attached to the desert parks in the Valley.	3.76	1.13	503
The desert parks in the Valley mean a lot to me.	3.64	1.11	503

4.4 Results

4.4.1 Variation in Comfort Living Near Wildlife

Respondents' reported comfort living near coyotes, foxes and rabbits varied among the three species and among neighborhoods. On average, respondents felt neutral-to-slightly comfortable near coyotes (mean = 3.13), slightly more comfortable living near foxes (mean = 3.30), and quite comfortable living near rabbits (mean = 4.42; Figure 4.1). 46.1% of respondents reported some level of comfort living near coyotes, as compared to the 48.3% of respondents comfortable around foxes and 82.9% comfortable around rabbits. Conversely, 38.3% of respondents reported being uncomfortable living near coyotes, 31.8% with foxes, and 5.6% with rabbits. 15.6% of respondents reported neutral attitudes toward coyotes, 19.9% were neutral toward foxes, and 11.5% were neutral toward rabbits.

Mean reported comfort living near each species also varied among neighborhoods, ranging between 2.24 and 3.92 for coyotes, 2.50 and 3.89 for foxes, and 3.60 and 4.78 for rabbits. Comfort living near coyotes and foxes was generally highest in higher-income neighborhoods closer to desert parks (Figure 4.2). Comfort also tended to be lower neighborhoods with more residents identifying as Hispanic/Latino and in neighborhoods where wildlife value orientations were generally lower (i.e., more anti-wildlife).

4.4.2 Factors Associated with Comfort Living near Wildlife

The relative associations of ideological, environmental, and sociodemographic factors with residents' reported comfort varied among the global models for each wildlife species, which were more supported lower AIC) than all partial models (Table 4.4). For all three species, pro-wildlife value orientation was the variable most positively associated with comfort – i.e. residents who were more comfortable living near each species tended to have wildlife values that were more mutualistic and less domination-oriented (Table 4.5; Table 4.6; Table 4.7; Figure D.1). We did not detect a significant relationship between comfort living near any species and either desert identity, urbanization, or vegetation. Female respondents and respondents living further from desert parks reported lower comfort living near coyotes and foxes (Figure 4.2a,b). Higher-income respondents were more comfortable living near coyotes (Figure 4.2a), while older respondents were generally less comfortable living near foxes. Comfort near foxes and rabbits was more positive among pet owners and more negative among older and Latino respondents.

Although the most supported model for each species was the global model, certain variables not found to have significant effects in the global model showed significant relationships in the partial model containing that variable, and vice versa (Table 4.8). For instance, pet ownership was positively associated with comfort living near coyotes in the sociodemographic-only partial model, but not in the global model. Conversely, comfort living near foxes was lower among older and Latino respondents in the global model, but not in the partial model.

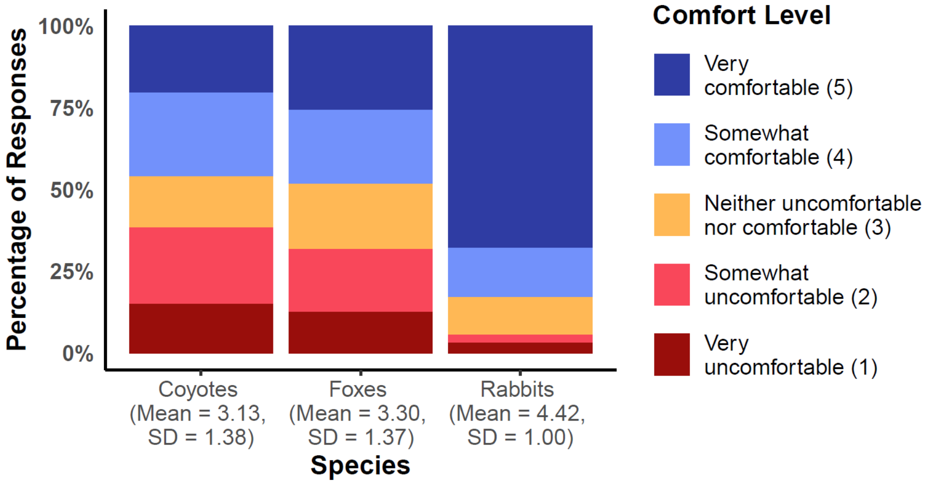

Figure 4.1: Summary of levels of comfort living near three wildlife groups – coyotes, foxes, and rabbits – as reported by metropolitan residents surveyed across twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USA

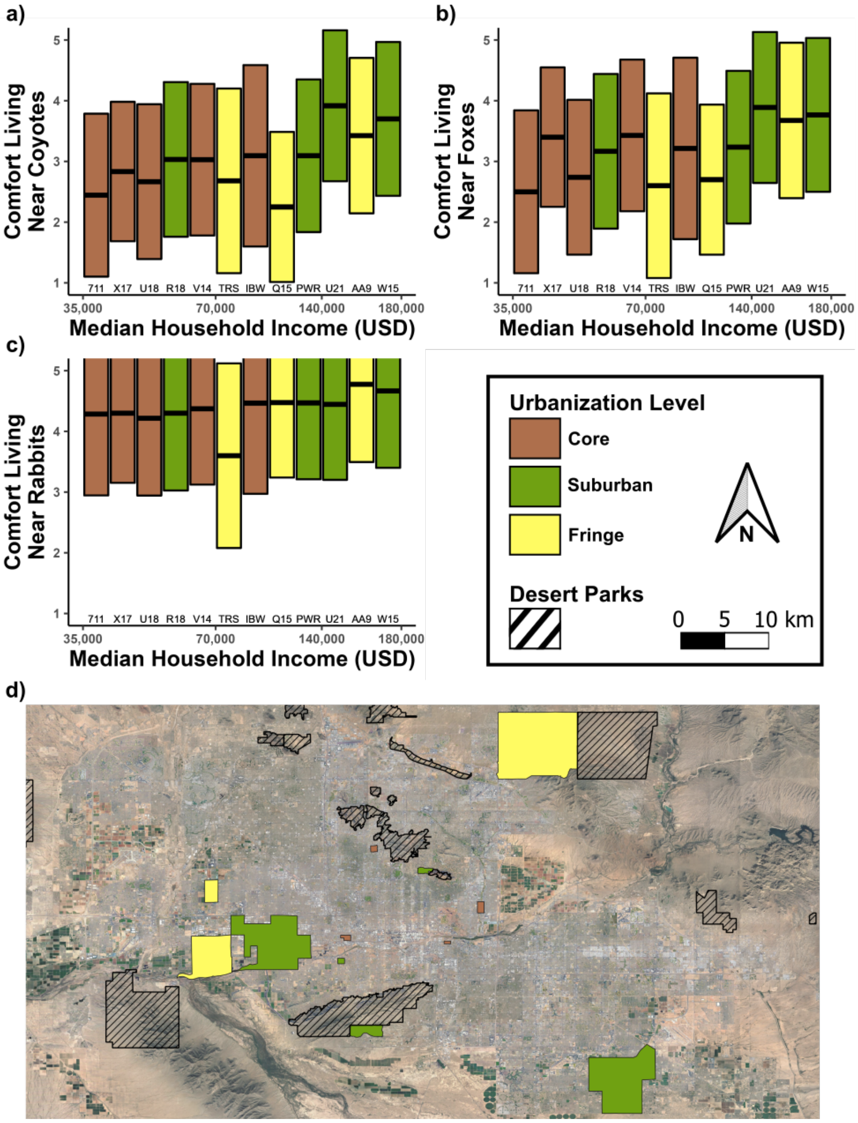

Figure 4.2: Average levels of comfort living near (a) coyotes, (b), foxes, and (c) rabbits, as reported within (d) twelve neighborhoods in the Phoenix Metropolitan Area, Arizona, USA. Midlines indicate neighborhood-mean comfort level, while upper and lower ends of the boxes depict one standard deviation above and below the mean (approximating a 68% confidence interval). We present average comfort in relation to each neighborhood's median household income, from the 2020 US Census. Neighborhoods are depicted by their broad level of urbanization (based on mean percentage of impervious surface cover), with Fringe neighborhoods being located along the edge of the metropolitan area and having <20% impervious surface, Suburban neighborhoods being moderately urbanized (20%-50% impervious surface), Core neighborhoods representing areas nearer the urban core with relatively high urbanization (< 50% impervious surface).

Table 4.4: Summary of model selection results for mixed-effects models of comfort living near three wildlife species. Values depict the number of parameters (K) and Akaike Information Criterion (AIC) for each global or partial model. Lower AIC values indicate higher relative quality (i.e., better fit), with the value of the best-fit model for each species indicated in boldface.

Model	K	Coyote	Foxes	Rabbits
Global	**14**	**1534.55**	**1521.79**	**1302.82**
Ideological only	5	1660.25	1653.52	1395.31
Environmental only	6	1684.23	1686.16	1416.15
Sociodemographics only	9	1592.47	1589.74	1321.44

Table 4.5: Multivariate generalized linear mixed model results for comfort living near coyotes, showing beta estimates (standardized effect sizes) with significance levels indicated using p-values and 95% confidence intervals (CI). Boldface emphasizes relationships with a significance level of $p < 0.01$. Conditional $R^2 = 0.23$.

All Variables			
Fixed Effects	**Beta Estimate**	**p-value**	**95% CI**
Intercept	3.29	<0.001	3.07, 3.53
Ideological			
Wildlife Value Orientation	0.41	<0.001	0.29, 0.53
Desert Identity	0.00	0.96	-0.13, 0.12
Environmental			
Urbanization	-0.10	0.13	-0.22, 0.02
Vegetation	-0.05	0.52	-0.20, 0.08
Distance to Desert Parks	-0.20	0.03	-0.37, -0.05
Sociodemographic			
Income	0.24	<0.001	0.11, 0.41
Education	-0.06	0.34	-0.19, 0.07
Age	0.00	0.99	-0.12, 0.12
Pet Ownership	0.10	0.41	-0.14, 0.34
Gender	-0.39	<0.001	0.34, -0.16
Latino Identity	-0.01	0.96	-0.35, 0.30

Random effects	**Variance**	**SD**
Neighborhood	0.025	0.16

Table 4.6: Multivariate generalized linear mixed model results for comfort living near foxes, showing beta estimates (standardized effect sizes) with significance levels indicated using p-values and 95% confidence intervals (CI). Boldface emphasizes relationships with a significance level of $p < 0.01$. Conditional $R^2 = 0.23$.

	All Variables		
Fixed Effects	**Beta Estimate**	**p-value**	**95% CI**
Intercept	3.47	<0.001	3.25, 3.69
Ideological			
Wildlife Value Orientation	0.44	<0.001	0.32, 0.56
Desert Identity	-0.03	0.60	-0.16, 0.09
Environmental			
Urbanization	-0.09	0.13	-0.20, 0.03
Vegetation	-0.01	0.92	-0.13, 0.12
Distance to Desert Parks	-0.25	<0.001	-0.39, -0.11
Sociodemographic			
Income	0.12	0.12	-0.03, 0.26
Education	-0.12	0.08	-0.25, 0.01
Age	-0.16	0.01	-0.28, -0.03
Pet Ownership	0.27	0.03	0.03, 0.50
Gender	-0.45	<0.001	-0.68, -0.22
Latino Identity	-0.40	0.02	-0.71, -0.08

Random effects	**Variance**	**SD**
Neighborhood	0.00	0.00

Table 4.7: Multivariate generalized linear mixed model results for comfort living near rabbits, showing beta estimates (standardized effect sizes) with significance levels indicated using p-values and 95% confidence intervals (CI). Boldface emphasizes relationships with a significance level of $p < 0.01$. Conditional $R^2 = 0.17$.

All Variables			
Fixed Effects	**Beta Estimate**	**p-value**	**95% CI**
Intercept	4.40	<0.001	4.21, 4.58
Ideological			
Wildlife Value Orientation	0.23	<0.001	0.14, 0.32
Desert Identity	0.00	0.96	-0.09, 0.10
Environmental			
Urbanization	-0.07	0.19	-0.16, 0.04
Vegetation	0.02	0.78	-0.10, 0.13
Distance to Desert Parks	0.02	0.80	-0.12, 0.14
Sociodemographic			
Income	0.11	0.06	0.00, 0.24
Education	-0.04	0.48	-0.14, 0.06
Age	-0.17	0.001	-0.26, -0.06
Pet Ownership	0.24	0.01	0.06, 0.43
Gender	-0.12	0.22	-0.29, 0.07
Latino Identity	-0.40	0.002	-0.65, -0.15

Random effects	**Variance**	**SD**	
Neighborhood	0.03	0.17	

Table 4.8: Summary of model results across all global and partial models for all three dependent variables (i.e., comfort living near coyotes, foxes, and rabbits). Text indicates whether each explanatory variable was significantly associated with the dependent variables in only the global model containing all variables, only the partial model including that variable, in both the global and partial models, or in neither. Parentheticals after each significant effect indicate the directionality of the relationship between that variable and comfort around wildlife. R^2 values indicate the proportion of variance explained by both the fixed and random effects in each global or partial model (bolded and un-bolded, respectively).

Explanatory Variables	**Coyotes** ($R^2 = 0.21$)	**Foxes** ($R^2 = 0.23$)	**Rabbits** ($R^2 = 0.17$)
Ideological	($R^2 = 0.17$)	($R^2 = 0.16$)	($R^2 = 0.09$)
Wildlife Value Orientation	***Both (+)***	***Both (+)***	***Both (+)***
Desert Identity	Neither	Neither	Neither
Environmental	($R^2 = 0.09$)	($R^2 = 0.08$)	($R^2 = 0.07$)
Urbanization	Neither	Neither	Neither
Vegetation	Neither	Neither	Neither
Distance to Desert Parks	***Both (-)***	***Both (-)***	Neither
Sociodemographic	($R^2 = 0.12$)	($R^2 = 0.13$)	($R^2 = 0.11$)
Income	***Both (+)***	Neither	Neither
Education	Neither	Neither	Neither
Age	Neither	**Global Only (-)**	***Both (-)***
Pet Ownership	*Partial Only (+)*	***Both (+)***	***Both (+)***
Gender	***Both (-)***	***Both (-)***	Neither
Latino Identity	Neither	**Global Only (-)**	***Both (-)***

4.5 Discussion

Overall, residents of Metropolitan Phoenix, Arizona, USA are somewhat comfortable living near mammals, which bodes well for coexistence. Yet the degree to which residents tolerate and accept the presence of coyotes, foxes, and rabbits in and around their neighborhoods depends upon various combinations of personal, social, and environmental characteristics. In our study, the data supported our hypotheses that comfort living near wildlife was most strongly associated with an individual's value-based judgements. Residents with more mutualistic, pro-wildlife value orientations were more likely to express greater comfort living near coyotes, foxes, and, to a lesser degree, rabbits. These varying levels of ideologically-based comfort may indicate different points along the conflict-coexistence continuum (Glikman *et al.*, 2021), where discomfort could signify the potential for conflict whereas moderate comfort might signal tolerance, and high levels of comfort even opportunities for wildlife acceptance and stewardship (Bhatia, 2021).

By showing that values are the primary predictor of comfort, our results indicate that people's ideological beliefs may present a key challenge to influence attitudes, given that value-based beliefs tend to be static and resistant to change (Manfredo, 2008c). However, given recent generational shifts toward mutualism, especially in metropolitan areas, changing wildlife value orientations may forecast growing potential for wildlife appreciation and stewardship in urbanizing regions (Heberlein, 2012; Dietsch *et al.*, 2019; Manfredo *et al.*, 2020). Finally, since comfort levels were mediated by residents' local environmental context and sociodemographic characteristics, and by the traits of the wildlife involved, alternative strategies for promoting pro-coexistence attitudes may be tailored to particular places, people, and wildlife taxa.

4.5.1 Roles of Environment and Sociodemographics

Although residents' comfort living near wildlife may be strongly grounded in their wildlife values, differences in comfort also reflect people's potential experiences with wildlife and natural environments more broadly. For instance, living closer to the region's desert preserves was associated with higher comfort living near coyotes and foxes, the two larger carnivores species that may threaten pets and small children (although attacks on people are rare; Curtis and Hadidian, 2010; Hudenko *et al.*, 2010; Nardi *et al.*, 2020; Poessel *et al.*, 2013). These results support the hypothesis that living in environments where wildlife are more likely to be present and interact with people can lead to residents becoming more familiar with wildlife and developing attitudes more consistent with tolerance and acceptance (Soulsbury and White, 2019; Glikman *et al.*, 2021).

Differences in comfort living near wildlife may also be mediated by certain sociodemographic characteristics, particularly those associated with two types of concerns that are often involved in conflict: that is, for the well-being of people and their households and for the protection and well-being of wildlife. Harm to pets is a major form of human-wildlife interaction and potential conflict within metropolitan regions (Curtis and Hadidian, 2010; Reidinger and Miller, 2013; Nardi *et al.*, 2020). However, our partial (sociodemographic variables only) model indicated that pet owners may be more comfortable living near coyotes, signaling relative tolerance of urban-adapted coyotes among people who might be negatively impacted by concerns about their pets. Furthermore, our global and partial model results indicated even greater comfort living near foxes and rabbits among pet owners, suggesting the potential for appreciation of relatively benign wildlife. The increased comfort of pet owners near wildlife may additionally reflect emotional dispositions in favor of animals more broadly, whether innate (biophilic), conditioned (through experiences), or the confluence of both (Slagle and Bruskotter, 2019).

Additional personal factors that are associated with people's variable tolerance of wildlife risks and damages, such as gender identity, may further influence the outcomes of human-wildlife interactions and people's resulting wildlife attitudes and behaviors (Soulsbury and White, 2019; Zinn and Pierce, 2002). For instance, we found that men in our study generally reported greater comfort living near coyotes and rabbits, consistent with previous studies indicating generally lower wildlife risk aversion (Kellert and Berry, 1987; Zinn and Pierce, 2002). However, further research is needed to better understand how perceptions of human-wildlife encounters (i.e., positive, neutral, or negative; acceptable or acceptable) affect their wildlife attitudes through people's prior expectations, emotional dispositions, and perceptions of risks (Jacobs and Vaske, 2019; Slagle and Bruskotter, 2019).

4.5.2 Roles of Species Traits

The nature of encounters between people and wildlife depends on the varied characteristics of wildlife species, particularly as they pertain to hazards to and benefits for human well-being. The potential for attitudes representing wildlife tolerance and acceptance to vary among individuals as a function of their values and experiences may be greatest for species that have been more historically stigmatized (George et al., 2016), including larger mammalian carnivores and venomous snakes (Bateman and Fleming, 2012; Bateman *et al.*, 2021). This concept was supported by our findings that residents living closer to desert parks were generally more comfortable living near coyotes and foxes, but not necessarily rabbits. Since greater experiences with nature and exposure to associated risks have been linked to lower risk perceptions and positive wildlife attitudes (Slovic, 1987; Zaradic *et al.*, 2009), increasing people's familiarity with potentially threatening wildlife and their behaviors may help to gradually build tolerance and acceptance of these species (Carter and Linnell, 2016). Thus, improving access to positive nature-based experiences – particularly among youth, whose environmental values are generally more dynamic (Manfredo, 2008c; Soga *et al.*, 2016) – is vital to enhancing the long-term growth in potential for coexistence.

Attitudes toward less-feared wildlife, such as rabbits, whose presence typically elicits more positive affective and cognitive responses of joy and appreciation (Jacobs and Vaske, 2019; Kellert, 1993, 1985; George *et al.*, 2016), appear less associated with environmental experiences and more closely associated with people's sociodemographic characteristics. For instance, our results indicated that variation in comfort living near rabbits (which was generally high to begin with) was not associated with residents' proximity to desert parks or as strongly influenced by wildlife value orientations. However, even relatively benign wildlife can exhibit traits and behaviors that directly impact people's livelihoods and lifestyles, shaping attitudes toward those species in subtler, less certain ways (Hudenko *et al.*, 2010). For example, comfort living with rabbits may be lower within areas of greater agricultural activity and in more extensively landscaped neighborhoods, where concerns over potential damage to plants valued by people may decrease tolerance of rabbit presence (Abu Baker *et al.*, 2015; Simes *et al.*, 2015). In such cases, coexistence might be more effectively facilitated through approaches that move beyond the ecological factors driving nature-based experiences to approaches that more strongly consider the personal and social factors that influence people's wildlife perceptions and attitudes.

4.5.3 Limitations and Future Research

To build a deeper understanding of the human and environmental factors that shape wildlife attitudes, future research could test relationships in different social-ecological contexts, including other species, other human populations, and other places. As it was not our intention to obtain a representative, generalizable sample in this study, we have focused our interpretation on local relationships with the explanatory variables within this study neighborhoods. Although we were limited by available data to a select few species and environmental variables, our survey methods coupled with geospatial data enabled us to detect substantial patterns of residents' attitudes in relation to the environmental and social characteristics of neighborhoods. However, we were unable to determine causal relationships such as the direct impacts of wildlife encounters on residents' attitudes and behaviors. Further exploration of causality requires follow-up studies that incorporate qualitative and experiential research methods to examine people's interactions with wildlife and how they have shaped their tolerance, acceptance, and stewardship, which requires approaches that align and integrate social and ecological data to better understand patterns of co-occurrence (Soulsbury and White, 2019). Finally, further teasing apart the roles of species traits as drivers of people's emotional and cognitive responses to wildlife is a key area of future study (Jacobs and Vaske, 2019), one that requires examining more taxonomically and functionally diverse wildlife taxa that have various ways of coexisting with people.

4.5.4 Implications for Coexistence

Different levels of comfort living near wildlife can signal alternative strategies for promoting human-wildlife coexistence, as comfort considers both positive and negative responses to wildlife and associated predictors of those responses, especially people's wildlife values. Our results indicated that the ability to expand wildlife acceptance and stewardship will be closely tied to shifts in wildlife value orientations away from domination and toward mutualism across the U.S. (Manfredo *et al.*, 2020), which may also be a major source for future human-human conflict due to the potential for disagreements over how best to manage wildlife populations and their coexistence with people in heterogeneous urbanizing regions (Lute and Gore, 2019). As such, we recommend that wildlife management practices continue to move beyond the prediction and mitigation of human-wildlife conflicts and toward the addressing human-human conflicts and the promotion of environmental stewardship (Lute and Gore, 2019; Bhatia, 2021). For instance, greater understanding of how wildlife attitudes, including comfort, may facilitate the incorporation of coexistence into multi-scale conservation planning efforts within landscapes increasingly dominated by human activity (Parris *et al.*, 2018; Marchini *et al.*, 2019; Apfelbeck *et al.*, 2020; Kay *et al.*, 2022). The success of these conservation efforts and the identification of stakeholders fall along the conflict-to-coexistence continuum depend upon human and wildlife behaviors rooted in complex social, ecological, and place-based relationships (Dietsch *et al.*, 2019; Carter and Linnell, 2023).

4.5.5 Conclusion

Metropolitan residents express a great degree of comfort living near mammals, possibly indicating broad wildlife acceptance and tolerance, and thus, the potential for human-wildlife coexistence. Not only did we show that the ability to enhance coexistence is tied to broader cultural trends, due to the strongly ideological foundation of wildlife comfort, our results highlighted how the influences of sociodemographic, environmental, and species characteristics on attitudes suggest additional place-based and individualized opportunities to enhance wildlife tolerance, acceptance, and stewardship. With wildlife attitudes serving as significant indicators of behavioral intent regarding people's willingness to coexist, further exploration of wildlife attitudes and their drivers remains vital to the success of conservation efforts in an urbanizing world.

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APPENDIX A

SUPPLEMENTARY DATA FOR CHAPTER 1

Table A.1: Pearson correlations among urbanization and metrics of spatial landscape heterogeneity for 50 sites across a gradient of urbanization in the Phoenix Metropolitan Area, Arizona, USA. All metrics were derived from the 2019 National Land Cover Database and measured at fine (100 m), medium (1 km), and broad (5 km) spatial scales. We measured urbanization as percentage of impervious surface cover and quadratic urbanization as the standardized then squared values of urbanization, such that a variable that was negatively correlated with quadratic urbanization would be said to peak at moderate levels of urbanization.

Landscape Metric	**Scale**	**Urbanization**	**Quadratic Urbanization**
Patch Richness	100 m	-0.18	-0.44
	1 km	-0.12	-0.45
	5 km	-0.19	-0.36
Patch Diversity	100 m	-0.19	-0.47
	1 km	-0.24	-0.70
	5 km	-0.50	-0.39
Patch Density	100 m	-0.22	-0.41
	1 km	-0.15	-0.59
	5 km	-0.26	-0.53
Edge Density	100 m	-0.15	-0.47
	1 km	-0.29	-0.48
	5 km	-0.51	-0.15
Contagion	100 m	0.19	0.47
	1 km	0.33	0.49
	5 km	0.73	-0.17

Table A.2: Model selection results for nine univariate dynamic community occupancy models fit to multi-season data of multi-species occurrence across the Phoenix Metropolitan Area, Arizona, USA, where species patch use, persistence, and colonization was a function of a single covariate (urbanization, including the quadratic urbanization term; landscape heterogeneity; vegetation greenness). M_{100m}, M_{1km}, and M_{5km} correspond to sets of univariate models fit using each covariate measured within 100 m, 1 km, and 5 km radius buffers, respectively. Values depict the relative fit of models for each covariate using the summary statistic $-\Sigma_{k,t} log(CPO_{k,t}$ for data point k and Markov chain Monte Carlo (MCMC) step t. CPO represents the conditional predictive ordinate for each data point. '*' indicates the lowest CPO summary statistic value (i.e, best-fit model) for each covariate.

Covariate	M_{100m}	M_{1km}	M_{5km}
Urbanization with Quadratic Term	2619.89	2603.90*	2663.68
Landscape Heterogeneity	2903.24	2911.44	2897.61*
Vegetation Greenness	2920.47	2913.37*	2924.23

Table A.3: Relationships of environmental predictor variables with wildlife community-level (among-species average) site use response variables, based on a dynamic (multi-season) community occupancy model that excluded the 'quadratic urbanization' term. ** = high (>95%) probability of detecting relationship, * = moderate (>85%) probability of detecting relationship

Response Variable	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
Initial use, ψ	Urbanization	-1.60	-5.41, -2.99	100.0%**
	Heterogeneity	-0.25	-0.53, 0.02	96.7%**
	Greenness	0.25	-0.16, 0.62	90.0%*
Persistence, ϕ	Urbanization	-0.20	-0.71, 0.35	78.6%
	Heterogeneity	0.05	-0.45, 0.57	59.1%
	Greenness	0.08	-0.60, 1.04	52.7%
Colonization, γ	Urbanization	-1.38	-1.99, -0.79	100.0%**
	Heterogeneity	-0.20	-0.63, 0.22	83.1%
	Greenness	0.16	-0.39, 0.69	74.0%

APPENDIX B

SUPPLEMENTARY DATA FOR CHAPTER 2

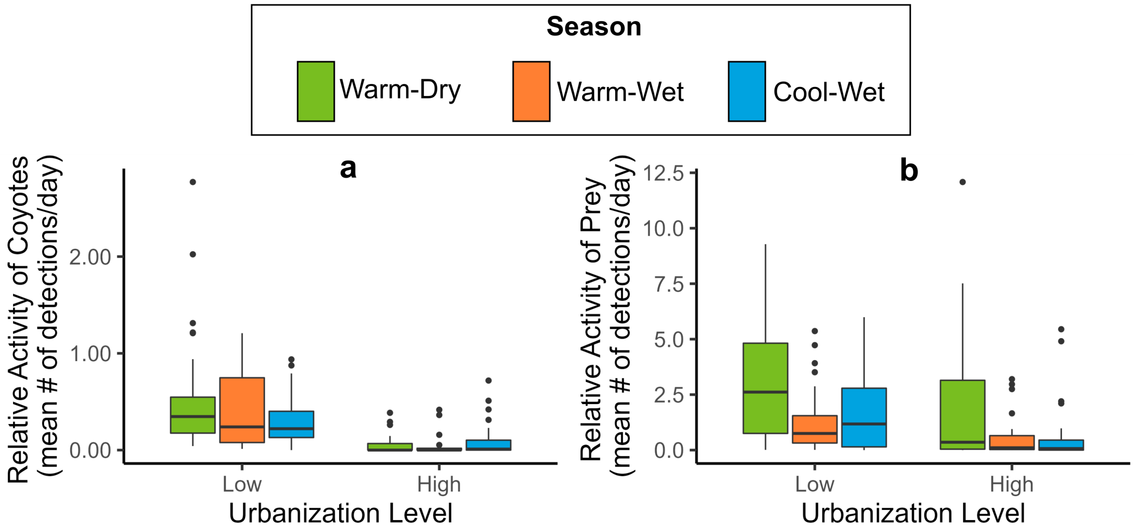

Figure B.1: **(a)** relative activity (# of independent detections per day sampled) of coyotes and **(b)** mesocarnivore prey species at low urbanization (<38% impervious surface) and high urbanization sites (>38% impervious surface)

Table B.1: List of prey species observed within the study area, including their number of independent detections and relative abundance across the three seasons. Indices of relative prey activity were calculated by summing independent observations (>30 minutes apart) of all three prey groups at each site during each season, and then dividing by the number of days in each site was sampled.

Prey Group	**Species Included**
Lagomorphs	Cottontail rabbit (*Sylvilagus audubonii*) and Black-tailed Jackrabbit (*Lepus californicus*)
Small Mammals	Rock Squirrel (*Otospermophilus variegatus*), Harris' Antelope Squirrel (*Ammospermophilus harrisii*), Round-tailed Ground Squirrel (*Xerospermophilus tereticaudus*), Woodrats (*Netotoma* spp.), Kangaroo Rat (*Dipodomys* spp.), all other unidentified species in Order *Rodentia*
Birds	Gambel's Quail (*Callipepla gambelii*), Doves (Family *Columbidae*), all other unidentifed species in Class *Aves*

Table B.2: List of candidate conditional two-species occupancy models (Richmond et al., 2010) used to assess how the presence of a dominant species A (i.e., coyotes) affects the presence and detection of mesocarnivore species B (gray foxes, bobcats, raccoons) within the Phoenix Metropolitan Area, Arizona, USA.

Model Name	**Presence**	**Detection**	**Description**
No-interaction	ψ^A; $\psi^{BA} = \psi^{Ba}$	$p^B = r^{BA} = r^{Ba}$	No interaction
OccA-OccB	ψ^A; $\psi^{BA} \neq \psi^{Ba}$	$p^B = r^{BA} = r^{Ba}$	Presence (but not detection) of B depends on presence of A
OccA-DetB	ψ^A; $\psi^{BA} = \psi^{Ba}$	$p^B \neq r^{BA} = r^{Ba}$	Detection (but not presence) of B depends on presence of A
OccA-OccB + OccA-DetB	ψ^A; $\psi^{BA} \neq \psi^{Ba}$	$p^B \neq r^{BA} = r^{Ba}$	Both presence and detection of B depend on presence of A

Table B.3: List of candidate Royle-Nichols occupancy models (Royle and Nichols, 2003) used to assess effects of environmental characteristics and competition (relative activity of coyotes) on the relative habitat use of three mesocarnivore species (gray foxes, bobcats, raccoons) within the Phoenix Metropolitan Area, Arizona, USA.

Model Name	**Relative Site Use Covariates**
Global	$RA_{Coyote} + RA_{Prey} + PlantProductivity$
Competition + Resources	$RA_{Coyote} + PlantProductivity$
Prey + Resources	$RA_{Prey} + PlantProductivity$
Competition + Prey	$RA_{Coyote} + RA_{Prey}$
Competition Only	RA_{Coyote}
Prey Only	RA_{Prey}
Resources Only	$PlantProductivity$

Table B.4: Estimated occupancy and detection probability parameters results from two-species models of mesocarnivore occupancy conditioned on the presence of coyotes at high and low urbanization sites in three seasons. Values depict the mean (Est.), standard error (SE), and 95% confidence interval (CI) for each parameter estimates from the top (lowest AICc) model for each species, season, and urbanization level. In cases where the top model was the one that assumed the occupancy or detection of the mesocarnivores species to be independent of the presence of coyotes (e.g., $\psi^{BA} = \psi^{Ba}$), we use '=' to indicate that parameter estimates were the same as the row immediately above. 'NA' values indicate failure of any model to converge for a particular combination of species, season, and urbanization level.

	Warm-Dry				**Warm-Wet**				**Cool-Wet**			
Probabilities, by species	**Low Urb.**		**High Urb.**		**Low Urb.**		**High Urb.**		**Low Urb.**		**High Urb.**	
	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI
Occupancy							—					
Coyote	1 (1)	0-1	0.44 (0.6)	0.25-0.64	1 (1)	0-1	0.44 (0.61)	0.26-0.65	0.98 (0.87)	0.53-1	0.53 (0.6)	0.33-0.72
Gray fox, coyotes absent	0.30 (0.60)	0.16-0.49	0.16 (0.68)	0.04-0.46	0.41 (0.6)	0.24-0.6	0 (1)	0-1	0.49 (0.6)	0.31-0.67	0.22 (0.62)	0.09-0.43
Gray fox, coyotes present	=	=	=	=	=	=	0.44 (0.67)	0.16-0.76	=	=	=	=
Bobcat, coyotes absent	0.65 (0.6)	0.45-0.81	0.05 (0.74)	0.01-0.3	0.62 (0.6)	0.41-0.78	NA	NA	0.68 (0.61)	0.48-0.83	1 (1)	0-1
Bobcat, coyotes present	=	=	=	=	=	=	NA	NA	=	=	=	=
Raccoon, coyotes absent	0.16 (0.64)	0.06-0.37	0.24 (0.66)	0.08-0.53	0.19 (0.62)	0.08-0.38	0.08 (0.76)	0.01-0.45	0.2 (0.62)	0.08-0.41	0 (1)	0-1
Raccoon, coyotes present	=	=	=	=	=	=	0.54 (0.67)	0.23-0.82	=	=	0.37 (0.66)	0.14-0.69
Detection												
Coyote	0.92 (0.57)	0.86-0.95	0.64 (0.57)	0.51-0.75	0.83 (0.55)	0.76-0.88	0.48 (0.57)	0.35-0.62	0.87 (0.56)	0.80-0.91	0.57 (0.56)	0.45-0.68
Gray fox, coyotes absent	0.6 (0.57)	0.46-0.73	0.49 (0.65)	0.23-0.76	0.56 (0.56)	0.43-0.67	0.32 (0.63)	0.15-0.57	0.61 (0.56)	0.50-0.72	0.65 (0.6)	0.45-0.81
Gray fox, coyotes present	=	=	=	=	=	=	=	=	=	=	=	=
Bobcat, coyotes absent	0.46 (0.55)	0.36-0.56	0.29 (0.74)	0.05-0.76	0.46 (0.55)	0.36-0.56	NA	NA	0.57 (0.55)	0.47-0.66	0.01 (0.73)	0.00-0.05
Bobcat, coyotes present	=	=	=	=	=	=	NA	NA	=	=	=	=
Raccoon, coyotes absent	0.34 (0.62)	0.17-0.58	0.13 (0.71)	0.02-0.37	0.45 (0.6)	0.28-0.64	0.37 (0.60)	0.22-0.56	0.39 (0.60)	0.22-0.59	0.34 (0.62)	0.17-0.57
Raccoon, coyotes present	=	=	0.58 (0.65)	0.30-0.82	=	=	=	=	=	=	=	=

Table B.5: Summary of seasonal detections for nine mammal and ground-dwelling bird species observed at both urbanization levels across three seasons in the Phoenix Metropolitan Area, Arizona, USA. Values include the total numbers of independent detections across each season and urbanization level (n), and the among-site mean relative activity (RA; the number of independent detections over the total number of trap-days in each season) of each species.

Species	**Season**	**Low Urbanization**		**High Urbanization**	
		n	RA	n	RA
Black-tailed Jackrabbit	All Seasons	3293	0.458	308	0.050
	Warm-Dry	950	0.406	184	0.086
	Warm-Wet	581	0.233	79	0.040
	Cool-Wet	1762	0.748	45	0.022
Bobcat	All Seasons	298	0.041	3	0.000
	Warm-Dry	95	0.041	2	0.001
	Warm-Wet	74	0.030	0	0.000
	Cool-Wet	129	0.055	1	0.000
Coyote	All Seasons	2996	0.417	435	0.071
	Warm-Dry	1316	0.562	125	0.059
	Warm-Wet	944	0.379	97	0.049
	Cool-Wet	736	0.313	213	0.106
Desert cottontail rabbit	All Seasons	4760	0.662	2678	0.437
	Warm-Dry	1944	0.830	964	0.451
	Warm-Wet	1095	0.439	526	0.265
	Cool-Wet	1721	0.731	1188	0.594
Gambel's quail	All Seasons	2784	0.387	344	0.056
	Warm-Dry	1960	0.837	267	0.125
	Warm-Wet	565	0.227	39	0.020
	Cool-Wet	259	0.110	38	0.019
Gray fox	All Seasons	293	0.041	286	0.047
	Warm-Dry	68	0.029	16	0.007
	Warm-Wet	106	0.043	122	0.061
	Cool-Wet	119	0.051	148	0.074
Raccoon	All Seasons	71	0.010	52	0.008
	Warm-Dry	13	0.006	15	0.007
	Warm-Wet	34	0.014	22	0.011
	Cool-Wet	24	0.010	15	0.007
Roadrunner	All Seasons	616	0.086	86	0.014
	Warm-Dry	270	0.115	41	0.019
	Warm-Wet	275	0.110	40	0.020
	Cool-Wet	71	0.030	5	0.002
Rock squirrel	All Seasons	199	0.028	491	0.080
	Warm-Dry	66	0.028	249	0.117
	Warm-Wet	68	0.027	198	0.100
	Cool-Wet	65	0.028	44	0.022

Table B.6: Results for overlap in wildlife activity patterns between carnivore species at low and high levels of urbanization during the warm-dry season, including the sample sizes for both wildlife species (n_A and n_B), mean estimate of activity pattern overlap (overlap estimate), and 95% confidence intervals for the overlap estimate, for four mammalian carnivore species in the Phoenix Metropolitan Area, Arizona, USA. 'NA' indicates where reliable overlap estimates could not be produced due to a low minimum sample size (<20 independent observations).

Species A	**Species B**	**Urbanization Level**	n_A	n_B	**Overlap Estimate**	**95% CI**	
						Lower	Upper
Coyote	Gray fox	Low	1316	68	0.77	0.70	0.84
		High	125	16	NA	NA	NA
Coyote	Bobcat	Low	1316	95	0.83	0.78	0.88
		High	125	2	NA	NA	NA
Coyote	Raccoon	Low	1316	13	NA	NA	NA
		High	125	15	NA	NA	NA
Gray fox	Bobcat	Low	68	95	0.90	0.80	0.96
		High	16	2	NA	NA	NA
Gray fox	Raccoon	Low	68	13	NA	NA	NA
		High	16	15	NA	NA	NA
Bobcat	Raccoon	Low	95	13	NA	NA	NA
		High	2	15	NA	NA	NA

Table B.7: Results for overlap in wildlife activity patterns between carnivore species at low and high levels of urbanization during the warm-wet season, including the sample sizes for both wildlife species (n_A and n_B), mean estimate of activity pattern overlap (overlap estimate), and 95% confidence intervals for the overlap estimate, for four mammalian carnivore species in the Phoenix Metropolitan Area, Arizona, USA. 'NA' indicates where reliable overlap estimates could not be produced due to a low minimum sample size (<20 independent observations).

Species A	**Species B**	**Urbanization Level**	n_A	n_B	**Overlap Estimate**	**95% CI**	
						Lower	Upper
Coyote	Gray fox	Low	944	106	0.82	0.76	0.88
		High	97	122	0.79	0.67	0.88
Coyote	Bobcat	Low	944	74	0.84	0.77	0.90
		High	97	0	NA	NA	NA
Coyote	Raccoon	Low	944	34	0.80	0.71	0.86
		High	97	22	0.84	0.70	0.93
Gray fox	Bobcat	Low	106	74	0.90	0.79	0.96
		High	122	0	NA	NA	NA
Gray fox	Raccoon	Low	106	34	0.87	0.76	0.94
		High	122	22	0.81	0.64	0.91
Bobcat	Raccoon	Low	74	34	0.88	0.74	0.95
		High	0	22	NA	NA	NA

Table B.8: Results for overlap in wildlife activity patterns between carnivore species at low and high levels of urbanization during the cool-wet season, including the sample sizes for both wildlife species (n_A and n_B), mean estimate of activity pattern overlap (overlap estimate), and 95% confidence intervals for the overlap estimate, for four mammalian carnivore species in the Phoenix Metropolitan Area, Arizona, USA. 'NA' indicates where reliable overlap estimates could not be produced due to a low minimum sample size (<20 independent observations).

Species A	**Species B**	**Urbanization Level**	n_A	n_B	**Overlap Estimate**	**95% CI**	
						Lower	Upper
Coyote	Gray fox	Low	736	119	0.81	0.75	0.87
		High	213	145	0.84	0.73	0.93
Coyote	Bobcat	Low	736	129	0.90	0.86	0.94
		High	213	1	NA	NA	NA
Coyote	Raccoon	Low	736	24	0.78	0.66	0.87
		High	213	15	NA	NA	NA
Gray fox	Bobcat	Low	119	129	0.85	0.76	0.92
		High	145	1	NA	NA	NA
Gray fox	Raccoon	Low	119	24	0.85	0.71	0.93
		High	145	15	NA	NA	NA
Bobcat	Raccoon	Low	129	24	0.84	0.71	0.93
		High	1	15	NA	NA	NA

APPENDIX C

SUPPLEMENTARY DATA FOR CHAPTER 3

Table C.1: Summary characteristics of 20 study areas (cities) included in the analysis of mammal presence and community composition. Species observation data from each city were collected via motion-triggered camera traps during the same 35-day summer period within different sampling years within different study areas. We represented sampling effort of each city using the total number of sites sampled (n_{site}) and the across-site sum of its camera trap-days (CT Days), the number of days in which each site was functional and collecting data. Total sampling effort was 20,176 camera trap-days across all 725 sites. We used four regional environmental variables to differences in among-city environment in our analysis: regional vegetation greenness (Enhanced Vegetation Index; EVI); regional temperature (mean annual temperature, in degC; MAT); regional urbanization (% urban land cover; URB); regional city age (years since colonization; AGE).

City	Sampling Year	n_{site} (CT Days)	EVI	MAT	URB	AGE
Atlanta, Georgia	2019	30 (913)	0.32	15.9	64.8	182
Austin, Texas	2018	13 (336)	0.27	20.0	63.2	183
Chicago, Illinois	2019	95 (2,531)	0.20	9.8	80.9	239
Denver, Colorado	2018	34 (842)	0.18	10.4	75.8	160
Edmonton, Alberta	2018	42 (1,431)	0.19	2.7	60.5	223
Fort Collins, Colorado	2017	27 (708)	0.18	9.0	35.8	153
Indianapolis, Indiana	2018	42 (1,293)	0.30	11.2	74.5	197
Iowa City, Iowa	2018	37 (885)	0.25	9.9	23.6	179
Manhattan, Kansas	2016	52 (1,353)	0.23	12.8	16.7	161
Metropolitan Los Angeles, California	2020	31 (930)	0.20	17.1	65.8	145
National Capitol, District of Columbia	2019	22 (409)	0.29	13.2	75.4	270
Phoenix, Arizona	2019	50 (1,666)	0.14	21.8	57.2	152
Rochester, New York	2020	15 (451)	0.25	9.2	50.1	232
Sanford, Florida	2019	24 (502)	0.34	22.0	42.8	177
Salt Lake City, Utah	2019	54 (977)	0.19	7.0	25.6	172
Seattle, Washington	2019	31 (965)	0.23	10.9	52.5	168
San Francisco Bay Area, California	2020	34 (1,139)	0.17	14.0	47.0	244
St. Louis, Missouri	2019	33 (1,128)	0.27	13.4	68.9	255
Tacoma, Washington	2019	34 (1,036)	0.24	10.8	57.8	155
Wilmington, Delaware	2019	24 (681)	0.31	12.5	54.0	381

Table C.2: List of observed species and species groups. The number of daily observations indicates the total camera trap-days in which the species was detected across all camera sites (N_{obs}), out of a total of 20,206 camera trap-days. Average body mass (in kg) and carnivory (% vertebrates in diet) were derived from the EltonTraits 1.0 database. Due to limitations in the ability to distinguish congeneric mammal species based solely on wildlife camera photographs, seven 'species' used in the estimation of species presence, detection, and community composition are represented by groupings of multiple taxonomic species (Antelope Ground Squirrel, Chipmunks, Cottontail Rabbits, Flying Squirrels, Gray Squirrels, Jackrabbits, Weasels), with their species traits representing the mean values across each group.

Species Common Name	**Species Binomial(s)**	N_{obs}	**Body Mass (kg)**	**Carnivory (%)**
Antelope Ground Squirrel	*Ammospermophilus harrisii, A. leucurus*	52	0.11	0
Armadillo	*Dasypus novemcinctus*	82	4.20	0
Black Bear	*Ursus americanus*	8	99.95	20
Bobcat	*Lynx rufus*	73	8.90	100
California Ground Squirrel	*Otospermophilus beecheyi*	53	0.58	0
Chipmunks	*Tamias minimus, T. striatus*	285	0.12	0
Cottontail Rabbits	*Sylvilagus audubonii, S. bachmani, S. floridanus, S. nuttallii, S. palustris*	1211	0.99	0
Cougar	*Puma concolor*	7	51.60	100
Coyote	*Canis latrans*	1149	13.41	70
Douglas Squirrel	*Tamiasciurus douglasii*	42	0.26	30
Elk	*Cervus canadensis*	29	165.02	0
Flying Squirrels	*Glaucomys sabrinus, G. volans*	5	0.11	0
Fox Squirrel	*Sciurus niger*	693	0.76	0
Gray Fox	*Urocyon cinereoargenteus*	73	3.83	30
Gray Squirrels	*Sciurus griseus, S. carolinensis*	2230	0.62	0
Hooded Skunk	*Mephitis macroura*	2	0.80	30
Jackrabbits	*Lepus americanus, L. californicus, L. townsendii*	209	1.90	0
Javelina	*Pecari tajacu*	29	21.27	20
Kit Fox	*Vulpes macrotis*	23	4.50	70

Species Common Name	**Species Binomial(s)**	N_{obs}	**Body Mass (kg)**	**Carnivory (%)**
Moose	*Alces alces*	32	357.00	0
Mountain Beaver	*Aplodontia rufa*	2	1.00	0
Mule Deer	*Odocoileus hemionus*	650	54.21	0
North American Badger	*Taxidea taxus*	25	7.11	90
North American Beaver	*Castor canadensis*	6	21.82	0
North American Mink	*Neogale vison*	23	1.15	90
North American Porcupine	*Erethizon dorsatum*	17	7.09	0
Raccoon	*Procyon lotor*	2900	5.52	20
Red Fox	*Vulpes vulpes*	516	5.48	70
Red Squirrel	*Tamiasciurus hudsonicus*	86	0.20 3	0
Richardson's Ground Squirrel	*Urocitellus richardsonii*	2	0.41	0
Rock Squirrel	*Otospermophilus variegatus*	79	0.69	0
Round-tailed Ground Squirrel	*Xerospermophilus tereticaudus*	11	0.16	0
Striped Skunk	*Mephitis mephitis*	291	2.09	30
Virginia Opossum	*Didelphis virginiana*	1090	2.20	30
Weasels	*Mustela nivalis, M. erminea, M. frenata*	2	0.12	96.67
White-tailed Deer	*Odocoileus virginianus*	1999	55.51	0
Woodchuck	*Marmota monax*	119	3.80	0

Table C.3: Effects of local (within-city) environmental predictors on species-level occupancy predicted across 20 North American cities. We estimated effects using a Bayesian multi-city community occupancy modeling approach, depicting the modeled effect of each predictor on occupancy by calculating means (β_{mean}) and 95% Bayesian credible intervals (CRI) across each effect parameter's posterior distribution. We additionally represented the probability that a substantial relationship was detected between each predictor and response variable using the percentage of each effect parameter's Bayesian posterior distribution that shares a sign (positive or negative) with the mean of the distribution.

Species Common Name	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
Antelope Ground Squirrel	Local Urbanization	-0.01	-1.07, 0.97	49.4
	Local Patch Density	0.05	-0.37, 0.46	60.5
	Local Agricultural Footprint	-0.17	-0.66, 0.28	77.8
Armadillo	Local Urbanization	-0.67	-1.56, 0.15	94.8
	Local Patch Density	0.02	-0.38, 0.41	56.1
	Local Agricultural Footprint	-0.19	-0.64, 0.24	81.3
Black Bear	Local Urbanization	-1.11	-2.12, -0.19	99.0
	Local Patch Density	0.04	-0.38, 0.43	58.4
	Local Agricultural Footprint	-0.18	-0.64, 0.25	79.3
Bobcat	Local Urbanization	-0.81	-1.53, -0.14	99.1
	Local Patch Density	0.16	-0.16, 0.50	84.4
	Local Agricultural Footprint	-0.15	-0.53, 0.21	79.0
California Ground Squirrel	Local Urbanization	-0.07	-0.92, 0.71	56.9
	Local Patch Density	0.06	-0.33, 0.45	63.4
	Local Agricultural Footprint	-0.12	-0.56, 0.31	72.6
Chipmunks	Local Urbanization	-0.32	-0.85, 0.19	89.3
	Local Patch Density	0.07	-0.25, 0.37	67.8
	Local Agricultural Footprint	-0.17	-0.51, 0.15	84.6
Cottontail Rabbits	Local Urbanization	0.21	-0.12, 0.52	90.8
	Local Patch Density	0.04	-0.18, 0.25	64.9
	Local Agricultural Footprint	-0.11	-0.38, 0.15	79.5
Cougar	Local Urbanization	-0.85	-1.92, 0.14	95.5
	Local Patch Density	0.07	-0.34, 0.47	63.8

Species Common Name	Predictor Variable	β_{mean}	95% CRI	Probability of Relationship
	Local Agricultural Footprint	-0.17	-0.64, 0.27	77.8
Coyote	Local Urbanization	-0.46	-0.77, -0.15	99.8
	Local Patch Density	0.10	-0.11, 0.30	82.5
	Local Agricultural Footprint	-0.04	-0.26, 0.19	62.8
Douglas Squirrel	Local Urbanization	-0.12	-1.25, 0.85	57.6
	Local Patch Density	0.05	-0.37, 0.46	61.7
	Local Agricultural Footprint	-0.18	-0.68, 0.27	79.1
Elk	Local Urbanization	-1.32	-2.36, -0.39	99.6
	Local Patch Density	0.05	-0.35, 0.44	61.6
	Local Agricultural Footprint	-0.11	-0.55, 0.32	70.6
Flying Squirrels	Local Urbanization	-0.15	-1.04, 0.67	63.3
	Local Patch Density	0.09	-0.30, 0.48	68.3
	Local Agricultural Footprint	-0.19	-0.65, 0.24	81.2
Fox Squirrel	Local Urbanization	0.00	-0.47, 0.46	51.0
	Local Patch Density	0.04	-0.27, 0.35	60.7
	Local Agricultural Footprint	-0.19	-0.56, 0.16	86.2
Gray Squirrels	Local Urbanization	-0.43	-1.13, 0.23	89.9
	Local Patch Density	0.02	-0.36, 0.38	55.2
	Local Agricultural Footprint	-0.15	-0.58, 0.24	77.4
Gray Fox	Local Urbanization	0.04	-0.30, 0.37	61.3
	Local Patch Density	0.10	-0.15, 0.36	77.7
	Local Agricultural Footprint	-0.30	-0.62, 0.00	97.5
Hooded Skunk	Local Urbanization	-0.28	-1.29, 0.62	72.9
	Local Patch Density	0.07	-0.36, 0.49	63.9
	Local Agricultural Footprint	-0.16	-0.64, 0.30	76.1
Jackrabbits	Local Urbanization	-0.45	-1.26, 0.33	88.1
	Local Patch Density	0.07	-0.32, 0.44	64.7
	Local Agricultural Footprint	-0.12	-0.55, 0.29	72.4
Javelina	Local Urbanization	-0.78	-1.74, 0.13	95.6
	Local Patch Density	0.05	-0.38, 0.46	60.1
	Local Agricultural Footprint	-0.17	-0.66, 0.29	77.1

Species Common Name	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
Kit Fox	Local Urbanization	-0.53	-1.59, 0.4	86.9
	Local Patch Density	0.06	-0.38, 0.47	61.6
	Local Agricultural Footprint	-0.16	-0.64, 0.3	76.1
Moose	Local Urbanization	-1.30	-2.44, -0.23	99.0
	Local Patch Density	0.12	-0.29, 0.55	72.8
	Local Agricultural Footprint	-0.14	-0.6, 0.30	74.4
Mountain Beaver	Local Urbanization	-0.50	-1.42, 0.36	87.9
	Local Patch Density	0.03	-0.39, 0.43	57.2
	Local Agricultural Footprint	-0.17	-0.65, 0.26	78.5
Mule Deer	Local Urbanization	-1.22	-1.98, -0.49	99.9
	Local Patch Density	0.20	-0.13, 0.55	88.6
	Local Agricultural Footprint	-0.11	-0.48, 0.23	73.9
North American Badger	Local Urbanization	-0.60	-1.68, 0.37	89.3
	Local Patch Density	0.06	-0.36, 0.47	62.7
	Local Agricultural Footprint	-0.17	-0.64, 0.29	77.5
North American Beaver	Local Urbanization	-0.34	-1.18, 0.54	79.1
	Local Patch Density	0.11	-0.27, 0.49	72.5
	Local Agricultural Footprint	-0.16	-0.6, 0.25	77.9
North American Mink	Local Urbanization	-0.20	-0.90, 0.49	71.4
	Local Patch Density	0.12	-0.25, 0.50	75.1
	Local Agricultural Footprint	-0.19	-0.61, 0.20	82.6
North American Porcupine	Local Urbanization	-0.45	-1.33, 0.39	86.2
	Local Patch Density	0.11	-0.26, 0.48	73.1
	Local Agricultural Footprint	-0.21	-0.65, 0.19	84.5
Raccoon	Local Urbanization	-0.05	-0.37, 0.27	62.5
	Local Patch Density	0.10	-0.13, 0.34	80.6
	Local Agricultural Footprint	-0.02	-0.29, 0.25	54.5
Red Fox	Local Urbanization	0.02	-0.51, 0.53	54.4
	Local Patch Density	0.18	-0.12, 0.48	88.5
	Local Agricultural Footprint	-0.16	-0.52, 0.18	82.1
Red Squirrel	Local Urbanization	-0.15	-0.99, 0.64	63.7

Species Common Name	**Predictor Variable**	β_{mean}	**95% CRI**	**Probability of Relationship**
	Local Patch Density	0.08	-0.29, 0.44	67.4
	Local Agricultural Footprint	-0.26	-0.77, 0.18	87.9
Richardson's Ground Squirrel	Local Urbanization	-0.19	-1.2, 0.74	64.9
	Local Patch Density	0.10	-0.32, 0.52	68.8
	Local Agricultural Footprint -	0.18	-0.66, 0.27	78.4
Rock Squirrel	Local Urbanization	-0.23	-1.12, 0.59	71.1
	Local Patch Density	0.09	-0.31, 0.48	68.8
	Local Agricultural Footprint	-0.13	-0.57, 0.30	72.2
Round-tailed Ground Squirrel	Local Urbanization	0.14	-0.79, 1.04	63.2
	Local Patch Density	0.10	-0.31, 0.50	69.3
	Local Agricultural Footprint	-0.18	-0.66, 0.25	80.0
Striped Skunk	Local Urbanization	-0.26	-0.74, 0.2	87.3
	Local Patch Density	-0.04	-0.37, 0.27	59.3
	Local Agricultural Footprint	-0.15	-0.51, 0.19	79.9
Virginia Opossum	Local Urbanization	-0.12	-0.53, 0.26	73.4
	Local Patch Density	0.08	-0.19, 0.35	72.2
	Local Agricultural Footprint	-0.08	-0.35, 0.19	71.6
Weasels	Local Urbanization	0.03	-1.04, 1.06	53.0
	Local Patch Density	0.05	-0.36, 0.45	61.4
	Local Agricultural Footprint	-0.13	-0.58, 0.32	72.0
White-tailed Deer	Local Urbanization	-1.25	-1.7, -0.80	100.0
	Local Patch Density	0.12	-0.15, 0.39	81.4
	Local Agricultural Footprint	0.01	-0.34, 0.36	51.8
Woodchuck	Local Urbanization	-0.27	-0.90, 0.35	80.8
	Local Patch Density	0.03	-0.31, 0.36	57.5
	Local Agricultural Footprint	-0.13	-0.51, 0.24	76.8

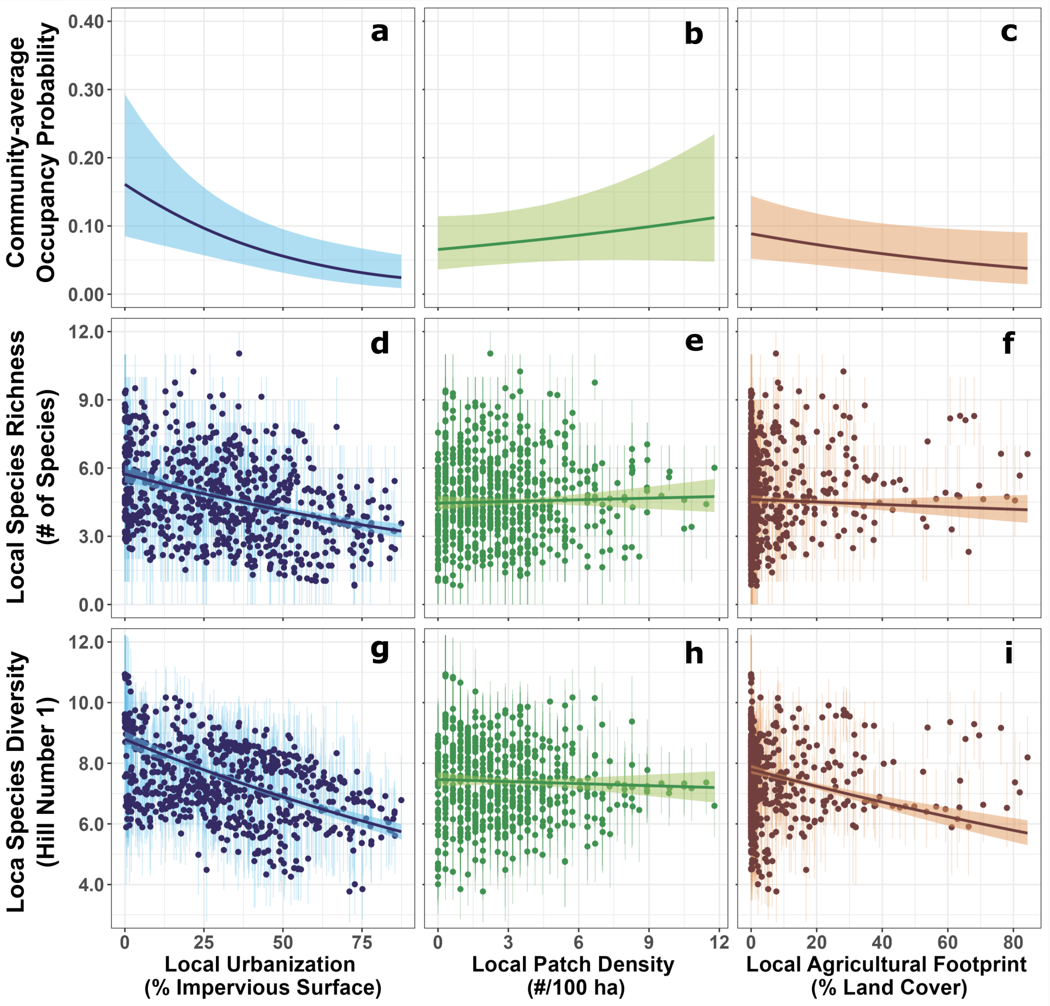

Figure C.1: Community-average occupancy probability, species richness, and species diversity across 725 sites in 20 North American cities, relative to three local, within-city predictor variables: urbanization (**a,b,c**), natural patch density (**d,e,f**), and agricultural footprint (**g,h,i**). The response variables species richness and species diversity, respectively, refer to the total number of species at each site (Hill Number 0) and the number of species at each site weighted by species evenness (the exponentiated Shannon index; Hill Number 1). Based on modeled effects of within-city variables on occupancy (Table 1, Effect Type 1) and on richness and diversity (Table 2, Effect Type 1), we predicted occupancy, richness, and diversity values across hypothetical ranges of each within-city variable, with all other variables held constant at their mean values; we then represented the median and 95% Bayesian credible interval of these predicted values using the trendlines and their corresponding shaded regions. The points and bars correspond to the mean and 95% CRI of 10,000 posterior estimates of richness and diversity at each camera site, based on actual ranges of within-city variables.

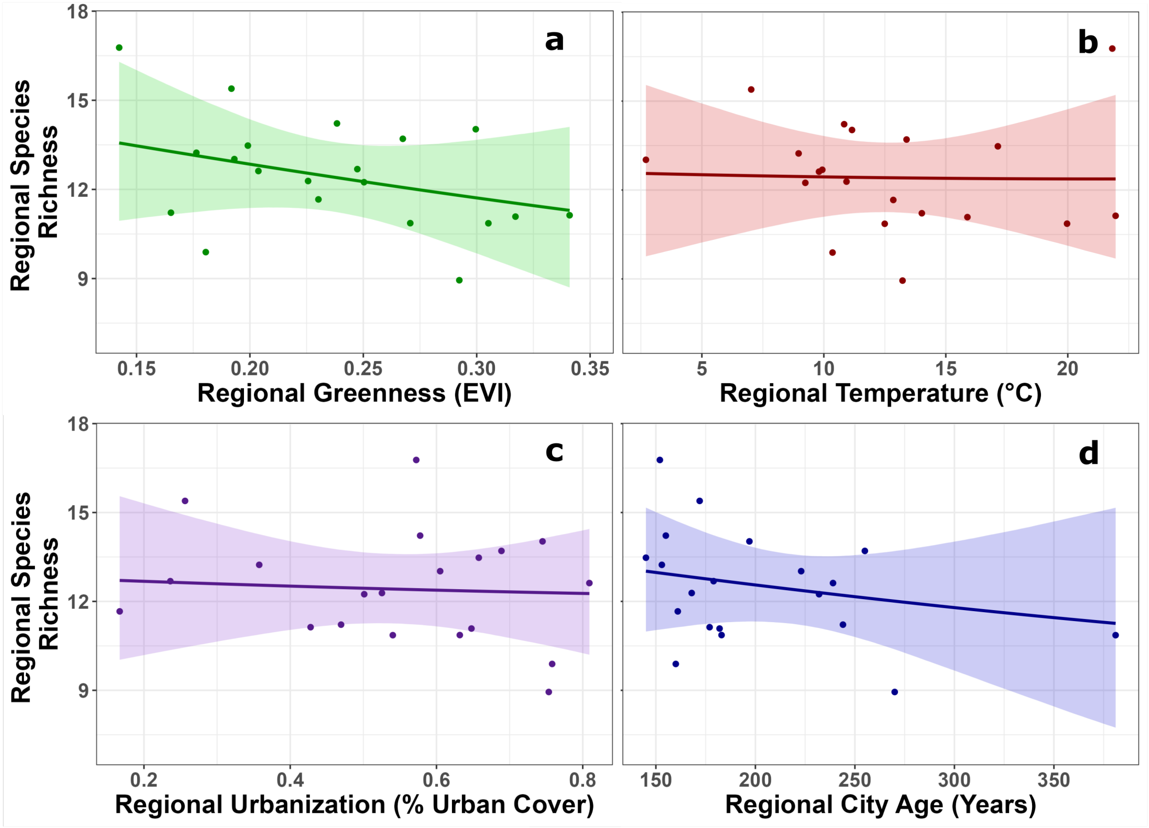

Figure C.2: Regional species richness (γ_r) in relation to regional environmental covariates: greenness (**a**); temperature (**b**); urbanization (**c**); and city age (**d**). Estimates of γ_r were calculated as the sum of predicted species presence with a region ($\gamma_r = \sum_s^S \omega_{s,r}$), using the probability of regional species presence Ω_r to correct observed species richness for the region-wide imperfect detection of species. Points correspond to the mean each of 20 city's γ_r, drawn from 60,000 Bayesian posterior estimates. Trendline and shaded region respectively depict the median and 95% Bayesian credible interval of γ_r predicted across hypothetical ranges of among-city covariate values, where all other covariates are held constant at their mean. We represented regional greenness using the Enhanced Vegetation Index (EVI), regional temperature corresponds to mean annual temperature, regional urbanization was estimated as the region's overall percentage of urban land cover types, and we measured city age as the approximate number of years since Euroamerican colonization of the metropolitan region.

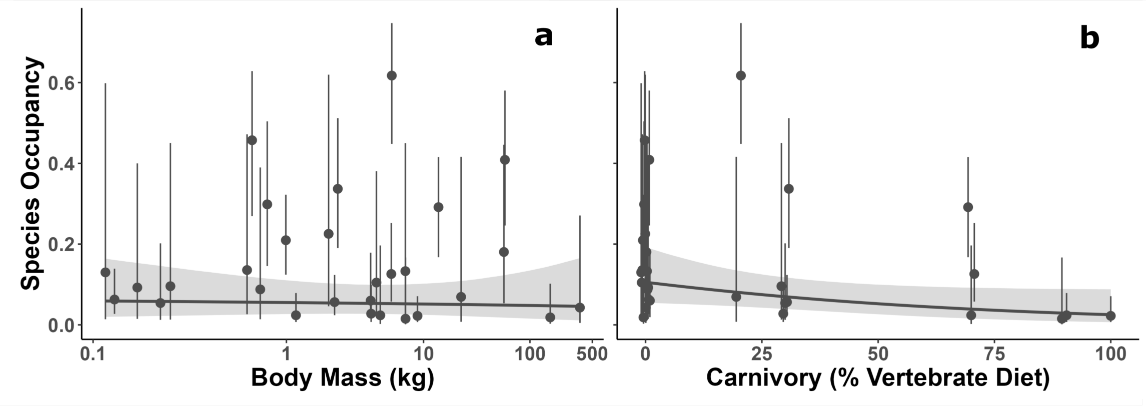

Figure C.3: Influences of species traits on site-level mammal occupancy in North America. **a**, body mass represented by the log-transformed mean body mass of each species (in kg). **b**, carnivory, calculated as the percentage of vertebrate prey in each species' diet. Each point and bar respectively represent the mean and 95% Bayesian credible interval (CRI) of estimated occupancy probabilities for 29 commonly detected mammal species (excluding eight species detected in fewer than 10 days total). Trendline and shaded region depict the median and 95% CRI of response variables predicted across a hypothetical range of trait values. Results primarily demonstrate that more carnivorous species are generally rarer.

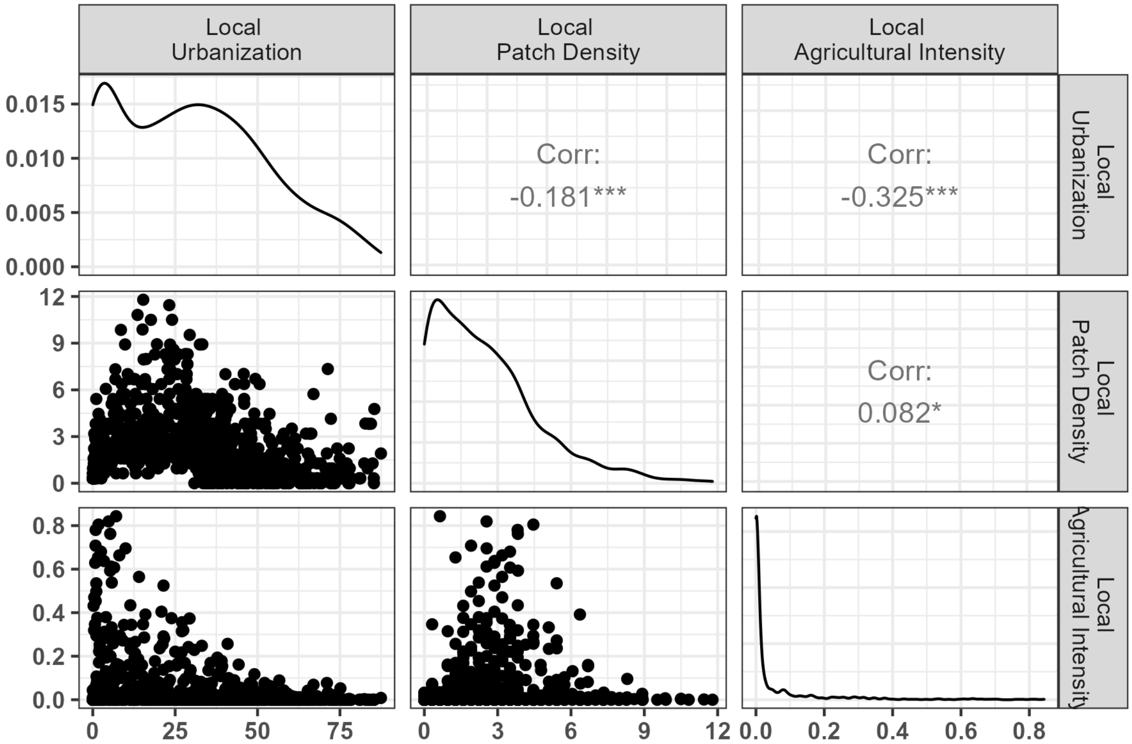

Figure C.4: Collinearity between pairs of within-city covariates (urbanization, natural patch density, and agricultural intensity) across 725 sites in 20 North American cities. The diagonal cells of the figure depict the frequency distribution of values for each covariate, upper-right half of the figure depicts the Pearson correlation between each pair of covariates, and the lower-left half visualizes each correlation in the form of a scatterplot.

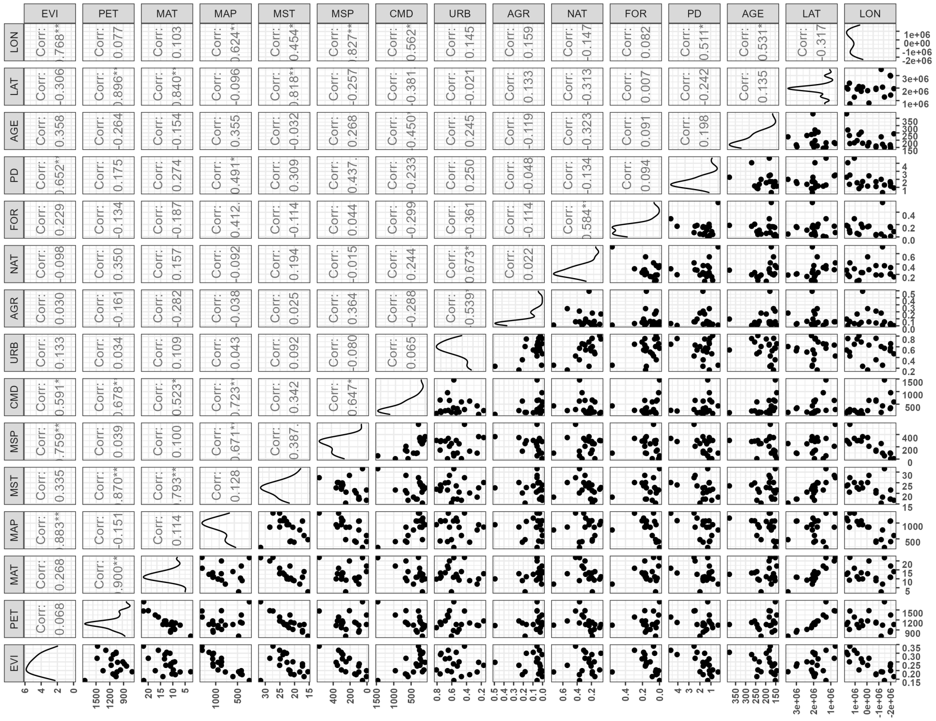

Figure C.5: Collinearity between pairs of regional variables assessed for potential inclusion as predictors of species occupancy, richness, and diversity among 20 North American cities. The diagonal cells of the figure depict the frequency distribution of values for each variable, upper-right half of the figure depicts the Pearson correlation between each pair of variables, and the lower-left half visualizes each correlation in the form of a scatterplot. We selected four variables to include in our final analysis as among-city covariates: vegetation greenness, mean annual temperature, regional urbanization, and city age. EVI = Enhanced Vegetation Index; PET = potential evapotranspiration; MAT = mean annual temperature; MAP = mean annual precipitation; MST = mean summer temperature; MSP = mean summer precipitation; CMD = climatic moisture deficit; URB = urban land cover (regional urbanization); AGR = agricultural land cover (regional agricultural area); NAT = natural land cover; FOR = woody vegetation (forest, shrubland) cover; PD = natural patch density; AGE = city age (years since colonization); LAT = latitude of city center; LON = longitude of city center.

APPENDIX D

SUPPLEMENTARY DATA FOR CHAPTER 4

Table D.1: Results for tests of multi-collinearity among explanatory variables in global mixed effect models of wildlife attitudes. Values depict the Variable Importance Factor (VIF) and tolerance levels, and their corresponding 95% confidence interval (CI), for each explanatory variable.

Variable Subset	Explanatory Variable	VIF (95% CI)	Tolerance (95% CI)
Ideological	Wildlife Value Orientation	1.18 (1.09, 1.36)	0.84 (0.74, 0.91)
	Desert Identity	1.18 (1.09, 1.35)	0.85 (0.74, 0.92)
Environmental	Urbanization	1.08 (1.02, 1.29)	0.93 (0.77, 0.98)
	Vegetation	1.20 (1.11, 1.37)	0.83 (0.73, 0.90)
	Distance to Desert Parks	1.35 (1.23, 1.54)	0.74 (0.65, 0.82)
Sociodemographic	Income	1.50 (1.35, 1.71)	0.67 (0.58, 0.74)
	Education	1.27 (1.16, 1.44)	0.79 (0.69, 0.86)
	Age	1.19 (1.10, 1.37)	0.84 (0.73, 0.91)
	Pets	1.12 (1.05, 1.30)	0.89 (0.77, 0.95)
	Gender	1.06 (1.01, 1.31)	0.94 (0.76, 0.99)
	Latino Identity	1.23 (1.13, 1.40)	0.81 (0.71, 0.88)

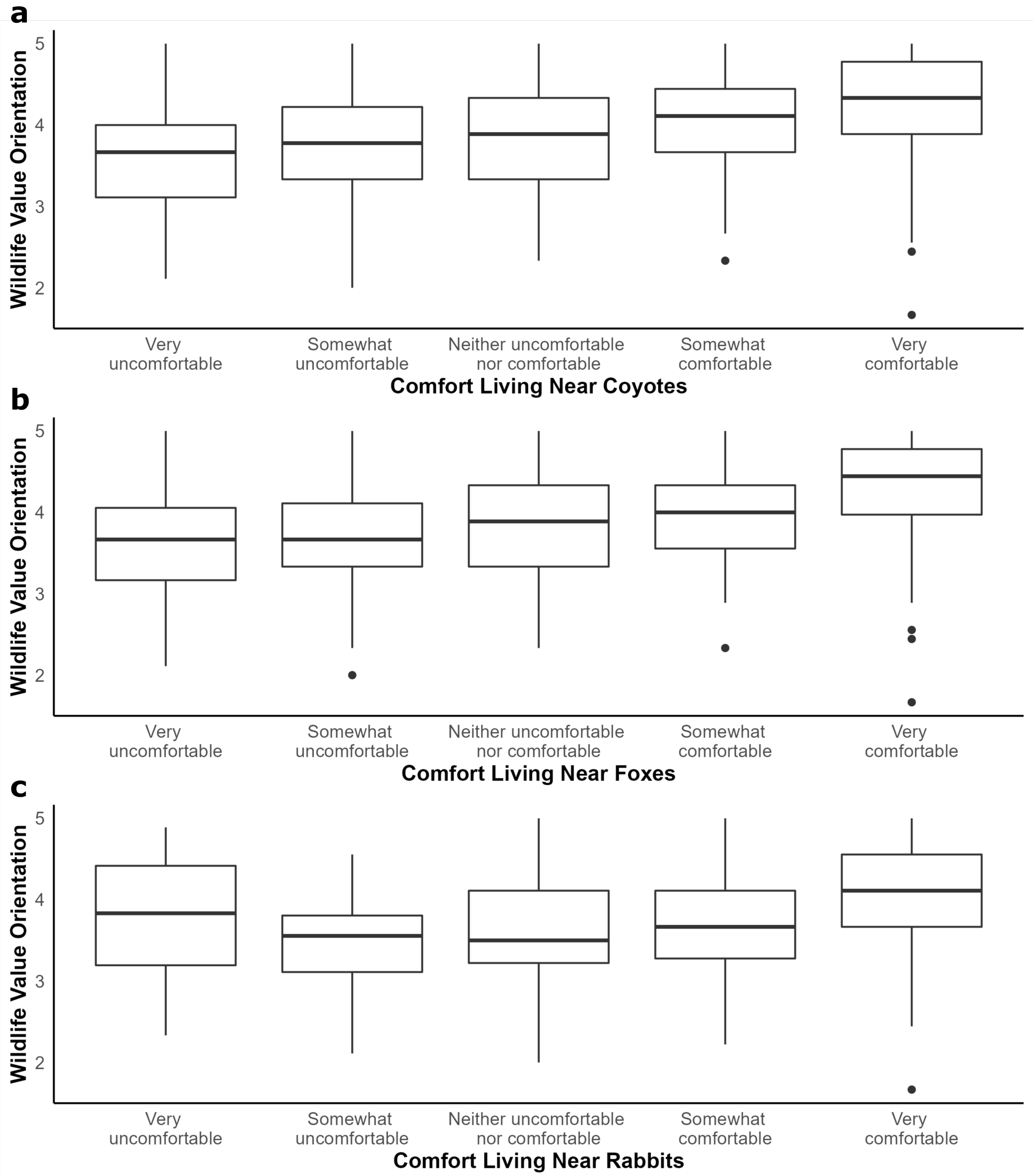

Figure D.1: Wildlife value orientations of residents from twelve neighborhoods across the Phoenix Metropolitan Area, Arizona, USA, relative to their reported levels of comfort living near three wildlife groups: coyotes (a), foxes (b), and rabbits (c).