Landscape-scale differences among cities alter common species' responses to urbanization

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Abstract. Understanding how biodiversity responds to urbanization is challenging, due in part to the single-city focus of most urban ecological research. Here, we delineate continent-scale patterns in urban species assemblages by leveraging data from a multi-city camera trap survey and quantify how differences in greenspace availability and average housing density among 10 North American cities relate to the distribution of eight widespread North American mammals. To do so, we deployed camera traps at 569 sites across these ten cities between 18 June and 14 August. Most data came from 2017, though some cities contributed 2016 or 2018 data if it was available. We found that the magnitude and direction of most species' responses to urbanization within a city were associated with landscape-scale differences among cities. For example, eastern gray squirrel (*Sciurus carolinensis*), fox squirrel (*Sciurus niger*), and red fox (*Vulpes vulpes*) responses to urbanization changed from negative to positive once the proportion of green space within a city was >~20%. Likewise, raccoon (*Procyon lotor*) and Virginia opossum (*Didelphis virginiana*) responses to urbanization changed from positive to negative once the average housing density of a city exceeded about 700 housing units/km^2. We also found that local species richness within cities consistently declined with urbanization in only the more densely developed cities (>~700 housing units/km^2). Given our results, it may therefore be possible to design cities to better support biodiversity and reduce the negative influence of urbanization on wildlife by, for example, increasing the amount of green space within a city. Additionally, it may be most important for densely populated cities to find innovative solutions to bolster wildlife resilience because they were the most likely to observe diversity losses of common urban species.

Key words: camera trap; mammal; multi-city survey; occupancy; species richness; urbanization; wildlife.

INTRODUCTION

More people live in cities than in rural areas worldwide (Seto et al. 2012). To meet the demands of their

human inhabitants, cities are expanding in area commensurate to roughly twice their population growth rate (Angel et al. 2011). This urban expansion drives global environmental change and threatens biodiversity (Grimm et al. 2008, Seto et al. 2012). And although some species can inhabit and possibly thrive in cities (Goddard et al. 2010), explorations into their urban ecology were historically rare and have only increased in recent decades (Magle et al. 2012, McPhearson et al. 2016, Fidino and Magle 2017a). Despite these increased levels of urban ecological research, there is still much to understand about how urbanization influences Earth's ecology.

Most urban ecological studies focus on a single city, which limits our understanding of urban areas as ecosystems (Magle et al. 2019). Single-city research can identify ecological responses to local patterns of urban development, but these responses cannot be extrapolated to other cities that differ in age, size, climate, or human population density, among other variables (Ramalho and Hobbs 2012, Aronson et al. 2016, Magle et al. 2019). Current multi-city assessments, for example, show that differences in bird and plant richness among cities are correlated with among-city differences in land cover and age (Aronson et al. 2014). Likewise, the location of water bodies or railways within a city can facilitate or hinder movement between wildlife populations and therefore influence where in a city that species may persist (Beninde et al. 2016). As a result, a single species may respond to urbanization in different ways among cities. Multi-city comparative approaches are therefore necessary to understand whether species' responses to urbanization are generalizable across cities, or if they vary due to landscape-scale differences among cities (Aronson et al. 2014, Beninde et al. 2016, Magle et al. 2019). Such assessments, however, remain challenging because few coordinated efforts monitor biodiversity in multiple cities.

Here we show how landscape-scale differences among cities influence the within-city distribution of urban-adapted mammals by leveraging data collected by the Urban Wildlife Information Network (UWIN), a systematic multi-city biodiversity monitoring survey (Magle et al. 2019). Our goals were to determine if the distribution and richness of terrestrial mammals within cities changed as a function of among-city differences in (1) greenspace availability and (2) average housing density. These two landscape-scale metrics are respectively associated with the average habitat potential in a city and its intensity of urbanization, which may collectively indicate the overall quality of a city as habitat for a species (Aronson et al. 2016, Magle et al. 2019). We predicted that the expected proportion of habitat patches a species occupies within a city (i.e., the relative occupancy of a species) would increase in cities with more greenspace but decrease in cities with higher average housing density. Likewise, we predicted that within cities, species would exhibit a stronger negative response to urbanization (i.e., be less likely to occur closer to an urban core) in cities with higher average housing density or less greenspace. We advance previous multi-city biodiversity assessments by quantifying whether the magnitude and direction of a species' response to urbanization changes due to landscape-scale differences among cities. This unique approach allows us to begin to identify the degree to which results from a single city can generalize to other cities or if species' responses to urbanization are unique to individual cities.

MATERIALS AND METHODS

Cities

Ten UWIN cities provided data for this study: Austin, Texas; Chicago, Illinois; Denver, Colorado; Fort Collins, Colorado; Iowa City, Iowa; Indianapolis, Indiana; Manhattan, Kansas; Madison, Wisconsin; Orange County, California; and Wilmington, Delaware. The cities are spread across the entire contiguous United States and range from about 43° N (Madison, Wisconsin) to 30° N (Austin, Texas) and 118° W (Orange County, California) to 75° W (Wilmington, Delaware; Appendix S1: Fig. S1). Overall city areas ranged from 44.52 km^2 (Wilmington, Delaware) to 2,460 km^2 (Orange County, California; see Appendix S1: Table S1 for all city areas). Population estimates for 2019 ranged from 54,604 (Manhattan, Kansas) to 3,175,692 (Orange County, California; see Appendix S1: Table S1 for all population estimates; United States Census Bureau 2019).

Sites

All cities followed a standard protocol to select sampling locations along a gradient of urbanization (Magle et al. 2019). Sampling locations (hereafter "sites") include an array of potential wildlife habitat such as parks, cemeteries, golf courses, natural areas, and backyards. Transects originated in an urban core of each city and extended outward through suburban, exurban, and/or rural areas across gradients of impervious land cover and housing density. The average number of sites per city was 51 (minimum 23, maximum 104). All sites were separated by at least 1 km. This distance was selected because it exceeds the home range extent of most city dwelling mammals surveyed in this study, save for the coyote (*Canis latrans*) and red fox (*Vulpes vulpes*; Gehrt et al. 2010).

Biological sampling

The focus of UWIN to date has been to use motion-triggered trail cameras (hereafter "camera traps") to monitor medium to large-sized mammals, which can be identified to the species level from camera trap images (Magle et al. 2019). One camera trap was placed at each site for at least 28 consecutive days between 18 June and

14 August. Camera traps were strapped to a tree, fence post, or other object and angled downward so that the camera's field of view captured another tree or fence post 2.5–6 m away. To potentially increase species detectability, a synthetic fatty acid scent tablet (USDA Wildlife Services, Pocatello, Idaho, USA) was placed in a mesh bag and attached roughly 30 cm from the ground to the object, toward which the camera trap was angled.

Photo data were uploaded and processed using a custom Microsoft Access (Redmond, Washington, USA) database built for camera trapping research (Ivan and Newkirk 2016). A custom R package, uwinr, was used to check each city's respective database for errors and to prepare data for analysis (Fidino 2018). We generated daily detection histories with these data for each site, species, and sampling season. A detection history took the value of 1 if a species was detected at a site on a given day, the value 0 if a species was not detected on that day, and the value NA if the camera malfunctioned (e.g., batteries ran out) or the camera was not deployed on a given day. For example, the detection history {0, 0, 1, NA} indicates that a species was not detected on the first two days, detected on the third, and then either the camera malfunctioned or was removed on the fourth day.

Data

Most data for this analysis were collected during 2017. However, two cities contributed data from 2016 and six cities contributed data from 2018 (Appendix S1: Table S1). Yearly differences in data availability among cities was due to either the year a city joined UWIN or whether camera trap images for a given season had been completely classified at the time of this analysis.

Statistical analysis

We fit a Bayesian hierarchical single-season occupancy model to each species' data to estimate if their average occupancy probability within a city changed due to among-city differences in greenspace availability and average housing density (MacKenzie et al. 2017). We also quantified relative changes in the likelihood of occupancy along each city's urbanization gradient (i.e., a species response to urbanization) as a function of among-city differences in greenspace availability and average housing density. Four candidate models were fit to each species' data to determine the relative influence of our two among-city variables. We explain the global model below. The remaining three models are reduced versions of this global model.

To represent each city's urbanization gradient, the global model included the housing density (1,000 units/km^2) within a 1-km buffer around each site. We also included two among-city covariates: overall greenspace availability and average housing density. To calculate overall greenspace availability, we first extended the width of each transect in a city by its respective length.

A straight 20-km transect, for example, became a square with 20 km length sides wherein the transect line bisects the center of the square. This method was used to increase the sampled area in proportion to transect length and enabled us to apply a consistent definition of greenspace availability across cities with transects of different lengths. Overlapping squares resulting from multiple transects within a city were spatially dissolved to create a single sampling area. We then calculated the proportion of available greenspace in a city's study area, following the U.S. EPA's EnviroAtlas definition (Pickard et al. 2015), by combining the forest, herbaceous, shrub & grass, and developed open space (e.g., golf courses, cemeteries, parks, etc.) land cover classes from the National Land Cover Database (Yang et al., 2018) and divided the summed area of those classes by the total sampled area for each city. We calculated the average housing density of each city as the mean housing density within a 1-km buffer of all sites in a city from the Silvis housing density data layer (Hammer et al. 2004). To estimate if a species' response to urbanization (i.e., the associated slope term to our "within-city" covariate) changed due to structural differences among cities, we included statistical interactions between our two "among-city" covariates (i.e., overall greenspace availability and average housing density of a city) and our single within-city covariate (i.e., the housing density at each site). For a single species, the logit-linear predictor of the probability of occupancy (Ψ_{js}) at j in $1,...,10$ cities and s in $1,...,S_j$ sites was

$$\text{logit}\left(\psi_{js}\right) = \beta_{0j} + \beta_{1j}\left(\text{hden}_{js} - \overline{\text{hden}_j}\right) + r_j + I\left(\delta_j\right) + I\left(\theta_j\right) \tag{1}$$

where

$$\beta_{0j} = \gamma_{00} + \gamma_{01}\text{greenspace}_j + \gamma_{02}\overline{\text{hden}_j} \tag{2}$$

and

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{greenspace}_j + \gamma_{12}\overline{\text{hden}_j}. \tag{3}$$

In Eq. 1, β_{0j} represents the average log-odds species s occupies an average site in city j and can be biologically interpreted as a species average occupancy probability within a city. It is derived from the intercept term γ_{00} and the effect of the two between-city covariates, overall greenspace availability (greenspace$_j$) and the average housing density of a city ($\overline{\text{hden}_j}$) via Eq. 2. Among-city covariates were centered and scaled to have a mean of 0 and standard deviation of 1, were poorly correlated (Pearson's $r^2 = 0.22$), and therefore represent relatively independent covariates (Appendix S1: Table S2). β_{1j} is a slope term that represents the relative log-odds change in occupancy at city j and site s given the within-city site-level housing-density covariate, hden$_{js}$, and can be

biologically interpreted as a species response to urbanization. Unlike the among-city covariates, hden_{js} is group-mean centered by subtracting the respective city average, $\overline{\mathrm{hden}}_j$, from each hden_{js}. This scaling, combined with multi-level structure of our model, eases parameter interpretation, ensures the slope terms in Eq. 2 and Eq. 3 (i.e., $\gamma_{01}, \gamma_{02}, \gamma_{11}$, and γ_{12}) represent among-city effects (Aguinis et al. 2013), and make parameter estimates far less sensitive to unequal sample sizes among cities (Milliren et al. 2018, Luke 2019). As with β_{0j}, β_{1j} is allowed to vary in magnitude or direction via Eq. 3 as a function of the two among-city covariates. By algebraically inputting Eqs. 2 and 3 into Eq. 1, it is evident that the parameters γ_{01} and γ_{02} are slope terms that vary by city while γ_{11} and γ_{12} are interaction terms between our among- and within-city covariates.

To account for additional among-city variation we included a city-specific random effect (r_j; Eq. 1). We also accounted for multiple years of sampling with two indicator functions, $I(\delta_j)$ and $I(\theta_j)$. The parameter δ_j is the log-odds difference in average occupancy at city j in 2016. If a city had 2016 data this term was estimated, otherwise it was 0. Conversely, θ_j is the log-odds difference in average occupancy at city j in 2018 if and only if city j had 2017 data. For the detection model, we allowed the species-specific detection probability (ρ_{sj}) to vary among cities such that the logit-linear predictor was $\mathrm{logit}\left(\rho_{sj}\right) = a_0 + a_j$ where a_0 is the average log-odds of detecting a species while a_j is a city-level random effect.

Model set, prior specification, and model selection

The four candidate models fit to each species' data differed in the number of among-city variables (Eq. 2) and represented separate hypotheses about which differences in urban form among cities were correlated with the average occupancy of a species in a city (Eq. 2) or where a species was most likely to occur within a city (Eq. 3). The global model (M_{global}) described above contained both among-city variables, our greenspace model only included the proportion of greenspace in a city ($M_{\mathrm{greenspace}}$), and our housing density model only included the average housing density of a city (M_{housing}). We also included a null model that contained no among-city variables (M_{null}). All models included the site-level housing density covariate (hden_{js}; Eq. 1), which represents the urbanization gradient in each city, and used the same detection model. Cities that were outside the distributional range of a species were omitted from that species' analysis, and models were only fit to a species' data if they were detected at a minimum of five participating UWIN cities (50% of sampled cities). This five-city cutoff was selected for two reasons. First, the among-city random effect term failed to converge for species that were detected in four or fewer cities. Second, to keep the city-level sample size relatively high to estimate among-city parameters in Eq. 2 and Eq. 3 because a minimum

sample size of five clusters (i.e., cities in our case) has been suggested to estimate the cross-level interactions of our model (Stegmueller 2013).

We used a Bayesian framework to parameterize and evaluate our models. All logit-scale parameters, save for the random effect terms, were drawn from Logistic (0,1) distributions, which represent a vague logit-scale prior. Random effects were drawn from $N(0,\sigma)$ distributions where $\sigma \sim$ Inv-gamma(0.001, 0.001). To compare the relative fit of each model we calculated the conditional predictive ordinate (CPO) of each data point at each Markov chain Monte Carlo (MCMC) step (Geisser 1993). Overall model performance was evaluated with the summary statistic $-\Sigma_{kt}\log(\mathrm{CPO}_{k,t})$ for data point k and MCMC step t and the lowest value indicates the best relative fit (Hooten and Hobbs 2015). Models were fit in JAGS version 4.3.0 (Plummer 2003) via the R programming language version 3.5.3 (R Core Team 2019). After a 60,000 step adaptation and 60,000 step burn-in, each model was sampled 1,250,000 times across five chains. Due to the computational intensity of tracking the CPO of each data point, chains were thinned by 10 for a total of 125,000 samples. To verify model convergence, we ensured that Gelman-Rubin diagnostics for each parameter were <1.10 and examined trace plots of parameters from the MCMC chains to visually confirm proper mixing (Gelman et al. 2014). While the number of parameters could differ for the best-fit model of each species, we referenced parameters as we did for the global model (i.e., Eqs. 1–3) for consistency.

Quantifying species richness within and among cities

We used posterior simulations of species occurrences from each species' best-fit model to derive (1) within-city species richness at sites surrounded by less than or more than a city's average housing density and (2) the most likely medium to large-mammal community to occur at the estimated median species richness.

RESULTS

A total of 25,115 camera trap nights occurred from 808 camera deployments at 569 sites across the 10 U.S. cities (Appendix S1: Fig. S1 and Table S1). Eight species were detected in at least five cities, representing a common suite of widely distributed, urban-adapted, medium-to-large mammals throughout North America: raccoon (*Procyon lotor*, 5504 detections across 10 cities), eastern gray squirrel (*Sciurus carolinensis*, 2,465 detections across 6 cities), Virginia opossum (*Didelphis virginiana*, hereafter opossum, 2,210 detections across 7 cities), cottontail rabbit (*Sylvilagus floridanus* or *Sylvilagus audubonii*, hereafter cottontail, 1,731 detections across 9 cities), fox squirrel (*Sciurus niger*, 1,508 detections across 8 cities), coyote (*Canis latrans*, 821 detections across 9 cities), striped skunk (*Mephitis mephitis*, 548 detections across 9 cities), and red fox (*Vulpes vulpes*,

368 detections across 8 cities). For a summary of the range and extent of within and among-city covariates see Appendix S1: Fig. S2 and Table S2.

Model selection

Differences in the urban form of cities were typically associated with the within-city habitat dynamics of widespread species. Models including average housing density, proportion of greenspace, or both (global model) outperformed the null model for all but one species, the striped skunk (Table 1). The global model (M_{global}) was the best-fit model for gray squirrel, the housing model ($M_{housing}$) for coyote, opossum, and raccoon, and the greenspace model ($M_{greenspace}$) for cottontail, fox squirrel, and red fox (Table 1; Fig. 1).

Changes in average occupancy associated with differences among cities

The average occupancy of raccoon and cottontail were influenced by differences among cities (Fig. 2A). Raccoon occupancy was highest in cities with a low average housing density (Fig. 2A, $\gamma_{02,raccoon} = -0.58$, 95% CI = -1.18 to-0.01). Raccoon had the highest average occupancy (i.e., the most positive intercept, Fig. 1A) across cities they were present at 74.41% (95% CI = 62.52–82.85%), followed by opossum (53.82%, 95% CI = 41.42–64.13%), fox squirrel, (51.51%, 95% CI = 30.98–71.30%), gray squirrel (48.58%, 95% CI = 17.13–81.76%), coyote (38.39%, 95% CI = 31.49%–45.62%), cottontail (37.54%, 95% CI = 31.46–44.14%), red fox (26.22%, 95% CI = 8.86–62.67%), and striped skunk (15.26%, 95% CI = 10.76–20.81%). There was some evidence that cottontail relative occupancy decreased in cities with more greenspace (Fig. 2B, $\gamma_{02,cottontail} = -0.22$, 95% CI = -0.49–0.03). All other among-city effects on average occupancy greatly overlapped 0 (Fig. 1A).

TABLE 1. Model selection results of the four candidate models fit to each species' data collected across 10 U.S. cities.

Species	M_{global}	$M_{housing}$	$M_{greenspace}$	M_{null}
Gray squirrel	**2,128.28**	2,131.34	2,128.63	2,129.17
Coyote	1,211.06	**1,209.59**	1,210.46	1,215.48
Opossum	2,205.11	**2,204.39**	2,204.95	2,205.8
Raccoon	4,400.48	**4,399.26**	4,401.09	4,400.87
Cottontail	1,962.64	1,962.4	**1,961.38**	1,961.93
Fox squirrel	1,610.9	1,612.69	**1,610.11**	1,632.01
Red fox	547.87	548.47	**547.82**	549.79
Striped skunk	915.16	913.63	913.88	**911.55**

Notes: Models were compared with the summary statistic $-\Sigma_{kt}\log(CPO_{kt})$ for data point k and Markov chain Monte Carlo (MCMC) step t, where CPO is the conditional predictive ordinate. Lower values indicate better model fit. The lowest score, which represents the best-fit model, is shown in boldface type for each species. Species are sorted by their best-fit model.

Species-specific responses to urbanization within a city associated with differences among cities

Fox squirrel, gray squirrel, and red fox responses to urbanization, which we estimated as their log-odds changes in occupancy due to differences in site-level housing density, changed as a function of greenspace availability in a city (Fig. 1B). When greenspace availability in a city was <19.70% (95% CI = 16.90–22.69) fox squirrels responded negatively to urbanization and were less likely to occupy sites surrounded by high levels of housing density within a city (Fig. 3A). Conversely, fox squirrel responded positively to site-level housing density if greenspace availability in a city was greater than 19.70% (Fig. 3A). Gray squirrel and red fox followed a similar pattern and both species responded positively to site-level housing density in cities that had more greenspace (~28% for both species; Fig. 3B,C).

The among-city response to urbanization of coyote, opossum, and raccoon changed as a function of a city's average housing density (Fig. 1B). Opossum and raccoon responded negatively to site-level housing density in densely populated cities (Fig. 4A, B). For example, Chicago had the highest average housing density (1316.70 houses/km^2) and there was strong evidence that raccoon and opossum responded negatively to site-level housing density in Chicago ($\beta_{Chicago,raccoon} = -0.55$, 95% CI = -0.77 to -0.35; $\beta_{Chicago,opossum} = -0.56$, 95% CI = -0.80 to -0.33). However, raccoon and opossum responded positively to urbanization in cities with a low average housing density (Fig. 4A-B). Manhattan, Kansas had the lowest average housing density (313.35 houses/km^2) and there was some evidence that raccoon and opossum responded positively to site-level housing density in that city ($\beta_{Manhattan,raccoon} = 0.41$, 95% CI = -0.34 to 1.18; $\beta_{Manhattan,opossum} = 0.27$, 95% CI = -0.37 to 0.92). Thus, the spatial distribution of raccoon and opossum within a city varied depending on a city's average housing density. Coyote, however, always responded negatively to site-level housing density in a city, but the strength of this effect was reduced in more densely populated cities (Fig. 4C). Thus, although coyote were most likely to occur at sites near less populated areas, this relationship was strongest in sparsely populated cities.

Species richness within and among cities

The cumulative effect of among-city differences in greenspace availability and average housing density resulted in altered mammal community composition and diversity (Fig. 5). Across all cities, sites with less-than-average housing density had a mean of 3.17 mammal species from this study (95% CI = 0–6), while sites with more-than-average housing density had 2.84 (95% CI = 0–6). For cities with more than 710 houses/km^2 on average, species richness was consistently lower at sites surrounded by greater than average housing density (Fig. 5). Of species we analyzed, the raccoon was lost
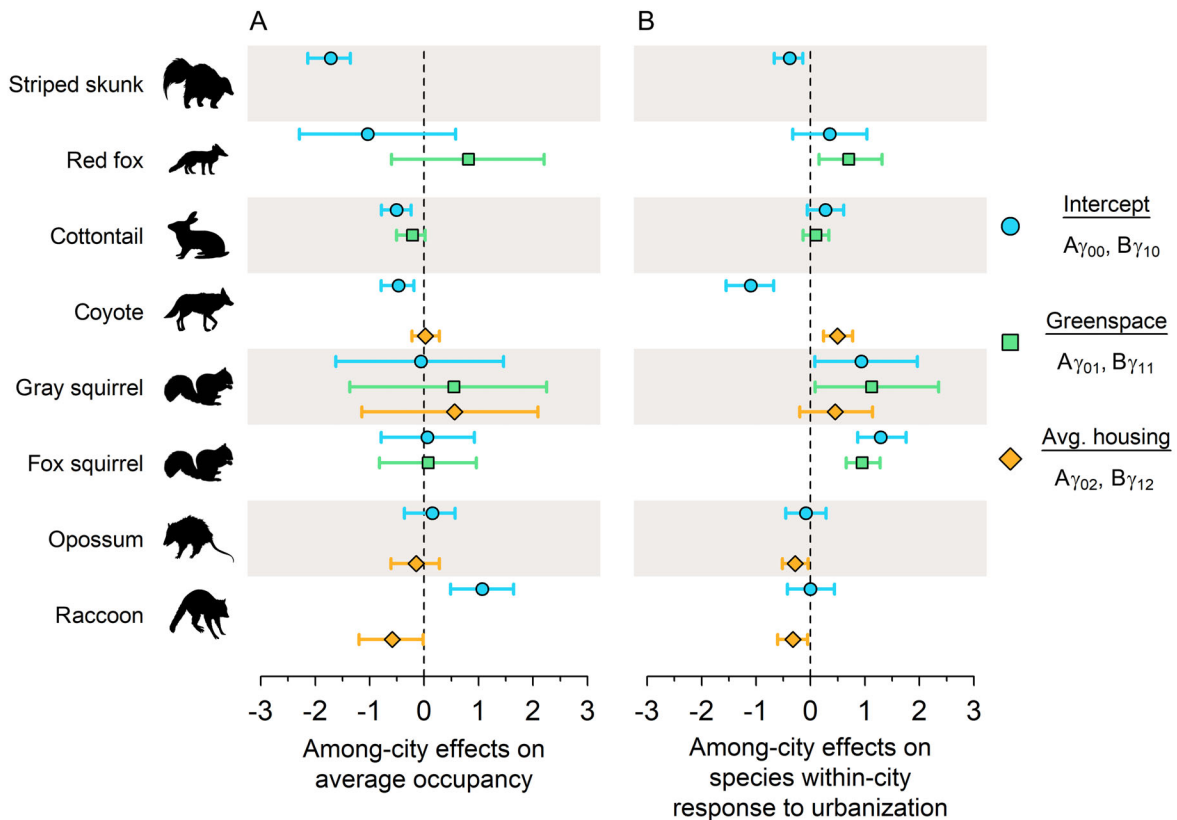
Fig. 1. Among-city effects from the best-fit model of each species estimated from data collected in 10 U.S. cities between 2016 and 2018. Panel A illustrates the average log-odds that a species occupies a habitat patch within a city and how that changes due to differences in greenspace availability or average housing density among cities. For example, the average log-odds occupancy for raccoon decreases in cities with a higher average housing density. Panel B demonstrates the magnitude and direction of a species' response to site-level housing density (i.e., urbanization) within a city and how that may change due to differences in greenspace availability or average housing density among cities. For example, the fox squirrel's response to urbanization (panel B) is more positive in cities with more greenspace. Parameters are on the logit scale.

most often from the wildlife community as the average housing density increased in a city. Within-city differences in species richness were equivocal for cities with an average housing density less than or equal to 710 houses/km² and could be positive, negative, or unchanged.

DISCUSSION

As the Earth urbanizes and cities increase in size and population density (Angel et al. 2011), it is imperative to understand how differences in urbanization patterns within and among cities influences biodiversity. This analysis clearly demonstrates associations between landscape-scale differences among cities and changes in the magnitude and, at times, the direction of species' responses to urbanization. Within-city distributions of gray squirrel, fox squirrel, and red fox, for example, were associated with differences in greenspace availability among cities (Fig. 3). Within-city distributions of coyote, opossum, and raccoon varied with the average housing density of a city (Fig. 4). If these data were analyzed as independent single-city studies we would infer

dissimilar species-specific responses to urbanization (Fig. 1). Analyzing them together, as we have done here, allows us to see that these apparent disagreements are explained by landscape-scale differences among cities. Most importantly, these results indicate that generality is possible between cities that are similar, for example, cities that have similar average housing densities. To facilitate cross-study syntheses and allow for a broader understanding of urban biodiversity it is therefore imperative that future urban ecological research describe the broader context of urbanization within a city.

We described each city's broader context of urbanization with two metrics: the proportion of greenspace and the average housing density of a city. While simple, these metrics described the habitat potential, or lack thereof, within a city and were correlated with differences in how species respond to urbanization (Fig. 1). These metrics were also correlated with among-city changes in average occupancy of raccoon and cottontail (Fig. 2A). Cottontail, however, responded negatively to greenspace availability within a city, which was contrary to our predictions. It is possible that additional greenspace
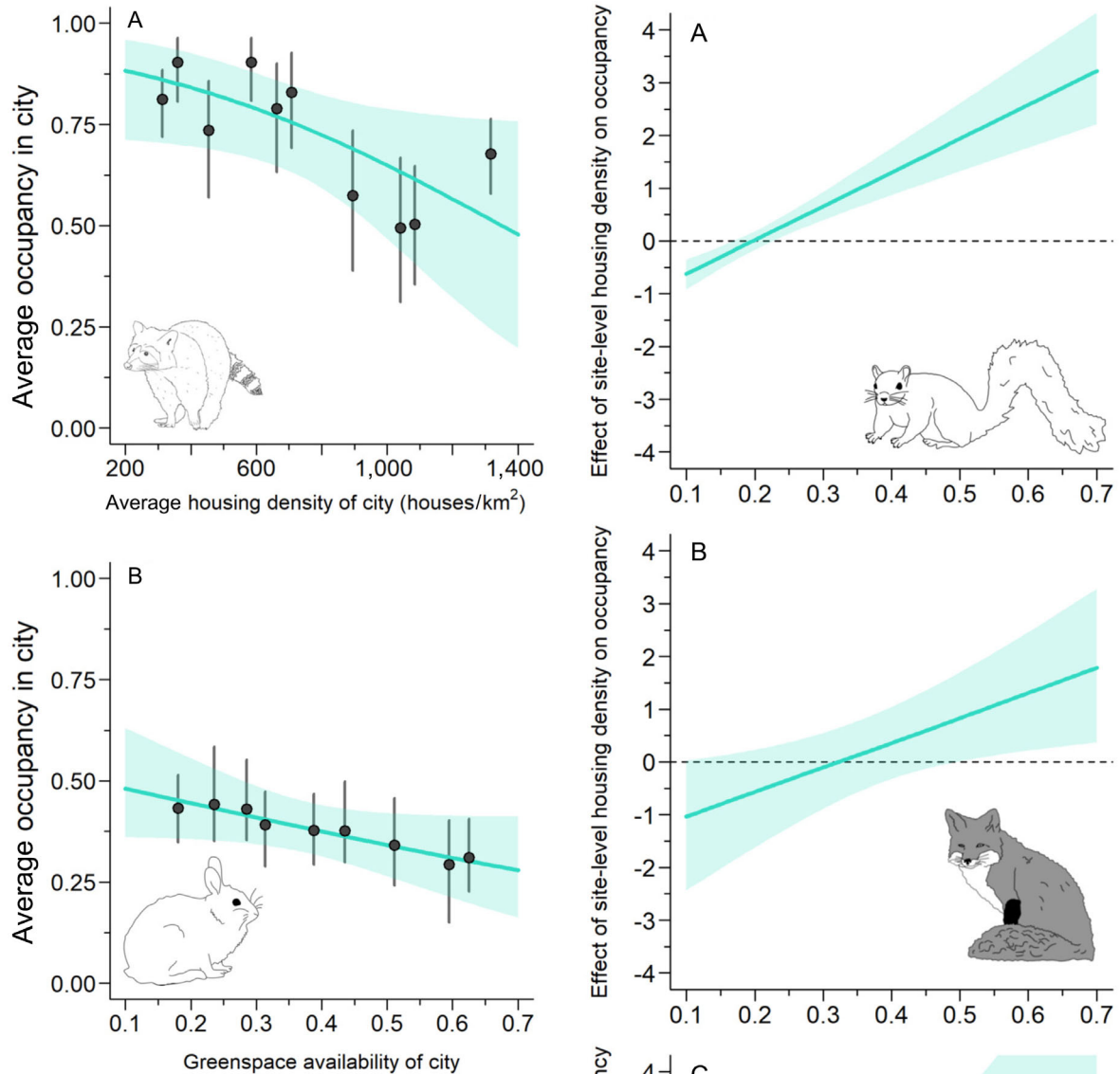
FIG. 2. The within-city relative occupancy of (A) raccoon decreased with average housing density whereas (B) cottontail decreased in cities with more greenspace. Solid lines are median model predictions of a species relative occupancy in a city while shaded ribbons are 95% credible intervals of this prediction. Gray dots represent city-specific occupancy estimates for the UWIN cities that detected the species while vertical bars are 95% credible intervals. Raccoon (A) had more among-city variability from the median predicted response than eastern cottontail (B).

FIG. 3. The among-city response to urbanization, which we estimated as the log-odds change in occupancy due to differences in site-level housing density, of (A) fox squirrel, (B) red fox, and (C) gray squirrel changes in magnitude and direction as a function of greenspace availability in a city. Solid horizontal lines are median model predictions of a species response to urbanization in a city that varies in greenspace availability while shaded ribbons are 95% credible intervals.
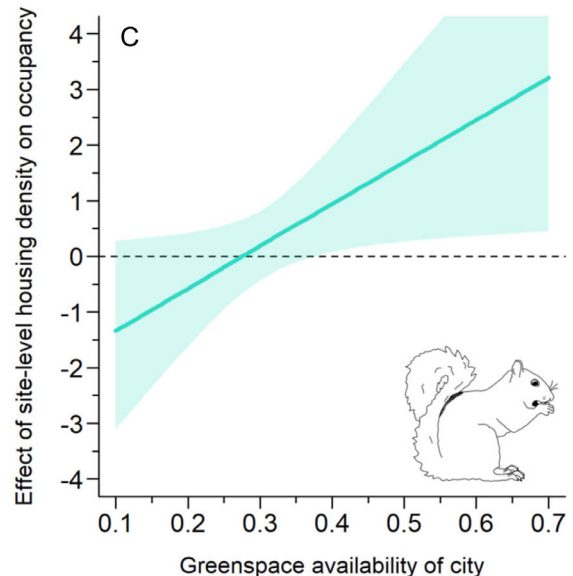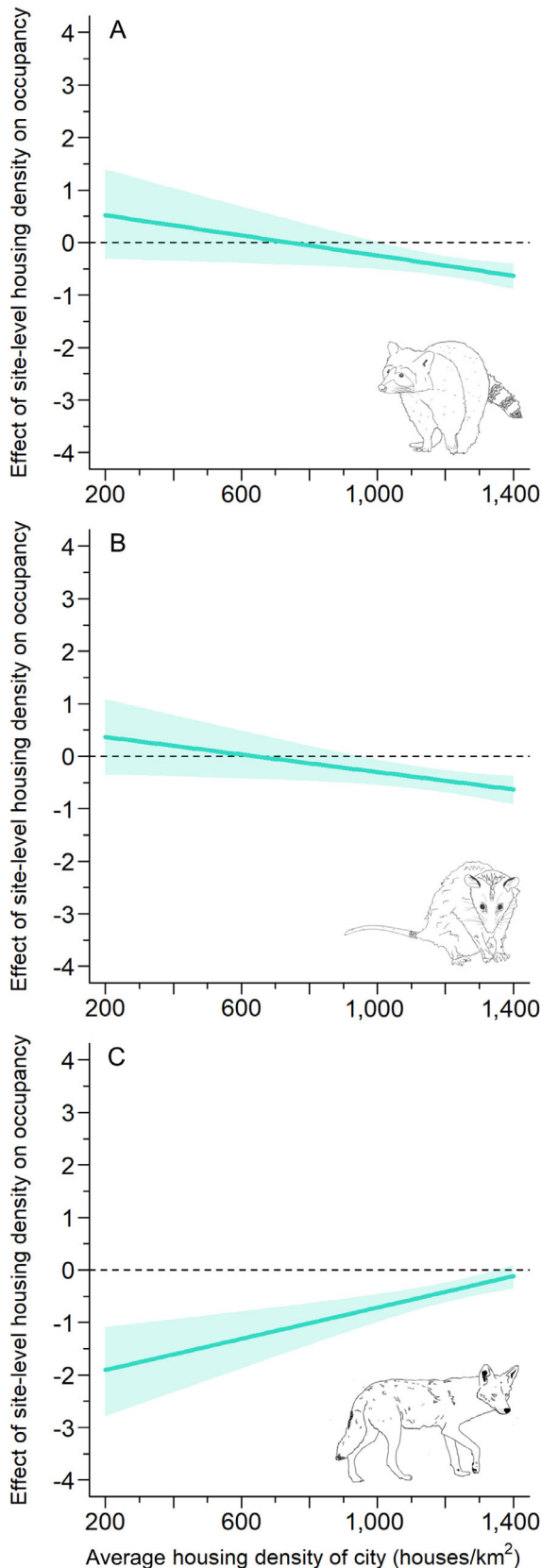
Fig. 4. The among-city response to urbanization, which we estimated as the log-odds change in occupancy due to differences in site-level housing density, of (A) raccoon, (B) opossum, and (C) coyote changed in magnitude and/or direction as a function of the average housing density of a city. Solid horizontal lines are mean model predictions of a species response to urbanization in a city that varies in average housing density while shaded ribbons are 95% credible intervals.

within a city increased the presence of predators and therefore constricted cottontail distributions (Crooks 2002). Although the importance of scale is well recognized in ecology (Wiens 1989, Levin 1992, Schneider 2001), the single-city focus of past urban ecological research prevented explorations into how landscape-scale differences influence urban ecological phenomena. Yet, as we have begun to show here, there is a need to explore how variables at the city-scale or larger drive species' distributions within and among cities (Aronson et al. 2014, Steenweg et al. 2017, Magle et al. 2019).

For vertebrates, increased urbanization generally results in decreased species richness at the local scale (Pautasso 2007, McKinney 2008, Ordeñana et al. 2010). In our analysis, cities with an average housing density greater than 710 housing units/km^2 ($n = 3$) consistently lost species at the local scale with increasing urbanization (Fig. 5), which validates this pattern. Conversely, species richness either increased ($n = 3$), decreased ($n = 1$), or did not change ($n = 2$) along the urbanization gradient of less densely built cities (Fig. 5). These results indicate that larger cities are more likely to observe diversity losses of common species, which may have dramatic consequences on ecosystem function (Gaston 2010). As such, it may be imperative for growing cities to find innovative solutions to reduce the likelihood of local extinctions and bolster wildlife resilience.

An advantage of our multi-level analysis is that differences in community composition within and among cities can be attributed to species-specific responses to urbanization. For example, we found the fox and gray squirrel's within-city response to urbanization went from positive to negative if a city had <~20% greenspace. As the distribution and abundance of these species are closely tied to tree availability, it is likely that increased greenspace within a city equates to additional tree-cover (Bonnington et al. 2014). We also found that coyotes always responded negatively to urbanization. However, the magnitude of that response was smaller in cities with greater average housing density. We suspect this is a result of behavioral shifts in coyotes, who typically have small urban home ranges, but have been shown to increase them in highly urban areas like downtown Chicago to access sufficient green space (Gehrt et al. 2010, Ellington and Gehrt 2019). Striped skunks, on the other hand, responded negatively to urbanization, but the strength or direction of this effect did not vary across cities as a function of average housing density or greenspace (i.e., the null model was the best-fit model). It may
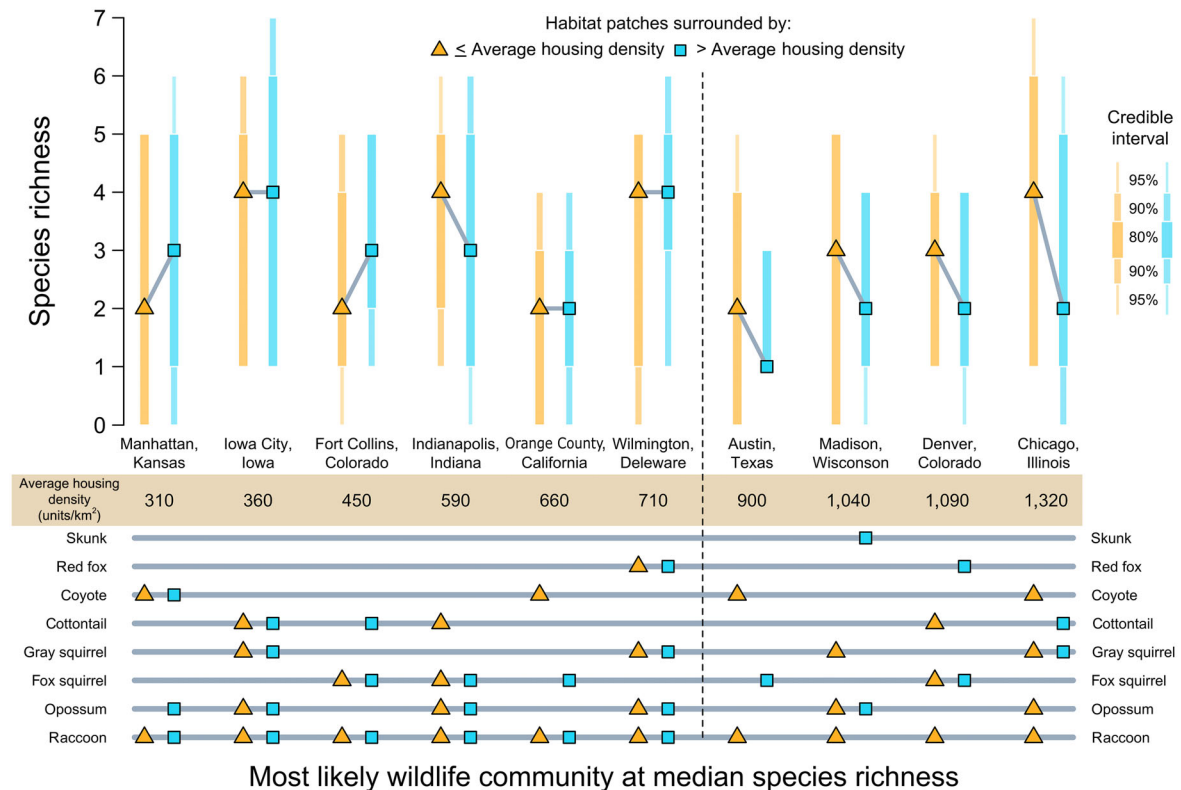
FIG. 5. A comparison of the estimated species richness at sites surrounded by less or more than the average housing density in a city. Cities are ordered from left to right, lowest to highest, by average housing density. The lower plot represents the most likely wildlife community represented by the median estimated species richness in urban greenspace in a city surrounded by less than or more than the average housing density for that city. The vertical dotted line represents an apparent shift in differences between species richness: cities with an average housing density >710 houses/km^2 always had fewer species in habitat patches surrounded by dense human populations.

be that greater levels of urbanization reduce available skunk habitat or increases skunk mortality due greater road traffic. That nearly every species response to urbanization was associated to landscape-scale differences among cities demonstrates that community level patterns should vary among cities and implies that other species' responses to urbanization are associated to land-scale differences among cities as well. Other multi-city analyses could use a similar modeling approach to this study to quantify such patterns for a wide array of species found in urban areas or on the urban fringe of cities.

Another core feature of our analysis is that the results can be used to develop quantitative and testable predictions for how common urban species are distributed throughout any city where they are known to exist or may exist in the future. Since some species' average occupancy (Eq. 2) and responses to urbanization (Eq. 3) are a function of landscape-scale variables, species distributions can be easily estimated within cities that vary in greenspace availability and average housing density. Given current levels of global change, there is great need for increased predictive power in ecology (Maris et al. 2018), especially as it is simpler to manage a system's

ecological characteristics if they are predictable (Dietze 2017). As we live in an increasingly urban world, it is not only essential to understand and predict how biodiversity responds to urbanization, but also to identify ways to advance urban conservation and reduce the negative impacts of urbanization on biodiversity. While we expect deviations from our model predictions, such discrepancies are welcome as they likely point to other landscape-scale variables that influence species distributions or could possibly highlight within-city species adaptations. For example, we simplified each city's urbanization gradient and represented it with a single metric: the housing density within 1,000 m of each camera trap. As urbanization is inherently composed of multiple variables (Moll et al. 2019), and there may be significant urbanization with low housing density (e.g., industrial or commercial districts), discrepancies from our model predictions may indicate other urban metrics that are important predictors of species' responses to urbanization. Likewise, the connectivity among habitat patches within a city may also relate to shifts in species distributions among cities (Beninde et al. 2015), though such metrics are notoriously difficult to quantify in urban settings given that species persist within the urban matrix

(Anderson and Minor 2017, Soanes et al. 2019). We also only quantified a species response to urbanization during the summer season. As many of these species have among-season variation in their colonization and extinction rates (Fidino and Magle, 2017*b*), exploring this relationship across space and time would be a promising avenue of future research. As long-term research networks like UWIN grow, the data they provide can be used to address these potential limitations.

Although cities are the hallmark of urbanization, they each have their own structural signature penned by land-use policy, coastlines or inland waterways, and topography (Bounoua et al. 2018, Magle et al. 2019). It is a promising finding that species occupancy patterns are associated with differences among cities because it implies that growing cities can be planned in such a way to reduce the negative influence of urbanization on biodiversity. Other research has also shown that increasing greenspace generally increases biodiversity (Beninde et al. 2015). We found that this may particularly be the case for tree squirrels and red fox (Fig. 3), as increasing greenspace within a city reduced the negative influence of urbanization on these species (Fig. 3). The positive benefits of green cities go beyond wildlife as urban greenspace also improves human health and wellbeing (Twohig-Bennett and Jones 2018, Bratman et al. 2019, Rojas-Rueda et al. 2019) and contributes to reduced urban heat island effects, better stormwater management, and cleaner air (Gómez-Baggethun and Barton, 2013). Yet, city planners must also weigh the benefits of increasing greenspace or decreasing housing density to benefit wildlife as this can come at the cost of increased sprawl, commute times, and housing prices for people. If planned correctly, urban greening can be an opportunity for cities to simultaneously benefit their human and non-human inhabitants, but to better understand this relationship additional studies are sorely needed that involve an even larger number of cities and a wider range of species, both urban-adapted and not.

However, it is also crucial to recognize urban greening as an environmental justice issue (Wolch et al. 2014). Communities of color disproportionately live in parts of a city where green space is either deficient or poorly maintained (Rigolon 2016) and are marked by significant environmental legacies (e.g., persistence of lead in urban soils; Morrison et al., 2013). Furthermore, while adding greenspace to these locations increases public health and neighborhood attractiveness, it can also displace the residents that the greenspace was meant to benefit via gentrification (Wolch et al. 2014). Equitably increasing access to greenspace, and thus biodiversity, in a city therefore requires appropriate regulation and anti-gentrification policy, which would, in turn, increase public health and advance social-environmental justice for urban communities (Kennedy and Leonard, 2001, Wolch et al. 2014, Bounoua et al. 2018). To illustrate the effectiveness of such policies, data will be necessary. As such, multi-city wildlife assessments could provide such data for cities to evaluate the potential impacts of regulation and policy on biodiversity, taking into account the desired outcomes of communities directly impacted by such changes.

Our results highlight the critical importance of considering the broader context of urbanization in urban ecological research given that differences between single-city findings may be a function of landscape-scale differences among cities. For cities that are structurally dissimilar, a given species' response to urbanization may even be in opposing directions (Figs. 3, 4). However, because species respond to the form of a city, it may be possible to design cities to decrease the negative influence of urbanization on biodiversity. Achieving this goal at broad scales requires us to understand and predict how variability within and among cities influences ecological phenomena. This understanding will, in turn, require multi-city collaborative approaches to tease apart how factors at varying scales influence Earth's urban biodiversity.

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