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PRIMARY RESEARCH ARTICLE

Wealth and urbanization shape medium and large terrestrial mammal communities

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Abstract

Urban biodiversity provides critical ecosystem services and is a key component to environmentally and socially sustainable cities. However, biodiversity varies greatly within and among cities, leading to human communities with changing and unequal experiences with nature. The “luxury effect,” a hypothesis that predicts a positive

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correlation between wealth, typically measured by per capita income, and species richness may be one indication of these inequities. While the luxury effect is well studied for some taxa, it has rarely been investigated for mammals, which provide unique ecosystem services (e.g., biological pest control) and exhibit significant potential for negative human–wildlife interactions (e.g., nuisances or conflicts). We analyzed a large dataset of mammal detections across 20 North American cities to test whether the luxury effect is consistent for medium- to large-sized terrestrial mammals across diverse urban contexts. Overall, support for the luxury effect, as indicated by per capita income, was inconsistent; we found evidence of a luxury effect in approximately half of our study cities. Species richness was, however, highly and negatively correlated with urban intensity in most cities. We thus suggest that economic factors play an important role in shaping urban mammal communities for some cities and species, but that the strongest driver of urban mammal diversity is urban intensity. To better understand the complexity of urban ecosystems, ecologists and social scientists must consider the social and political factors that drive inequitable human experiences with nature in cities.

KEYWORDS

environmental justice, human–wildlife interactions, luxury effect, urban ecology, urban wildlife

1 | INTRODUCTION

Urban biodiversity is an essential part of sustainable, healthy cities (Chamberlain et al., 2020; Lambert & Donihue, 2020; Lepczyk et al., 2017). As urban populations increase, the need for biodiverse landscapes becomes all the more important. Urban species underpin many ecosystem services (Mace et al., 2012) and act as ecosystem service providers; for example, urban trees mitigate urban heat, air and water pollution, and flooding, and provide recreational and aesthetic benefits (Kowarik, 2011). Interactions with urban organisms can also enhance human mental and physical health and build connections to wildlife and nature that benefit well-being (Bell et al., 2018; Fuller et al., 2007; Liddicoat et al., 2018; Lovell et al., 2014; Luck et al., 2011; Wolf & Robbins, 2015). Given the importance of biodiversity to urban ecosystem function and society, it is therefore critical to identify how biodiversity is distributed within cities to ensure urban communities equitably benefit.

Urban environments are inherently heterogeneous due partly to an unequal distribution and proportion of green space, vegetative diversity, impervious cover, and human population density. Such factors structure urban biodiversity (e.g., Fidino et al., 2020; Guetté et al., 2017; Magle et al., 2016; Morelli et al., 2018; Ordeñana et al., 2010), in ways that often lead to lower species richness in the densely developed urban core relative to less developed areas (Fidino et al., 2020; Gagné et al., 2016). However, these biodiversity trends along urban gradients may also result from social dynamics that lead to heterogeneity in land cover across the urban landscape. Social–ecological systems research has repeatedly emphasized how social dynamics affect land management decisions that ultimately

structure human-driven disturbances, shape urban wildlife community dynamics, and influence biodiversity (Andrade et al., 2021; Liu et al., 2007; Wood & Esaian, 2020). As such, many social variables have been linked to urban biodiversity and land management decisions. Per capita income, for example, has been positively associated with the diversity and distribution of plant (Clarke et al., 2013; Hope et al., 2003), avian (Kinzig et al., 2005; Loss et al., 2009), lizard (Ackley et al., 2015), arthropod (Leong et al., 2016), and bat communities (Li & Wilkins, 2014). More recently, this emergent positive spatial correlation between neighborhood wealth and biodiversity has been viewed as driving the structure of urban vegetation and biotic communities. This relationship, termed the “luxury effect” (Hope et al., 2003; Leong et al., 2018), has received considerable attention as it may represent a universal governing principle of urban wildlife distribution (Chamberlain et al., 2019; Kuras et al., 2020).

While the luxury effect appears to hold true across a majority of studies (Chamberlain et al., 2019; Hassell et al., 2021; Kuras et al., 2020), the single-city nature of most urban ecological research makes it difficult to assess patterns across cities. In fact, the reverse effect—for example, high vegetation levels associated with low-income areas—has been found in some single-city studies (Li et al., 2019; Rigolon, 2016) while other studies demonstrate variable relationships derived from factors such as land-use history, vacancy, and race (Berland & Hopton, 2014; Berland et al., 2020; Gerrish & Watkins, 2018; Watkins & Gerrish, 2018). Meanwhile, features of the built environment (e.g., roads, buildings) may limit habitat and obscure the effects of income on wildlife. While a meta-analysis on the results of single-city studies could provide insights on the luxury effect across diverse contexts (Kuras et al., 2020), this approach is

hindered by differences in sampling methodology among studies. To control for such biases, well-designed multi-city comparative approaches that follow systematic protocols are necessary (Magle et al., 2019).

Through a multi-city collaborative project, the Urban Wildlife Information Network (UWIN), we were able to conduct a systematic analysis to compare the extent to which income levels are linked to medium- and large-sized mammal species richness across 20 North American cities (Figure 1) while assessing the effect of urban intensity within and among cities. Very few studies have simultaneously investigated relationships between socioeconomics (i.e., median household income) and development (i.e., urban intensity) on terrestrial mammal distributions (but see Magle et al., 2016). The majority of luxury effect studies thus far have focused on avian species (Chamberlain et al., 2019; Lerman & Warren, 2011), which tend to rely less on habitat connectivity than terrestrial mammals and, as a result, may be less influenced by urbanization and more by the socioeconomic characteristics of a neighborhood. Medium-sized mammals are ideal target species to evaluate the luxury effect across broad regions as they are more likely to demonstrate pronounced responses to terrestrial heterogeneities in the landscape, often garner public attention

and are frequently targeted for both conservation and pest management (Gehrt et al., 2010).

We tested the hypothesis that the luxury effect exists for medium- to large-sized North American mammals with camera trap data from 20 UWIN cities (Magle et al., 2019). We predicted that if a luxury effect exists for urban mammals, positive relationships would exist between species richness in urban habitat patches and per capita income of the neighborhood surrounding the camera sites. Likewise, as mammal species richness at the local scale typically decreases with urban intensity (Fidino et al., 2020; Ordeñana et al., 2010), we sought to assess the strength of this relationship across multiple cities. To quantify these relationships, we used a Bayesian multi-city, multi-species occupancy model which estimates species richness along and species-specific responses to environmental gradients (Sutherland et al., 2016). Our results not only advance knowledge of habitat use for a large number of high-profile urban wildlife species, they also provide insights into inequities in urban human-wildlife interactions across the United States and Canada and in the distribution of potential ecosystem services and disservices associated with such interactions. Furthermore, such investigations provide an unparalleled opportunity to develop innovative, sustainable strategies for supporting urban environmental equity and health.

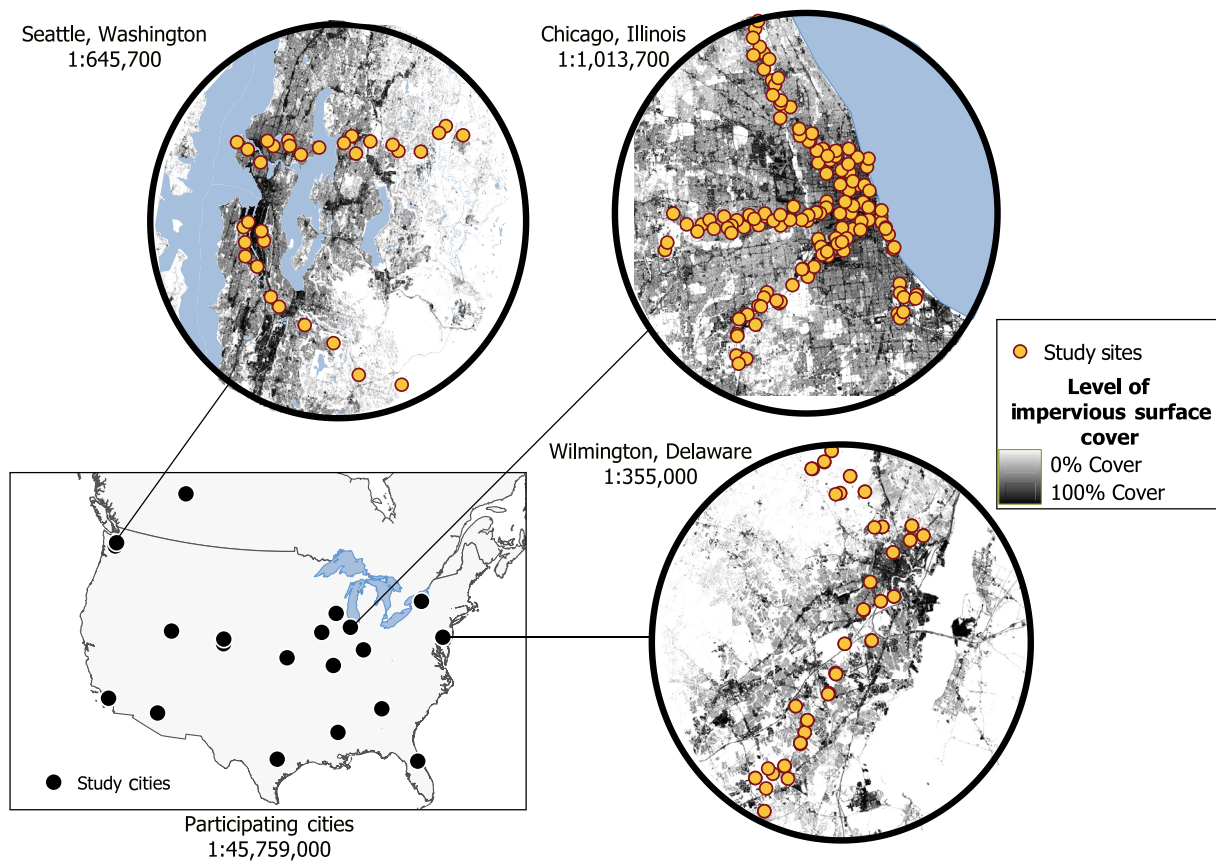


FIGURE 1 Map of the distribution of the 20 cities across North America that contributed data for this analysis (bottom left) as well as three representative examples of the distribution of camera trapping study sites along each city's respective urbanization gradient. Points for Tacoma, Washington and Seattle, Washington are partially overlapping, as are points for Denver, Colorado and Fort Collins, Colorado. For a map with the study sites for all cities see Figure S1

2 | MATERIALS AND METHODS

2.1 | Sampling

In all, 20 UWIN cities provided data to evaluate the luxury effect (Figure 1). In each of these cities, researchers followed a standard protocol to select sites for camera trapping along a gradient of urbanization (for more details, see Fidino et al., 2020; Magle et al., 2019). These locations, hereafter sites, represented a diversity of habitable formal and informal greenspace for wildlife such as city parks, cemeteries, natural areas, school yards, private property, and golf courses. Sites were separated by at least 1 km, which exceeds the home range extent of most city-dwelling mammals (Feldhamer et al., 2003). Larger carnivores, however, likely have home ranges that far exceed this distance and therefore estimates associated with these species or others with large home range extents should be interpreted as metrics of relative use instead of true occupancy.

A camera trap was placed at each site for at least 28 consecutive days in January, April, July, and October (i.e., four primary sampling periods per year) between July 2016 and January 2020. Because UWIN researchers joined the network in different years, the number of sampling periods varied among cities. During camera deployments, we initially placed a scented synthetic fatty acid disk in view of the camera to possibly increase species detectability, though we later found this lure to have little to no effect for most urban-dwelling mammals (Fidino et al., 2020). As such, lure use was discontinued starting in October 2019. Camera trap images were identified to the species level by trained experts. For each site, sampling period, and species, we calculated the number of days a species was detected as well as the number of days a camera trap was operational. These data were then used to quantify species occupancy and detectability among and within cities. All detected species were native to North America.

2.2 | Statistical analysis

We used a multi-city multi-species occupancy model to estimate medium- to large-sized mammal species richness at each site as well as the overall medium- to large-sized mammal richness of each city (Sutherland et al., 2016). This approach was necessary because some cities fell outside the known range of some mammals and therefore we needed an additional probability model to estimate whether a species was available for sampling within a city. We briefly describe this model because their formulation has been covered in depth (Sutherland et al., 2016).

The first level of this hierarchical model estimated if a species was available for sampling in a city. For s in $1, \dots, S$ species and c in $1, \dots, C$ cities, let $\pi_{s,c}$ be the probability species s was present in city c and $x_{s,c}$ be a Bernoulli random variable that equaled one if species s is in city c , otherwise it was zero, such that $x_{s,c} \sim \text{Bernoulli}(\pi_{s,c})$. Because of this, $\sum_{s=1}^S x_{s,c}$ represented the overall richness of the S species in city c . Using the logit-link, we let $\pi_{s,c}$ be a linear function

of the distance (km) city c was from the edge of the known range of species s . Species ranges came from IUCN red list data (IUCN, 2020). Because the IUCN data may not be fully accurate, we opted to include this as a covariate within the model to estimate how strongly a species presence in a city was related to their known range rather than simply excluding cities that fell outside of a species range boundary. Distances from a species range boundary were negative if a city fell outside a species range and were positive if a city fell within. Large bodies of freshwater (e.g., the Great Lakes) were filled in for these distance calculations otherwise distances generated for Chicago, Illinois were always to Lake Michigan. Species had their own intercept and slope term for this layer of the model, though these species-level coefficients varied around a community-level mean (i.e., this was a varying intercept, varying slope model with species as a random effect).

The next level of the model estimated site occupancy within each city. In addition to the S species and C cities, there were i_c in $1, \dots, I_c$ sites and t_c in $1, \dots, T_c$ sampling periods, which are indexed by c because the number of sites and sampling periods varied among cities. We drop the additional subset of i and t throughout the model explanation for simplicity. Let z_{scit} be a Bernoulli random variable that equaled one if species s was present at city c , site i , and sampling period t , $z_{scit} \sim \text{Bernoulli}(\psi_{scit} \times x_{s,c})$, where ψ_{scit} is the probability of occupancy. Therefore, if a species was present in a city, $x_{s,c} = 1$, then $z_{scit} = 1$ with $\Pr(\psi_{scit})$. Unlike a multi-season occupancy model that estimates colonization and extinction rates among sampling periods, we have opted to estimate occupancy during each time step because some cities had insufficient data for the additional model complexity.

We used the logit-link to let ψ_{scit} vary as a function of median household income and an urban intensity metric we created using principal component analysis within a 1 km buffer of each site. We used a 1 km buffer because it encompassed the average home range of many mammals in our analysis save for some large-bodied carnivores and ungulates (Feldhamer et al., 2003). As sites were a minimum of 1 km apart, the 1 km buffer we used therefore created overlapping landscapes, which has traditionally been perceived to violate the assumption of statistical independence among sampling locations (Zuckerberg et al., 2020). This concern, however, is misdirected as overlapping landscapes do not increase spatial autocorrelation in model errors (Zuckerberg et al., 2012). Income data were calculated as the average median household income for all census blocks that intersected a 1 km buffer around each site from the 2014–2018 American Community Survey for all US cities and the 2016 Canadian Census for Edmonton, Alberta (Statistics Canada, 2016; U.S. Census Bureau, 2018). Because the cost of living varies among cities, we scaled median income by the average cost of a one-bedroom apartment in each city. Apartment data were collected from the Apartment List's rent estimate database for all cities other than Sanford, Florida; Wilmington, Delaware; and Edmonton, Alberta (Popov et al., 2020). Sanford and Wilmington data came from Rent Jungle while Edmonton data came from the Government of Alberta's Regional Dashboard (Government of Alberta, 2020;

Rent Jungle, 2020). We calculated the urban intensity metric as the first principal component of mean normalized difference vegetation index (NDVI), impervious cover (percent), and population density (1000s of people km⁻²) within 1 km of each site, which explained 66.46% of the variation in these data. Loadings for NDVI, impervious cover, and population density were, respectively, -0.57, 0.63, and 0.52. As such, this metric represented a gradient of increased levels of NDVI (i.e., vegetation) when negative to increased levels of impervious cover and population density when positive. Mean NDVI was calculated from the MODIS Vegetation Index (Didan et al., 2015), impervious cover was calculated from the 2016 National Landcover Database Developed Imperviousness product for all cities in the United States and from building footprint and road data from the City of Edmonton's Open Data Portal (2018, 2019; Xian et al., 2011; Yang et al., 2003), and population density was calculated from the Silvis Lab's block-level housing density change database for U.S. cities and the 2016 Canadian Census for Edmonton (Helmets, 2010; Radeloff et al., 2010; Statistics Canada, 2016). To make parameters less sensitive to unequal sample sizes among cities and increase interpretability of parameters, we group mean-centered covariates by subtracting the respective city-specific mean (Milliren et al., 2018).

Because we sampled multiple species across multiple cities and sampling periods, we used a partially crossed random effect structure to parameterize the log-odds coefficients for ψ_{scit} . We used a nearly identical parameterization for the intercept and slope terms. As such, we explain this hierarchy once, for the intercept, and then describe how the slope terms differ. The top level of this hierarchy estimated a global average (ω_{global}) that partially informed the average response of each species (u_s) across cities and sampling periods. The variation of each species average from the global average (σ_{global}) was assumed to be normally distributed such that:

$$\omega_{\text{global}} \sim \text{Cauchy}(0, 2.5),$$

$$\sigma_{\text{global}} \sim \text{Inv} - \text{Gamma}(1, 1),$$

$$u_s \sim \text{Normal}(\omega_{\text{global}}, \sigma_{\text{global}}).$$

Each species average response, u_s , was then used to estimate species-specific coefficients for each city (u_{sc}). We again assumed the variation of u_{sc} around u_s was normally distributed with the standard deviation term σ_s . However, to accommodate rare species or those only detected in a few cities, we incorporated hyperpriors for the shape (a_1) and rate (b_1) terms of the inverse-gamma distribution that informs σ_s such that:

$$a_1 \sim \text{Uniform}(0, 10),$$

$$b_1 \sim \text{Uniform}(0, 10),$$

$$\sigma_s \sim \text{Inv} - \text{Gamma}(a_1, b_1),$$

$$u_{sc} \sim \text{Normal}(u_s, \sigma_s).$$

For slope terms, the parameter hierarchy stops at this level. The final level of the parameter hierarchy allowed the model intercept (u_{1sc} , the 1 indicates this is the model intercept) to vary (σ_c) across multiple sampling periods around (u_{sc}). Because some cities only had one sampling period of data, we again used hyperpriors for the shape (a_2) and rate (b_2) terms of the inverse Gamma distribution that informs σ_c :

$$a_2 \sim \text{Uniform}(0, 10),$$

$$b_2 \sim \text{Uniform}(0, 10),$$

$$\sigma_c \sim \text{Inv} - \text{Gamma}(a_2, b_2),$$

$$u_{sc} \sim \text{Normal}(u_{sc}, \sigma_c).$$

Using this parameter hierarchy for the intercept and two slope terms made the linear predictor $\text{logit}(\psi_{scit}) = u_{1sc} + u_{2ct} \times \text{income}_{cit} + u_{3ct} \times \text{URB}_{cit}$.

We also corrected for imperfect species detection. Let y_{scit} be a binomial random variable that represents the number of days species s was detected at city c , site i , and sampling period t . Likewise, let j_{cit} be the number of days sampled at city c , site i , and sampling period t . The observation level of the model is then $y_{scit} \sim \text{Binomial}(j_{cit}, p_{scit} \times z_{scit})$, where p_{scit} is the probability of detecting a species given $z_{scit} = 1$. As with occupancy, we used the logit-link to let p_{scit} vary as a function of median income and urban intensity. We used the same hierarchy described for occupancy to parameterize detection model coefficients.

We used a Bayesian framework to estimate model parameters. Models were fit in JAGS v 4.3.0 (Plummer, 2003) via the R programming language v 4.0.0 (R Core Team, 2020). Following a 1000 step adaptation and 55,000 step burn in, the posterior was sampled 180,000 times across three chains. Chains were thinned by 3 due to the complexity of tracking every model parameter for a total of 60,000 posterior samples. To verify model convergence, we checked to see that the Gelman-Rubin diagnostic for each parameter was <1.10 and visually inspected plots of the MCMC chains to ensure proper mixing (Gelman et al., 2014). We considered slope terms in the model as informative if their 95% credible interval did not include zero.

2.3 | Deriving correlations between species richness and environmental gradients within cities

We estimated species richness per city, site, and sampling period from posterior simulations as $\sum_{s=1}^S z_{scit}$. We did this for 9000 random draws from our 60,000 posterior samples. With each of the 9000 draws per city, site, and sampling period, we calculated a Pearson correlation coefficient between richness and median income as well as between richness and urban intensity. This process provided a posterior sample of correlations between richness and the two

environmental gradients (i.e., median income and urban intensity), which we used to calculate median correlations and their associated 95% credible intervals. We considered a city to have a positive luxury effect if the median correlation between income and species richness was positive and the associated 95% credible interval of the estimate excluded zero. Likewise, we considered a city to have a negative luxury effect if the median correlation between income and species richness was negative and the associated 95% credible intervals excluded zero. We used an identical approach with median correlations and 95% credible intervals between urban intensity and species richness to evaluate positive and negative relationships for each city. Code and data to reproduce all analyses are available here: <https://doi.org/10.5281/zenodo.5093795>.

3 | RESULTS

We collected medium- and large-sized mammal detections during 117,964 camera trapping days from 3924 camera deployments at 905 unique sites across 20 North American cities (Figure 1). Study cities varied in degree of urbanization, population density, wealth, and wildlife community composition, among other differences. The data covered four sampling periods per year in January, April, July, and October between July 2016 and January 2020 (i.e., 15 total sampling periods). The number of sampling periods varied among cities (mean = 5.25; min = 1 from Phoenix, Arizona and Seattle, Washington; max = 13 from Chicago, Illinois). The number of sites sampled along each city's urbanization gradient also varied (mean = 45.25; min = 22 from Madison, Wisconsin; max = 129 from Salt Lake City, Utah). For a detailed map with city names (see Figure S1).

We detected a total of 45 species, although roughly half of them were too rare to be analyzed in our multi-city multi-species occupancy model (i.e., parameters failed to converge for these species). Therefore, we analyzed the data from the remaining 26 species, which represented a diverse medium-to-large North American mammal community that varied in their urban tolerance (Gehrt et al., 2010; Magle et al., 2019). The most common species was the raccoon (*Procyon lotor*; 22,242 detections across 19 cities), and the most rare species was the North American porcupine (*Erethizon dorsatum*; 29 detections across 2 cities). Median species richness among cities was 14 (95% CI = 9, 18). Iowa City, Iowa had the greatest species richness (median = 18, 95% CI = 18, 19) whereas Phoenix, Arizona had the lowest species richness (median = 10, 95% CI = 8, 13). Distance to a species range boundary was strongly associated with the probability a species was available for sampling within a city. On average, a city 500 km outside a given species range boundary had a 0.12 (95% CI = 0.04, 0.22) probability the species was available for sampling, whereas a city 500 km inside a species range boundary had a 0.87 (95% CI = 0.77, 0.95) probability. This probability exceeded 0.95 for cities 760 km within a species range boundary. See Supporting Information for a list of all species as well as a summary of their detections.

3.1 | Evidence for the luxury effect

We observed a luxury effect (i.e., a positive correlation between income and species richness whose 95% credible interval did not overlap zero) in 9 of the 20 cities, though median estimates were positive for 18 of the 20 cities (Figure 2). Of these nine cities, the most positive correlation between species richness and median income was Saint Louis, Missouri ($r = .54$; 95% CI = 0.37, 0.67). In Saint Louis, the average species richness at the five sites with the highest median income was 7.23 (95% CI = 6.23, 8.38) and was approximately 78% greater than the five sites with the lowest median income (mean = 4.07; 95% CI = 3.33, 5.00). Of the cities where we observed a luxury effect, the weakest positive correlation between richness and income was Indianapolis, Indiana ($r = .22$; 95% CI = 0.08, 0.36). In Indianapolis, average species richness at the five sites with the highest median income was 7.45 (95% CI = 6.90, 8.23) and was only about 9% greater than the five sites with the lowest median income (mean = 6.84; 95% CI = 6.38, 7.38).

3.2 | Urban intensity and species richness

Species richness was negatively correlated with urbanization in 16 of the 20 cities (Figure 3). Phoenix, Arizona had the strongest negative correlation ($r = -.72$; 95% CI = $-0.82, -0.57$). Average species richness in Phoenix's five most urban sites was 2.0 (95% CI = 1.0, 3.2), which was one-third the species richness in their least urban sites (mean = 6.0; 95% CI = 5.0, 7.4). Chicago, Illinois also had a strong negative correlation between species richness and urban intensity ($r = -.57$; 95% CI = $-0.63, -0.49$). Average species richness in Chicago's five most urban sites was 4.21 (95% CI = 3.85, 4.90) and was roughly 55% lower than the five least urban sites (mean = 7.56; 95% CI = 7.17, 8.14).

3.3 | Differences in occupancy among species and cities

The hierarchical structure of the log-odds parameters provided an average occupancy estimate of the medium- and large-sized mammal community among cities, average occupancy estimates for each species among cities, and species-specific occupancy estimates within each city (Figure 4). Across species and cities, the community average occupancy was only 0.14 (95% CI = 0.08, 0.24). Variation in species-specific occupancy around this community average, however, was high (median standard deviation = 1.40, 95% CI = 1.03, 1.95). The average among-city occupancy of raccoon, for example, was roughly 4.5 times greater than the community average (median = 0.65; 95% CI = 0.50, 0.77). Likewise, the average among-city occupancy of muskrat was roughly 10 times lower than the community average (median = 0.01; 95% CI = 0.00, 0.04), though it should be noted camera traps are not optimized for detecting muskrat. In general, common urban-adapted species such as raccoon had

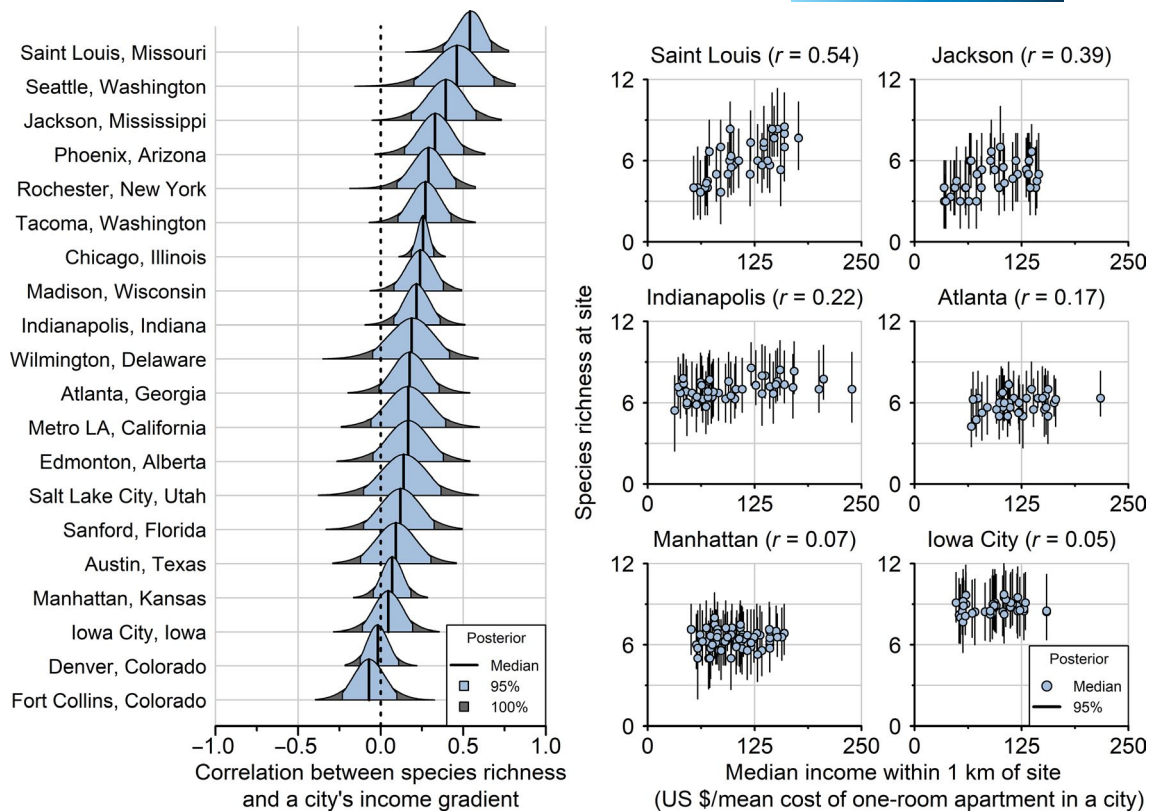


FIGURE 2 Nine of the twenty cities showed evidence of the luxury effect, although the magnitude of the correlation between median income and species richness at sites differed among cities. We estimated species richness with our multi-city multi-species occupancy model using data from 3924 camera deployments at 905 unique sites throughout 20 North American cities. The left plot shows the city-specific correlation between mammalian species richness and median income. For each city, Pearson correlation coefficients were calculated between median household income within 1 km of each study site (US \$ scaled by the average cost of a one-bedroom apartment per city) and 9000 posterior draws of the detection-corrected species richness estimate per site and sampling period. For reference, we have placed a vertical dotted line at 0 (i.e., no correlation) to compare with the posterior correlation estimates for each city. The right plots demonstrate the varying relationships between average species richness and the income gradient across six cities that demonstrate a strong luxury effect (top two) to weak (middle two) or no effect (bottom two). Point estimates on the right plots represent the average species richness for a site across sampling periods while vertical lines are 95% credible intervals

average occupancy estimates greater than the community average, whereas those less common such as woodchuck had among-city estimates on par with or less than the community average (Figure 4). Species occupancy within cities also varied around their respective among-city average. Red fox occupancy in Wilmington, Delaware was 0.91 (95% CI = 0.84, 0.96), roughly 3.3 times greater than the average red fox occupancy among cities (median = 0.28; 95% CI = 0.14, 0.45). Conversely, although the among-city occupancy of raccoon was high, their occupancy in Phoenix, Arizona was only 0.31 (95% CI = 0.07, 0.85). In general, species occupancy estimates within cities were more variable for species with a higher among-city average occupancy (Figure 4).

3.4 | Differences in species' responses to income and urbanization

The hierarchical structure of the slope terms similarly provided an average log-odds response of this mammal community to income

and urbanization gradients among cities, average log-odds responses for each species to income and urbanization gradients among cities, and species-specific log-odds responses to income and urbanization gradients within each city (Figure 5). In general, species responded less strongly to the income gradient of a city than the urbanization gradient.

Across species and cities, the average log-odds response of this mammal community to income was negligible (community median = 0.02; 95% CI = -0.16, 0.19). The average response of these mammals to urban intensity among cities, however, was negative (community median = -0.25; 95% CI = -0.46, -0.04), indicating that species occupancy on average was highest at lower levels of urban intensity. Additionally, as the 95% credible interval of every species' among-city average response to income bounded zero, there was little evidence of species uniformly increasing or decreasing their occupancy along the income gradient of cities (Figure 5). Conversely, 8 of the 26 species (i.e., white-tailed deer, moose, mule deer, bobcat, nine-banded armadillo, elk, striped skunk, and coyote) responded negatively to urban intensity among cities at the 0.95 level.

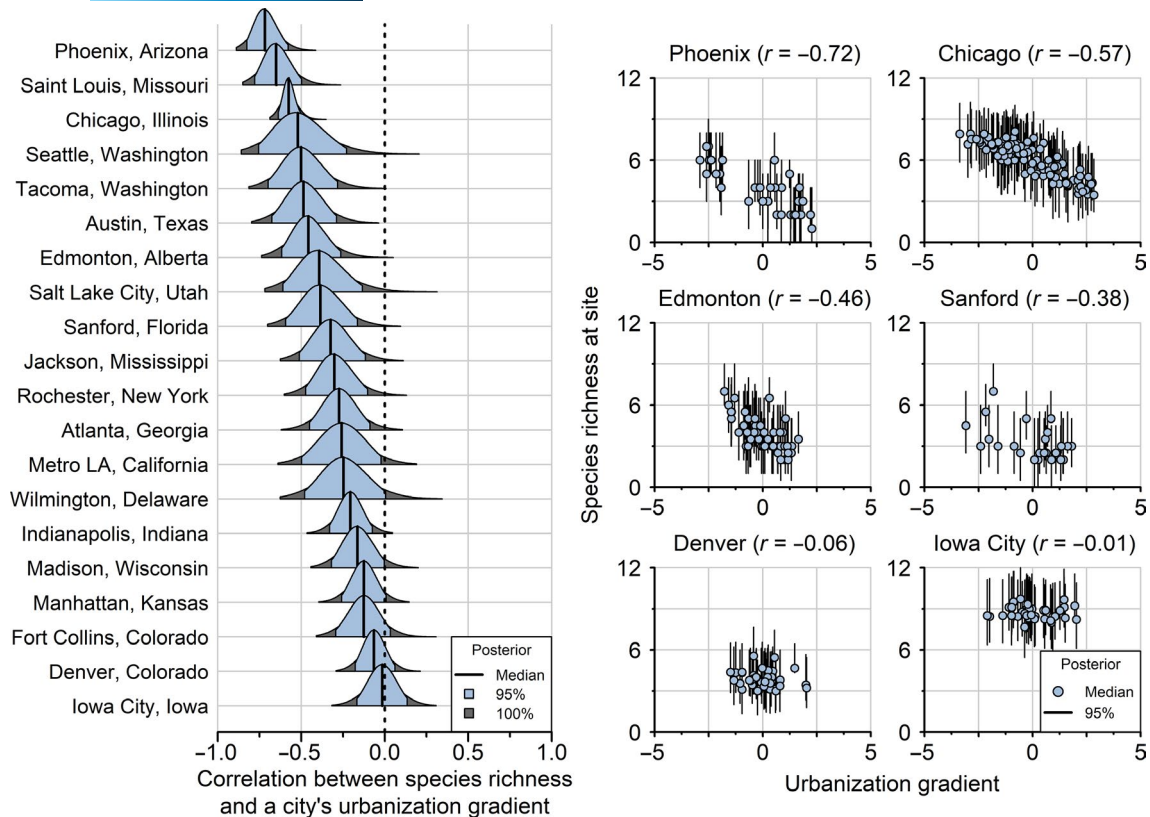


FIGURE 3 Sixteen of the twenty cities showed a negative correlation between mammalian species richness and the urbanization gradient of a city at the 0.95 level. We estimated species richness with our multi-city multi-species occupancy model with data from 3924 camera deployments at 905 unique sites throughout 20 North American cities. We quantified urbanization as the first principal component of mean NDVI, impervious cover, and population density within 1 km of a sampled site. Positive urbanization values indicate increased levels of impervious cover and population density while negative urbanization values indicate higher NDVI (i.e., more vegetation). The left plot shows the city-specific correlation between mammalian species richness and urbanization. For each city, Pearson correlation coefficients were calculated between urbanization and 9000 posterior draws of the detection-corrected species richness estimate per site and sampling period. For reference, we have placed a vertical dotted line at 0 (i.e., no correlation) to compare with the posterior correlation estimates for each city. The right plots demonstrate the varying relationship between average species richness and the urbanization gradient of six cities that exhibit a strong urbanization effect (top two) to weak (middle two) or no effect (bottom two). Point estimates on the right plots represent the average species richness for a site across sampling periods while vertical lines are 95% credible intervals

Across all species-specific responses to the income gradient of the 20 sampled cities, we only detected 11 positive associations and 9 negative associations at the 0.95 level. Conversely, we detected 17 positive associations and 55 negative associations between species occupancy and urban intensity at the 0.95 level. See Supporting Information material for a summary of all model coefficients.

4 | DISCUSSION

4.1 | Luxury effect

Our data supported the existence of a luxury effect in approximately half of the cities surveyed, although the strength of household income was decidedly weaker than urban intensity in explaining mammalian occupancy. Thus, for medium to large mammals, it appears that income alone is a relatively modest explanatory variable for

species richness, relative to the robust effects of the built environment. Although the effect size for the luxury effect was much lower than that of urban intensity, we show that socioeconomic factors are also key predictors of urban species communities in some cities.

We believe there are three reasons why the luxury effect may not be universal, especially for medium to large mammals. First, despite its widespread use in empirical studies, recent meta-analyses emphasize that income as a standalone variable is an incomplete predictor of community-level ecological patterns (Chamberlain et al., 2020; Gerrish & Watkins, 2018; Kuras et al., 2020). We chose to examine income to allow for broader comparison across studies; however, more insight could be gained by exploring some of the underlying causes of economic inequities, such as the historical and racist practice of redlining in some cities as well as development policies and patterns, including those linked to gentrification (Schell et al., 2020). Second, other social mechanisms may dilute or negate income-related differences in species richness, which could vary

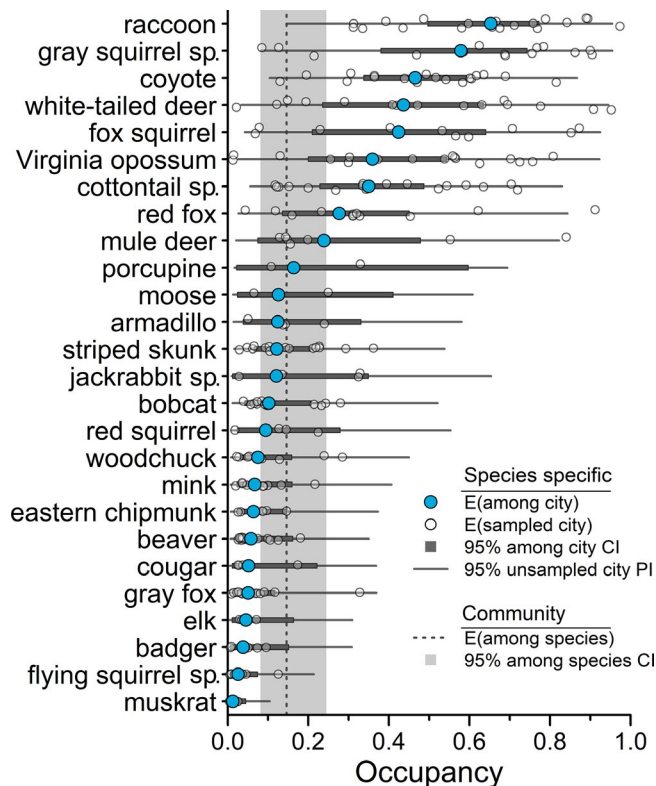


FIGURE 4 Among-city occupancy of species varies around the community average. Likewise, the city-specific occupancy of species varied around their respective among-city mean. The thick horizontal gray bars represent 95% credible intervals of a species among-city occupancy estimate, whereas the thin horizontal gray bars are 95% prediction intervals of a species occupancy in unsampled cities. The vertical gray box represents the 95% credible interval of the community average occupancy. Occupancy estimates were made with a multi-region multi-species occupancy model with data from 3924 camera trap deployments at 905 unique sites across 20 North American cities between July 2016 and January 2020

among cities. For instance, neighborhood norms compel individual homeowners to follow a specific landscape aesthetic, for example, by upholding traditional lawns or planting a set list of nonnative or ornamental plants (Avolio et al., 2018; Nassauer et al., 2009). Because of this, homeowners may favor plants and landscape designs that are less useful to local wildlife (Avolio et al., 2018; Grove et al., 2014). Third, the inception of the luxury effect hypothesis predicted positive relationships between income and plant community composition (Hope et al., 2003). This initial focus on plant communities may explain the mixed relationships we detected for medium- to large-sized mammal diversity, as well as no overall relationship with medium- to large-sized mammal occupancy (Figure 5). For example, while some mammals in our sample are dependent on plant resources (e.g., rabbits), several others are omnivores that make extensive use of anthropogenic resources, and their distribution may be decoupled from plant communities (e.g., raccoon, opossum, Gross et al., 2012). Taken together, we conclude that more sophisticated

predictors are needed to quantify social mechanisms and how the built environment shapes urban ecological dynamics for diverse taxonomic groups.

Nevertheless, our mixed results with respect to the luxury effect still have implications for biodiversity conservation and environmental justice. Lower-income neighborhoods, for example, can be characterized by modified vegetative communities and associated disservices such as urban heating, which, in turn, can lead to depauperate or primarily invasive plant and animal communities (Larsen & Harlan, 2006, but see Berland et al., 2020). Conversely, wealthier neighborhoods often have more and better quality green space (Li et al., 2019; Rigolon, 2016; de Vries et al., 2020). Research on the luxury effect also often assumes that 'financial wherewithal' (Hope et al., 2003) is the mechanism underlying positive relationships between income and vegetation, biodiversity, or other forms of nature. In reality, a more complex set of social-ecological factors is likely at play, including legacy effects that have driven the geography of urban development (Grove et al., 2018; Roman et al., 2018), associated socioeconomic and political factors (Nyhus, 2016), individual- and community-level value and belief systems toward wildlife (e.g., Manfredo et al., 2018; Teel & Manfredo, 2009), as well as the traits of local wildlife in particular places. Thus, deeper research is needed to understand the mechanisms driving the relationship between income and biodiversity.

4.2 | Urbanization and species effects

With our multi-city collaborative approach, we identified three broad trends. First, medium to large mammals, on average, responded negatively to urban intensity across cities (Figure 5). As such, our results indicate that urban intensity is a driving factor for medium to large mammals throughout North America, where higher levels of urban intensity are associated with decreased species richness at the local scale. Yet, some species are disproportionately lost with increasing urban intensity, which brings us to our second trend. We found that many large-bodied mammals, especially ungulates, exhibited uniformly negative relationships to urban intensity across cities (Figure 5). Thus, within a city, it is likely that these large species are disproportionately filtered out as urban intensity increases and habitat becomes more fragmented and less available. However, it may not only be habitat loss impacting ungulates. Larger-bodied species are also more likely to be impacted by roads as sources of mortality (Forman et al., 2003). As the urban intensity metric we used represented a gradient of vegetation replaced by buildings and impervious cover (e.g., roads), it may be that ungulates responded primarily to an increase in roads. To further evaluate this relationship, perhaps more refined classifications of urban intensity that separate the green (e.g., habitat) and gray (e.g., roads) parts of a city are necessary.

Finally, common urban species exhibited greater intraspecific variation in occupancy among cities than less common species (Figure 4). For instance, raccoon occupancy demonstrated substantial among-city

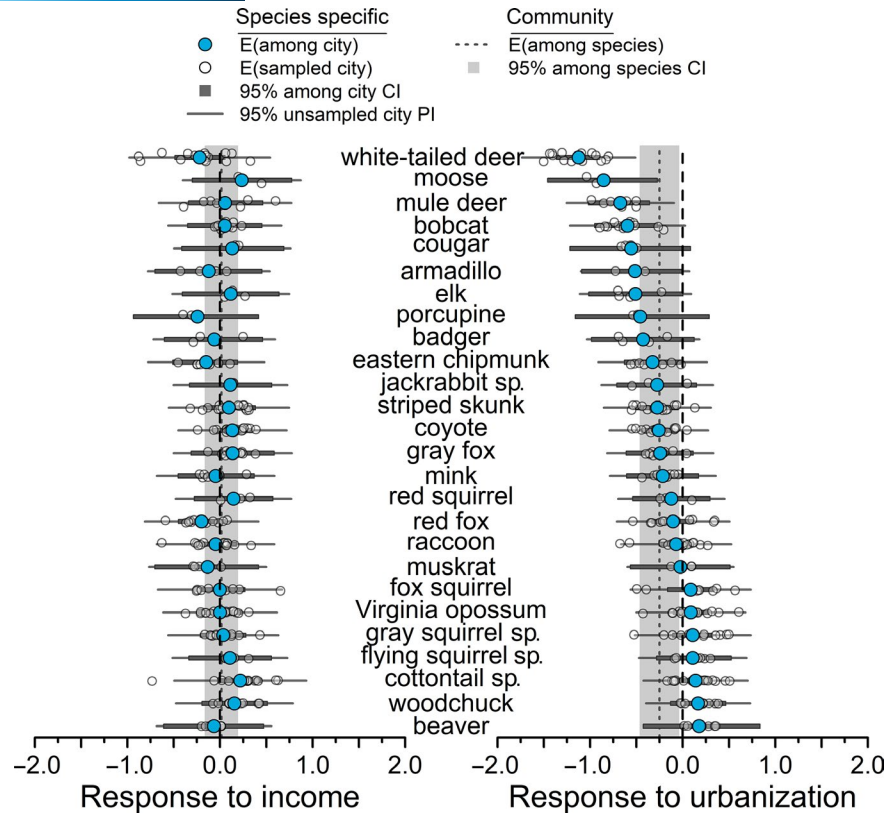


FIGURE 5 Changes in species occupancy within a city were more often associated with urbanization than the income gradient of a city. Responses are on the log-odds scale, and species are ordered by urbanization response. Thick horizontal gray bars represent 95% credible intervals of a species average log-odds response to income (left) or urbanization (right) among cities. Thin horizontal gray bars are 95% prediction intervals of a species response to these gradients in unsampled cities. The vertical gray box represents the 95% credible interval of the community-level response to income or urbanization among cities. For reference, we placed a vertical line at 0 to compare with the 95% credible intervals. Occupancy estimates were made with a multi-region multi-species occupancy model with data from 3924 camera trap deployments at 905 unique sites across 20 North American cities between July 2016 and January 2020

variation, ranging from 0.97 occupancy (Iowa City, Iowa) to only 0.31 (Phoenix, Arizona). We observed similar among-city occupancy variability for eight other species (Figure 4). While species such as raccoon, eastern gray and fox squirrel, coyote, and white-tailed deer are often considered quintessential urban species within their respective ranges (Adams, 2009), our analysis indicates that these species are not equally common across cities. We suggest that landscape-level differences among cities may contribute to this phenomenon, including differences in average housing density or greenspace availability, which were found to influence urban mammals in 10 U.S. cities (Fidino et al., 2020). In addition, it is possible that species respond to other among-city differences such as land-use legacies, patterns of human activity, cultural or other socioeconomic variables we did not measure (Aronson et al., 2016). Of course, factors at even larger scales than the city, such as climate, could also be partially driving these differences (Magle et al., 2019). As large-scale research networks such as UWIN continue to grow, so too will the opportunities to evaluate how forces at multiple spatial scales bring about observed differences within and among cities, regions, or continents. By identifying the context in which results from one city may generalize to others, such a multi-scalar approach would no doubt help facilitate an impressive synthesis of urban

ecological research and provide sorely needed information for conservation (Aronson et al., 2016).

4.3 | Integrating large-scale research and management

Our results emphasize the power of multi-city investigations in assessing explanatory variables impacting wildlife in cities. The robust effects of impervious surfaces, heightened human densities, and reduced vegetation cover in cities spotlight both the potential and need for building wildlife-friendly features in cities to mitigate the adverse effects of built structures on mammalian occupancy. For example, increased urban intensity reduced occupancy of ungulates, so modifying landscape permeability by creating greenways over major roads or reducing human activity in specific natural areas may promote colonization for these species while prohibiting the establishment of other well-represented urban species. Some species, such as bobcat and moose, have particularly pronounced responses to urban development and would require extraordinary effort and resources to conserve in

urbanizing landscapes, likely including creation of very large urban preserves. To achieve this balance, cities with different levels of urbanization, resources, and priorities will require different types of wildlife management plans. Stewarding a healthy urban wildlife community is an essential component of urban conservation and sustainability, and will require interdisciplinary teams that connect urban wildlife ecologists and social scientists with landscape ecologists and architects, urban planners and policy analysts, and municipality leaders and developers to shape urban environments that support both humans and wildlife (Apfelbeck et al., 2020).

4.4 | Caveats/limitations

Our study does have some limitations. We may have detected relatively weak evidence of the luxury effect in some cities because our study design limited camera placement to formal and informal green spaces such as parks, school yards, golf courses, cemeteries, and private property. Communities with low municipal investment and/or a lack of resources to invest in natural space may lack many types of public green spaces. Habitats located on private property could be underrepresented in our analysis. Future studies could work with residents to monitor wildlife communities in yards, alleys, or vacant lots to include data across the full spectrum of neighborhood wealth. Additionally, UWIN's study design focused on capturing the urbanization gradient in partner cities and did not explicitly seek to capture socioeconomic gradients. While sites within cities did have substantial variation in per capita income, it is likely that sampling in some cities fails to capture the full range of socioeconomic variation. Incorporating factors such as income, educational attainment, and racial and ethnic composition of populations in the selection of survey sites could improve the ability of future studies to assess the luxury effect.

5 | CONCLUSION

Despite the profound impact of urban intensity on mammalian dynamics, the relative importance of societal mechanisms in shaping urban biodiversity cannot be overlooked. Socioeconomic status and political influence, as well as prestige and legacy effects, can coalesce or diverge to mediate decisions in how the built environment is structured, and for whom (Schell et al., 2020). While the overall negative impact of urban intensity is not surprising, the inter-city variation we identify suggests the existence of unmeasured facets of urban systems that influence which medium- and large-sized mammalian species will thrive. These facets likely include historical legacies and land development patterns, temporal changes in neighborhood structure and wealth through gentrification and disinvestment, zoning policies and land governance, individual attitudes and sociocultural norms toward wildlife and their management, and systems of oppression that perpetuate inequality in access to nature and resources (Grove et al., 2018; Roman et al., 2018). Understanding the linkages between human and wildlife communities is a critical

first step toward building cities where the benefits and burdens of living with wildlife are equitably shared.

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CONFLICT OF INTEREST

We declare no competing interests.

AUTHOR CONTRIBUTION

SBM, MF, TG, and CJS conceptualized the manuscript. MF conducted all the statistical analyses. All authors contributed data and assisted with drafting and editing the manuscript.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available on Zenodo at <https://doi.org/10.5281/zenodo.5093795>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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