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# Urbanization, climate and species traits shape mammal communities from local to continental scales

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Human-driven environmental changes shape ecological communities from local to global scales. Within cities, landscape-scale patterns and processes and species characteristics generally drive local-scale wildlife diversity. However, cities differ in their structure, species pools, geographies and histories, calling into question the extent to which these drivers of wildlife diversity are predictive at continental scales. In partnership with the Urban Wildlife Information Network, we used occurrence data from 725 sites located across 20 North American cities and a multi-city, multi-species occupancy modelling approach to evaluate the effects of ecoregional characteristics and mammal species traits on the urbanization–diversity relationship. Among 37 native terrestrial mammal species, regional environmental characteristics and species traits influenced within-city effects of urbanization on species occupancy and community composition. Species occupancy and diversity were most negatively related to urbanization in the warmer, less vegetated cities. Additionally, larger-bodied species were most negatively impacted by urbanization across North America. Our results suggest that shifting climate conditions could worsen the effects of urbanization on native wildlife communities, such that conservation strategies should seek to mitigate the combined effects of a warming and urbanizing world.

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[1–3], while finer-scale patterns of resource availability, ecological disturbance and species traits influence local community composition through habitat use, species interactions and population processes[4–7]. 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 (that is, species richness) and related metrics that account for species evenness (that is, species diversity indices)[2,8]. Despite the critical influences that broader-scale environmental factors can have on the mechanisms by which local human activities shape community composition[9–13], 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[14–16].

Human-driven landscape changes can influence the distribution and diversity of species across multiple scales and along urbanization gradients, ranging from undeveloped to urban[17,18]. Greater levels of urbanization negatively affect wildlife communities across scales[9,10,15,16,19,20], with community composition varying within and among cities according to each city's broad biophysical characteristics[6,11,21]. Regionally, urban species pools can be associated with variation in climate, city size and land cover[1,11,18]. For instance, warmer, mesic ecoregions and more recently urbanized regions often exhibit greater

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biodiversity[2,22,23]. Locally, communities may respond differently to urbanization due to regional differences in urban footprint[16,24], vegetation[9,10] and age of development[9,25]. These multi-scale landscape changes can individually influence biodiversity patterns[3], but their combined effects on communities are poorly understood[8,18].

Species' functional traits may also influence relationships between human development and community composition. Life history traits such as body size, home range and diet can mediate species' tolerance of urbanization[26–28]. Wider-ranging, larger-bodied and more carnivorous mammals, for example, are often most negatively affected by human development or persecution[29–31]. The few urbanization-tolerant species that remain can become abundant in human-dominated landscapes, resulting in lower species evenness and diversity[32–35]. Community composition within cities is thus a consequence of species traits and multi-scale landscape factors[6]. However, it is unclear how these factors interact across scales to drive biodiversity patterns[14,36].

Here we tested whether local-scale and regional-scale environmental factors and species traits influenced mammal presence, community composition and the relationships of both with anthropogenic landscape changes. We conducted this study across 20 North American cities in the Urban Wildlife Information Network (UWIN; Fig. 1 and Extended Data Table 1), a long-term, multi-region study with the purpose of systematically monitoring biodiversity across cities of varying sizes, histories and ecoregional contexts[18]. We used data from a continent-wide camera-trap array and a multi-city, multi-species occupancy model to address three research objectives[37]. 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.

## 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) (Extended Data Table 1)[38]. 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 in fewer than 0.05% of the total trap-days (ten daily detections) and were excluded from species-level analyses (Supplementary Table 1).

### Within cities

Mammal species occupancy was associated with variations in human landscape modification within cities (Table 1, Effect Type 1; see also Extended Data Fig. 1a–c). Across all sites, community-average occupancy probability (that is, the among-species mean, community-level occupancy hyperparameter) strongly decreased with increasing local urbanization (the mean impervious surface percentage around each site), with the city-average modelled relationship (Table 1) predicting occupancy probabilities of 0.16 (95% Bayesian credible interval (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 (Extended Data Fig. 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 1), relationships on 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 (Extended Data Fig. 1b). Community-average occupancy also demonstrated a moderate negative relationship with local agricultural footprint (Table 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 (Extended Data Fig. 1c).

Metrics of local community composition—specifically, species richness (the total number of species) and diversity (the exponentiated Shannon entropy index, or the number of species weighted by species evenness; see the Methods for additional details)—also exhibited associations with gradients of landscape modification (Table 2, Effect Type 1). Across all sites, local urbanization demonstrated negative relationships with richness and diversity (Table 2 and Extended Data Fig. 1d–f). The average sites with the most impervious surface cover were predicted 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 (Extended Data Fig. 1d,g). Local patch density was probably not associated with either richness or diversity (Table 2 and Extended Data Fig. 1e,h). Conversely, local agricultural footprint demonstrated negative relationships with both richness and diversity (Table 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 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 (Extended Data Fig. 1f,i). Variation in diversity—as a metric positively associated with species evenness—partially resulted from how the effects of human landscape changes varied within the community, because the occupancy of several species exhibited stronger negative relationships with urbanization than that of others (Supplementary Table 2 and Supplementary Data 1).

### 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 (that is, the overall probability of regional species presence) and regional environmental variables (Table 1, Effect Type 2; see also Extended Data Fig. 2), including vegetation greenness (enhanced vegetation index (EVI)), temperature (mean annual temperature), regional urbanization (the percentage of the city consisting of urban land-cover types) or city age (years since colonization). However, species were more common across all sites (that is, community-average occupancy was higher) in cities with greater vegetation greenness, lower regional urbanization and colder temperatures (Table 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 (Fig. 2a,b) but probably did not vary among cities of different ages or with different levels of regional urbanization (Fig. 2c,d and Table 1, Effect Type 4). For instance, the negative effect of local urbanization on occupancy in the relatively low-temperature and highly vegetated city of Tacoma, Washington, was predicted to be 0.65 times weaker than that in the similarly vegetated but warmer St. Louis, Missouri, and 0.50 times weaker than that in 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 (Supplementary Data 1).

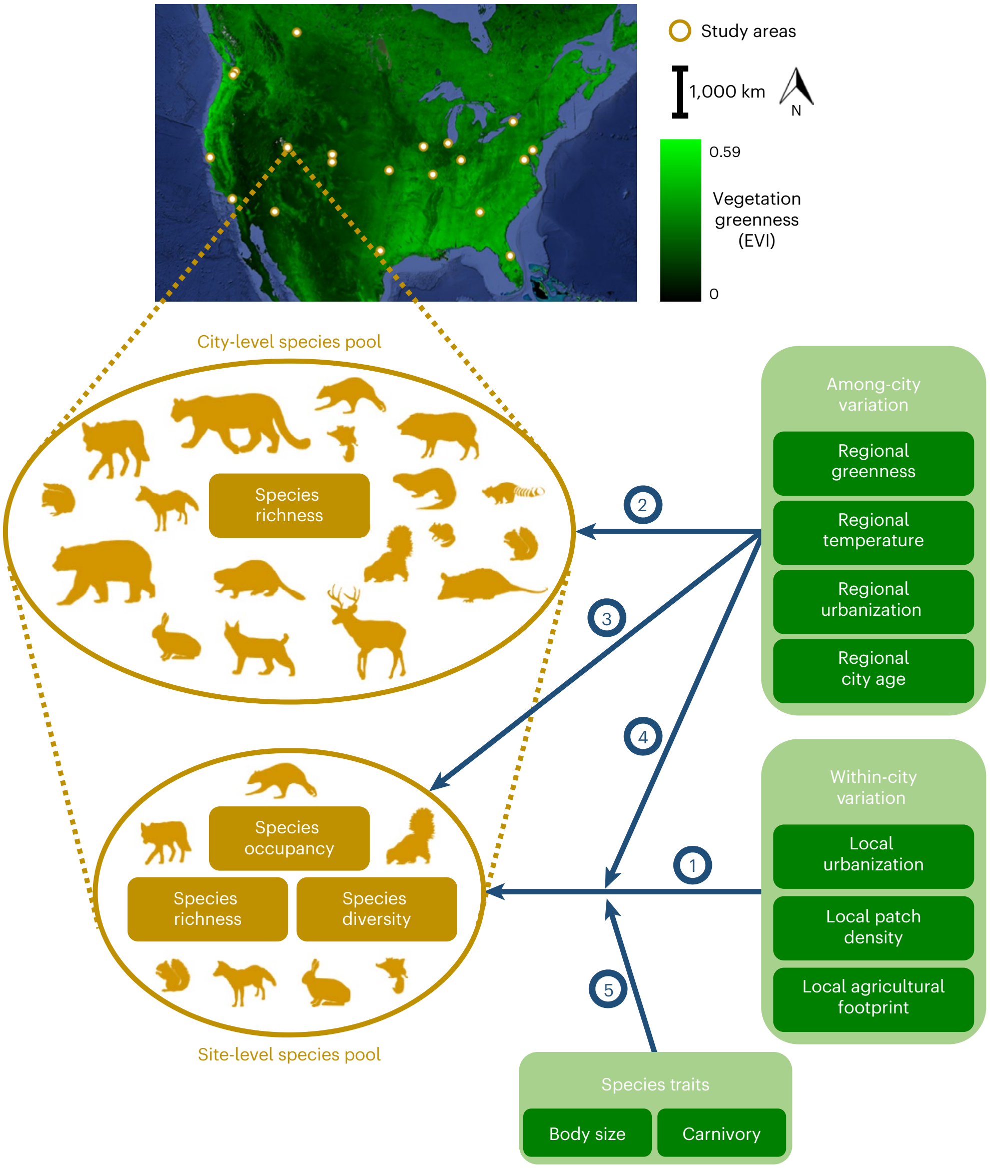

**Fig. 1 | Study cities across North America and the study's modelling approach.** We depict the locations of 20 cities participating in the long-term monitoring of wildlife species, as part of UWIN, across a continental gradient of vegetation greenness (EVI). The arrows represent the five types of effects modelled in this study, 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 (for example, local urbanization) influencing site-level species pools (for example, average species occupancy or alpha diversity); (2) environmental variation among cities (for example, EVI) driving differences in regional species pools (for example, 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 shape local communities; and (5) species traits shaping local species pools by mediating among-species differences in within-city responses to environmental predictors. All animal graphics were sourced from PhyloPic (https://www.phylopic.org/) and were utilized as part of the public domain or under the CC BY 3.0 licence (for the full list of image attributions, please see the data repository archived at https://github.com/jhaight-eco/uwin-multiregioncommcomp).

For example, interaction effects for cottontail rabbits (*Sylvilagus* spp.) indicated that the species responded more negatively to urbanization in warmer cities ($\beta_{\text{mean}} = -0.27$; 95% CRI, −0.62 to 0.09; 93.5% of posterior distribution negative) and in cities with lower vegetation greenness ($\beta_{\text{mean}} = 0.21$; 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 2, Effect Type 3) and their within-city relationships with urbanization (Fig. 2e–l and Table 2, Effect Type 4). In cities with greener vegetation, site-level richness and diversity tended to be greater and less negatively associated with urbanization (Fig. 2e,i). For example, the negative effects of local urbanization on richness and diversity in the least vegetated city (Phoenix, Arizona) were predicted to be, respectively, 1.45 and 3.60 times stronger than 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 (Fig. 2f,j). For instance, local urbanization in 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 in Salt Lake City, Utah, one of the coldest cities with similar vegetation greenness. Cities with greater regional urbanization (that is, more intensively urbanized landscapes)

**Table 1 | Effects of local and regional environmental predictors on local community-average occupancy and regional species richness**

| Response variable | Predictor variable(s) | Effect type | $\beta_{mean}$ | 95% CRI (lower, upper) | Probability of relationship (%) |
|---|---|---|---|---|---|
| **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* |
| | 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 × local urbanization (interaction) | 4 | 0.12 | −0.08, 0.31 | 88.4* |
| | Regional temperature × local urbanization (interaction) | 4 | −0.13 | −0.38, 0.11 | 86.4* |
| | Regional urbanization × local urbanization (interaction) | 4 | −0.01 | −0.17, 0.15 | 54.7 |
| | Regional city age × 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 |

We estimated standardized effects using a Bayesian multi-city community occupancy modelling approach across 725 sites in 20 North American cities, determining the modelled effect of each set of predictor variables on each response variable by calculating means ($\beta_{mean}$) and 95% CRIs across each effect parameter's posterior distribution. We measured the response variable local community-average occupancy as the mean probability of site use among the mammal community and quantified regional species richness using the probability of the average species being present in each city (the proportion of a city's potential regional species pool that was present). We grouped effects into one of five types on the basis of the spatial scale(s) at which they were assumed to operate, as depicted in Fig. 1. The modelled effects included cross-scale interactions (Fig. 1, Effect Type 4), the combined effects of regional environmental predictors and local urbanization on local community characteristics (that is, average species occupancy; Fig. 2a–c). Because of the inclusion of interaction terms, local urbanization effects (Fig. 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 percentage of each effect parameter's Bayesian posterior distribution that shared a sign (positive or negative) with the mean of the distribution, with '*' indicating 'likely' relationships (>85% probability) and '**' indicating 'highly likely' relationships (>95% probability) (see the Methods for additional details).

had lower site-level richness and diversity, both of which also had more negative relationships with local urbanization than in less urbanized cities (Fig. 2g,k). Finally, site-level richness tended to be higher in older cities, whereas site-level diversity was lower (Fig. 2h,l).

### Among species

Species traits (that is, body size and carnivory) influenced each mammal species' occupancy and their responses to urbanization in cities (Fig. 3 and Extended Data Fig. 3). Although larger-bodied species were as common as (that is, had similar species-level occupancy to) smaller-bodied species overall (Extended Data Fig. 3a; $\beta_{mean} = -0.07$; 95% CRI, −0.66 to 0.51; 59.8% of posterior positive), body mass exhibited a negative relationship to the urbanization effect (Fig. 3a; $\beta_{mean} = -0.36$; 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 (Extended Data Fig. 3b; $\beta_{mean} = -0.53$; 95% CRI, −1.08 to 0.03; 96.9% of posterior distribution negative), but carnivory did not influence species' responses to urbanization (Fig. 3b; $\beta_{mean} = 0.03$; 95% CRI, −0.24 to 0.29; 58.5% of posterior distribution positive).

## 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 multi-city modelling approach and biodiversity data spanning North American biomes. As we hypothesized, local mammal communities varied substantially across gradients of human landscape change[11,15,16,19], and the broad environmental characteristics of cities shaped differences in how local communities related to urbanization[9–11], with urbanization demonstrating stronger negative influences on communities in warmer, less vegetated cities. Furthermore, the effects of urbanization on species presence were mediated by key life history traits[29]. 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[6].

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 loss due to urban development[11,20,33]. 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[39–42]. 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[35]. Similarly, natural patch and edge density, proxy measures of habitat fragmentation and landscape heterogeneity that tend to vary most in moderately urbanized areas[40,42], may be either positively or negatively associated with richness[43–45]. More fragmented landscapes can also favour edge-tolerant, generalist species, reducing evenness and further

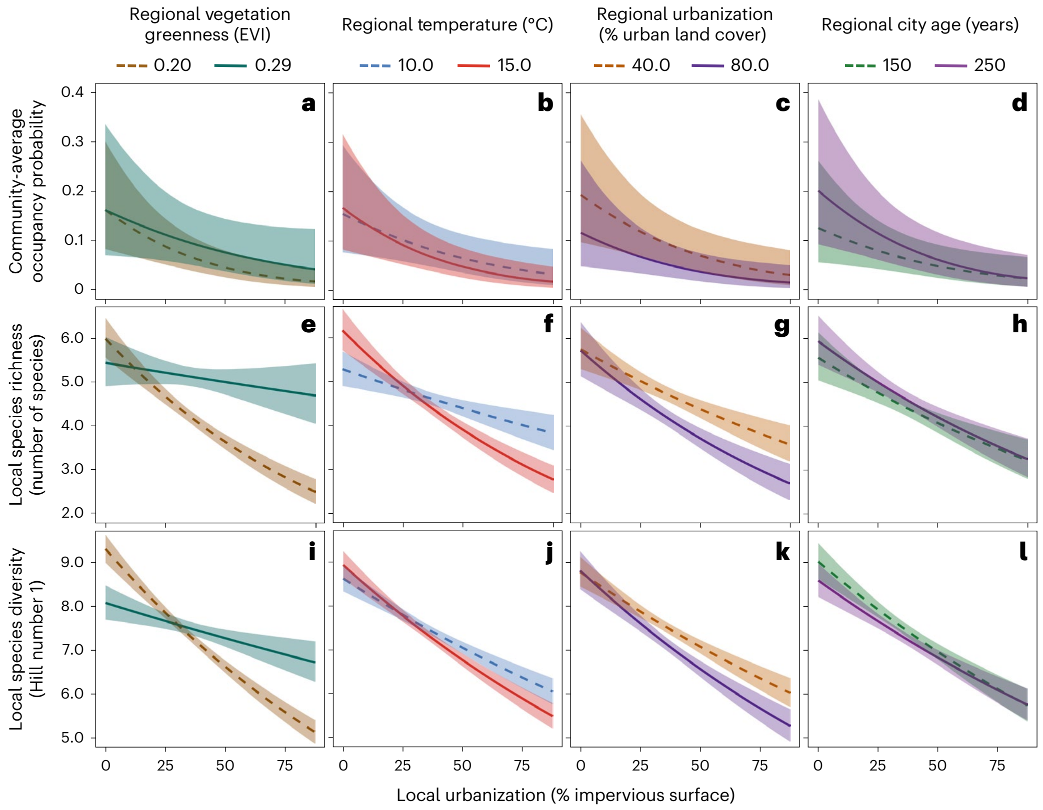

**Fig. 2 | Influences of regional variation in vegetation greenness, temperature, urbanization and city age on mammal community trends across local urbanization gradients. a–d**, Community-average occupancy probability, the average probability of site use among the mammal community. **e–h**, Local species richness, the total number of species at each site (Hill number 0). **i–l**, Local species diversity, the number of species at each site weighted by species evenness (Hill number 1, the exponentiated Shannon index). We estimated the response variables of community-average occupancy, local species richness and local species diversity across 725 sites in 20 North American cities using a Bayesian multi-city community occupancy model and accompanying community composition meta-analysis models. We visualized the modelled effects of within-city and among-city variables on occupancy (Table 1, Effect Types 1, 3 and 4) and on richness and diversity (Table 2, Effect Types 1, 3 and 4) by predicting the 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 depicted the median and 95% CRI of these predicted values using the trendlines and their corresponding shaded regions.

complicating relationships between landscape heterogeneity and community composition[20,33,46]. 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 (for example, recreational activity) and other behaviours (for example, wildlife feeding and yard management) across landscapes[7,13,21,47]. 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 with species in cooler cities (for example, Salt Lake City, Utah), species in warmer cities (for example, 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 in different ecoregions distinct, such as vegetation type, structure and evapotranspiration. Urban heat island effects (that is, higher temperatures in highly urbanized areas than in wildlands) may additionally be greater in warmer cities[48]. Particularly for endothermic species such as mammals, combined increases in temperature and urbanization can negatively impact health and survival[49,50]. Conversely, cities with greener vegetation (which also tend to have higher mean annual precipitation—for example, Sanford, Florida) were more likely than less vegetated, drier cities (for example, 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 such as food, water and refugia from predators associated with more vegetation and precipitation[16,51]. 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 on the unique sociocultural processes that characterize different cities. For example, local species diversity tended to be greater across sites in more recently developed and less urbanized cities in our study (for example, Salt Lake City, Utah; and 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[9,11,16,25]. Despite potential mechanistic connections between the overall age of

**Table 2 | Effects of local and regional environmental predictors on local community composition**

| Response variable | Predictor variable(s) | Effect type | $\beta_{mean}$ | 95% CRI (lower, upper) | Probability of relationship (%) |
|---|---|---|---|---|---|
| **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** |
| | 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 × local urbanization | 4 | 0.09 | 0.06, 0.12 | 100.0** |
| | Regional temperature × local urbanization | 4 | −0.04 | −0.07, −0.06 | 100.00** |
| | Regional urbanization × local urbanization | 4 | −0.03 | −0.05, 0.00 | 96.6** |
| | Regional city age × local urbanization | 4 | −0.01 | −0.04, 0.03 | 63.6 |
| **Local species diversity** | 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** |
| | Regional city age | 3 | −0.02 | −0.03, 0.00 | 97.5** |
| | Regional greenness × local urbanization | 4 | 0.05 | 0.03, 0.07 | 100.0** |
| | Regional temperature × local urbanization | 4 | −0.02 | −0.04, −0.01 | 99.9** |
| | Regional urbanization × local urbanization | 4 | −0.01 | −0.02, 0.00 | 97.2** |
| | Regional city age × local urbanization | 4 | 0.01 | −0.01, 0.02 | 75.2 |

We estimated standardized effects using a Bayesian meta-analysis on the basis of local species richness and diversity values derived from a multi-city community occupancy model across 725 sites in 20 North American cities, determining the modelled effect of each set of predictor variables on each response variable by calculating means ($\beta_{mean}$) and 95% CRIs 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 high evenness. The effects were grouped into one of five types on the basis of the spatial scale(s) at which they were assumed to operate, as depicted in Fig. 1. The modelled effects included cross-scale interactions (Fig. 1, Effect Type 4), the combined effects of regional environmental predictors and local urbanization on local community composition (that is, species richness and diversity; Fig. 2d–i). Because of the inclusion of interaction terms, local urbanization effects (Fig. 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 percentage of each effect parameter's Bayesian posterior distribution that shares a sign (positive or negative) with the mean of the distribution, with '*' indicating 'likely' relationships (>85% probability) and '**' indicating 'highly likely' relationships (>95% probability) (see the Methods for additional details).

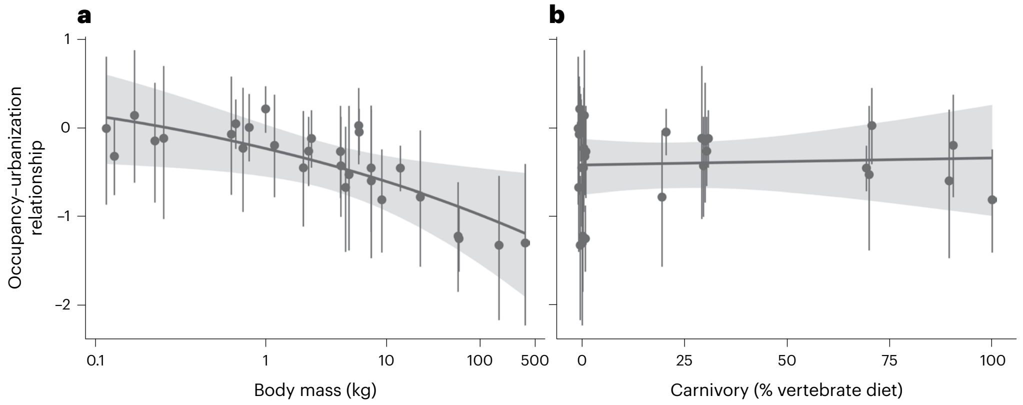

**Fig. 3 | Influences of species traits on within-city relationships between urbanization and mammal occupancy. a**, Influence of body mass, represented by the log-transformed mean body mass of each species (in kg). **b**, Influence of carnivory, calculated as the percentage of vertebrate prey in each species' diet. Each point and bar, respectively, represents the mean and 95% CRI of the estimated responses to urbanization for 29 mammal species commonly detected across 725 sites in 20 North American cities (excluding 8 species detected in fewer than 10 total trap-days). The trendline and shaded region depict the median and 95% CRI of response variables predicted across a hypothetical range of trait values. The results primarily demonstrate that larger-bodied species had more negative relationships with urbanization.

a city and local species extinction and colonization processes[11], city age has uncertain relationships with biodiversity[9], potentially due to cities growing more rapidly during different historical periods. Regardless of their overall ages, cities that have been more intensively built—either outwards (via urban sprawl) or upwards (via urban densification)—tend to be those in which human landscape changes most strongly impact biodiversity[9,16]. These biophysical landscape characteristics that drive differences in biodiversity relationships among cities are additionally influenced by heterogeneous socio-economic processes, including those associated with past and present distributions of wealth and social inequities[15,52]. Understanding what makes a city more supportive of biodiversity persistence requires further recognition of how complex human decision-making processes variably structure urbanizing landscapes and wildlife community patterns[6,14,53,54], 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[26,29]. Although the greater mobility of larger species can enable them to better access anthropogenic resources across fragmented landscapes[31,55], those species are also generally more sensitive to urbanization-driven habitat losses due to their greater space needs, lower reproductive rates and increased persecution by humans[25,26,29,30,56]. While obligate carnivores (for example, bobcats and mountain lions) are often regarded as intolerant of urban environments[29,31], 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 (for example, coyotes, foxes and raccoons), whose flexible, omnivorous diets enable them to exploit anthropogenic resources in urban environments[30]. 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[27,30]. It is also important to acknowledge that assessments of functional traits and taxonomic diversity depend on how wildlife communities were sampled across landscapes, where the use of multiple survey methods (for example, camera traps, hair traps and live traps) may help future studies reduce potential biases, such as the under-sampling of smaller-bodied species[57,58]. Nevertheless, species functional traits play critical roles in community assembly across urbanization gradients by driving individual species distributions[6], and our results indicate the importance of further examining 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[14].

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-level 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[59]. For instance, during winter seasons, urban environments in 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[60]. Furthermore, the use of human-dominated environments by wildlife communities can vary substantially across years, driven by changes in human land use/land cover and fluctuations in resource availability and human activity[29,47,59,61–63]. 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 examining and understanding how wildlife communities vary in relation to changing landscapes and climates through time[64].

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[3,8,14]. 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[65–67]. However, there are other key differences in warmer and greener cities that can drive these patterns (for example, biome characteristics, vegetation communities, water availability and size of the regional species pool), and future studies could further explore potential mechanisms underlying these cross-scale relationships[8,14]. 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[16].

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[11,66–68]. 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[53,69]. 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[53,70,71]. Towards this end, identifying key areas in which region-specific conservation priorities align with existing human-centred urban sustainability goals and management practices should be a priority for future research[54]. Finally, we emphasize that research networks spanning multiple cities and continents can identify interconnected biodiversity threats and offer recommendations to mitigate the impacts of global change[14,18,68]. 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.

## Methods

### 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 (Fig. 1 and Extended Data Table 1)[38]. The data were collected using a camera-trapping protocol established by UWIN for the long-term monitoring of ground-dwelling wildlife species[18]. In each city, passive infrared-triggered wildlife cameras were located along likely wildlife travel corridors (for example, parks, preserves, riparian corridors, trails, alleys and canals) across a gradient of urbanization (defined as the percentage of impervious surface cover) and positioned a minimum of 1 km apart from one another to increase the independence of each sampling site.

### 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 the basis of wildlife camera photographs, observations of seven sets of closely related congeneric species (antelope ground squirrels, chipmunks, cottontail rabbits, flying squirrels, grey squirrels, jackrabbits and weasels) were grouped for estimating species presence, detection and community composition. Although certain small mammals were also widely detected and identified across all cities (for example, squirrel species), mid-to-large-sized mammal species were probably over-represented, and many smaller-bodied species were under-represented or not detected at all in our sampling, a potential source of bias typical of camera trapping as a method for sampling wildlife communities[58].

We analysed 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 (29 June–2 August; Supplementary Table 1). Each UWIN partner began and ended data collection at different times between 2016 and 2020, with certain cities having only a single full or partial year's worth of data available at the time of this analysis (for example, Manhattan, Kansas, stopped collecting data in 2016). We thus 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 in each city (Extended Data Table 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-trap sites that were sampled for a minimum of 12 days and a maximum of 35 days. From 2016 through 2020, 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 ten daily detections (0.05% of the total trap-days). As described in our statistical modelling 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.

## 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, on the basis of the combination of data from the 2016 National Land Cover Database Imperviousness dataset (for all US cities) and road and building footprint data (for Edmonton)[72–74]. In the R programming language version 4.0.1 (ref. 75), 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 30-metre dataset[76,77] and the R package landscapemetrics[78]. 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, which are observably greater in areas of moderate urbanization (Extended Data Fig. 4). To reduce the influence of differences in sample size (the number of wildlife cameras) among cities, the values of all within-city covariates were standardized by city prior to model implementation, following best-practice recommendations for multilevel modelling[79,80]. 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 (Extended Data Fig. 5). We included four of these variables as among-city covariates in our model on the basis of their alignment with regional environmental characteristics hypothesized to drive regional species diversity and influence urbanization–community relationships. We measured vegetation greenness using the EVI, calculated in Google Earth Engine on the basis of Landsat 5 TM 32-Day composite imagery from 1984 to 2012[81]. We considered the EVI to be associated with metrics of precipitation, aridity, natural patch density and latitude, based on an arbitrary cut-off of Pearson's coefficient > 0.5 (Extended Data Fig. 5). Mean annual temperature (MAT) was derived from 1 km downscaled climate data for the 1981–2010 normal period produced by ClimateNA[82] and was associated with mean summer temperature, potential evapotranspiration, aridity and latitude (Extended Data Fig. 5). 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 (Extended Data Fig. 5). We measured city age (AGE) using the years since the approximate date of the earliest Euroamerican colonization or settlement of each city's metropolitan area, following the methods of Aronson et al.[9]. Although we chose to model the effects of these four city-level characteristics on the basis of 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 (for example, human population density and precipitation).

**Species trait covariates.** We assessed among-species variation in species occupancy and urbanization effects on the basis of species trait data for all 37 species sourced from the EltonTraits and PanTHERIA databases[83,84]. 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[26–29]: 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, grey squirrels, chipmunks and weasels), we calculated mean trait values among the known species in each assemblage.

## Multi-city community occupancy model

We estimated site-level 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 probably 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[15]. On the basis of the multi-region community occupancy model structures described by Sutherland et al.[37] and Tenan et al.[85], our model estimates the probability that (1) a species is present in the species pool of a given city; (2) a species is present at a site in a city, given its 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 $1, \ldots, S$ species in each of $r$ in $1, \ldots, R$ cities, we treat $\omega_{s,r}$ as a Bernoulli random variable that denotes whether species $s$ is in the species pool of city

$r$, and we let $\Omega_r$ (the completeness of each regional species pool) be the probability that all $S$ species are in the species pool of city $r$, such that

$$\omega_{s,r} \sim \text{Bernoulli}(\Omega_r) \tag{1}$$

We further define the regional species richness ($\gamma_r$) as $\sum_s^S \omega_{s,r}$, representing the number of species in the species pool of city $r$. If a species was ever observed in city $r$, then $\omega_{s,r}$ was initially set to 1 (that is, presence). If a species was not observed in city $r$ during the sampling period but is known to exist in the regional species pool on the basis of previous observation by UWIN partners or known species ranges (for example, Mammals of North America and the USGS Gap Analysis Project)[86,87], then the model estimated $\omega_{s,r}$ with uncertainty. We did not augment matrices of species occurrence in cities beyond the total number of observed species ($S = 37$) because the purpose of this study was to evaluate patterns of known species richness while correcting for imperfect detection, not to estimate numbers of unknown species.

We used the logit link to allow the completeness of the regional species pool ($\Omega_r$) to vary from the logit-scale intercept $\bar{\Omega}$ as a function of standardized among-city (regional) covariates ($m_{\text{EVI}}$, $m_{\text{MAT}}$, $m_{\text{URB}}$ and $m_{\text{AGE}}$), such that

$$\begin{aligned} \text{logit}(\Omega_r) = {} & \bar{\Omega} + \theta_{\text{EVI}} \times m_{\text{EVI},r} + \theta_{\text{MAT}} \times m_{\text{MAT},r} \\ & + \theta_{\text{URB}} \times m_{\text{URB},r} + \theta_{\text{AGE}} \times m_{\text{AGE},r} \end{aligned} \tag{2}$$

where the $\bar{\Omega}$ and slope terms ($\theta$) were all given vague normal priors (for example, $\bar{\Omega} \sim \text{Normal}\left(0, \frac{1}{\sqrt{0.1}}\right)$).

**Site-level species presence.** The second level of the model estimated species presence at a site in a city given that a species is in that city's species pool. For $j$ in 1, ..., $J$ sampled sites in city $r$, let $z_{s,j,r}$ be a Bernoulli random variable that takes the value of 1 when species $s$ is present at site $j$ in city $r$ and is otherwise zero. Furthermore, let $\psi_{s,j,r}$ be the probability of occupancy such that

$$z_{s,j,r} \sim \text{Bernoulli}(\psi_{s,j,r} \times \omega_{s,r}) \tag{3}$$

Given this specification, if a species is not in 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 ($m_{\text{EVI}}$, $m_{\text{MAT}}$, $m_{\text{URB}}$ and $m_{\text{AGE}}$), within-city covariates ($m_{\text{Urbanization}}$, $m_{\text{PatchDensity}}$ and $m_{\text{AgriculturalFootprint}}$) and the interactions between the two (for example, $m_{\text{EVI}} \times m_{\text{Urbanization}}$) via the logit link, such that

$$\begin{aligned} \text{logit}(\psi_{s,j,r}) = {} & \varphi_{0,s,r} + \varphi_{\text{Urbanization},s,r} \times m_{\text{Urbanization},j,r} \\ & + \varphi_{\text{PatchDensity},s,r} \times m_{\text{PatchDensity},j,r} \\ & + \varphi_{\text{AgriculturalFootprint},s,r} \times m_{\text{AgriculturalFootprint},j,r} \\ & + \varphi_{\text{EVI},s,r} \times m_{\text{EVI},r} + \varphi_{\text{MAT},s,r} \times m_{\text{MAT},r} + \varphi_{\text{URB},s,r} \\ & \times m_{\text{URB},r} + \varphi_{\text{AGE},s,r} \times m_{\text{AGE},r} + \varphi_{\text{EVI}\times\text{Urbanization},s,r} \\ & \times m_{\text{EVI},r} \times m_{\text{Urbanization},j,r} + \varphi_{\text{MAT}\times\text{Urbanization},s,r} \\ & \times m_{\text{MAT},r} \times m_{\text{Urbanization},j,r} + \varphi_{\text{URB}\times\text{Urbanization},s,r} \\ & \times m_{\text{URB},r} \times m_{\text{Urbanization},j,r} + \varphi_{\text{AGE}\times\text{Urbanization},s,r} \\ & \times m_{\text{AGE},r} \times m_{\text{Urbanization},j,r} + \in_{\text{Year},t} \end{aligned} \tag{4}$$

where each $\varphi_{s,r}$ represents each species' city-specific logit-scale occupancy intercept and slope parameters and $\in_{\text{Year},t}$ 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 vary from community-level (that is, among-species average) hyperparameters $\beta$ on the basis of species-level traits. In the model, among-species covariates were assumed to partially influence the degrees to which each species' occupancy within a city $\varphi_{0,s,r}$ and among-city average relationship with urbanization $\delta_{\text{Urbanization},s}$ both vary from their respective community-average mean parameters $\beta_0$ and $\beta_{\text{Urbanization}}$.

$$\begin{aligned} \varphi_{0,s,r} \sim {} & \text{Normal}\,(\,\beta_0 + \beta_{\text{OccupancyMass}} \times m_{\text{Mass},s} \\ & + \beta_{\text{OccupancyCarnivory}} \times m_{\text{Carnivory},s}, \sigma_{\beta_0}\,) \\ & \delta_{\text{Urbanization},s} \\ \sim {} & \text{Normal}\,(\,\beta_{\text{Urbanization}} + \beta_{\text{UrbanizationMass}} \times m_{\text{Mass},s} \\ & + \beta_{\text{UrbanizationCarnivory}} \times m_{\text{Carnivory},s}, \sigma_{\beta_{\text{Urbanization}}}\,) \end{aligned} \tag{5}$$

where $\beta_{\text{OccupancyMass}}$, $\beta_{\text{OccupancyCarnivory}}$, $\beta_{\text{UrbanizationMass}}$ and $\beta_{\text{UrbanizationCarnivory}}$ 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 in equations (4) and (5). As such, we explain only the model intercept prior specification, which was

$$\begin{aligned} \beta_0 & \sim \text{Normal}(0, 1.5) \\ \delta_{0,s} & \sim \text{Normal}(\beta_0, \sigma_{\beta_0}) \\ \sigma_{\beta_0} & \sim \text{Inverse gamma}(0.1, 0.1) \\ \varphi_{0,s,r} & \sim \text{Normal}(\delta_{0,s}, \sigma_{\delta_{0,s}}) \\ \sigma_{\delta_{0,s}} & \sim \text{Inverse gamma}(0.1, 0.1) \end{aligned} \tag{6}$$

where $\beta_0$ 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 varies around $\beta_0$ via the standard deviation term $\sigma_{\beta_0}$; and $\varphi_{0,s,r}$ is the species-specific and city-specific logit-scale intercept that varies 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 its presence, such that

$$\begin{aligned} y_{s,j,r} & \sim \text{Binomial}(\rho_{s,j,r} \times z_{s,j,r}, k_{s,j,r}) \\ \text{logit}(\rho_{s,j,r}) & = \eta_{0,s,r} \end{aligned} \tag{7}$$

where $\eta_{0,s,r}$ is the species-specific and city-specific logit-scale parameter for detection probability. We specified priors for the detection intercept parameters following a hierarchical parameterization identical to that of the occupancy parameters shown in equation (6).

**Model fitting.** We implemented our multi-city community occupancy model in a Bayesian framework using R version 4.0.1 (ref. 75) and JAGS version 4.3.0 (ref. 88). 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 the model parameters, resulting in a total of 60,000 posterior samples. We verified convergence by examining the Gelman–Rubin diagnostics ($\hat{R} < 1.1$) and by visually inspecting traceplots for all modelled parameters[89].

**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: species richness ($q = 0$, the absolute sum of species present) and species diversity ($q = 1$, an exponentiated Shannon entropy index)[85,90]. 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[15,91]. Following the methods of Broms et al.[92] and Tenan et al.[85], we used occupancy estimates as stand-ins for abundance in the calculation of species diversity[85,92]. We chose the metric of species diversity ($^1D$) 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 higher evenness.

### 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 modelled 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 to allow species richness ($^0D$) and species diversity ($^1D$) to individually vary as functions of the same set of covariates from the multi-city community occupancy model (for example, within-city covariate $m_{\mathrm{Urbanization}}$, among-city covariate $m_{\mathrm{EVI}}$ and the combined interaction between the two $m_{\mathrm{EVI}} \times m_{\mathrm{Urbanization}}$), such that

$$\begin{aligned}
\ln({}^qD_{j,r}) = {} & \propto_{0,j} + \propto_{\mathrm{Urbanization}} \times m_{\mathrm{Urbanization},j,r} + \propto_{\mathrm{PatchDensity}} \\
& \times m_{\mathrm{PatchDensity},j,r} + \propto_{\mathrm{AgriculturalFootprint}} \\
& \times m_{\mathrm{AgriculturalFootprint},j,r} + \propto_{\mathrm{EVI}} \times m_{\mathrm{EVI},r} + \propto_{\mathrm{MAT}} \\
& \times m_{\mathrm{MAT},r} + \propto_{\mathrm{URB}} \times m_{\mathrm{URB},r} + \propto_{\mathrm{AGE}} \times m_{\mathrm{AGE},r} \\
& + \propto_{\mathrm{EVI\times Urbanization}} \times m_{\mathrm{EVI},r} \times m_{\mathrm{Urbanization},j,r} \\
& + \propto_{\mathrm{MAT\times Urbanization}} \times m_{\mathrm{MAT},r} \times m_{\mathrm{Urbanization},j,r} \\
& + \propto_{\mathrm{URB\times Urbanization}} \times m_{\mathrm{URB},r} \times m_{\mathrm{Urbanization},j,r} \\
& + \propto_{\mathrm{AGE\times Urbanization}} \times m_{\mathrm{AGE},r} \times m_{\mathrm{Urbanization},j,r} + \in_{j,r} \\
{}^qD_{j,r} \sim {} & \mathrm{Normal}(\bar{D}, \sigma_D)
\end{aligned} \tag{8}$$

where $\propto_{0,j}$ is the log-scale intercept of each community composition metric, the remaining $\propto$ terms are slope parameters representing the effects of each covariate or combination of covariates, and $\in_{j,r}$ is an additional error term that allowed each data point to vary from the modelled relationship (that is, the standard residual error term in a log-linear model). All intercept and slope parameters were given vague normal priors (for example, $\alpha_{0,r} \sim \mathrm{Normal}(0, 10)$). We parameterized normal priors for $^qD$ on the basis of $\bar{D}$ and $\sigma_D$, 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.

### Evaluating modelled covariate relationships

We evaluated the hypothesized influences of the 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 CRIs and whether or not they overlap zero. In multilevel models such as ours, estimates of lower-level random parameters (for example, our species-specific parameters) tend to be drawn towards the mean value of the upper-level parameters from which they are derived (for example, our community-mean parameters), resulting in the shrinkage of lower-level parameters[93]. When necessary to account for the effect of parameter shrinkage in 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'[29,94].

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

All data that support the findings of this study and that were used in the production of all figures are publicly available on Zenodo at https://doi.org/10.5281/zenodo.8083504.

## Code availability

All code that supports the findings of this study and that was used in the production of all figures is publicly available on Zenodo at https://doi.org/10.5281/zenodo.8083504.

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J.D.H., J.S.L., S.J.H. and M.F. conceptualized the manuscript and wrote the initial draft. J.D.H. and M.F. designed and conducted all the statistical analyses. All authors (J.D.H., J.S.L., S.J.H., M.F., S.A.A., A.A.A., J.A., W.J.B.A., E.B., M.K.C., B.D., T.G., A.M.G., L.H., M.J.J., C.A.M.K., E.W.L., R.A.L., B.M., S.B.M., D.E.M., C.M., M.M., K.N., M.E.P., K.R.R., T.R., C.S., C. J. Schell, Ç.H.Ş., C. J. Shier, K.C.S., C.C.S.C., T.S., C. J. Stevenson, L. Wayne, D.W., J.W., L. Wilson and A.J.Z.) contributed data and assisted with drafting and editing the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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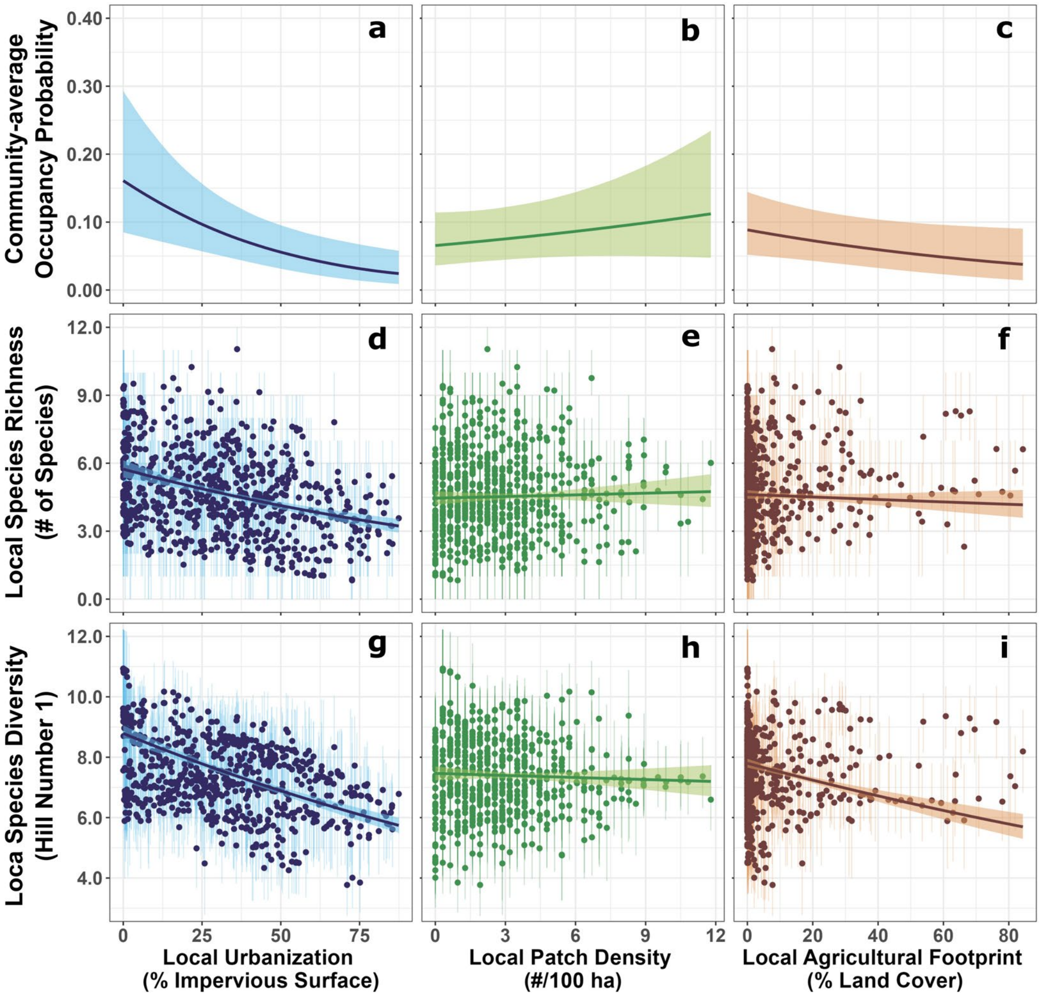
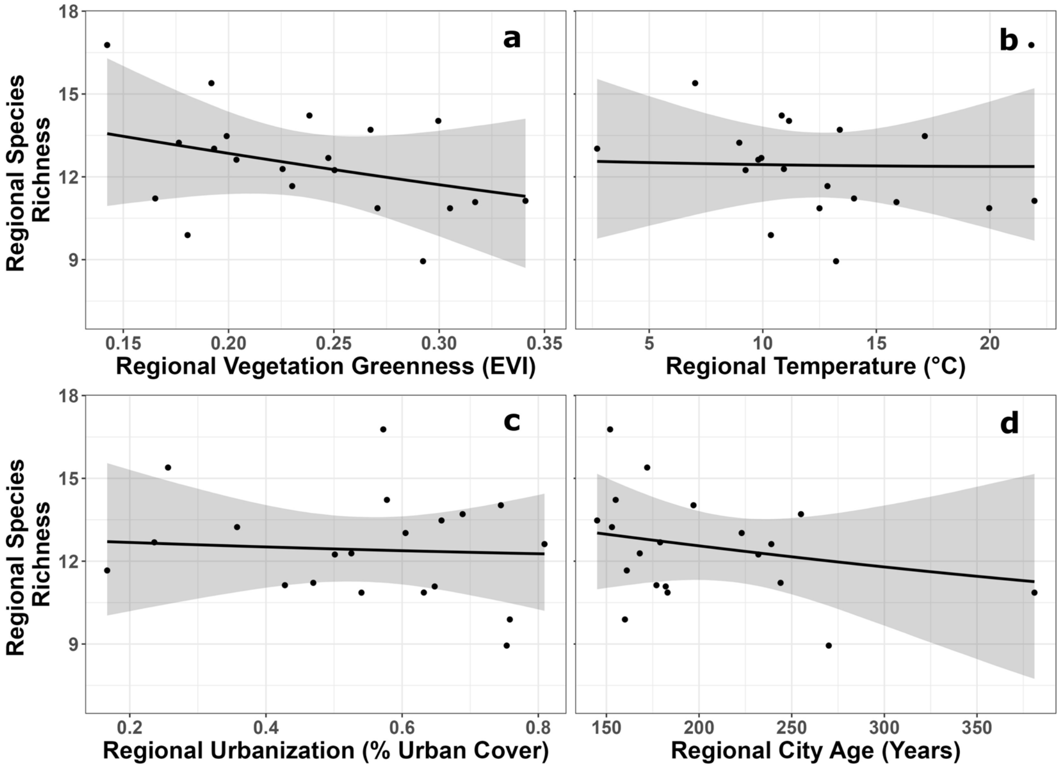
| City | Sampling Year | Number of Sites (Camera Trap-Days) | EVI | MAT | URB | AGE |
|---|---|---|---|---|---|---|
| **Atlanta, Georgia** | 2019 | 30 (913) | 0.32 | 15.9 | 64.8 | 182 |
| **Austin, Texas** | 2018 | 13 (336) | 0.27 | 20.0 | 63.2 | 183 |
| **Chicago, Illinois** | 2019 | 95 (2,531) | 0.20 | 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 |

**Extended Data Fig. 1 | Community-average occupancy probability, species richness, and species diversity across gradients of local environmental predictors. a-c**, urbanization. **d-f**, natural patch density. **g-i**, agricultural footprint. Across 725 sites in 20 North American cities, we used a Bayesian multi-city community occupancy model and accompanying community composition meta-analysis models to estimate the local, within-city response variables *community-average occupancy* (**a,d,g**), *species richness* (**b,e,h**) and *species diversity* (**c,f,i**). These three response variables respectively refer 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 (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.



**Extended Data Fig. 2 | Regional species richness in relation to regional environmental covariates. a-d**, vegetation greenness (**a**); temperature (**b**); urbanization (**c**); and city age (**d**). Estimates of regional species richness $\gamma_r$ were calculated as the sum of predicted species presence values within each of 20 cities ($\gamma_r = \sum_s^S \omega_{s,r}$), using the probability of regional species presence $\Omega_r$ to correct observed species richness for the region-wide imperfect detection of species. Points correspond to each city's mean value of $\gamma_r$ across 60,000 Bayesian posterior estimates. Trendline and shaded region respectively depict the median and 95% Bayesian credible interval of $\gamma_r$ predicted across hypothetical ranges of among-city covariate values, where all other covariates were held constant at their mean. We represented regional vegetation greenness using the Enhanced Vegetation Index (EVI), regional temperature corresponds to mean annual temperature (in °C), regional urbanization was estimated as the city'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.



**Extended Data Fig. 3 | Influences of species traits on site-level mammal occupancy. 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 mammal species commonly detected across 725 camera sites in 20 North American cities (excluding eight species detected in fewer than 10 total trap-days). 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.

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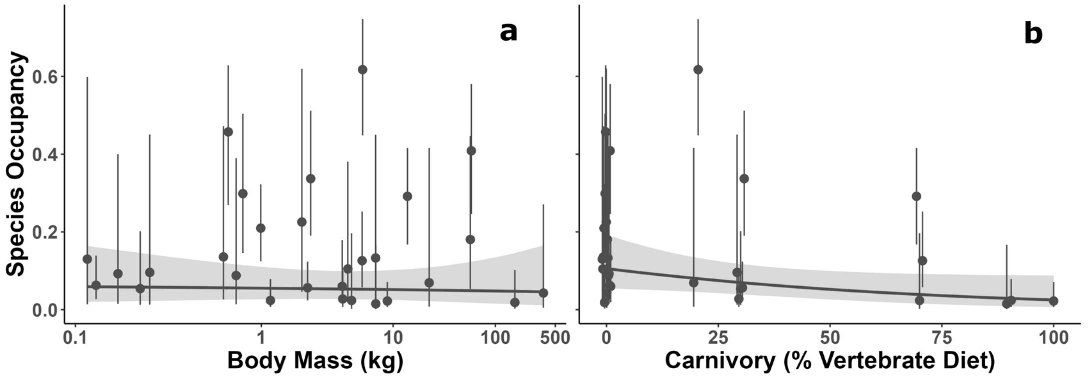
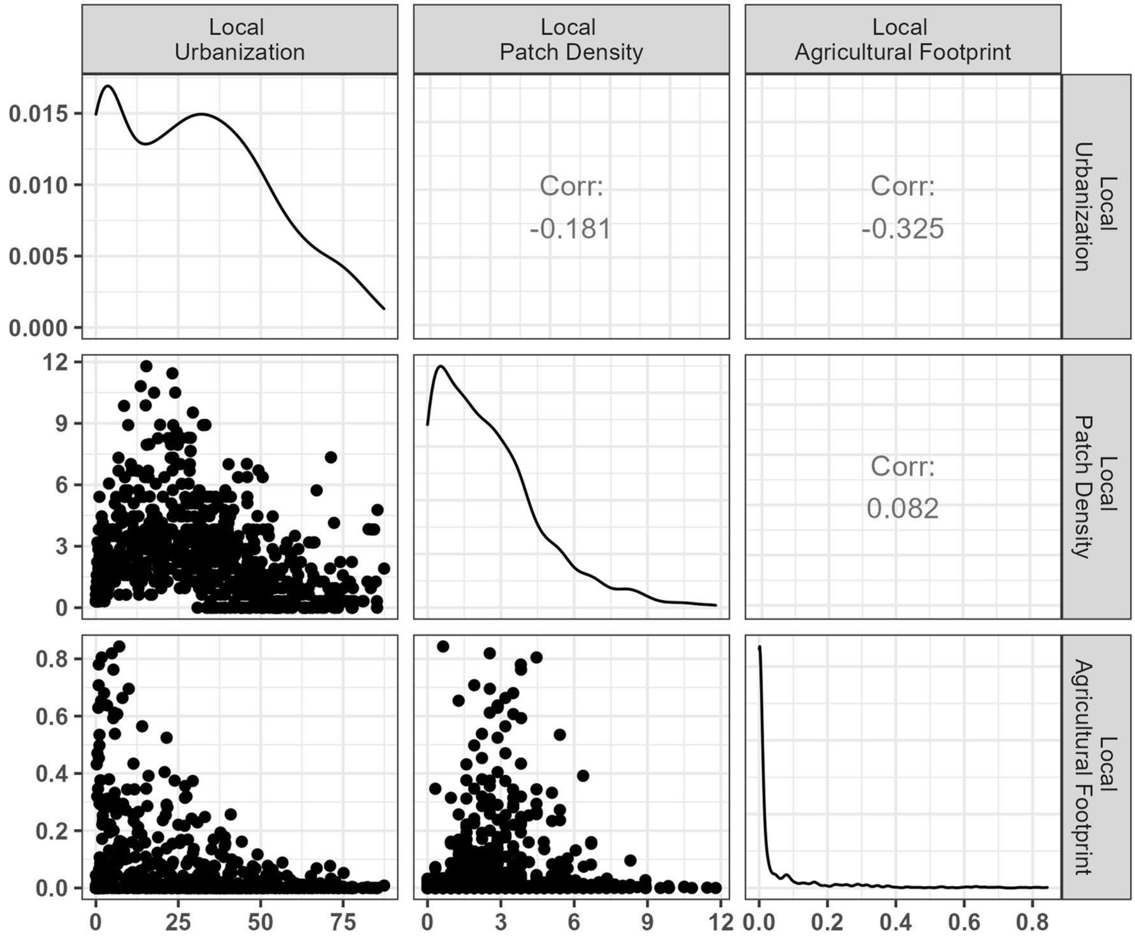
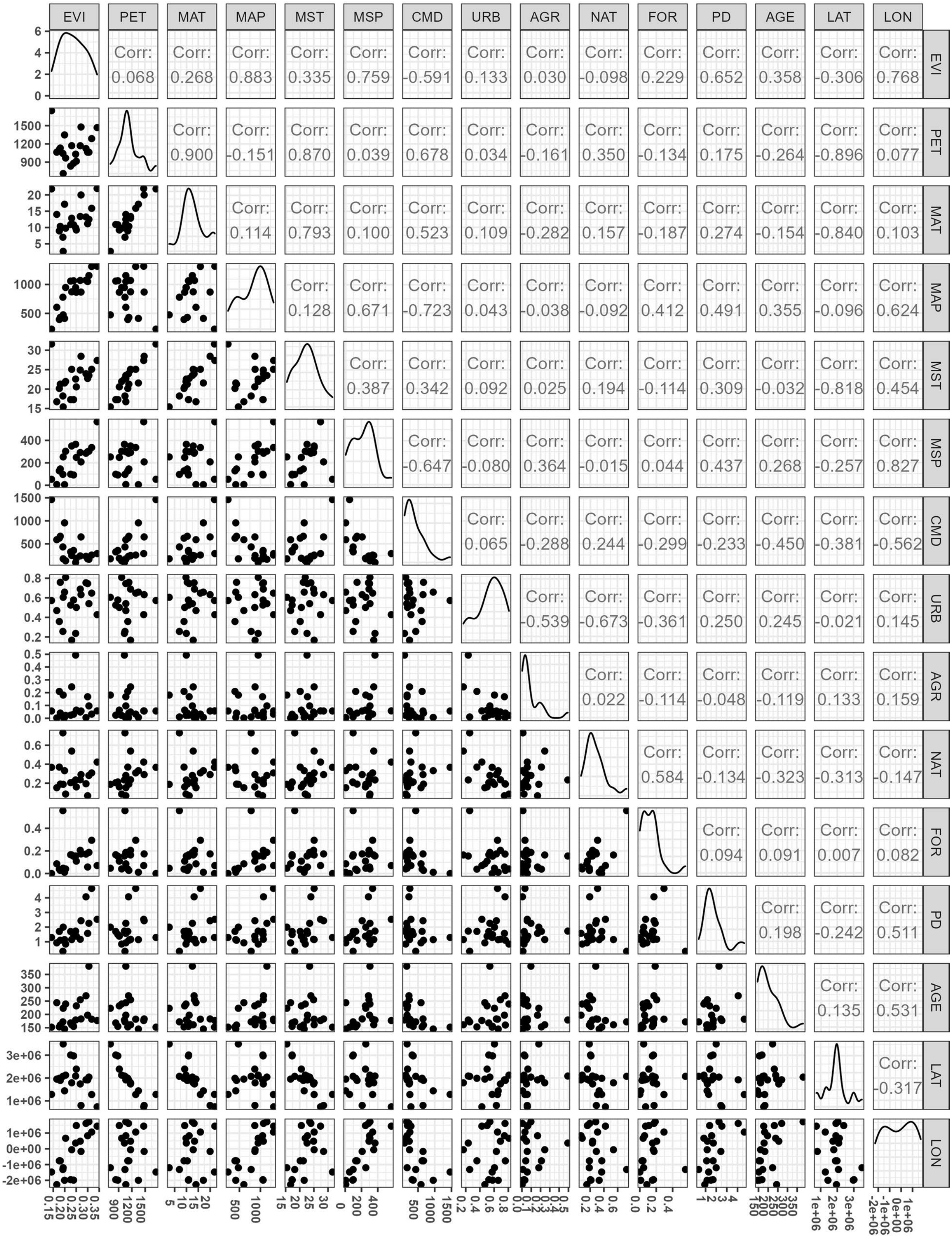


**Extended Data Fig. 4 | Collinearity between pairs of local (within-city) covariates.** Within-city covariates include local urbanization, natural patch density, and agricultural intensity across 725 sites in 20 North American cities. The diagonal cells of the figure depict the frequency distribution 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.



**Extended Data Fig. 5 | Collinearity between pairs of regional variables of 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.

**Extended Data Table 1 | Summary characteristics of 20 study 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 and the across-site sum of its camera trap-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 °C; MAT); regional urbanization (% urban land cover; URB); regional city age (years since colonization; AGE)



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| | |
|---|---|
| Data collection | No software were used for collection of original data. Any additional data used to conduct the analyses featured in this study (i.e., covariate data) were obtained from various online, open-access sources and are cited in the manuscript where appropriate. |
| Data analysis | All data and code that support the findings of this study and that were used in the production of all figures are publicly available on Zenodo at https://doi.org/10.5281/zenodo.8083504. |

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

## Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data and R code that support the findings of this study and that were used in the production of all figures are stored in Github and can be made available to reviewers upon request. Pending acceptance of this manuscript, all data and code will be archived with a DOI and made publicly available on Zenodo. Additional data used to conduct the analyses featured in this study (i.e., covariate data) were obtained from various online, open-access sources and are cited in the manuscript where appropriate.

## Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

| | |
|---|---|
| Reporting on sex and gender | N/A |
| Population characteristics | N/A |
| Recruitment | N/A |
| Ethics oversight | N/A |

Note that full information on the approval of the study protocol must also be provided in the manuscript.

# Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|---|---|
| Study description | Analyses included a Bayesian multi-species, multi-region (hierarchical) occupancy model and accompanying Bayesian meta-analysis models. All models included covariates on occupancy, species richness, and species diversity at multiple levels (site, region, species), as well as interactions among covariates (site*region, site*species). We analyzed data points from 725 sites across 20 regions (cities), each of which was sampled repeatedly for 35 days. A full description of the analyses in this study can be found in the Methods section of the manuscript. |
| Research sample | Motion-triggered wildlife cameras were used to take photographs recording occurrences of endothermic, vertebrate wildlife species at sites distributed across North American cities/metropolitan regions. We included only mammal species in this study as they were the taxon most reliably detected and identifiable in wildlife cameras photos. A full list of 35 species included in this study is reported in the Extended Data section of the manuscript. |
| Sampling strategy | Full description of the sampling strategy can be found on the Resources page of the Urban Wildlife Information Network (UWIN) website (https://www.urbanwildlifeinfo.org/gettingstarted), specifically in the Camera Trapping Design Overview document (https://www.dropbox.com/s/cuex75fuw3igaep/Design%20Overview.pdf?dl=0). Sampling was conducted by UWIN partners, who included university faculty and students and wildlife professional in governmental and non-governmental organizations. Wildlife camera sites in each city were located across an urbanization gradient within each city following a stratified pseudo-random sampling design (based on strata representing levels of urbanization). Based on minimum sample sizes typically necessary for fitting occupancy models, each UWIN partner city aimed to sample a minimum of 25 camera sites, though sample sizes (number of camera sites) varied among cities due to logistical limitations (equipment availability, camera failures, etc.). |
| Data collection | Wildlife camera photos were collected by UWIN members and uploaded to UWIN's online database for processing (species identification). Photos processed into tagged species observation data within the online database by trained personnel, including university students and faculty, community member volunteers, and wildlife professionals in governmental and non-governmental organizations. |
| Timing and spatial scale | Since 2016, UWIN partner cities have been regularly sampling during four distinct seasons during which data were continuously collected for a minimum of one calendar month: summer (July), fall (October), winter (January), and spring (April). Different UWIN cities began at and ended sampling during different years (e.g. Fort Collins stopped sampling in 2017, Salt Lake City started sampling in 2019). |
| Data exclusions | Due to the objectives our analysis (single-season occupancy modeling) and the availability of data from different cities, we included only data from a single 35-day summer sampling season (June 29th-August 2nd) from each city in this study. |
| Reproducibility | All code and data necessary for replicating the results of this study will be archived with a DOI and made publicly available on Zenodo, pending acceptance of the manuscript. |
| Randomization | Allocation of sampling sites among cities was non-random. City-level (regional) covariates were used to control for variation among cities. Allocation of sampling sites within each city followed a stratified pseudo-random sampling design (briefly described above) and variation among sites was controlled for using site-level covariates. |

| | |
|---|---|
| Blinding | Use of wildlife cameras allowed for the collection of study species occurrence data in the absence of researchers, minimizing impacts of the researchers on the behaviors of the study species. |

Did the study involve field work? ☒ Yes ☐ No

## Field work, collection and transport

| | |
|---|---|
| Field conditions | Field conditions have varied wildly across the multi-year, multi-season sampling effort of UWIN. This study includes data from the summer sampling season, during which conditions at all sites were relatively warm, though temperatures varied across cities located within different climate zones. |
| Location | Sampling in all 20 cities occurred across a gradient of human development from natural environments to highly urbanized city centers. Cities ranged across North America, between roughly -122.4 and -75.5 degrees W longitude and 28.8 to 53.5 degrees N latitude, including sites in hot, dry cities (e.g. Phoenix, Arizona) and cold, wet cities (e.g. Seattle, Washington). |
| Access & import/export | In establishing each study site, all UWIN partners were responsible obtaining the necessary permission or permits from all public and private owners and/or managers whose land on which wildlife cameras were to be located and accessed. |
| Disturbance | No significant disturbance was caused to each site |

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

| n/a | Involved in the study | |
|---|---|---|
| ☒ | ☐ | Antibodies |
| ☒ | ☐ | Eukaryotic cell lines |
| ☒ | ☐ | Palaeontology and archaeology |
| ☐ | ☒ | Animals and other organisms |
| ☒ | ☐ | Clinical data |
| ☒ | ☐ | Dual use research of concern |

### Methods

| n/a | Involved in the study | |
|---|---|---|
| ☒ | ☐ | ChIP-seq |
| ☒ | ☐ | Flow cytometry |
| ☒ | ☐ | MRI-based neuroimaging |

## Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

| | |
|---|---|
| Laboratory animals | This study did not involve laboratory animals. |
| Wild animals | This study involved the use of motion-triggered wildlife cameras to observe (i.e., photograph) all detectable mammal species. The full list of 35 species included in this study is reported in the Extended Data section of the manuscript. No wild animals were caught or transported during this study. |
| Reporting on sex | This information was not collected. |
| Field-collected samples | Field-collected samples consisted of only photographs, which were stored within the UWIN online database. |
| Ethics oversight | No ethical approval or guidance was required, due to the use of minimally-invasive observation methods. |

Note that full information on the approval of the study protocol must also be provided in the manuscript.