SYMPOSIUM

Are Urban Vertebrates City Specialists, Artificial Habitat Exploiters, or Environmental Generalists?

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Synopsis Although urbanization is a major threat to biodiversity, some species are able to thrive in cities. This might be because they have specific adaptations to urban conditions, because they are able to cope with artificial habitats in general or because they are generalists that can live in a wide range of conditions. We use the latest version of the IUCN database to distinguish these possibilities in 25,985 species of the four classes of terrestrial vertebrates with the help of phylogenetically controlled methods. We first compare species occurrence in cities with that of the five other artificial habitats recognized by the IUCN and use principal components analyses to ask which of these most resembles cities. We then test whether urban species have a wider habitat breadth than species occurring in other, non-urban, artificial habitats, as well as species that occur only in natural habitats. Our results suggest that the proportion of terrestrial vertebrates that occur in urban environments is small and that, among the species that do occur in cities, the great majority also occur in other artificial habitats. Our data also show that the presence of terrestrial vertebrates in urban habitats is skewed in favor of habitat generalists. In birds and mammals, species occurrence in urban areas is most similar to that of rural gardens, while in reptiles and amphibians, urban areas most resemble pasture and arable land. Our study suggests that cities are likely not unique, as is often thought, and may resemble other types of artificial environments, which urban exploiters can adapt to because of their wide habitat breadth.

Introduction

The expansion of urbanization during the last centuries has created severe threats for biodiversity (Marzluff 2005; Chace and Walsh 2006; Sol et al. 2014), a trend that is predicted to continue in the future (McDonald et al. 2008). Yet while most species avoid cities or respond poorly to urban encroachment of their previously pristine habitats, some readily adjust to, and proliferate in, urban environments (McKinney 2006). Although ecological pressures are expected to vary across and within cities, some common features such as a predominance of artificial resources and a high level of human disturbance could make some challenges more common in cities than elsewhere. Given the unique features of urbanized environments, it is tempting to explain the proliferation of organisms in cities in terms of adaptive specializations.

However, there is at present little evidence for the existence of such specializations. Instead, urban exploiters seem to be able to cope with a wide variety of environmental challenges. Analyses in birds, for example, suggest that urban exploiters are characterized by a wider ecological niche (Evans et al. 2011; Sol et al. 2014; Marzluff 2017), broad environmental tolerance (Bonier et al. 2007), and disproportionally larger brains linked to enhanced behavioral plasticity (Maklakov et al. 2011; Møller and Erritzøe 2015). From this perspective, urban dwellers might be extreme habitat generalists and their uniqueness could, paradoxically, be this broad ecological tolerance that allows them to thrive in multiple environments, including cities.

Aside from extreme generalism and specific adaptations to city life, a third, intermediate, possibility is that urban species are good at exploiting many kinds of anthropogenically-modified environments, of which cities are only one example. Cleared expanses like pastures or planted areas like farms, gardens, and orchards might offer conditions that share many features with cities. For example, coping with the ubiquity of humans, domestic animals, and machinery, as well as the presence of anthropogenic sources of food and shelter, might require similar adaptations in both cities and other forms of artificial environments.

Disentangling whether urban species are city specialists, extreme generalists, or artificial habitat exploiters requires data that quantify these three habitat use dimensions on a broad range of taxa. The IUCN database is a useful tool for this purpose (IUCN 2018). It lists for over 25,000 species of terrestrial vertebrates their presence or absence in cities, in 5 other kinds of artificial habitats, and in 94 non-artificial habitat categories. Here, we combine phylogenetically-controlled principal components analyses (PCAs) with phylogenetic generalized linear mixed models (PGLMMs) to describe the distribution of species across artificial and natural habitats, and test whether their occurrence in cities is best explained by urban specialization, extreme generalism, and/or tolerance to human-altered habitats. Our assessment of generalism is based on previous work that validated and tested on a similar sample of vertebrate species a novel index of species co-occurrences within habitats (Ducatez et al. 2014, 2015). If urban exploiters are specialists, they should occur in few habitats besides the city. If city dwellers are artificial habitat exploiters, they should be found in some of the five other artificial habitats recognized by the IUCN (2018), arable land, pasture land, plantations, rural gardens, and degraded former forests. Finally, if urban exploiters are extreme generalists, they should be present in a wide array of non-artificial habitats. We test these predictions in each of the four classes of terrestrial vertebrates, amphibians, reptiles, birds, and vertebrates.

Methods

Habitat data

We used the latest available IUCN database (IUCN 2018) to determine whether or not an avian, mammalian, reptilian, or amphibian species occurs in each of the 100 IUCN habitat subcategories (the habitat category "other" was excluded). To make the data comparable across classes, we restricted the analysis to subcategories that contained at least one species.

Taxa listed as "extinct," "extinct in the wild," "data deficient," or with an unknown habitat were excluded. We obtained a matrix of 100 habitat types by 25,985 species, filled with 1s and 0s according to whether or not each species occurred in each habitat type. Our analyses are thus based on data that cover close to 100% of extant avian species, 81% of mammals, 72% of amphibians, and 55% of reptiles.

Habitat breadth indices

As a measure of habitat breadth, we calculated the habitat co-occurrence index (HCI) previously described in Ducatez et al. (2014, 2015), using the updated IUCN database (new data extracted in January 2018). The idea behind this index, first proposed by Colwell and Futuyma (1971), is that a species that occurs in habitat categories that vary considerably in species composition can be considered more of a generalist than a species that occurs in habitats that contain a consistent suite of other species. Fridley et al. (2007) applied this idea to plants and Ducatez et al. (2014, 2015) extended it to over 22,000 species in four classes of terrestrial vertebrates, validating the index against four traditional estimates of habitat breadth, with correlations ranging from 0.711 and 0.995 depending on the measure and the class.

Briefly, HCI for a given species is measured as $\beta = \gamma/\mu(\alpha)$, where γ is the cumulative number of different species that occur in the habitats used by the species considered and $\mu(\alpha)$ is the mean habitat species richness calculated over the different habitats used by that species. Values are higher for more generalist species, that is for species that occur in a large number of habitats with a wide range of values for species diversity (see Ducatez et al. [2014, 2015] for more details). Artificial terrestrial habitats (IUCN categories 14.1–14.6) were excluded when measuring this index to avoid spurious effects in our analyses. The HCI was thus calculated here over a total of 94 habitat subcategories. To test for the robustness of our results, we also estimated (as in Ducatez et al. [2014, 2015]) a more classical habitat breadth measure, the number of habitat categories occupied by each species, classified according to Bennett and Owens (2002) and constructed by clustering IUCN habitat types into eight broader groups, excluding the category "urban."

Analyses

Which species occur in cities?

For each order in the four vertebrate classes, we graphed the proportion of species present in cities
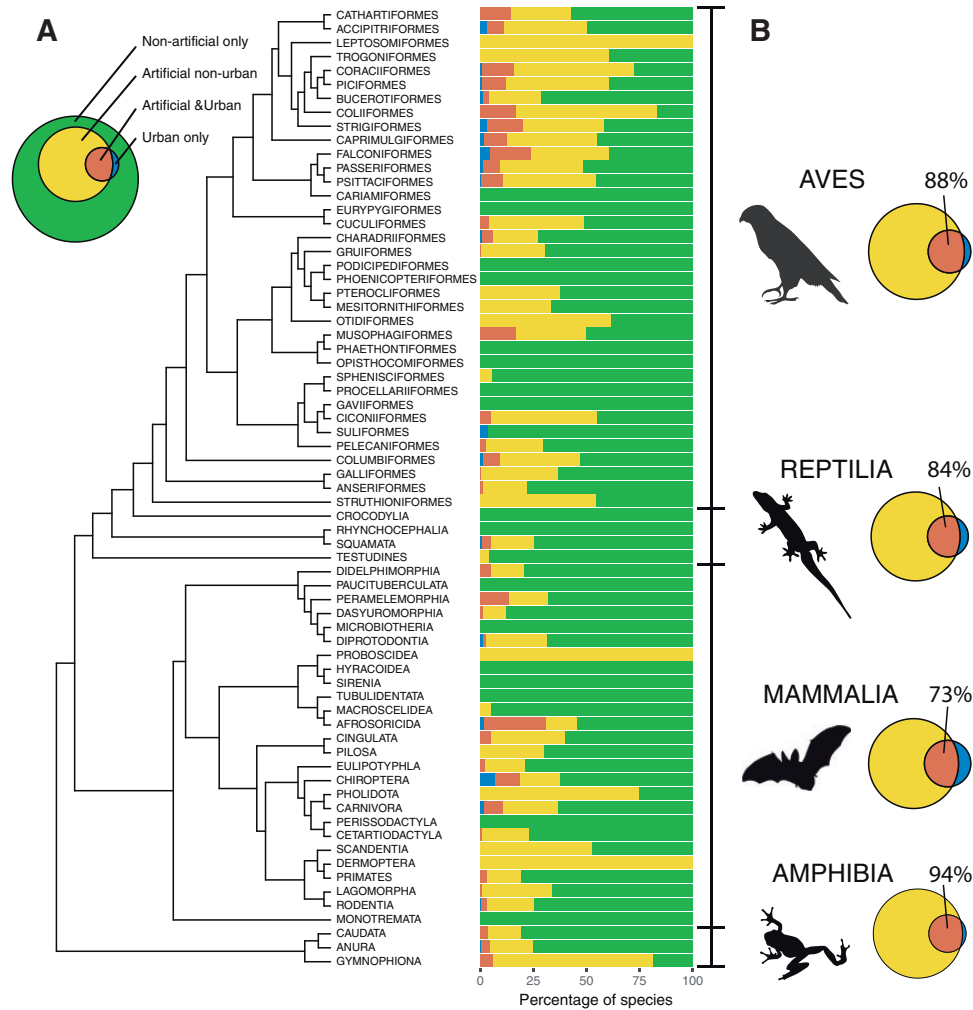
Fig. 1 Phylogenetic distribution of presence in cities and artificial habitats. (**A**) Proportion of species in each order that occur in the habitat categories "urban only," "urban and artificial," "artificial non-urban," and "non-artificial". (**B**) For each of the four classes of terrestrial vertebrates, overlap in the proportion of species that occur in urban areas only (white or blue) and those that also occur in at least one of the five other artificial terrestrial habitats (light gray or red). Species that not occur in any artificial habitat are excluded from this section.

only, as well as those occurring both in cities and other artificial habitats, artificial habitats but not cities, and finally those occurring only in natural habitats. We then assessed the phylogenetic signal of urban dwelling by estimating the proportion of variance in species occurrence explained by phylogeny. We used PGLMM with ordinal family and Markov chain Monte Carlo (MCMC) techniques in the R package MCMCglmm. The proportion of variance was calculated as VP/(VP+VR), with VP the variance explained by phylogeny and VR the residual variance. We used the most complete phylogenetic information currently available for mammals (Bininda-Emonds et al. 2007), birds (Jetz et al. 2012), amphibians (Isaac et al. 2012), and squamate reptiles (Pyron et al. 2013). For birds, Jetz et al. (2012) do not provide a unique consensus tree, but sample trees from a pseudo-posterior distribution.

In this case, we sampled 15 different trees for our analyses and after running the analysis in the tree subset, we averaged the model parameters over the 15 phylogenies. Reliable phylogenetic data suitable for large-scale analyses do not include all species for which IUCN habitat data are available. For this reason, we ran both phylogenetically-controlled and non-phylogenetically-controlled analyses to insure the robustness of our conclusions. The phylogenetically-controlled analyses included 8141 species of birds, 3942 amphibians, 3596 mammals, but only 1649 reptiles.

Which artificial habitat has the most similar species composition to cities?

We addressed this question by asking whether species that occur in urban environments also tend to occur in other human-altered environments by
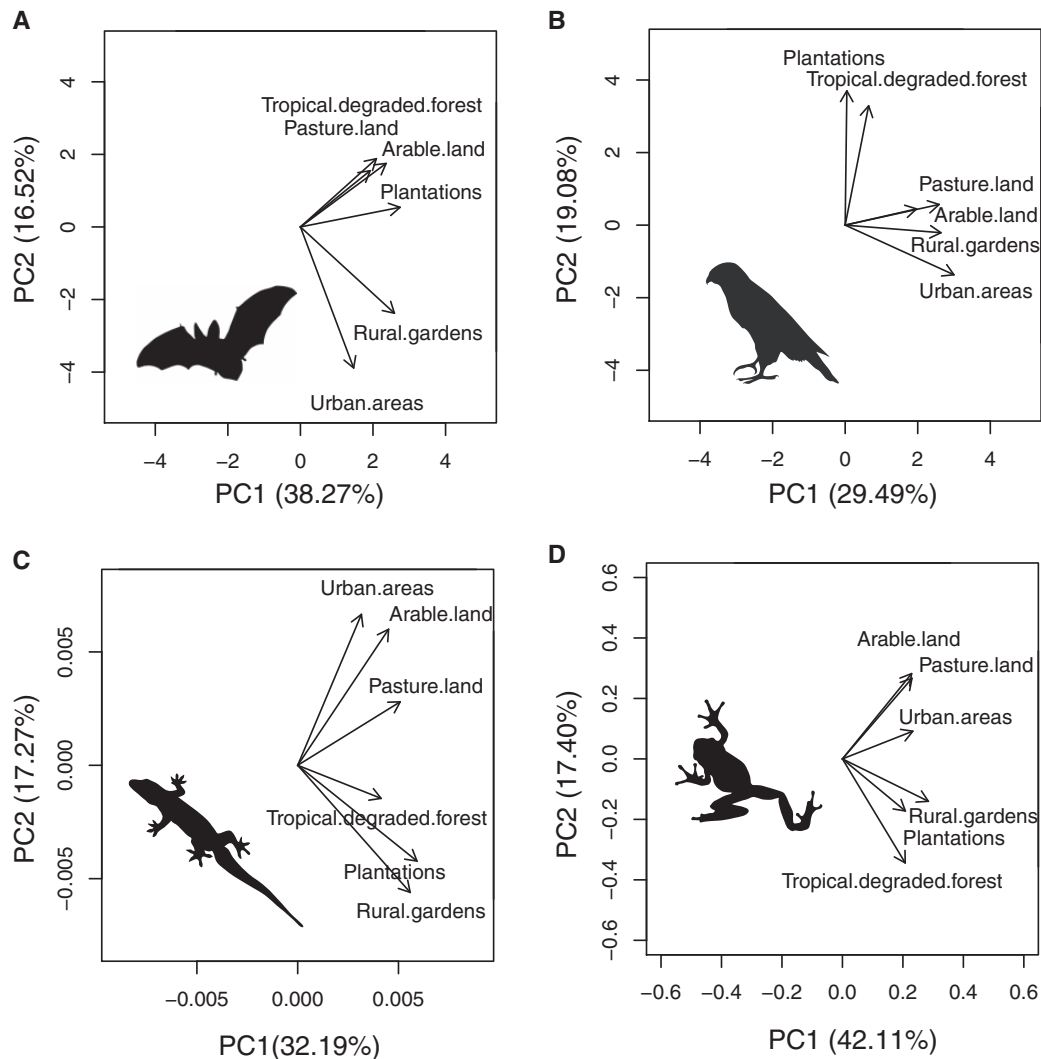
Fig. 2 PCA controlled for phylogeny on species occurrence in artificial habitats for 3596 mammals (**A**), 8141 birds (**B**), 1649 reptiles (**C**), and 3942 amphibians (**D**). The proportion of variance explained by each PC is given along each axis.

performing phylogenetically controlled PCAs. PCAs were conducted independently for each of the four classes. Presence or absence within each of the six terrestrial artificial habitats was included in the PCA, and we used the "phyl.pca" function from the "phytools" (Revell 2012) R package to extract the first and second components. Because some of the available phylogenies, for reptiles in particular, included a reduced number of the species for which we had habitat data, we also built classical PCAs (i.e., without phylogenetic controls), using the "PCA" function from the "FactoMineR" (Lê et al. 2008) R package, this time including all species with habitat data.

Are urban species habitat generalists?

This question was addressed by asking whether habitat breadth differs between species that occur or not in cities. For each class, we built two PGLMMs

(one for HCI and the other for the eight broad categories) with occurrence in cities as the response variable, habitat breadth as a fixed effect, and phylogeny as a random effect. We used ordinal generalized linear-mixed models with MCMC techniques in the R package MCMCglmm (Hadfield 2010). In addition, we tested whether species occurring in urban habitats are more generalist than species occurring in non-urban artificial habitats. For this purpose we built the same PGLMMs as described above, but this time focusing only on species occurring in at least one of the six categories of artificial habitats (i.e., excluding species that do not occur in any artificial habitat). For all models, the MCMC chains were run for 550,001 iterations with a burn-in interval of 50,000 to ensure satisfactory convergence. A total of 1000 iterations were sampled to estimate parameters for each model. We verified that autocorrelation levels among samples were lower than

0.1. Following Hadfield (2010), we used weakly informative priors (improper prior with $\mu =0.02$) for the variance. All explanatory variables were standardized to a mean of 0 and a variance of 1.

Results

Which species occur in cities?

In the IUCN database, only a small proportion of species are reported in cities in the four vertebrate classes. Birds are the one with the highest proportion (1012 of 11,112 species or 9%), followed by mammals (7%), reptiles (5%), and amphibians (4%). Within each class, clades differ strongly in their proportion of species that are urbanized (Fig. 1A), suggesting that some groups, but not others, share adaptations to urban living. The intra-class coefficients estimated within each class confirm that a large part of this variation is phylogenetic: the proportion of variance in urbanization explained by the phylogeny is very high in birds (0.907, CI =[0.883, 0.930]), mammals (0.834, CI =[0.716, 0.906]), and amphibians (0.846, CI =[0.723, 0.935]), but lower in squamate reptiles (0.591, CI =[0.402, 0.758]).

Which artificial habitat has the most similar species composition to cities?

As illustrated in Fig. 1B, the majority of urban species in all four classes also occur in one or more of the five other artificial habitats, with amphibians having the largest proportion (94%) and mammals the lowest (73%), confirming the idea that urban species tend to also live in other artificial habitats. Among these artificial habitats, Fig. 2 and Table 1 show that for birds and mammals, rural gardens are the environmental category most similar to urban habitats in terms of species occurrence. In reptiles and amphibians, pasture and arable lands are the habitats whose species composition has the strongest resemblance to cities. Despite this difference, the four classes share one clear trend: all artificial habitats cluster on the same pole of PC1, differing only on PC2. In addition, in all four clades, species occurring in tropical degraded forests and plantations clearly differ from cities on the PC2 axis. Phylogenetically controlled PCAs and standard PCAs without phylogenetic controls yield similar conclusions for birds, mammals, and amphibians (see Figs. 2 and 3, Tables 1 and 2). For reptiles, the urban environment places close to arable land instead of rural gardens and tropical degraded forests in the phylogenetically controlled PCAs, likely because the phylogenetic dataset was much smaller and taxonomically restricted (Squamata

Table 1 PCA controlled for phylogeny on species occurrence in artificial habitats for 3596 mammals (**A**), 8141 birds (**B**), 1649 reptiles (**C**), and 3942 amphibians

Class	Variable	PC1	PC2
Amphibians	Arable land	0.636	−0.504
	Pastureland	0.639	−0.476
	Plantations	0.579	0.308
	Rural gardens	0.791	0.251
	Urban area	0.647	−0.164
	Degraded forest	0.578	0.615
	Eigenvalue	2.526	1.044
	% explained	42.106	17.396
Birds	Arable land	0.504	0.092
	Pastureland	0.663	0.117
	Plantations	0.012	0.763
	Rural gardens	0.676	−0.043
	Urban area	0.768	−0.282
	Degraded forest	0.166	0.678
	Eigenvalue	1.769	1.145
	% explained	29.491	19.088
Mammals	Arable land	0.647	0.344
	Pastureland	0.670	0.320
	Plantations	0.670	0.099
	Rural gardens	0.674	−0.435
	Urban area	0.504	−0.710
	Degraded forest	0.522	0.283
	Eigenvalue	2.296	1.003
	% explained	38.273	16.728
Reptiles	Arable land	0.531	−0.517
	Pastureland	0.599	−0.241
	Plantations	0.696	0.364
	Rural gardens	0.657	0.483
	Urban area	0.372	−0.574
	Degraded forest	0.487	0.126
	Eigenvalue	1.931	1.036
	% explained	32.190	17.274

only). The clustering of the six artificial habitats on the same pole of PC1 was still consistent across all four classes, whether or not we controlled for phylogenetic effects.

Are urban species habitat generalists?

Table 3 presents the results of the Bayesian phylogenetic mixed models on presence or absence in urban areas against habitat breadth indices. All four vertebrate classes show a significant effect of habitat breadth on the probability of occurring in the urban
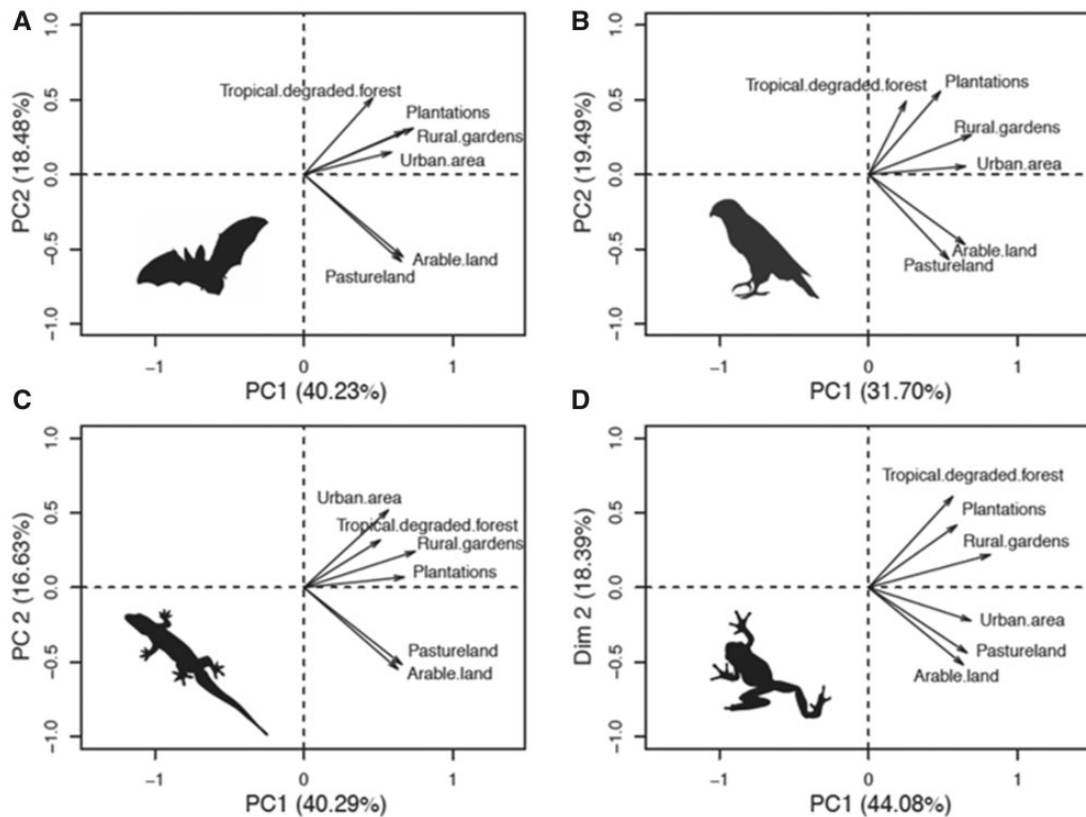
Fig. 3 Non-phylogenetically-controlled PCA on species occurrence in artificial habitats for 4782 mammals (**A**), 10,903 birds (**B**), 5241 reptiles (**C**), and 5059 amphibians (**D**). The proportion of variance explained by each PC is given along each axis.

environment, whether we measure this with the co-occurrence index or the number of habitat categories. The four classes also show a significant, positive effect of habitat breadth on the probability of occurring in the urban habitat when we restrict the analysis to species that occur in at least one artificial habitat (Table 4 and Fig. 4).

Discussion

Three main conclusions can be drawn from our analyses: (1) The proportion of terrestrial vertebrates that occur in urban environments is small (Fig. 1A); (2) among the species that do occur in cities, the great majority are also present in other artificial habitats (Fig. 1B); (3) these urban species also use a broad array of natural habitats (Fig. 4). Urban vertebrates are thus generalists that can exploit a wide variety of habitats, among them those that are altered by human activities.

Given that urbanization is predicted to continue expanding in the next decades (Seto et al. 2012), our finding that only a small proportion of vertebrates occur in urban environments suggests that this may substantially reduce biodiversity on a global scale. This is unsurprising considering that urbanization

is one of the most drastic and sudden alterations of natural environments, which may generate adaptive mismatches and reduce evolutionary responses (Johnson and Munshi-South 2017). In fact, there is ample evidence that most species do not tolerate urbanized environments very well (Evans et al. 2011; Sol et al. 2014).

If urban tolerance is generally low, why is it that some species thrive and proliferate in such altered environments? Our observation that most urban species also occur in other artificial habitats suggests that they have adaptations to cope with environmental disturbances in general. Dealing with disturbances is crucial to succeed in these habitats because an animal that, for example, does not tolerate the presence of humans or is incapable of using artificial resources is likely to go extinct. However, the success of some species in cities cannot be merely attributed to adaptations that allow tolerance for disturbed conditions and human proximity. Instead, our results suggest that the adaptations that lead to urbanization in some species are based on a generalist strategy that allows them to thrive in many habitats, including cities. Our study thus confirms and extends previous work showing that urban birds have a wide ecological niche (Evans et al. 2011;

Table 2 PCA (without phylogenetic correction) on species occurrence in artificial habitats for 4782 mammals, 10,903 birds, 5241 reptiles, and 5059 amphibians

Class	Variable	PC1	PC2
Amphibians	Arable land	0.636	−0.518
	Pastureland	0.660	−0.437
	Plantations	0.592	0.418
	Rural gardens	0.816	0.220
	Urban area	0.686	−0.222
	Degraded forest	0.564	0.610
	Eigenvalue	2.645	1.104
	% explained	44.083	18.394
Birds	Arable land	0.646	−0.469
	Pastureland	0.538	−0.570
	Plantations	0.483	0.557
	Rural gardens	0.690	0.266
	Urban area	0.650	0.054
	Degraded forest	0.251	0.490
	Eigenvalue	1.90	31.70
	% explained	1.17	19.49
Mammals	Arable land	0.663	−0.552
	Pastureland	0.653	−0.582
	Plantations	0.674	0.291
	Rural gardens	0.733	0.309
	Urban area	0.587	0.149
	Degraded forest	0.461	0.512
	Eigenvalue	2.414	1.109
	% explained	40.234	18.475
Reptiles	Arable land	0.631	−0.547
	Pastureland	0.657	−0.515
	Plantations	0.672	0.070
	Rural gardens	0.746	0.242
	Urban area	0.566	0.519
	Degraded forest	0.511	0.317
	Eigenvalue	2.418	0.998
	% explained	40.294	16.632

Notes: The contribution of each variable to the first two PCA axes, and the eigenvalue and proportion of variance explained by the first two PCA axes are given.

Sol et al. 2014; Marzluff 2017) and a broad environmental tolerance (Bonier et al. 2007). These same features have also been found to predict invasion success (reviewed in Sol et al. 2017), suggesting that they are general adaptations to cope with environmental novelty. Coping with a wide variety of environments should increase the likelihood of finding an appropriate habitat within the city (Devictor et al. 2008), and also reduce the effect of habitat fragmentation that is typical of urbanization.

Our analyses are based on a dataset of unprecedented geographic and taxonomic coverage. Although this means that knowledge might be limited for some species, the patterns we found are highly consistent across the four classes of terrestrial vertebrates and the two habitat breadth measures. The conclusions are also robust to methodological decisions, such as using phylogenetic and non-phylogenetic analyses, and hold even when sample sizes differ by as much as 25%. The consistency in our findings on habitat breadth across the four classes of terrestrial vertebrates is particularly remarkable, as the classes are expected to use different features of each artificial habitat. While for birds and mammals rural gardens most resemble cities in terms of species composition, in reptiles and amphibians the closest artificial habitats are pastures and arable land. Realizing that the same artificial habitat may pose different problems and opportunities for different taxa is an important piece of knowledge in predicting biodiversity loss in anthropogenically-modified environments.

Our approach provides general conclusions that apply across taxa and over broad regions, but it is also susceptible to several caveats. The most obvious one, the possibility that the patterns we observe reflect biases in species coverage, seems unlikely given that cities are among the habitats that are most closely monitored on Earth. However, our evaluation of the impact of urbanization is probably an overestimation, as the absence of a species in the city does not necessarily mean that it cannot thrive in this habitat; absence may indicate that the species has had few opportunities to colonize the urban habitat (Clergeau et al. 2001; Sol et al. 2014), for example because the species is too scarce in natural environments to generate propagules or because it lives in remote regions too far away from human settlements. While limitations in dispersal seem to account for only a small fraction of the observed loss of species richness in birds (Sol et al. 2014), in other vertebrates with more modest dispersal abilities the fraction might be substantially higher. Another limitation of our analyses is their reliance on simple species presence or absence. Estimates of actual urban populations are important, as in many cases species that live in cities are scarce and probably only thrive there thanks to the influx of individuals from surrounding areas (see Sol et al. 2014). Finally, the IUCN definition of urban habitats does not specify the intensity of urbanization, pooling areas with varying degrees of human imprint such as lawns, parks, and developed zones with asphalt and buildings. The use of such a broad definition is not

Table 3 Result of the phylogenetically controlled mixed linear models on the HCI and the number of habitat categories exploited as predictors of presence or absence of species in urban areas

Class	Explanatory variable	pm	CI	pMCMC
Amphibians *n*=3942	Habitat co-occurrence	0.878	[0.789, 0.977]	<0.001
	Phylogeny	0.401	[0.034, 0.838]	—
	Number of habitats	0.672	[0.588, 0.764]	<0.001
	Phylogeny	0.930	[0.588, 0.764]	—
Birds *n*=8141	Habitat co-occurrence	0.600	[0.539, 0.662]	<0.001
	Phylogeny	7.098	[4.836, 9.162]	—
	Number of habitats	0.504	[0.447, 0.567]	<0.001
	Phylogeny	6.615	[4.674, 8.860]	—
Mammals *n*=3596	Habitat co-occurrence	0.556	[0.472, 0.650]	<0.001
	Phylogeny	4.756	[2.248, 7.877]	—
	Number of habitats	0.558	[0.462, 0.651]	<0.001
	Phylogeny	4.271	[2.209, 6.788]	—
Reptiles *n*=1649	Habitat co-occurrence	0.260	[0.181, 0.331]	<0.001
	Phylogeny	1.438	[0.272, 2.937]	—
	Number of habitats	0.256	[0.182, 0.333]	<0.001
	Phylogeny	1.245	[0.204, 2.618]	—

Table 4 Results of the phylogenetically controlled linear mixed models on the HCI and the number of habitat categories exploited as predictors of presence or absence of species in urban areas, considering only species that occur in at least one artificial habitat category

Class	Explanatory variables	pm	CI	pMCMC
Amphibians *n*=1229	Co-occurrence index	0.880	[0.741, 1.013]	<0.001
	Phylogeny	0.301	[0.014, 0.708]	—
	Number of habitats	0.650	[0.535, 0.760]	<0.001
	Phylogeny	0.172	[0.003, 0.462]	—
Birds *n*=3860	Co-occurrence index	0.543	[0.470, 0.616]	<0.001
	Phylogeny	6.983	[4.789, 9.445]	—
	Number of habitats	0.415	[0.348, 0.487]	<0.001
	Phylogeny	6.774	[4.514, 9.350]	—
Mammals *n*=1206	Co-occurrence index	0.626	[0.467, 0.766]	<0.001
	Phylogeny	4.689	[2.220, 7.787]	—
	Number of habitats	0.538	[0.396, 0.683]	<0.001
	Phylogeny	4.441	[1.933, 7.509]	—
Reptiles *n*=592	Co-occurrence index	0.266	[0.154, 0.371]	<0.001
	Phylogeny	1.394	[0.223, 3.230]	—
	Number of habitats	0.240	[0.126, 0.350]	<0.001
	Phylogeny	1.463	[0.185, 3.733]	—

necessarily inappropriate for the purpose of our study, as it merely reflects the fact that cities are a mosaic of habitats. However, it implies that the proportion of terrestrial vertebrates that occur in urban environments could have been substantially lower had our analyses been restricted to intensely urbanized environments (e.g., Sol et al. 2014, 2017).

The importance of these caveats will have to be revisited in the future as species coverage improves for both large-scale molecular phylogenies and IUCN data, in particular for clades with smaller sample sizes like reptiles.

Cities are exceptional in many aspects, including their high degree of human-related disturbances and
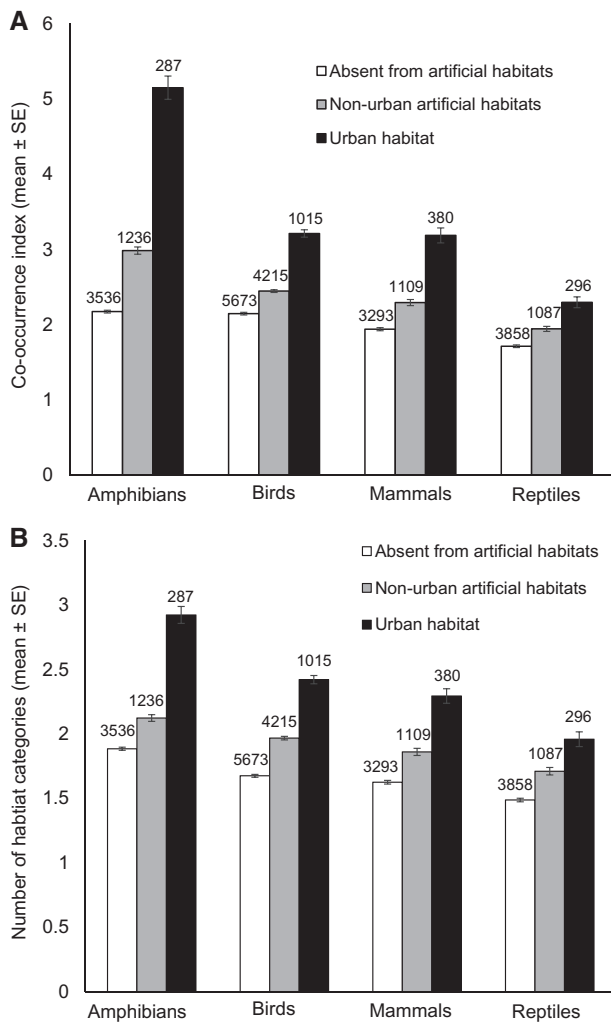
Fig. 4 Differences in habitat breadth (co-occurrence index [**A**] or number of habitat categories [**B**]) between species that do not occur in artificial habitats, species that occur in artificial but not urban habitats, and species exploiting the urban habitat. The number of species per category is given above each bar; note that these numbers differ from the ones included in the phylogenetically corrected analyses (all species with habitat use data are included in this figure, including species that were absent from the phylogenetic trees).

a predominance of artificial resources due to the loss and fragmentation of native vegetation. In terms of vertebrate composition, however, our study highlights the fact that cities are likely not unique, as is often thought. More likely, cities resemble other types of artificial environments, which urban exploiters can adapt to because of their outstanding capacities to exploit novel ecological opportunities and expand their niches.

Funding

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