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No consistent diversity patterns in terrestrial mammal assemblages along rural-urban forest gradients

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Abstract

Urbanization is increasing worldwide, fragmenting, isolating or destroying native habitats with a subsequent loss of biodiversity, structural and compositional changes of biotic communities and weakening of the functioning of biological processes and ecosystem services. In urban ecosystems, terrestrial mammals provide important functions and services, but we do not have a synthesis of the impacts of urbanization on terrestrial mammals. Terrestrial mammals are vulnerable to habitat loss and modification caused by urbanization, thus we hypothesised that the abundance and diversity of mammals would decrease as urbanization progresses. In addition, due to the declining number of predators and thus to decreasing predation pressure in urban habitats, we assumed that herbivore and omnivore mammals would gain dominance. To clarify the inconsistency of previous urbanization studies on terrestrial mammals, we synthetized and re-evaluated published results by meta-analysis. Based on 50 rural-urban comparisons, terrestrial mammals were not significantly more abundant or diverse in rural than urban habitats. This was not only found at the community level, but also at the level of taxonomic groups (carnivores, marsupials, rodents), feeding habit (carnivorous, herbivorous or omnivorous species) or at the level of their interactions. Our results suggest that the studied urban-dwelling mammal species are probably well adapted to environmental conditions and pressures accompanied by urbanization via individual-level adaptation.

Introduction

Human activities, especially agriculture, forestry and urbanization are among the main drivers of environmental change and their outcome is a patchwork of modified land-cover types world-wide (Forman, 2008). A major component of this "anthropization of the biosphere" is urbanization, which includes spatial expansion of urban infrastructures, as well as human population growth in urban settlements. Today 55.3% of the global human population (4.2 billion people) lives in cities, and this is even higher in the more urbanized "global North" (United Nations, 2018). When approaching a settlement from rural areas towards its centre, the ratio of native habitats is generally decreasing, while the number and density of the human population, the density of roads, and the amount of artificial surfaces increase (Carreiro & Tripler, 2005; McDonnell et al., 1997). With urban development, the remaining native habitats are

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drastically fragmented (Collins et al., 2000), while the remaining ones are either converted to managed areas or become ruderal spaces (Deutschewitz et al., 2003). Furthermore, urbanization causes changes in temperature, humidity (Liu et al., 2009), nutrient cycling and several other biological processes (Pouyat et al., 1997). Consequences include significant changes in community organization and composition of urban and peri-urban biota (Grimm et al., 2008; Magura et al., 2018).

Forests and urbanization also have a special relationship. Especially in the temperate regions, forested areas have been greatly reduced, while forest patches − usually in the form of parks − have long been favoured by designers and city dwellers alike (McKinney, 2002; Lin et al., 2019). Urban trees provide multiple benefits for urban environments and their inhabitants (Brzoska & Spage, 2020). Forests also support high biodiversity, including flora and fauna, and many of them are culturally very important. The contribution to biodiversity by forest-associated organisms is important also in urban settings (Nowak & Walton, 2005; Roeland et al., 2019). Among the animal groups associated with forests or trees, the group that resonates with people perhaps the most are the mammals (Leather, 2009). This can arise from a sense of kinship, but the evidence about a special relationship between people and mammals is vast. Numerous mammals can be classified as anthropophiles, and these can reach high densities in urban areas (Baker & Harris, 2007). Others may utilise human-modified habitats but their presence is underappreciated, due to their behaviour, activity times, or other biological features.

The effects of urbanization on forest-associated terrestrial mammals, however, seem to be inconsistent. Several mammal species suffer from changes in environmental conditions accompanied by urbanization and show lower abundance in urban environments compared to rural habitats (Fernández & Simonetti, 2013; Łopucki & Kitowski, 2017) while others are more abundant in urban than rural areas (Baker et al., 2003; Gentile et al., 2018; Parsons et al., 2018; Santini et al., 2019). Other studies found no difference in abundance between mammals in urban and rural habitats (Mollov et al., 2009; Riem et al., 2012).

We synthesize the results of urbanization impacts on forest-inhabiting terrestrial mammals by performing a meta-analysis, and to determine whether there is a consistent pattern of change in mammalian abundance and diversity in forest patches along rural-urban gradients. Specifically, we hypothesized that (1) the abundance and diversity of the terrestrial mammal communities would be higher in rural areas than those living in urban environments. This assumption is consistent with the increasing disturbance hypothesis (Gray, 1989), which predicts that along an urbanization gradient, disturbance is monotonously increasing, and this causes a similarly monotonous decrease in diversity. Habitat fragmentation, patch isolation and alteration due to urbanization are major threats to mammalian predators with generally extensive home ranges (Gering & Blair, 1999), so we

hypothesized that (2) the abundance of the predatory mammals should be higher in rural environments compared to urban ones. Furthermore, due to the decreasing predation pressure in urban habitats (Eötvös et al., 2018), we hypothesized that (3) herbivorous and omnivorous mammals should become more prominent in urbanized ecosystems.

Materials and methods

Literature search and data collection

The data search and selection process was as suggested by the PRISMA guidelines (Moher et al., 2009). We performed a literature search at University of Debrecen, Hungary, using the "all databases" option in Web of Science on 7 March 2017. We used the following search terms: TOPIC: (forest*) AND TOPIC: (urban*) AND TOPIC: (densit* OR richness OR divers*) AND TOPIC: (mammal*). We also checked the reference list of the papers found for additional, relevant publications. Our inclusion criteria were: 1) the study had to be conducted in clearly defined, forested rural (relatively large and undisturbed native forest stands) as well as in urban habitats (forested urban parks, remnant native forest fragments), 2) the study reported mean abundance and/or species richness values with their SD and sample sizes. In cases where a gradient was studied, we only considered the two extremes.

Data analyses

At the assemblage level, the mean abundance and species richness of terrestrial mammals were analysed. Species with different feeding habits (carnivore, herbivore, and omnivore) and different taxonomic affiliation (e.g. Carnivora, Marsupialia, Rodentia) may react differently to urbanization; therefore, we also classified the studied mammal species by feeding habit and taxonomy, and their mean abundances were evaluated separately. The necessary information was extracted from the original paper; if missing, we tried to retrieve it from Internet databases. Analyses were performed only for those levels (assemblage level, feeding habit level, taxonomic level, and their interactions) where at least five cases of the given response variable (abundance or species richness) were available.

As effect size, we calculated the unbiased standardized mean difference (Hedges' g), (Borenstein et al., 2009) for each rural-to-urban comparison as:

$$g = J\frac{X_R - X_U}{S_{within}} \tag{1}$$

$$S_{within} = \sqrt{\frac{(n_R - 1)S_R^2 + (n_U - 1)S_U^2}{n_R + n_U - 2}} \tag{2}$$

and

$$J = 1 - \frac{3}{4(n_R + n_U - 2) - 1} \qquad (3)$$

where X_R and X_U were the mean abundance or species richness of terrestrial mammals in rural (R) and urban (U) forested habitats, n_R and n_U were the sample sizes from rural (R) and urban (U) sites, and S_R and S_U were their SDs. A positive g value indicates higher mammal abundance or diversity in rural than urban habitats.

We calculated the mean effect size using a random-effects model, because of the variable locations, conditions, methods and experimental setups in the individual studies. Occasionally, more than a single effect size was calculated from one study, thus we included a publication-level random effect as a nesting factor. A significant mean effect size could not include zero in its 95% bootstrap confidence interval (which was calculated with 999 iterations). We also tested for heterogeneity in effect sizes by calculating Q, the weighted sum of squares within a data set (Borenstein et al., 2009), because if effect sizes vary across studies, the results should be carefully interpreted. Meta-analyses may suffer from publication bias, resulting in missing studies (Borenstein et al., 2009). Publication bias was tested by Egger's regression test with a mixed-effects meta-regression model. When significant asymmetry was found, Duval and Tweedies' (2000) trim and fill method was used (Duval & Tweedie, 2000). This method calculates the effect sizes as well as standard errors of the assumed missing studies; then after adding theses values of missing studies, the summary effect size is recomputed. All calculations were made in the R programming environment (R Core Team, 2017), using the packages *MAd* (Del Re & Hoyt, 2014) and *metafor* (Viechtbauer, 2010)

Results

The original literature search yielded 131 publications, and by scanning the reference list of these, we found three additional papers. After applying the inclusion criteria, 11 studies were retained (Appendix A: Fig. 1). Four papers reported data from Australia (Brady et al., 2011; Treby & Castley, 2016; Villaseñor et al., 2014, 2015), two from Europe (Chernousova, 2001; Croci et al., 2008), three from North-America (Kays et al., 2015; Randa & Yunger, 2006; Rytwinski & Fahrig, 2007), and one each from Asia (Morand et al., 2015), and South-America (Fernández & Simonetti, 2013). From these papers, we extracted 50 rural-urban comparisons (Appendix A: Table 1). Among the 50 comparisons, five evaluated the abundance of mammal communities, six focused on species richness, ten reported the abundance of predatory mammals, 14 of herbivores, and 15 concentrated on the abundance of omnivorous species. These 39 species-level comparisons referred to 31 mammal species. These 31 species belonged to the Carnivora order (five species), the Marsupialia infraclass (eight species), and to the Rodentia order (18 species; Appendix A: Table 2). None of these 31 mammalian species had data from at least five studies, so we could not perform species-level analyses.

Taken together as a group, mammals were neither significantly more abundant, nor more diverse in rural than urban habitats (Table 1 and Fig. 1). No significant heterogeneity was detected for either abundance or diversity (Table 1; Appendix A: Figs. 5 and 6). There was significant asymmetry in the funnel plot of the abundance data ($z = 2.300$, $p = 0.021$), but no such asymmetry existed for diversity ($z = -0.615$, $p = 0.538$). The trim and fill method added 1 data point to the abundance data, but this did not change the non-significance (Appendix A: Fig. 2 and Table 3).

At the level of taxonomic groups, the abundance of carnivore, marsupial or rodent species were not significantly different between the rural and urban sites (Table 1 and Fig. 1). Significant heterogeneity was revealed for all three taxonomic groups (Table 1; Appendix A: Figs. 7−9). There was no significant asymmetry for the abundance of carnivores or marsupials ($z = -1.408$, $p = 0.159$ and $z = -0.494$, $p = 0.621$, respectively), but significant asymmetry existed for rodent abundance ($z = -3.002$, $p = 0.003$). However, the trim and fill method with two added data points did not change the outcome (Appendix A: Fig. 3 and Table 3).

At the level of trophic groups, neither the abundance of carnivores, herbivores, nor omnivores differed significantly between the rural and urban habitats (Table 1 and Fig. 1). There was significant heterogeneity for the abundance of species in all three groups (Table 1; Appendix A: Figs. 10-12) without significant asymmetry (carnivores, $z = 0.079$, $p = 0.937$, herbivores, $z = -1.583$, $p = 0.113$ and omnivores, $z = -1.044$, $p = 0.296$).

At the level of the interactions between taxonomic and trophic groups, we observed no significant difference in the abundance of carnivorous species, omnivorous marsupials, herbivorous or omnivorous rodents (Table 1 and Fig. 1). Data on all groups but omnivorous marsupials displayed significant heterogeneity (Table 1; Appendix A: Figs. 13-16). No asymmetry existed for the abundance of carnivores ($z = -1.560$, $p = 0.119$), omnivorous marsupials ($z = -0.700$, $p = 0.484$) or of herbivorous rodents ($z = -0.498$, $p = 0.619$). Egger's test detected significant asymmetry for the abundance of omnivorous rodents ($z = -2.404$, $p = 0.016$), but the trim and fill method estimated no missing values (Appendix A: Fig. 4 and Table 3).

Discussion

Contrary to our hypotheses, we found that neither the abundance nor the diversity of terrestrial mammals were significantly higher in rural forests than urban forest fragments. Furthermore, the abundance of carnivorous, herbivorous or omnivorous mammals did not change as we
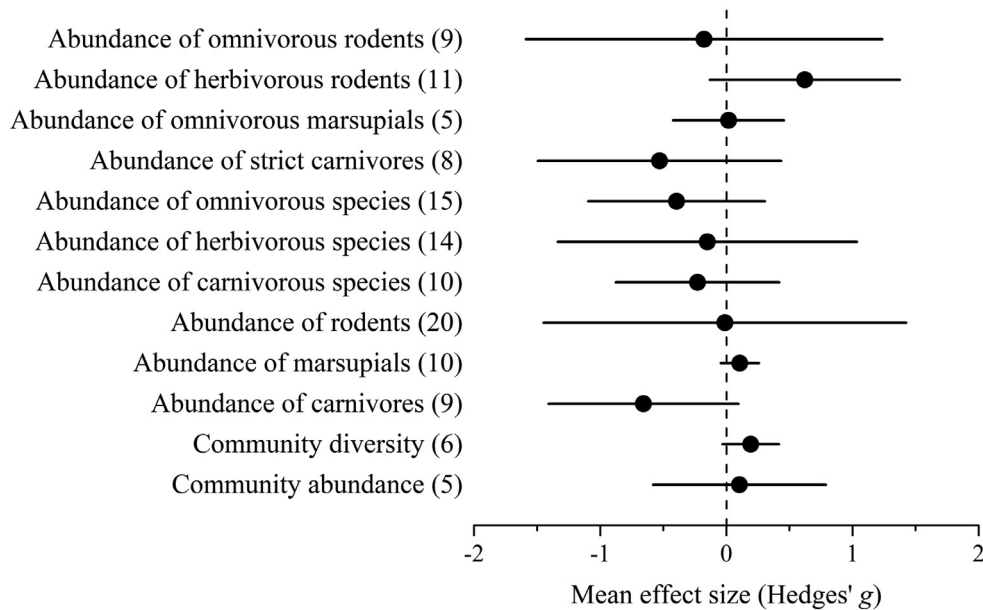
Fig. 1. Mean effect sizes (mean Hedges' *g* ± 95% confidence interval) for the abundance and diversity of terrestrial mammals in rural and urban forested habitats. Values in brackets refer to the number of comparisons from which the mean effect size was calculated. A positive *g* value means higher mammal abundance or diversity in rural habitats than in urban ones. The mean effect size was considered statistically significant if the 95% bootstrap confidence interval did not include zero.

hypothesised: carnivorous species were not more abundant in the rural, while herbivorous and omnivorous species were not more abundant in urban habitats compared to their counterparts.

The lack of significant difference in abundance and diversity could result from differential reactions of the various species to urbanization: some could be affected negatively, while others could utilise the ecological opportunities created by the process of urbanization, thus their densities could increase (Baker et al., 2003; Santini et al., 2019). In fact, urbanophile species can have larger populations inside than outside cities (McDonnell & Hahs, 2015). At a group or assemblage level, these species-specific reactions can cancel each other out.

With respect to their role and strength, both top-down and bottom-up forces can create conditions that are more favourable for mammals in urban than rural areas. Considering top-down factors, predators and parasites can be less common and less influential in urban than rural habitats, favouring non-predatory mammal species. Many of the predators present in urbanized environments are also opportunistic, ready to utilise food resources offered by urban habitats that can be more easily obtained, for example by scavenging. This can lower predation pressure (Eötvös et al., 2018), irrespective of predator densities, and would result in increased densities (although not necessarily the diversity) of other mammals in urban areas. Bottom-up factors can also have a positive impact. Food can be more available, because urban areas typically concentrate resources, importing many of them, and create surplus or waste. Much of this becomes available to non-human consumers.

Important determinants of urban success include flexible reproductive timing, large litter size, large body size, behavioural flexibility, and diet diversity (Santini et al., 2019). Higher reproductive output (large litter size) and behavioural plasticity seems to facilitate the exploitation of urban environments by mammals, and could counterbalance unfavourable factors such as roadkill, predation by domesticated species, mostly cats and dogs, whether they are pets or stray animals or by opportunistic urban-dwelling species (Bateman & Fleming, 2012; Santini et al., 2019). Predation risk by pets is highly dependent on cultural differences, such as tolerating or controlling stray pets. Large body size can deter predators, is beneficial when facing unpredictable food shortages, and useful for accessing patchy resources (Kelt & Van Vuren, 2001; Santini et al., 2019). Larger mammals usually have bigger home ranges, enabling them to use fragmented habitat patches, including urban ones, for feeding, reproduction, resting, overwintering, etc. and to move regularly between patches according to their needs (Kelt & Van Vuren, 2001). Moreover, higher dispersal capacity of large-bodied species allows the connection of spatially separated subpopulations, ensuring their long-term persistence in urban environments (Niemelä, 1999; Santini et al., 2019). Behavioural plasticity is a useful feature when facing unpredictable changes in environmental conditions and frequent novel challenges occurring in urban environments. In mammals, larger brain sizes may increase behavioural flexibility and the ability to deal with highly unpredictable environments (Santini et al., 2019; Sol et al., 2008). Urban populations of mammals actually have significantly bigger brains than rural ones (Santini et al., 2019; Snell-Rood &

Table 1. Estimates and heterogeneities in the models performed at the level of the whole mammal communities, the different taxonomic groups, and the species with different feeding habits.

	Mean effect size (model)	Lower CI bound (model)	Upper CI bound (model)	SE (model)	*p* value (model)	Q (hetero-geneity)	*p* value (hetero-geneity)
Community level							
Abundance	0.1045	−0.5800	0.7891	0.3493	0.7647	9.1173	0.0582
Diversity	0.1931	−0.0310	0.4173	0.1144	0.0913	7.4900	0.1867
Taxonomic group level							
Abundance, carnivores	−0.6571	−1.4089	0.0948	0.3836	0.0867	49.2291	< 0.001
Abundance, marsupials	0.1069	−0.0448	0.2586	0.0774	0.1671	65.7101	< 0.001
Abundance, rodents	−0.0121	−1.4486	1.4244	0.7329	0.9868	86.4462	< 0.001
Feeding type level							
Abundance, carnivorous spp.	−0.2282	−0.8762	0.4198	0.3306	0.4900	77.4697	< 0.001
Abundance, herbivorous spp.	−0.1507	−1.3361	1.0347	0.6048	0.8033	71.2608	< 0.001
Abundance, omnivorous spp.	−0.3944	−1.0942	0.3055	0.3571	0.2694	70.2125	< 0.001
Taxonomic group × feeding type level							
Abundance, strict carnivores	−0.5294	−1.4938	0.4351	0.4921	0.2820	41.8529	< 0.001
Abundance, omnivorous marsupials	0.0170	−0.4216	0.4557	0.2238	0.9393	6.8252	0.1454
Abundance, herbivorous rodents	0.6218	−0.1308	1.3744	0.3840	0.1054	34.9159	< 0.001
Abundance, omnivorous rodents	−0.1769	−1.5884	1.2346	0.7202	0.8060	47.4417	< 0.001

Wick, 2013). Anthropogenic food sources in urban habitats, such as pet food and garbage (also highly dependent on cultural differences) provide alternative resources for mammals (Withey & Marzluff, 2008). Bird feeding, now widespread in urban areas in the temperate regions also offers, directly and/or indirectly, food for mammals (Robb et al., 2008). The exploitation of such increased feeding opportunities can be important during adaptation to urban environments and can trigger aggregation of mammals in these habitats (Santini et al., 2019). Reproduction at an early age may provide faster adaptive responses, higher dispersal capacity and effective adaptation to unpredictable conditions (Bielby et al., 2007; Santini et al., 2016, 2019; Stearns, 2000). Indeed, urban-dwelling ungulates, primates and insectivores have earlier weaning age than their rural congeneric species (Santini et al., 2019).

In addition to the behavioural adaptation to urbanized environments, there may be other, community-level reasons for our findings. One of these potential reasons is the predator relaxation or safe habitat hypothesis (Gering & Blair, 1999). The reduced number of predators also allows potential prey to spend less time on vigilance, allowing more time for parental care, feeding, or social interactions (Valcarcel & Fernández-Juricic, 2009). Urban predators may switch from their usual prey range to either a few hyperabundant species or to food supplied by humans, thereby reducing the overall predation pressure (Stracey, 2011; Eötvös et al., 2018)

Our results at the community level seem to be consistent, as effect sizes were homogenous. Significant total heterogeneity at the taxonomic group and trophic group levels, however, indicates that besides the degree of the urbanization (urbanized or non-urbanized) other factors (size, isolation of the habitats, type and quality of adjacent habitats) must also

be considered for a more sophisticated understanding of the patterns found. The most likely of these are connected to the rural habitat features and their impact on the rural pool of species.

Most of the studies evaluated here came from the Northern Hemisphere where rural habitats are far from being undisturbed and many of them have been influenced, sometimes profoundly and over a long period, by human activities (Lerman et al., 2020). Small, disturbance-sensitive, ground-dwelling mammals (van der Ree & McCarthy, 2005) and large carnivores may have disappeared from these areas as part of the ongoing defaunation (Galetti & Dirzo, 2013). Consequently, the original mammal communities may have been reduced already, and the remaining rural species could have traits that make them 'pre-adapted' to urban conditions.

Further, the geographical distribution of urbanization studies is also very uneven by climatic regimes, originating mostly from temperate climates (McHale et al., 2013). This underlines the importance of studies to be conducted in other climatic regions (Seto et al., 2012), especially because current, rapid urbanization occurs in biodiverse, non-temperate regions of the world. The realization that contact with nature is essential for humans, and the emerging movement of "greening our cities" provides opportunities to enrich the biodiversity in cities, among them of mammals, but this calls for considering the social drivers of ecological processes (Johnson et al., 2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.02.004.

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