Mammalian functional diversity and trait responses to anthropogenic and environmental factors across the contiguous USA

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Abstract

Ongoing urbanization and land transformation drive profound changes in ecosystems worldwide, with wildlife responding in myriad ways. Particularly, functional homogenization of wildlife communities due to these widespread changes may reduce biodiversity and urban ecosystem resilience. However, there are benefits of urbanization (e.g., increased resources and survival) for some mammal species, likely supported by corresponding traits that facilitate the exploitation of human-dominated landscapes. Using data collected simultaneously from 107 sites throughout the contiguous United States, we explored how urban development, agricultural development, and environmental factors affected mammalian functional diversity (i.e., richness, evenness, and divergence of effect traits) and mean species' traits at two spatial scales. Although we expected that urbanization would lead to mammal community functional homogenization, we found that urban development was positively associated with functional richness at the camera-site and all three functional metrics at the camera-array scales, whereas environmental variables (i.e., primary productivity, temperature) were not associated with any functional diversity metric. Sampling locations with greater urban development were associated with mammals that had smaller average home ranges, smaller average body sizes, and decreased mean rates of carnivory and scavenging. Identifying the effects of anthropogenic development on ecosystem functioning, as mediated by species' traits, is crucial as urban landscapes continue to expand globally.

Keywords Divergence · Evenness · Functional · Homogenization · Traits · Urbanization

Introduction

The ecological consequences of human-mediated landscape transformation (e.g., urbanization, intensive agriculture, and landscape fragmentation) are profound and complex. Nearly three-quarters of Earth's terrestrial land surface is impacted by a myriad of human activities (Venter et al. 2016), and subsequent changes in community assembly and structure are often linked to reduced ecosystem integrity, resilience, and function across multiple spatial scales (Flynn et al.

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2009; Foley et al. 2005; McKinney 2006). For example, the reduction of native land cover and the conversion of complex natural systems to simplified, intensive agriculture is linked to biodiversity loss (Gámez-Virués et al. 2015), particularly for stream macroinvertebrates (Barnum et al. 2017), invertebrate pollinators (Deguines et al. 2014), amphibians (Hayes et al. 2010), birds (Donald et al. 2001; Sidemo-Holm et al. 2022), mammals (Sotherton 1998), and plants (McCune and Vellend 2013; Schwartz et al. 2006). Similarly, the process of urbanization is a leading cause of local species extinction, due to both direct and indirect effects on wildlife populations (McKinney 2006; Morelli et al. 2016; Sidemo-Holm et al. 2022). In the United States of America (hereafter USA), transformation of native land cover for urban development is more ubiquitous than other human activities (Czech et al. 2000), and the combination of urbanization and expansion of intensive agriculture has increased ecosystem homogenization (Flynn et al. 2009; Groffman et al. 2014; McKinney 2006). As a result, urban systems are often more similar to each other than to their natural counterparts (Groffman et al. 2014).

The hierarchical filtering of wildlife communities in cities can directly and indirectly influence the function of ecosystems (Fig. 1; Aronson et al. 2016). These shifts may occur at different scales, often through mediating species interactions, habitat, and climatic filters, while nested within human socioeconomic and cultural frameworks (Fig. 1; Aronson et al. 2016). For example, at local scales, urbanization may impact wildlife populations directly through the construction of roads that affect wildlife mortality and fragment habitat (Forman and Alexander 1998). At the regional or city-scale, urbanization can lead to significant changes in microclimates associated with heat absorption by human structures, which cause warmer localized temperatures (i.e., urban heat island effect) and shifts in precipitation rates, which may serve as an ecological filter for thermally-constrained species (Magura et al. 2020). Additionally, indirect effects of urbanization at more local scales include the introduction of exotic species that may outcompete native fauna and flora (Colléony and Shwartz 2020; Larson and Pool 2020; Mack and Lonsdale 2001) and increase the abundance of generalist species due to human-facilitated supplemental food resources (Hansen et al. 2020). Individuals within species can then filter into or out of cities at different scales, based on the traits they share that facilitate the occupation of these novel urban spaces (Aronson et al. 2016). Different species-level mean traits have been observed to pre-adapt mammal species to city living (e.g., Santini et al. 2018; Suraci et al. 2021). Yet, how traits influencing ecosystem health and processes (i.e., functional effect traits; Lavorel and Garnier 2002; Weiss and Ray 2019) filter into urban environments remains untested.

Functional homogenization (i.e., the reduction of community-wide functional trait diversity) is an important aspect of biotic homogenization, but has historically
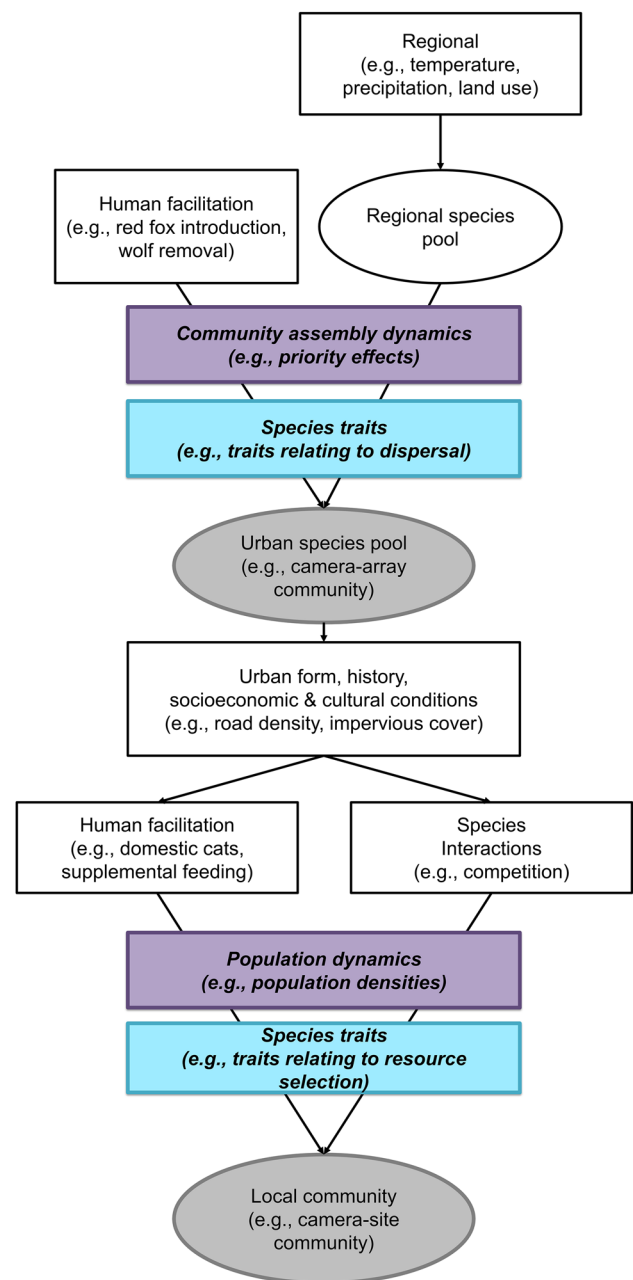

Fig. 1 Urban mammal species pools, following a series of hypothesized ecological and human modification filters, modified from Aronson et al. (2016) to reflect the multiple scales of our study approach (with analyses conducted at the urban species pool and local community scales). Rectangular icons represent filters hypothesized to influence species pools (ovals) at multiple scales

been understudied in mammal communities (Olden 2006; Rega-Brodsky et al. 2022). Functional diversity can be used to quantify how biodiversity governs ecosystem functioning, and accounts for how changes in community composition affect the diversity of or changes in functional effect traits (Lavorel and Garnier 2002; Naeem et al. 2012; but see Lavorel and Garnier 2002 and Weiss

and Ray 2019 for information on response traits). Effect traits are specific traits expected to influence ecosystem services, health, and processes, such as by mediating nutrient cycling, trophic dynamics, species-interactions, or environmental footprint (de Bello et al. 2010, 2021). Measures of functional diversity then quantify how much the effect traits assessed within the community diverge, are distributed, or vary (Botta-Dukát and Czúcz 2016; Hillebrand and Matthiessen 2009). Greater diversity in functional traits is associated with increased resilience to environmental change (de Bello et al. 2021; de Battisti 2021), whereas functional homogenization of mammal communities can reduce resilience and increase the precariousness to biotic change and stochastic environmental perturbations at scales from local communities to ecosystems and continents (Olden 2006). For instance, functionally-similar communities may respond in similar ways to changes in their environment, resulting in less resilient systems compared to those with greater functional heterogeneity. Further, literature focused on homogenization of mammal communities suggests that species introductions may be more influential in community-level functional similarity than species extinctions (Olden 2006; Spear and Chown 2008). Within the USA, specifically, past projections have revealed that urbanization may be the leading cause of biotic homogenization (Olden 2006). Since these projections were suggested, limited studies have focused on the functional homogenization of mammal communities, which have been especially lacking in the USA.

Range expansion of generalist or synanthropic species with traits that facilitate the exploitation of anthropogenic systems can also drive functional homogenization in cities (Gossner et al. 2016; McKinney and Lockwood 1999; McKinney 2006; Morelli et al. 2020; Pacifici et al. 2020). These range expansions can result in increasingly homogenized wildlife communities, composed primarily of synanthropic species that are both taxonomically and functionally similar (Baiser and Lockwood 2011; Flynn et al. 2009; McKinney 2006; Morelli et al. 2020). The species that inhabit anthropogenically altered ecosystems are directly influenced by the traits they share (Suraci et al. 2021), ranging from body size, diet type and flexibility, to home range size. Dietary plasticity allows some animals to exploit variable resources offered in anthropogenically altered ecosystems (Bateman and Fleming 2012; Contesse et al. 2004), whereas smaller body sizes and home ranges can reduce the impacts of landscape fragmentation that are common in anthropogenic environments (Crooks et al. 2017; Suraci et al. 2021). Trophic position within an ecological community further contributes to how species interact with humans and whether species may benefit from relaxed competition in areas with high anthropogenic activity (Moll et al. 2018;

Suraci et al. 2019). For example, many mid-sized carnivores persist in urban spaces where larger predators are less common, or where they can outcompete and limit smaller carnivores (Bateman and Fleming 2012). However, whether mammalian species traits related to ecosystem health and function (i.e., effect traits) homogenize or differentiate in response to urbanization remains unknown.

We sought to add to the paucity of data on mammal community functional homogenization and trait responses to urbanization by using camera-trap data collected simultaneously across the contiguous USA. Specifically, we investigated the influence of urbanization on ecosystem health and processes via alterations in species-level mammalian functional effect traits by answering two main research questions. 1) Does urbanization contribute to functional homogenization within mammal communities in the USA (i.e., decrease in functional richness, functional evenness, and functional divergence) at two spatial scales (individual camera sites and entire camera arrays)? We predicted that urbanization would correspond negatively with each aspect of functional diversity (i.e., richness, evenness, and divergence) for traits expected to influence ecosystem health and processes across spatial scales. For each species identified in our study, we also assessed effect traits expected to be particularly affected by urbanization, such as traits corresponding with nutrient cycling, top-down/bottom-up ecological control, ecological footprint, and competition. 2) Do particular anthropogenic habitats correspond with greater representation of species with traits that pre-adapt species to exploit anthropogenic environments? If yes, we predicted that urbanization would correspond with decreases in diet specialization, body mass, and home range size (Suraci et al. 2021). Importantly, by understanding how and in what way species-level functional traits homogenize or differentiate in association with urbanization in the USA, we can gain insight into how hierarchical filtering of mammal communities may affect ecosystem health and processes in general and at different spatial scales, thereby affecting ecosystem services and conservation objectives.

Materials

Study area

Snapshot USA (Cove et al. 2021) is a collaborative mammal survey that occurs across the USA each fall, using standardized methods. Our study used data from the inaugural sampling period (2019) in which data were collected by a network of 154 collaborators across 58 universities, 13 non-profit organizations, and 15 government agencies. We removed records from Alaska and Hawaii due to geographic distances and extreme differences in species assemblages compared to those within the contiguous USA. Data in the

remaining subset were collected from a coordinated survey of 1,512 individual camera trap sites from 107 study arrays between August 17, 2019 and November 24, 2019. Camera sites ranged from 25.17º to 48.14º latitude and from -124.02º to -69.10º longitude. These camera trap arrays were located across all major ecoregions as delineated by Bailey (1995) and represented anthropogenic disturbance regimes across the country (Cove et al. 2021). This disturbance regime includes a wide variability in human population density (range = 0—76,975 per km^2; median 5,697 per km^2) and housing density (range = 0—1,945 per km^2; median 9 per km^2).

Data collection

Camera traps are an efficient means of non-invasive sampling that adequately captures common and cryptic mammal species alike (Kays et al. 2020). Camera trap arrays were established by researchers participating in Snapshot USA with the goal of obtaining comparable mammal community data. These arrays were variable in size and extent, with each array consisting of an average of 14.13 camera sites (SD = 8.01, range = 4—49), with a minimum of 400 trap nights per array (Cove et al. 2021). Cameras were active for an average of 34.18 survey days (SD = 18.62, min = 1, max = 92), totaling 51,684 survey days. Evidence suggests that cameras detect most species present at a site after approximately two-weeks, with detection of new species leveling off after approximately 30 days, including in more biodiverse regions (Kays et al. 2020). Camera trap settings and models were all reasonably comparable with fast trigger speeds (< 0.5 s), high-resolution photos, and infrared flash. Cameras were deployed ~ 30–50 cm off the ground and set to take 1–10 photos per trigger without a quiet period between triggers. Bait and scent lures were not used. We considered species detections at the same camera independent only when > 1 min apart. All observations underwent a two-stage review process to ensure species were properly identified. Further details on camera trap establishment and specific camera models can be reviewed in Cove et al. (2021), but we identified differences in sampling effort of arrays by explicitly including sampling effort as a factor in our mammal community modeling as explained below.

We used 163,334 unique detections of 71 mammal species from across the contiguous USA (Supplementary Material 1). The taxa represented in the data include wild mammals weighing > 500 g that could be identified to species, as well as domestic cats (*Felis catus*), which were included because they often occur independently of humans as feral or semi-feral animals throughout the USA (Cove et al. 2018) and due to the substantial effects they can have on ecosystem health and processes (Loss et al. 2013). However, other domesticated species that are most often detected due to

co-occurrence with humans (e.g., domestic dogs [*Canis lupus familiaris*]) or species associated with agriculture, which is unevenly distributed throughout the USA (e.g., domestic cows [*Bos taurus*], domestic sheep [*Ovis aries*] and domestic horses [*Equus caballus*]) were excluded from our analyses. Although we recognize that domestic dogs have been demonstrated to kill wild and other domesticated species (Hughes and Macdonald 2013), most domestic dogs detected in this study were companion animals and accompanied by humans. Thus, we believe their ecological effect in this case to be minimal. Moreover, domesticated livestock were only present at a few locations; domestic cows only occurred at 15 sites across eight states, domestic sheep occurred at two sites, and domestic horses at 10 sites, most of which were linked to sites in agricultural or rural areas. We also omitted detections that could not be accurately identified to species, and we removed Mexican woodrats (*Neotoma mexicana*) and mountain cottontails (*Sylvilagus nuttalli*) from our analyses due to lack of available information to calculate their traits.

To determine if functional homogenization of the mammalian community was related to land cover features and urbanization, we identified functional traits for each mammal species assessed in our study (Supplementary Material 1). We included average species-level traits related to nutrient cycling and top-down/bottom-up ecological control (body mass [Jones et al. 2009; Wilman et al. 2014], percentage of carnivorous diet [Wilman et al. 2014], percentage of scavenging in diet [Wilman et al. 2014], and percentage of seed consumption in diet [Wilman et al. 2014]), and ecological footprint (home range size [Jones et al. 2009]). Herbivory was not assessed, as the average percent herbivorous diet was expected to be the inverse of the average percent carnivorous diet (Wilman et al. 2014). Additionally, as our research questions focused on effect traits rather than response traits (Lavorel and Garnier 2002), we also did not include response traits or demographic traits in our analyses. Additionally, response traits were not assessed as these require individual measures of organisms to identify how traits respond to changes in the environment (Weiss and Ray 2019), which was not possible with our camera trapping methods. However, effect traits can be assessed at broader, species-level scales. As such, all traits were assessed using mean-values of species traits provided in openly accessible trait databases (i.e., Pantheria [Jones et al. 2009] and Elton-Traits 1.0 [Wilman et al. 2014]).

We calculated functional richness, functional evenness, and functional divergence following Villéger et al. (2008). We used the *dbFD* function in the *FD* package (Laliberté and Legendre 2010) in program R (R Core Team 2021) to determine dissimilarity among quantifiable traits (Gower dissimilarity; Podani and Schmera 2006). We measured functional richness as the convex hull volume of the functional space

of the given community at the camera-site and the camera-array scale, functional evenness as the regularity of the distribution within this volume, and functional divergence as the divergence in the distribution in this volume. Because the method applied is based on the volume of the functional space, we were unable to calculate values for camera-sites or arrays with < 3 species. Ecologically, functional richness represents the amount of niche space occupied by species, based on their trait features; thus, low functional richness predicted in more urbanized areas would represent fewer functional traits represented in the community and more resources left unused in the habitat (Mason et al. 2005). Functional evenness represents the distribution of the functional niche space, with lower functional evenness representing an underutilization of resources in the habitat (Mason et al. 2005; Mouchet et al. 2010). Lastly, functional divergence represents niche differentiation, so communities with low functional divergence would indicate greater overlaps in resource use, increased competition, and low ecosystem functioning (Mason et al. 2005).

When possible, we extracted environmental and habitat covariate data for our models at two spatial scales: the camera site (a 100 m buffer around each site to represent the habitat and resources in the immediate vicinity of the camera) and the camera array (a 5 km buffer, which is a large enough area to encompass most arrays, around the centroid of the camera array to represent the habitat and resources available across the study array). The list included abiotic (temperature, precipitation), land cover (impervious cover, agricultural land, wildland vegetation), urbanization (human population density, housing density, road density), and vegetation (Gross Primary Productivity) variables (additional details in Supplementary Material 2). Due to the resolution of the available layer, values of Gross Primary Productivity, temperature, and precipitation were extracted only at the array scale. Similarly, we only analyzed road density at the camera-site scale because camera sites within an array may be clustered towards areas either farther or closer to roads than what that mean may suggest (i.e., average road density for the array may not reflect the average road density experienced by the species detected at camera sites). This issue was alleviated with a smaller buffer used in the camera-site analysis, which is why we retained this variable only for the camera-site scale. We extracted the landscape variables using ArcMap v10.8 (ESRI, Redlands, CA) and QGIS v3.12 (QGIS Development Team) and used weather station data for abiotic variables (Supplementary Material 2).

We ran a Principal Component Analysis (PCA) on the set of variables available at each scale to reduce dimensionality, while retaining important, but correlated, variables and to carry a more direct comparison between analysis at the camera-site and camera-array scales. As a minimum, we retained all the components necessary to explain a cumulative variance of at least 80%. At the camera-site scale, this process resulted in three components that we interpreted as urban development (51.1% of variance explained, named because of the large positive contributions of population density, housing density, and impervious surface cover and the large negative contribution of wildland vegetation), agricultural development (19.0%, named because of the large positive contribution of cultivated land and the large negative contribution of wildland vegetation), and suburban development (14.1%, named because of the positive contributions of housing density, cultivated land, and wildland vegetation and the negative contributions of road density and impervious surface cover), for a total of 84.2% of variance explained (Supplementary Material 3). At the camera-array scale, we retained the first four components, reaching a cumulative explained variance of 92.5%; we interpreted these components as urban development (41.6% of variance explained, named because of the large positive contributions of population density, housing density, and impervious surface cover and the large negative contribution of wildland vegetation), primary productivity (23.8%, named because of the large positive contributions of gross primary productivity and precipitation), agricultural development (15.6%, named because of the large negative contribution of cultivated land and the large positive contribution of wildland vegetation, with negative associations reflecting selection of agricultural lands), and temperature (11.5%, named because of the large positive contribution of temperature, with no other associated variables contributing strongly to the principal component; Supplementary Material 3). Since we were unable to test along a true urbanization gradient due to the constraints of the Snapshot USA study design, we determined how the dependent variables responded to a continuous assessment of urbanization and habitat features as represented within the principal components (PCs).

Statistical analyses

We characterized the mammal communities sampled by the Snapshot USA project (Cove et al. 2021) in 2019 to understand how patterns in functional metrics (functional richness, functional evenness, and functional divergence) and traits composition in these communities were affected by anthropogenic and environmental factors.

Functional metrics We first focused on the three functional responses: functional richness, functional evenness, and functional divergence, at the two spatial scales: camera-site and camera-array. At each scale, we assessed how the relative PCs identified in the previous step were associated with each of the three functional metrics.

Out of 1512 camera-sites, 539 (36%) detected < 3 species. Consequently, it was not possible to estimate functional
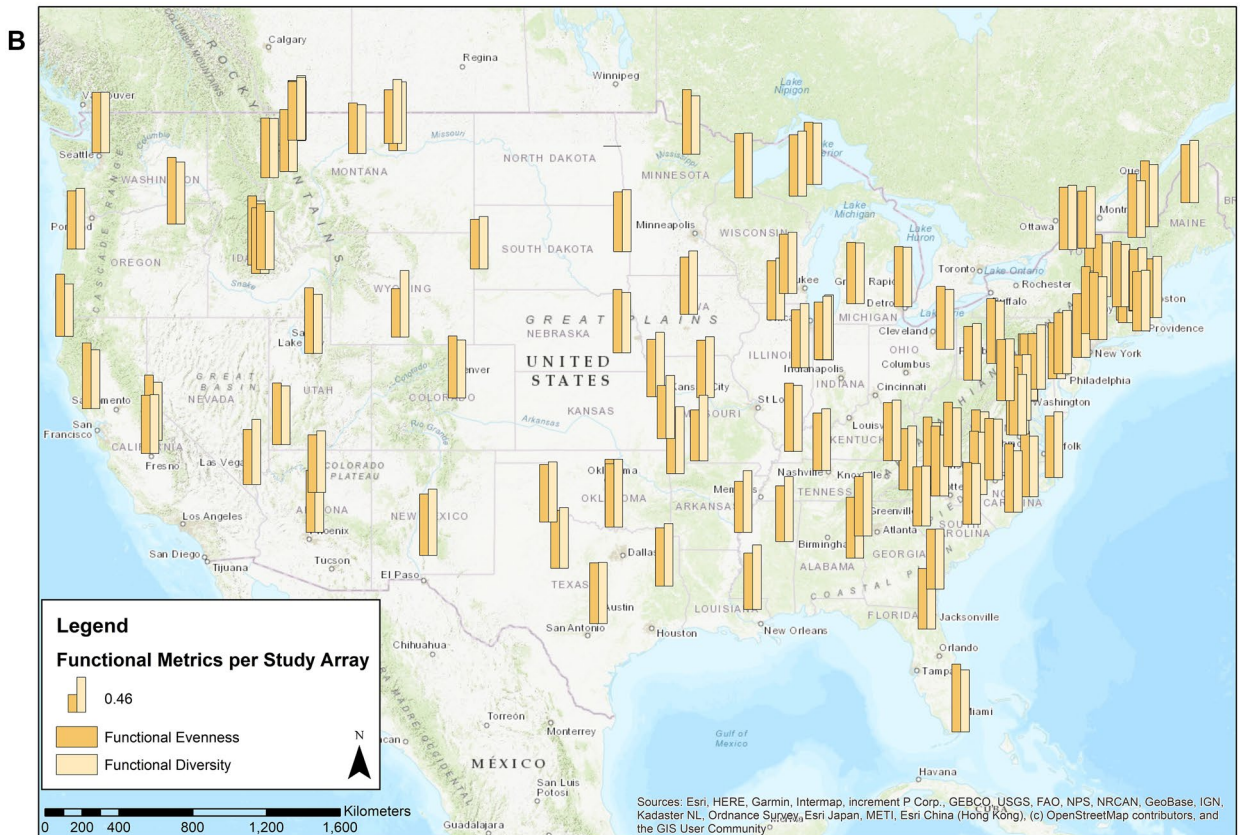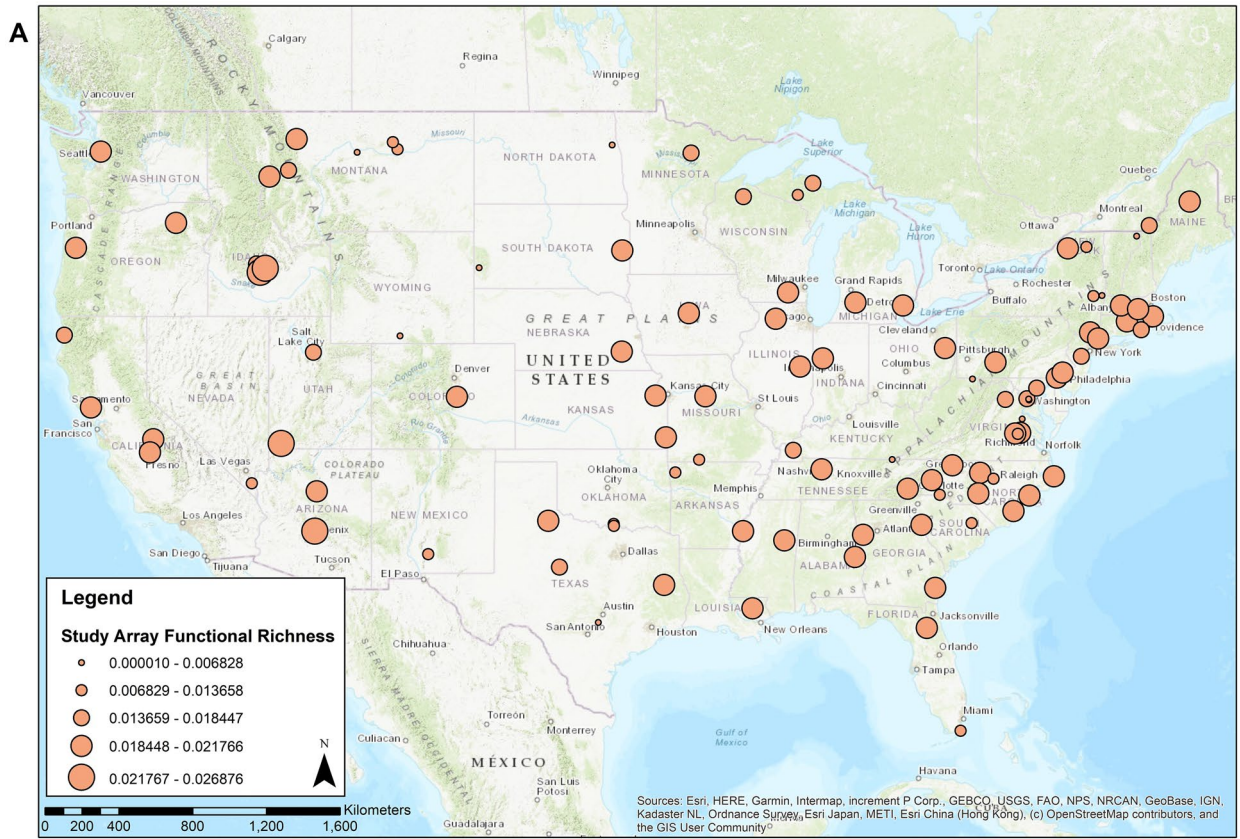
◀**Fig. 2** The nationwide camera trap survey of 1,512 individual camera-trap sites from 107 camera-arrays, across the contiguous United States used to assess mammal community characteristics, i.e., functional richness (**A**), functional evenness and divergence (**B**). Camera-arrays each represent a mammal community. Mammal data were collected as part of the Snapshot USA program

metrics for these sites at the camera-site scale. To account for the zero-inflated nature of our data, we opted to run Hurdle models (Heilbron 1994) for assessing whether any of the PCs identified were important predictors of 1) determining the detection/non-detection of a functional value for a specific functional metric; and 2) the value of the functional metrics considered. Hurdle models are two-component mixture models consisting of a binomial regression describing the probability of detecting a quantity of interest and a second component that explores the truncated distribution of the non-zero values. For the first part of the model, we applied a logistic model (with logit link) to each response metric (e.g. functional evenness) after converting all the non-zero values of the functional metric to 1. For the second part of the hurdle model, we retained only camera sites in which functional values were > 0 and ran a zero-left truncated linear regression model for each of the three metrics using package *truncreg* (Croissant and Zeileis 2018). For both components of the hurdle models, we added the number of active trap nights at a site to account for variability in effort at the different locations; we also included latitude and longitude to account for correlation in the spatial distribution of the sites in camera arrays, which we did not need to do for the camera-array scale (Supplementary Material 4).

At the camera-array scale, only 1 out of 107 sites had functional metric values equal to zero. Thus, we decided to only fit linear regression models at this scale to test if the three functional metrics were associated to one or more of the four PCs identified. We included the number of locations sampled per array (as a fixed effect) and number of active trap-nights (as an offset) to control for differential effort among arrays, after centering and scaling these variables (Supplementary Material 4).

Trait analysis We assessed the effects of anthropogenic and environmental factors on the average trait values measured at each camera-site. To calculate the average trait values, we first identified each species detected at a given camera-site. We then took the average trait values calculated across all species detected based on the same values used in the functional metrics analysis described above. Using these camera-site-specific values, we then ran models assessing how the average trait values calculated at each camera-site were affected by the same PCs included in the functional metrics analysis. Since percent carnivory, percent scavenging, and percent seed dispersing were each highly zero-inflated,

we elected to run Hurdle models on these variables, following the same two-component mixture model process as described in the functional metrics analysis above. This allowed us to model how each of the PCs affected both the detection of carnivores, scavengers, and seed dispersers, as well as the degree to which these traits occurred across camera-sites within our study system. Average home range size and body mass were analyzed using linear regressions models, as we did not detect zero-inflation in these values at the camera-site, and these traits were each log-transformed before analysis. As in the above analysis, we included camera-site-specific trap nights, latitude, and longitude in each trait model to address variation in survey effort and spatial autocorrelation, respectively.

Finally, we repeated this analysis at the camera-array scale, using the PCs calculated as explained above for each location. To calculate camera-array specific trait values, we aggregated the mean value from each of the camera-sites with the array area. We chose this method instead of calculating a value similar to the process outlined for the camera-site analysis to control for rare species with large trait values that may skew the results of a particular study site. In this manner, camera-array values become more reflective of all camera-sites contained within. As with the functional metric analyses, we included the number of cameras deployed per project (as a fixed effect) and number of active trap-nights (as an offset) to control for differential effort among study sites. We scaled all covariates at both the camera-site and camera-array scale prior to analysis so that they had a mean = 0 and a standard deviation = 1. All analyses were performed in R (R Core Team 2021), and statistical significance was assessed at the $\alpha = 0.05$ level for all models.

Results

Functional metrics

Across all camera-sites, functional richness ranged from 0 to 0.12 (mean = 0.04, SD = 0.04), functional divergence ranged from 0 to 0.99 (mean = 0.52, SD = 0.39), and functional evenness ranged from 0 to 1 (mean = 0.53, SD = 0.40) (Fig. 2). At the camera-array scale, functional richness ranged from < 0.01 to 0.03 (mean 0.02, SD = 0.01), functional divergence ranged from < 0.01 to 0.90 (mean = 0.80, SD = 0.09), and functional evenness ranged from < 0.01 to 0.91 (mean = 0.79, SD = 0.10).

At the camera-site scale, the probability of getting a non-zero value of one of the functional metrics considered (i.e., detection of functional divergence, evenness, and richness) was negatively affected by increasing suburban development (PC3-Camera) and positively affected by increasing urban

(PC1-Camera) and agricultural (PC2-Camera) development. However, only the effects of urban and agricultural development on the detection of functional richness, and suburban development on the detection of functional divergence and evenness were significant (p-values < 0.03; Fig. 3A).

Urban development (PC1-Camera) was positively associated with functional richness (p < 0.01), yet lacked a significant association with functional evenness and functional divergence (both p > 0.06). Agricultural development (PC2-Camera) was positively associated with functional richness (p < 0.001), and negatively associated with functional evenness (p = 0.03). Functional divergence was not associated with agricultural development (PC2-Camera; p = 0.16). Finally, increasing suburban development was positively associated with functional evenness (p < 0.001), yet lacked associations with functional richness (p = 0.59) and divergence (p = 0.13) (Fig. 3B).

At the camera-array scale, the responses to the four PCs were similar across the three functional metrics (Fig. 4). All functional metrics showed a strong positive association with urban development (PC1-Array; all p-values < 0.01). Primary productivity (all p-values > 0.15), agricultural development (all p-values > 0.07), and temperature (all p-values > 0.50) were not associated with any of the three functional metrics. The complete set of estimates of the functional metric analyses at the two scales are reported in Supplementary Material 4.

Trait metrics

Due to small numbers of detections across the entire Snapshot USA dataset, we were unable to assess the effects of our principal components on the seed dispersing trait value at the camera-site scale, as models failed to converge.
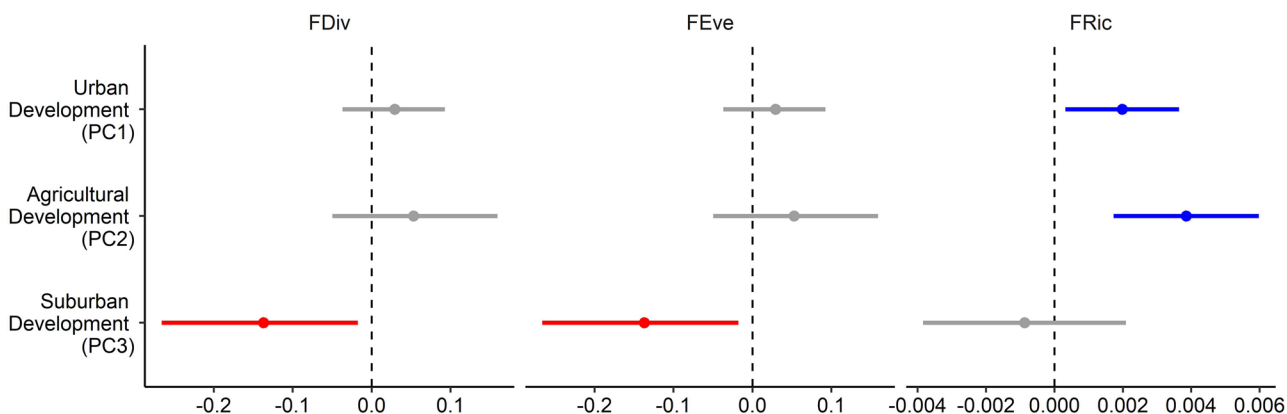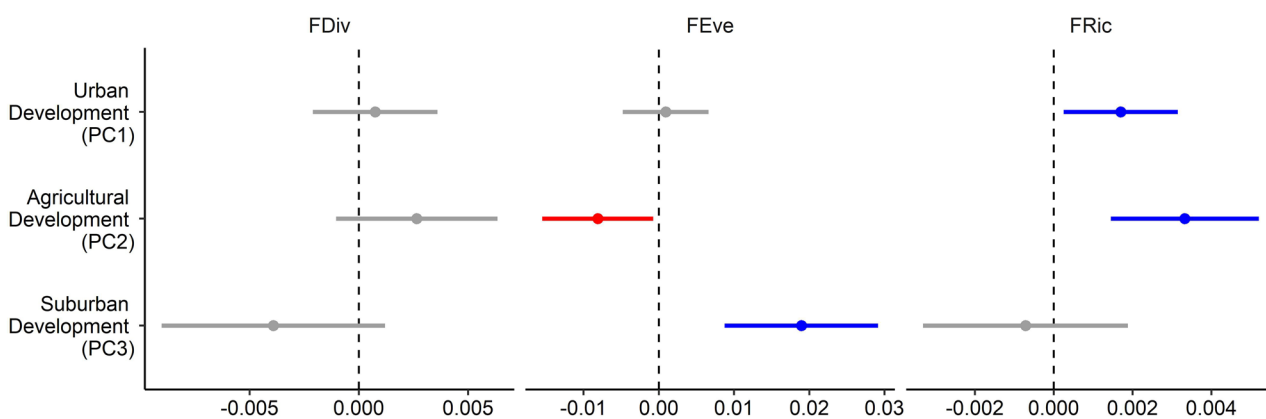

Fig. 3 Functional divergence (FDiv), functional evenness (FEve), and functional richness (FRic) in relation to principal components at the camera-site level based on hurdle models. Panel **A**: Coefficient estimates (means and 95% confidence intervals) describing the probability of having a zero value in each of the three functional metrics considered. Panel **B**: For cameras in which the functional values were > 0, coefficient estimates describing relationship between the different functional metrics and the three PCs. Blue and red colors represent significant (p < 0.05) positive and negative associations, respectively, while gray represents no association between the two variables. The complete set of coefficient estimates is reported in the Supplementary Material 4
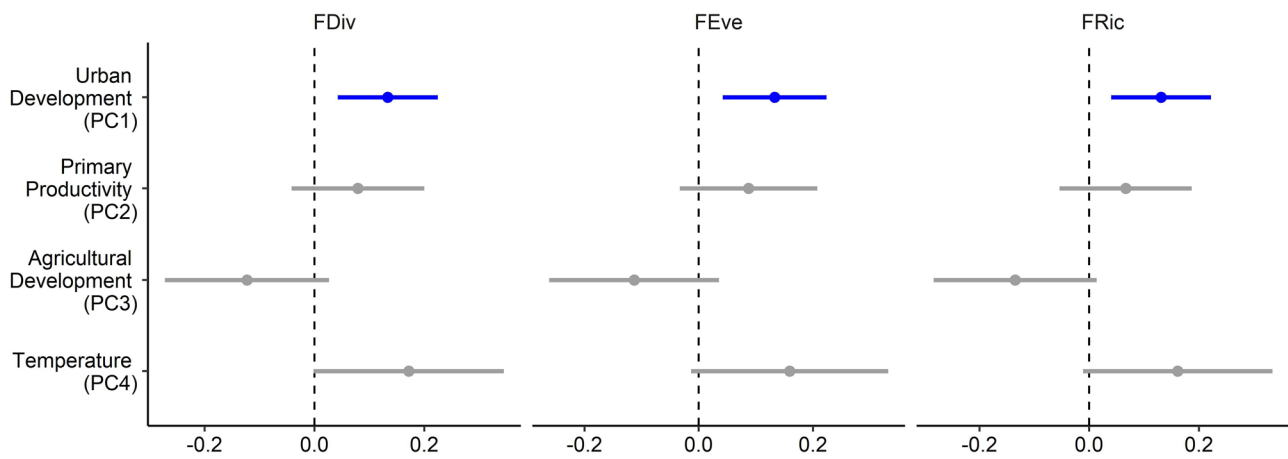
Fig. 4 Functional divergence (FDiv), functional evenness (FEve), and functional richness (FRic) in relation to principal components at the camera-array level based on linear regression models. Coefficient estimates (mean and 95% confidence intervals) describing the relationship between the different functional metrics and the four PCs. Blue colors represent significant ($p < 0.05$) positive associations, while gray represents no association between the two variables. The complete set of coefficient estimates is reported in the Supplementary Material 4

However, we were able to obtain estimates for all other trait values (Supplementary Material 5).

At the camera-site scale (Fig. 5), all measured trait values were negatively associated with camera locations that had increasing measures of urban development (PC1-Camera; all p-values < 0.01). The probability of carnivore and scavenger detection was positively associated with camera locations that had increasing agricultural development (PC2-Camera; both p-values < 0.01), while mammals with larger body mass were negatively associated with agricultural development ($p = 0.02$). Mammals with larger home ranges and body mass were positively associated with camera locations that had increasing suburban development (PC3-Camera; both p-values < 0.01). Responses to the other covariates, which served more as controls for sampling effort and geographic clustering, were mixed across traits (Supplementary Material). A full summary of the camera-site trait metric analysis is available in Supplementary Material 5.

At the camera-array scale (Fig. 6), mammals with larger body mass and home ranges were negatively associated with array sites with higher levels of urban development (PC1-Array; both p-values $= 0.01$). Mammals with larger home ranges were negatively associated with study sites that had higher levels of primary productivity (PC2-Array; $p = 0.03$). Scavenging was positively associated with study sites that had more agricultural development (negative effect of PC3-Array; $p = 0.03$). Carnivory, scavenging, and seed dispersing were all positively associated with study sites that had higher average temperature (PC4-Array; all p-values < 0.01). A full summary of the camera-array trait metric analysis is available in Supplementary Material 5.

Discussion

We used a large, standardized camera trap dataset to examine the relationship between urbanization and functional homogenization of mammal communities across the contiguous USA (Snapshot USA; Cove et al. 2021). Similar to previous studies' projections on the homogenization of wildlife communities along an urbanization gradient (e.g., Olden 2006), we predicted that urbanization in the USA would correspond with biotic homogenization in mammal communities. Instead, we found that the overall pattern across mammal communities in the USA indicated that urbanization led to biotic differentiation with increases in each of the functional metrics at the camera-array scale and increased functional richness at the camera-site scale, which may reflect the traits characterizing the species within these communities.

Early studies (e.g., Sotherton 1998) indicated biodiversity loss for mammal communities is driven by human-mediated change; however, these studies overlooked the benefits of urbanization (e.g., increased resources and survival) and the various traits that allow many mammals to exploit human-dominated environments. Exploitation of urban ecosystems is often by generalist or synanthropic species (Gossner et al. 2016; McKinney 2006; McKinney and Lockwood 1999; Morelli et al. 2020), potentially leading to assumptions that human-mediated change leads to the functional similarity of mammal communities. Instead, our results show that functional diversity in urban developments (i.e., areas with higher population density, housing density, impervious cover) is retained in communities with species characterized as having smaller body sizes, smaller home ranges, and a generalist diet. This may reflect commensal mammals taking
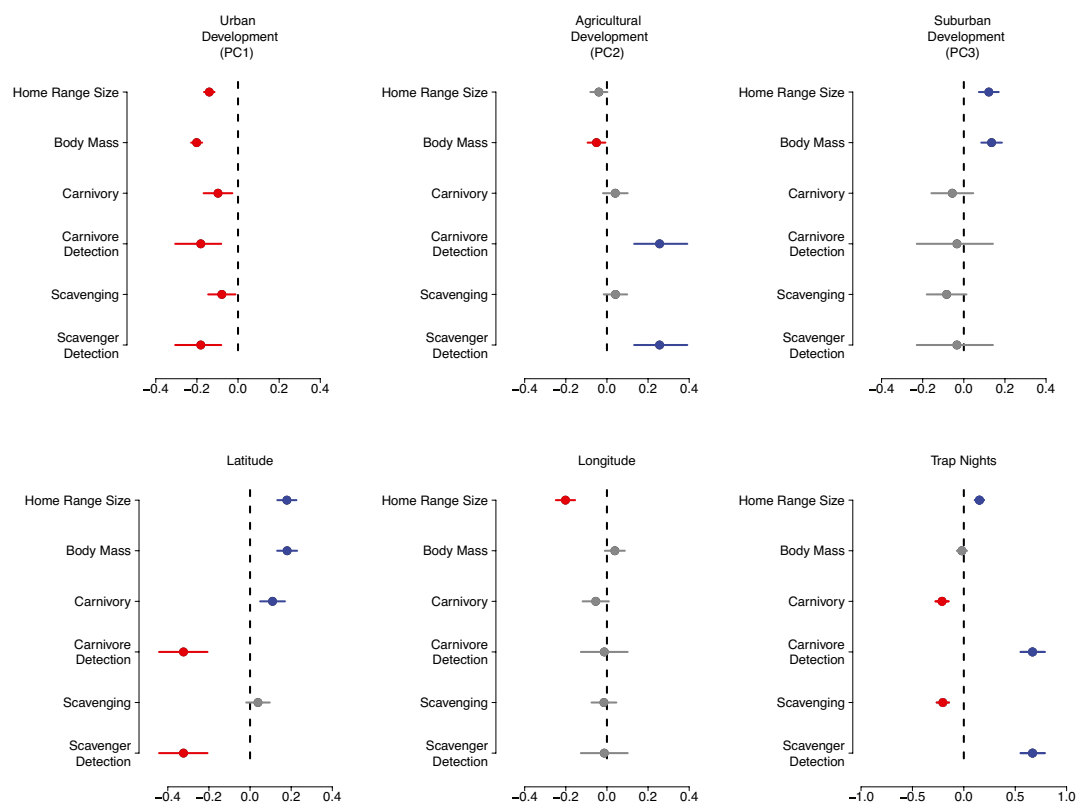
Fig. 5 Coefficient estimates (mean and 95% confidence intervals) from each model, in association with camera-site specific covariates, represented by their three camera-site PCs. The x-axis denotes the effect size and the y-axis lists the specific traits assessed. Blue and red colors represent significant ($p < 0.05$) positive and negative associations, respectively, while gray represents no association between the two variables

advantage of human-provisioned resources (e.g., anthropogenic foods/garbage) within smaller habitat patches in areas of heavy development, driving higher detections in urban environments compared to cameras placed within more rural areas (Mann et al. 2015).

Mammals with a smaller body mass and home range size were associated with urban development at both spatial scales, indicating these two traits' importance across the urban landscape (e.g., Rytwinski and Fahrig 2011, 2012). Consequently, the largest mammals (e.g., moose [*Alces alces*]), as well as many large carnivores with large home ranges (e.g., gray wolves [*Canis lupus*], pumas [*Puma concolor*], and wolverines [*Gulo gulo*]), are less likely to be present in urban environments (Rytwinski and Fahrig 2011; Suraci et al. 2021). Larger species need more space on average than smaller species and are also more vulnerable to the effects of roads, so their presence is greatly reduced in urban environments, leading to a trend in smaller body mass (Suraci et al. 2021).

We found that mammals with generalist diets (i.e., reduced rates of carnivory and scavenging specialization) were associated with urban development, but only at the camera-site scale. Urban environments offer substantial anthropogenic food sources (Bateman and Fleming 2012;

Contesse et al. 2004), including human refuse, crops (i.e., fruit and vegetables), synanthropic rodents and birds, pets, livestock and road-killed animals, or food made available through deliberate feeding. Although community-wide analyses may not indicate the functional homogenization of mammals due to human-mediated change, a decrease in large carnivores and scavengers is likely to lead to future food web destabilization and reduced ecosystem resilience (Ripple et al. 2014; Sebastián-González et al. 2019). Carnivore and scavenger detections were positively associated with agricultural development, indicating that diet specialists may be restricted to the urban periphery. Realistically, diet flexibility may be a key trait that allows species to move into and exploit urban environments, and a follow-up study on trait plasticity would be valuable.

Functional metrics and associated traits were variable within agricultural and suburban land uses, both of which may represent moderate levels of development and disturbances on the landscape. While areas with more cultivated agriculture had greater functional richness and less functional evenness at the camera-site scale, functional divergence was not associated with cultivated lands at either scale. Compared to areas without development, mammalian
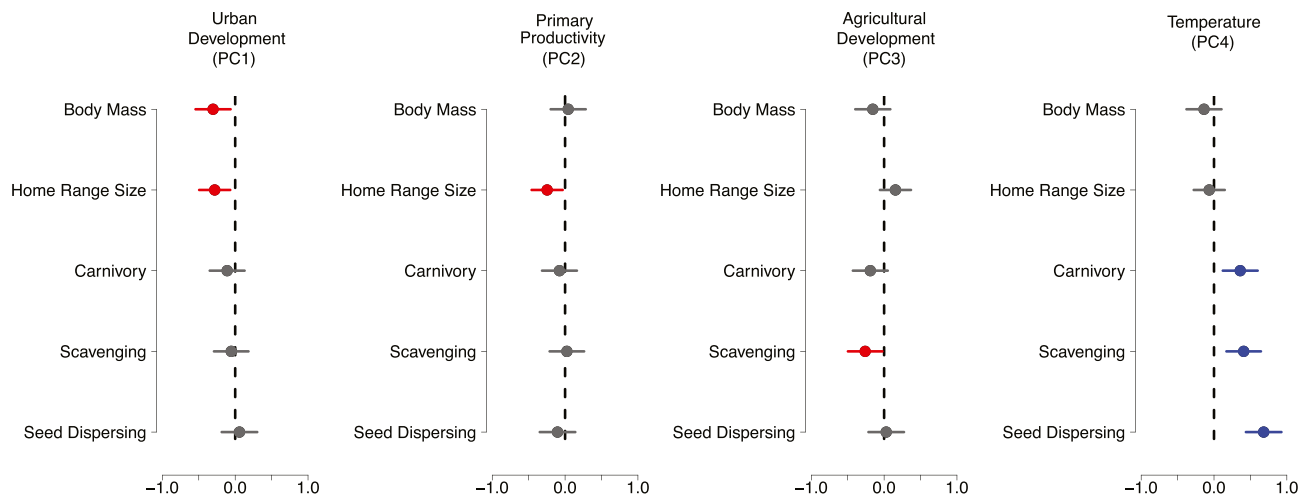
Fig. 6 Coefficient estimates (mean and 95% confidence intervals) from each model, in association with camera-array specific covariates, represented by their four camera-array PCs. The x-axis denotes the effect size and the y-axis lists the specific traits assessed. Note that for PC3, negative associations represent a positive response to cultivated lands and a negative response to undeveloped land (i.e., wildland vegetation). Blue and red colors represent significant ($p < 0.05$) positive and negative associations, respectively, while gray represents no association between the two variables

functional diversity can substantially decline in areas of agricultural intensification due to the loss of diet specialists, specifically those specializing on fish, fruit, seeds, or nuts (Flynn et al. 2009). Suburban landscapes, which were represented as areas with increased housing density mixed with greater rates of cultivated lands in our principal component analysis, may represent the land use gradient moving away from urban centers to more rural landscapes. Thus, mammal species with greater home range and body mass sizes were positively associated with this land use. Otherwise, with the heterogeneous nature of landscape gradients at the intermediate, suburban stage (Padilla and Sutherland 2021), it is no surprise that suburban development in our analyses yielded weak associations with functional metrics and limited associations to diet effect traits.

Climate variables had limited associations with the functional metrics and effect traits of mammal communities, as compared to anthropogenic land uses and cover. At global scales, species richness correlates with net primary productivity, precipitation, and temperature (Mittelbach et al. 2007), which could theoretically result in a positive association with functional richness as more species and their traits are represented in the community. However, we found that functional diversity metrics (i.e., richness, evenness, divergence of effect traits) were not associated with either temperature (PC4-Array) or primary productivity and precipitation (PC2-Array). We could only test these climate variables at the camera-array scale due to the resolution of these data; thus, associations between temperature and precipitation may strengthen if microclimate data collected at the camera were integrated into these models. Analyzing

patterns at different spatial scales minimizes the chance of mismatch between the scale at which species respond most strongly to environmental and anthropogenic factors and the scale at which these responses are assessed (Mertes and Jetz 2018) and it might highlight scale-dependent effects.

Although the Snapshot USA program is an excellent model for collecting large amounts of comparable data in a standardized sampling protocol, there are data limitations to consider. Snapshot USA is a unique program that sampled a large geographic area, including locations in all 48 contiguous states, to yield an enormous dataset of mammalian community data captured in one discrete time period. However, one constraint in this study design was unequal sampling across the landscape. Contributing scientists selected their locations independently, and forested locations were the most frequently sampled land cover (Cove et al. 2021). While these data encompassed diverse land cover types, sampling was not stratified to represent a range of urban microhabitats and the sites were not set up on a rigorous urbanization gradient, with locations biased towards more urban areas. Sampling in urban areas was also likely focused on greenspaces in suburban and exurban communities rather than true urban cores. These wealthier suburban and exurban areas have greater resources for wildlife, and wealth can be as great a driver of mammal communities as urbanization (Magle et al. 2021). In addition, sampling with camera traps limits the ability to detect very small mammals due to various sampling constraints of the many contributing scientists. The data are also limited to the Snapshot USA sample period (mid-August to late November), which does not encompass

seasonal weather patterns that occur at most survey locations and likely influence mammal behaviors and detectability. While these limitations should be considered and accounted for, the Snapshot USA program will likely continue for many years, providing a wealth of ecological data for exploring multi-scale changes in mammal communities across the USA (Cove et al. 2021).

Our study provides evidence that urbanization may not result in functional homogenization of mammal communities, but instead may increase functional richness of mammals and their ability to preadapt to anthropogenic environments. The ecological consequences of urbanization are complex and often linked with reduced ecosystem integrity, resilience, and function (Flynn et al. 2009; Foley et al. 2005; McKinney 2006). Our findings demonstrate that understanding both the positive and negative effects of urbanization on diverse members of the mammal community are critical for establishing effective management and conservation strategies in an increasingly human-dominated global ecosystem. Overall, our findings indicate that land use intensity more strongly explained variation in mammal community assemblages at both the camera-site and -array scales, while climate variables were not associated with mammalian functional diversity in the USA. Small- and large-scale actions within the urban landscape, such as increased development of green infrastructure and broad-scale biodiversity initiatives to stabilize food web trophic levels, may positively contribute to the resiliency of urban mammal communities. Beyond these efforts, we would benefit from future research that identifies the extent of variation and plasticity of mammalian traits, specifically diet patterns across urban gradients, as this may either constrain or enhance mammalian functional diversity with increasing levels of urbanization at multiple scales. We also encourage ecologists to use large-scale datasets when examining human-mediated global changes, as well as the use of multiple metrics to define urbanization and provide nuanced understanding of its effects. Overall, it is becoming increasingly more apparent that a diversity of wildlife exists in these urban landscapes and it is imperative that we better understand how to preserve the functioning of these ecosystems, both for the sake of wildlife and humans inhabiting these areas.

Declarations

References

Aronson MFJ, Nilon CH, Lepczyk CA et al (2016) Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963. https://doi.org/10.1002/ecy.1535

Bailey RG (1995) Description of the ecoregions of the United States. No. 1391. US Department of Agriculture, Forest Service. https://www.fs.fed.us/rm/ecoregions/downloads/ecoregions-united-states/data-sets/eco-us-shp.zip. Accessed 09 July 2020

Baiser B, Lockwood JL (2011) The relationship between functional and taxonomic homogenization. Glob Ecol Biogeogr 20:134–144. https://doi.org/10.1111/j.1466-8238.2010.00583.x

Barnum TR, Weller DE, Williams M (2017) Urbanization reduces and homogenizes trait diversity in stream macroinvertebrate communities. Ecol Appl 27:2428–2442. https://doi.org/10.1002/eap.1619

Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. J Zool 287:1–23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Botta-Dukát Z, Czúcz B (2016) Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. Methods Ecol Evol 7:114–126. https://doi.org/10.1111/2041-210X.12450

Colléony A, Shwartz A (2020) When the winners are the losers: invasive alien bird species outcompete the native winners in the biotic homogenization process. Biol Conserv 241:108314. https://doi.org/10.1016/j.biocon.2019.108314

Contesse P, Hegglin D, Gloor S et al (2004) The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mamm Biol 69:81–95. https://doi.org/10.1078/1616-5047-00123

Cove MV, Gardner B, Simons TR et al (2018) Free-ranging domestic cats (*Felis catus*) on public lands: estimating density, activity, and diet in the Florida Keys. Biol Invasions 20:333–344. https://doi.org/10.1007/s10530-017-1534-x

Cove MV, Kays R, Bontrager H et al (2021) SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. Ecology 102:e03353. https://doi.org/10.1002/ecy.3353

Croissant Y, Zeileis A (2018) truncreg: Truncated Gaussian Regression Models. R package version 0.2–5. https://CRAN.R-project.org/package=truncreg. Accessed 01 Feb 2022

Crooks KR, Burdett CL, Theobald DM et al (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proc Natl Acad Sci 114:7635–7640

Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. Bioscience 50:593. https://doi.org/10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2

De Battisti D (2021) The resilience of coastal ecosystems: a functional trait-based perspective. J Ecol 109:3133–3146. https://doi.org/10.1111/1365-2745.13641

de Bello F, Lavorel S, Díaz S et al (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers Conserv 19:2873–2893. https://doi.org/10.1007/s10531-010-9850-9

de Bello F, Botta-Dukát Z, Lepš J et al (2021) Towards a more balanced combination of multiple traits when computing functional differences between species. Methods Ecol Evol 12:443–448. https://doi.org/10.1111/2041-210X.13537

Deguines N, Jono C, Baude M et al (2014) Large-scale trade-off between agricultural intensification and crop pollination services. Front Ecol Environ 12:212–217. https://doi.org/10.1890/130054

Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc Lond B Biol Sci 268:25–29. https://doi.org/10.1098/rspb.2000.1325

Flynn DFB, Gogol-Prokurat M, Nogeire T et al (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Foley JA, DeFries R, Asner GP et al (2005) Global consequences of land use. Science 309:570–574. https://doi.org/10.1126/science.1111772

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29:207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Gámez-Virués S, Perović DJ, Gossner MM et al (2015) Landscape simplification filters species traits and drives biotic homogenization. Nat Commun 6:8568. https://doi.org/10.1038/ncomms9568

Gossner MM, Lewinsohn TM, Kahl T et al (2016) Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540:266–269. https://doi.org/10.1038/nature20575

Groffman PM, Cavender-Bares J, Bettez ND et al (2014) Ecological homogenization of urban USA. Front Ecol Environ 12:74–81. https://doi.org/10.1890/120374

Hansen CP, Parsons AW, Kays R, Millspaugh JJ (2020) Does use of backyard resources explain the abundance of urban wildlife? Front Ecol Evol 8. https://doi.org/10.3389/fevo.2020.570771

Hayes TB, Falso P, Gallipeau S, Stice M (2010) The cause of global amphibian declines: a developmental endocrinologist's perspective. J Exp Biol 213:921–933. https://doi.org/10.1242/jeb.040865

Heilbron DC (1994) Zero-altered and other regression models for count data with added zeros. Biom J 36:531–547. https://doi.org/10.1002/bimj.4710360505

Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecol Lett 12:1405–1419. https://doi.org/10.1111/j.1461-0248.2009.01388.x

Hughes J, Macdonald DW (2013) A review of the interactions between free-roaming domestic dogs and wildlife. Biol Conserv 157:341–351. https://doi.org/10.1016/j.biocon.2012.07.005

Jones KE, Bielby J, Cardillo M et al (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648. https://doi.org/10.1890/08-1494.1

Kays R, Arbogast BS, Baker-Whatton M et al (2020) An empirical evaluation of camera trap study design: how many, how long and when? Methods Ecol Evol 11:700–713. https://doi.org/10.1111/2041-210X.13370

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Larson ER, Pool TK (2020) Biological invasions drive biotic homogenization of North American crayfishes. Hydrobiologia 847:3795–3809. https://doi.org/10.1007/s10750-019-04164-2

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Loss SR, Will T, Marra PP (2013) The impacts of free-ranging domestic cats on wildlife of the United States. Nat Commun 4:1396. https://doi.org/10.1038/ncomms2380

Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. Bioscience 51:95. https://doi.org/10.1641/0006-3568(2001)051[0095:HAGPDG]2.0.CO;2

Magle SB, Fidino M, Sander HA et al (2021) Wealth and urbanization shape medium and large terrestrial mammal communities. Glob Chang Biol 27:5446–5459. https://doi.org/10.1111/gcb.15800

Magura T, Ferrante M, Lövei GL (2020) Only habitat specialists become smaller with advancing urbanization. Glob Ecol Biogeogr 29:1978–1987. https://doi.org/10.1111/geb.13168

Mann GKH, O'Riain MJ, Parker DM (2015) The road less traveled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodivers Conserv 24:531–545. https://doi.org/10.1007/s10531-014-0834-z

Mason NWH, Mouillot D, Lee WG et al (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

McCune JL, Vellend M (2013) Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. J Ecol 101:1542–1551. https://doi.org/10.1111/1365-2745.12156

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Mertes K, Jetz W (2018) Disentangling scale dependencies in species environmental niches and distributions. Ecography 41:1604–1615. https://doi.org/10.1111/ecog.02871

Mittelbach GG, Schemske DW, Cornell HV et al (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol Lett 10:315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x

Moll RJ, Cepek JD, Lorch PD et al (2018) Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosyst 21:765–778. https://doi.org/10.1007/s11252-018-0758-6

Morelli F, Benedetti Y, Ibáñez-Álamo JD et al (2016) Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Glob Ecol Biogeogr 25:1284–1293. https://doi.org/10.1111/geb.12486

Morelli F, Benedetti Y, Ibáñez-Álamo JD et al (2020) Insurance for the future? Potential avian community resilience in cities across Europe. Clim Chang 159:195–214. https://doi.org/10.1007/s10584-019-02583-7

Mouchet MA, Villéger S, Mason NWH et al (2010) Functional diversity measures: an overview of their redundancy and their ability to

discriminate community assembly rules. Funct Ecol 24:867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. Science 336:1401–1406. https://doi.org/10.1126/science.1215855

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. J Biogeogr 33:2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x

Pacifici M, Rondinini C, Rhodes JR et al (2020) Global correlates of range contractions and expansions in terrestrial mammals. Nat Commun 11:2840. https://doi.org/10.1038/s41467-020-16684-w

Padilla BJ, Sutherland C (2021) Defining dual-axis landscape gradients of human influence for studying ecological processes. PLoS One 16:e0252364. https://doi.org/10.1371/journal.pone.0252364

Podani J, Schmera D (2006) On dendrogram-based measures of functional diversity. Oikos 115:179–185. https://doi.org/10.1111/j.2006.0030-1299.15048.x

R Core Team (2021) R: The R project for statistical computing

Rega-Brodsky CC, Aronson MFJ, Piana MR et al (2022) Urban biodiversity: state of the science and future directions. Urban Ecosyst 25:1083–1096. https://doi.org/10.1007/s11252-022-01207-w

Ripple WJ, Estes JA, Beschta RL et al (2014) Status and ecological effects of the world's largest carnivores. Science 343:1241484. https://doi.org/10.1126/science

Rytwinski T, Fahrig L (2011) Reproductive rate and body size predict road impacts on mammal abundance. Ecol Appl 21:589–600. https://doi.org/10.1890/10-0968.1

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biol Conserv 147:87–98. https://doi.org/10.1016/j.biocon.2011.11.023

Santini L, Gonzalez-Suarez M, Russo D et al (2018) One strategy does not fit all: determinants of urban adaptation in mammals. Ecol Lett 22:365–376. https://doi.org/10.1111/ele.13199

Schwartz MW, Thorne JH, Viers JH (2006) Biotic homogenization of the California flora in urban and urbanizing regions. Biol Conserv 127:282–291. https://doi.org/10.1016/j.biocon.2005.05.017

Sebastián-González E, Barbosa JM, Pérez-García JM et al (2019) Scavenging in the Anthropocene: human impact drives vertebrate scavenger species richness at a global scale. Glob Chang Biol 25:3005–3017. https://doi.org/10.1111/gcb.14708

Sidemo-Holm W, Ekroos J, Reina García S et al (2022) Urbanization causes biotic homogenization of woodland bird communities at multiple spatial scales. Glob Chang Biol 28:6152–6164. https://doi.org/10.1111/gcb.16350

Sotherton NW (1998) Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. Biol Conserv 83:259–268. https://doi.org/10.1016/S0006-3207(97)00082-7

Spear D, Chown SL (2008) Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. J Biogeogr 35:1962–1975. https://doi.org/10.1111/j.1365-2699.2008.01926.x

Suraci JP, Clinchy M, Zanette LY, Wilmers CC (2019) Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol Lett 22:1578–1586. https://doi.org/10.1111/ele.13344

Suraci JP, Gaynor KM, Allen ML et al (2021) Disturbance type and species life history predict mammal responses to humans. Glob Chang Biol 27:3718–3731. https://doi.org/10.1111/gcb.15650

Venter O, Sanderson EW, Magrach A et al (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat Commun 7:12558. https://doi.org/10.1038/ncomms12558

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. https://doi.org/10.1890/07-1206.1

Weiss KCB, Ray CA (2019) Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. Ecography 42:2012–2020. https://doi.org/10.1111/ecog.04387

Wilman H, Belmaker J, Simpson J et al (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027. https://doi.org/10.1890/13-1917.1