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# A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers

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Urbanization contributes to the loss of the world's biodiversity and the homogenization of its biota. However, comparative studies of urban biodiversity leading to robust generalities of the status and drivers of biodiversity in cities at the global scale are lacking. Here, we compiled the largest global dataset to date of two diverse taxa in cities: birds (54 cities) and plants (110 cities). We found that the majority of urban bird and plant species are native in the world's cities. Few plants and birds are cosmopolitan, the most common being *Columba livia* and *Poa annua*. The density of bird and plant species (the number of species per km<sup>2</sup>) has declined substantially:

only 8% of native bird and 25% of native plant species are currently present compared with estimates of non-urban density of species. The current density of species in cities and the loss in density of species was best explained by anthropogenic features (landcover, city age) rather than by non-anthropogenic factors (geography, climate, topography). As urbanization continues to expand, efforts directed towards the conservation of intact vegetation within urban landscapes could support higher concentrations of both bird and plant species. Despite declines in the density of species, cities still retain endemic native species, thus providing opportunities for regional and global biodiversity conservation, restoration and education.

## 1. Introduction

Over half of humanity now live in cities [1], which cover less than 3% of the Earth's terrestrial surface [2]. Cities are often located in naturally species-rich regions [3–5] where native species are threatened by an array of anthropogenic factors, including habitat loss and species introductions [6] that present serious conservation challenges [7]. Given that the world's urban population is growing at nearly 1% per annum on average [1] and cities are expanding geographically at a higher rate than population growth, particularly in key biodiversity hotspots [8], a better understanding of the global patterns of urban species composition and its drivers is necessary for sustainable urban planning and conservation.

Despite recognition by the Convention on Biological Diversity [9] of the importance of biodiversity in cities and a history of urban ecology research [10–11], global-scale syntheses of urban biodiversity are lacking [12]. A few studies have compared the diversity of single taxa within cities across continents [13–16], but the majority of urban biodiversity research has focused on compositional patterns within individual cities. Generalities made on the effects of urbanization on the patterns and drivers of species diversity have been primarily based on studies of individual cities [17]. While it is clear that urbanization changes the local biota, comprehensive analyses determining the level to which urbanization has changed biodiversity at the global scale are lacking.

Commonalities in the development histories and spatial structure among cities, in combination with human-mediated biotic interchange, have been hypothesized to result in biotic homogenization, or an increase in compositional similarity over time, across the world's cities [13]. Cities are novel ecosystems [18], characterized by fragmented and disturbed environments, high densities of fabricated structures and impervious surfaces with strong heat-retaining abilities, and elevated levels of some resources [19]. In particular, invasions of a similar suite of exotic species owing to human-mediated biotic interchange and extinctions of indigenous native species owing to habitat alteration and destruction may lead to a homogenized biota across the world's cities, as has been shown for continent-wide analyses [20].

To facilitate global-scale comparative studies of urban biodiversity and analyse the global consequences of urbanization on biodiversity, we compiled urban bird species lists for 54 cities and city-wide floras of spontaneously established (species that establish and grow without human intent) vascular plants for 110 cities. The lists encompass 36 countries on six continents

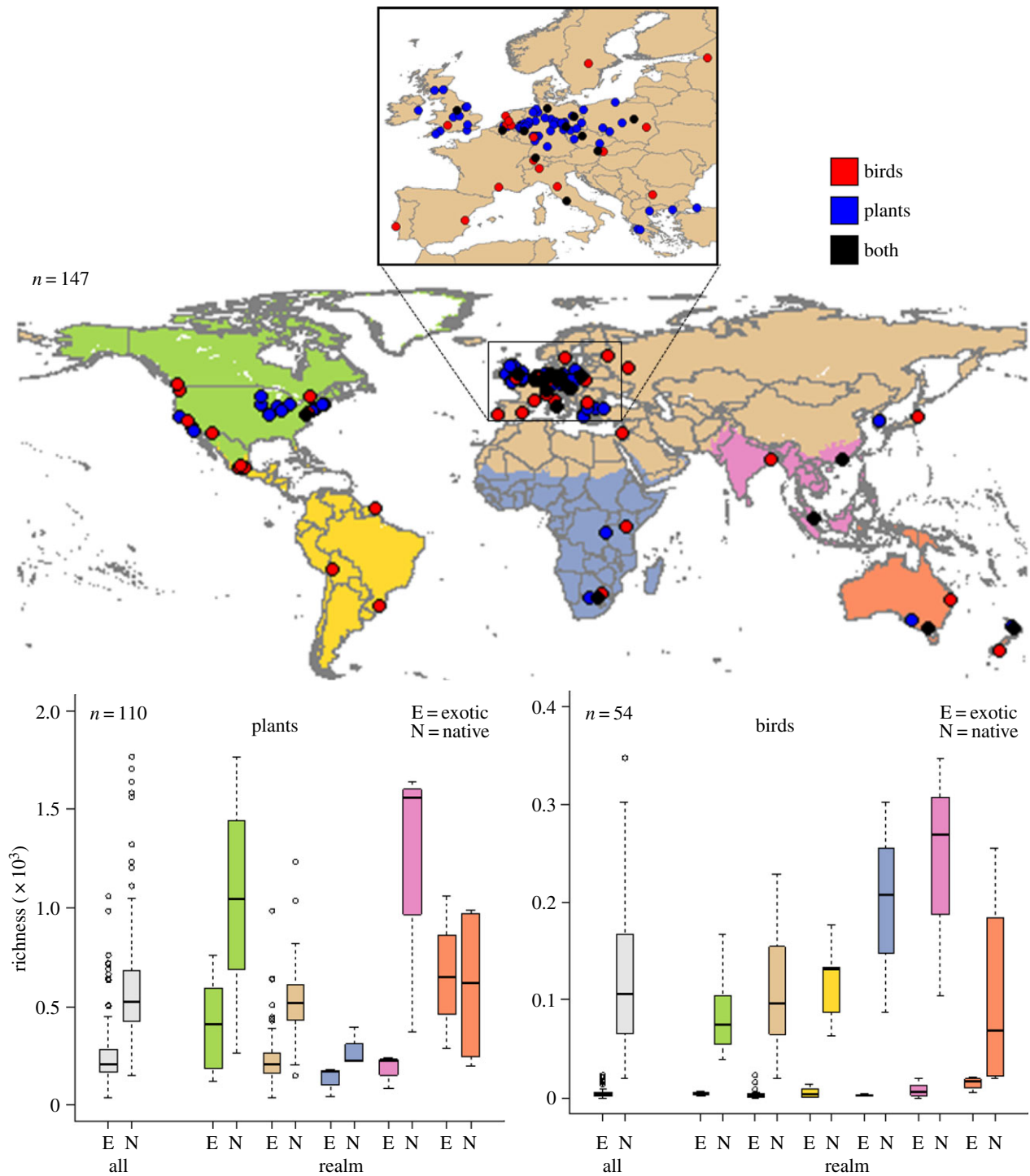
and six biogeographic realms (figure 1; and see the electronic supplementary material, tables S1 and S2), and represent the largest global compilation of urban biodiversity data to date. The cities cover a range of human population sizes ( $1.3 \times 10^4$  to  $1.8 \times 10^7$ ), geographical areas (15–2778 km<sup>2</sup>) and establishment dates (4000 BC to AD 1971). We examined the status of bird and plant diversity in the world's cities, homogenization of the biota, the density of species relative to estimates of non-urban levels, and the anthropogenic and environmental correlates of the density of species in cities.

## 2. Methods

### (a) Biological data

City lists of birds and plants were obtained from the literature, databases and expert surveys (see the electronic supplementary material, tables S1 and S2). Plant lists included surveys of natural and spontaneous vegetation (the sum of species that are not planted at a given site and reproduce without human intent) collected since 1950. Bird lists included all species recorded during surveys conducted since 1990 that used standardized methods (atlas, point count, territory mapping). Some datasets were based on intensive surveys conducted for 1 or 2 years, whereas others represented data collected over multiple time periods. Datasets were complete lists from within the administrative boundary of a city, often including inner urban as well as the peri-urban areas. Few datasets were from the inner urban area only. Differences among cities owing to variation in sampling design should be minimal, because our analyses rely on comprehensive species lists from each city and not, for example, weighted measures of diversity. Vagrant and accidental bird species were excluded by experts from each region, and each species was assigned as being exotic or native to each city using BirdLife International range maps [21]. We combined all varieties and subspecies of plants and birds into single species. Plant species were designated native or exotic to each city after consulting the literature and experts from each region. We classified bird and plant species as threatened with extinction if they were categorized as critically endangered (CR), endangered (EN) or vulnerable (VU) under the IUCN Red List [22] in their native range. We excluded threatened species that were non-native to a city. We standardized bird taxonomy using BirdLife International's Taxonomic Checklist [23] and plant taxonomy using the Taxonomic Name Resolution Service [24].

The density of species of extant birds, all plants and native plants was calculated as the number of species per km<sup>2</sup> for each city using estimates of city area (see the electronic supplementary material, table S6). We chose to examine the density of species within cities as this accounts for the large variability in area among the cities examined here, and species richness is strongly correlated with city area (log bird species richness and log city area: Pearson's  $r = 0.44$ ,  $t = 3.53$ ,  $p < 0.001$ ; log plant species richness and log city area: Pearson's  $r = 0.31$ ,  $t = 3.43$ ,  $p < 0.001$ ). We did not consider native birds separately, because the proportion of exotic bird species was very low for the majority of the cities considered (see the electronic supplementary material, figure S3). We used BirdLife International and NatureServe range maps [21] and the Kreft & Jetz [25] model of plant species richness to estimate the bird and plant species density of each city before urbanization (non-urban density of species). Non-urban density of bird species was estimated using range maps for the world's terrestrial birds from BirdLife International and NatureServe [21]. We considered breeding/resident ranges only and excluded marine species, resulting in a total of 9039 extant species. Range maps were rasterized using a cylindrical equal-area projection and a



**Figure 1.** The 147 cities considered in the analysis, and species richness of vascular plants (110) and birds (54). The box plots show the distribution of species richness for exotic (E) and native (N) species across all cities combined (all) and for cities in six biogeographic realms. The realms are identified by matching colours in the map and plots. The six realms are the Nearctic (green), Palearctic (brown), Neotropics (yellow), Afrotropics (blue), Indo-Malaya (pink) and Australasia (orange). No cities in the Neotropics contain plant data.

cell area of 3091 km<sup>2</sup>. Because range maps provide representations of species' extent of occurrence at coarse resolutions with little or no consideration of changes in occupancy owing to land-use change [26], they are ideally suited to estimate non-urban density of bird species within larger areas such as cities. Non-urban density of plant species was estimated using the co-kriging plant richness model from Kreft & Jetz [25]. This model quantified, at a coarse resolution, native patterns of plant species density where exotic species and other anthropogenic influences were minimized. This model is therefore well suited to estimating the non-urban density of plant species of cities. Density of plant species was gridded using a cylindrical equal-area projection and a cell area of 12 100 km<sup>2</sup>. The density of non-urban

bird and plant species was estimated for each city from these two sources based on the number of species in the equal-area cell divided by the cell area that contained the city centre.

### (b) Patterns of urban diversity

We used several metrics to examine the structure and composition of urban bird and plant communities for all cities combined and by biogeographic realm. We examined the representation of urban biotas within the world's biota using BirdLife International's Taxonomic Checklist [24] and a global list of vascular plant families with estimates of species richness compiled from multiple sources [27–31]. Patterns of species richness and the proportion of exotic

species of birds and plants within cities were examined by biogeographic realm [32] using Student's *t*-tests. We examined compositional similarity among cities using a hierarchical cluster analysis and the  $\beta$ -sim dissimilarity index [33,34]. The clustering method used unweighted pair-groups and arithmetic averages, and we identified the most prominent clusters using an adaptive branch-pruning technique [35]. This procedure represents a more flexible alternative to the constant or static height approach by detecting clusters based on the structure of the branches within the dendrogram. We used the 'dynamic hybrid' method with a minimum cluster size of one and the deepSplit option set to zero. All analyses were conducted in the statistical package R v. 2.15.2 [36]. The hierarchical cluster analysis was conducted using the *hclust* function in the *stats* library and the cluster identification using the *dynamicTreeCut* library.

### (c) Predictors of urban diversity

We considered 13 predictors of the density of bird and plant species and change in density of bird and plant species from non-urban levels (see the electronic supplementary material, table S6). Variables were selected to assess the role of potential anthropogenic and non-anthropogenic factors. Landcover was expected to be an important predictor of the density of species as it defines the quantity and quality of suitable habitats within the city [37,38]. The non-anthropogenic variables we chose have been shown to be important predictors of global patterns of species [39]. The landcover variables and all the non-anthropogenic variables were estimated within a 15 km radius circle of the city centre. We log-transformed the four density estimates and eight predictor variables to improve distributional properties. We evaluated variables for multi-collinearity and singularity using variance inflation factors (VIFs) where variables with  $VIF > 5$  indicate a cause for concern and  $VIF > 10$  indicate series collinearity [40]. We retained 10 predictors for analysis (see the electronic supplementary material, tables S4 and S5) after they were deemed to be statistically independent ( $VIF \leq 5$ ). We contrasted potential anthropogenic and non-anthropogenic factors using eight nested linear models and an information-theoretic approach [41]. To account for the inability of our data to meet all of the assumptions of least-squares regression, we used robust regression fitted using iterated reweighted least-squares with 10 000 maximum iterations within each model. The regression technique uses an M-estimator whose starting coefficients and fixed scale were given by an S-estimator [42]. Each model was run 1000 times, and the resulting Akaike information criterion with a correction for small sample size ( $AIC_c$ ) scores [41] were averaged across runs. We ranked the eight models based on their  $AIC_c$  scores, with smaller values indicating models with greater relative statistical support.

The eight models included a full model that contained all 10 predictors, one anthropogenic model with three predictors, and one non-anthropogenic model with seven predictors (see the electronic supplementary material, tables S4 and S5). The anthropogenic and non-anthropogenic models were further divided into three submodels (see the electronic supplementary material, tables S4 and S5). The anthropogenic models considered city age and landcover features within the city. The non-anthropogenic models considered the geographical, climatic and topographic features of the city. Robust regression was implemented using the *rlm* function in the library MASS [43], and *p*-values were estimated using robust *F*-tests in the library *fsmisc*.

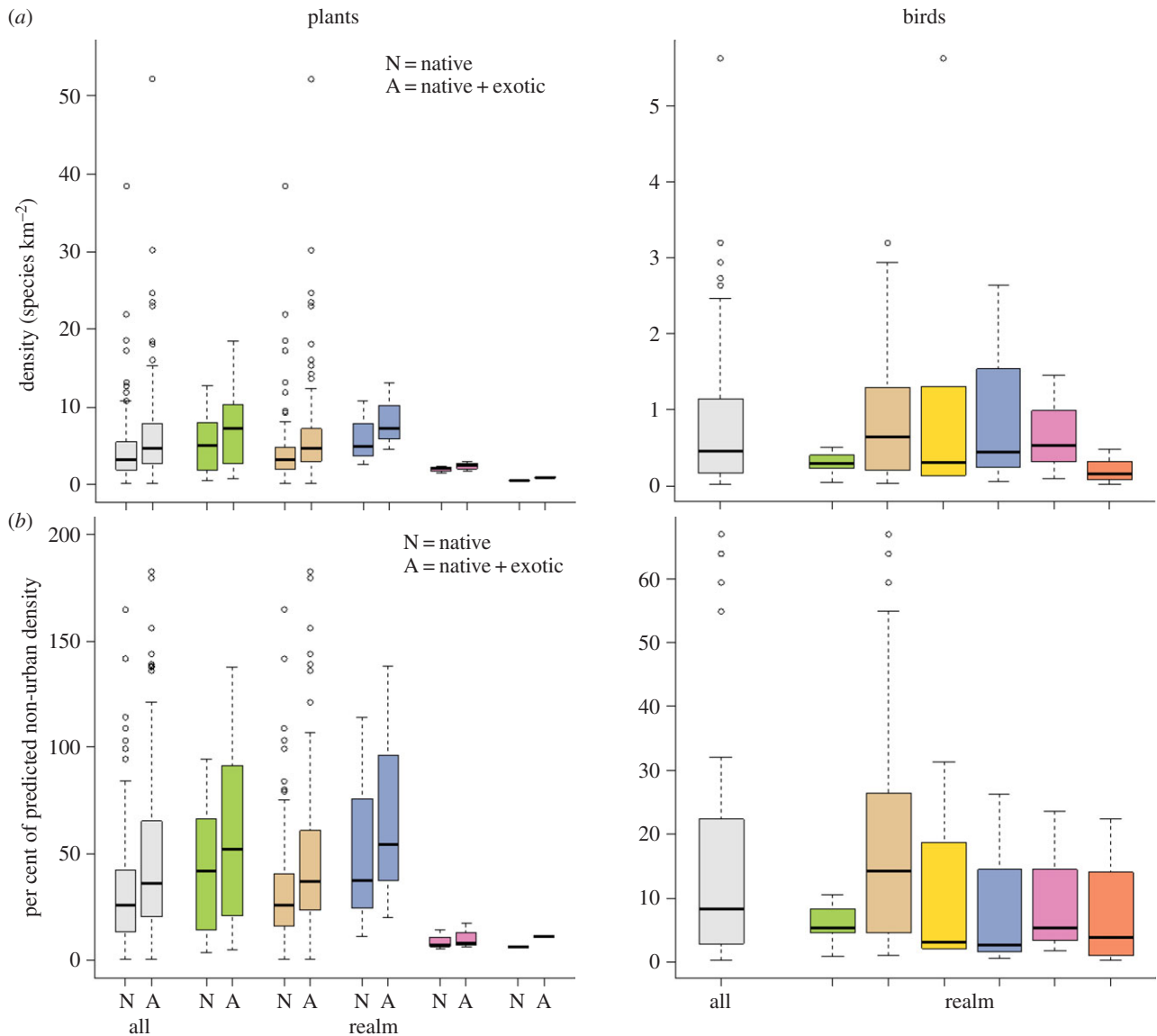
## 3. Results and discussion

Bird and plant species richness differ broadly among cities with a median of 112.5 for birds (range: 24–368) and 766 for plants

(range: 269–2528; figure 1; and see the electronic supplementary material, tables S1 and S2). Of the 10 052 recognized bird species worldwide, 2041 (20%) occur in our cities, representing nearly three-quarters of all bird families (144/198). Likewise, of the roughly 279 107 vascular plant species worldwide, 14 240 (5%) occur in these cities, representing two-thirds of all plant families (323/497). Hierarchical cluster analyses suggest that cities retain similar compositional patterns within biogeographic realms (see the electronic supplementary material, figures S1 and S2). We found that approximately 98% of urban bird assemblages correctly clustered and 79% of urban floras correctly clustered within realms. These findings show that, although some exotic species are shared across many cities, urban biotas have not yet become taxonomically homogenized at the global scale and continue to reflect their regional biogeographic species pool. Urban floras incorrectly clustered were primarily those in Australasia, which may be explained by the high proportion of exotic species from other regions in these cities (see the electronic supplementary material, figure S3), leading to more similar floras to these other regions. We did not analyse patterns of species abundance, owing to lack of data, which may increase similarity among cities in different biogeographic realms [44].

Exotic species are considered to be an increasing threat to global biodiversity [45]. The number of exotic species differs broadly among cities with a median of 3.5 exotic bird (range: 0–23) and 213 plant species (range: 38–1058; figure 1; and see the electronic supplementary material, tables S1 and S2). On average, cities have more native bird (paired Student's  $t = 11.45$ , d.f. = 53,  $p < 0.001$ ) and plant species (paired Student's  $t = 12.20$ , d.f. = 109,  $p < 0.001$ ; figure 1) than exotic species. The proportion of exotic bird and plant species is similar across realms except for Australasia (see the electronic supplementary material, figure S3), which is particularly skewed by the high proportions of exotic species in New Zealand cities (see the electronic supplementary material, tables S1 and S2), due primarily to deliberate introductions [46] and the presence of unfilled ecological niches. The relative proportion of exotic plant species is much greater than that of exotic bird species. Cities contain a median of 28% exotic plants and 3% exotic birds (see the electronic supplementary material, figure S3). These differences suggest that urban bird and plant communities are assembled under different processes. Greater propagule pressure, introduction rates [47] and establishment rates for exotic plants, in addition to differing environmental requirements for survival and success in urban environments, are likely to underlie these differences. Clearly, human-mediated global biotic interchange has played a considerable role in the development of urban plant communities [13].

Only a few cosmopolitan species occur across cities. In the case of birds, four occur in more than 80% of cities: *Columba livia* (rock pigeon, 51 cities); *Passer domesticus* (house sparrow, 48 cities); *Sturnus vulgaris* (European starling, 44 cities); and *Hirundo rustica* (barn swallow, 43 cities). For plants, 11 occur in more than 90% of cities, with the most common, *Poa annua* (annual meadow grass), occurring in 96% of the cities and in all biogeographic realms. Additional species that occur in all biogeographic realms include *Capsella bursa pastoris* (95% of cities), *Stellaria media* (94% of cities), *Plantago lanceolata* (93% of cities) and *Phragmites australis* (90% of cities). The majority of these cosmopolitan plant species are archaeophytes, exotic species introduced into Europe before AD 1500, suggesting that the most widespread and successful urban plant species



**Figure 2.** (a) The density and (b) the percentage of predicted non-urban density of plant and bird species in cities for all cities combined and cities in six biogeographic realms. The realms are identified by colour as in figure 1: the Nearctic (green), Palearctic (brown), Neotropics (yellow), Afrotropics (blue), Indo-Malaya (pink) and Australasia (orange). No cities in the Neotropics contain plant data.

first developed urban populations in European anthropogenic landscapes before becoming established in cities outside of Europe through human immigration and commerce [13,48].

In our cities, we found 36 birds and 65 plants identified by the IUCN global Red List as threatened with extinction (see the electronic supplementary material, table S3) [22]. Threatened bird species occur in 14 cities (30%), with Singapore having the greatest number ( $n = 12$ ). Threatened plant species are found in a much smaller proportion of cities (8%), with the greatest numbers found in Singapore ( $n = 41$ ) and in Hong Kong ( $n = 13$ ). Among realms, the greatest number of threatened bird ( $n = 15$ ) and plant species ( $n = 54$ ) are found in Indo-Malaya, whereas the Nearctic has the fewest threatened bird species ( $n = 2$ ), and the Palearctic has the fewest threatened plant species ( $n = 3$ ). This assessment of rare species in cities is expected to be conservative, particularly for plant species, as national lists may highlight additional species not assessed by the IUCN. For example, Australasian plant species are not included in the IUCN Red List, and endangered species are known to be present within cities in this realm.

We further examined patterns of biodiversity in cities using the density of species. The density of bird species in cities was 0.5

species km<sup>-2</sup> (median), which differed among realms (robust ANOVA,  $F_{1,5} = 5.6$ ,  $p = 0.016$ ), with the highest densities in the Palearctic (figure 2), primarily European cities, and lowest in Nearctic and Australasia. A median of 3.3 species km<sup>-2</sup> was found in these cities for native plants and 4.7 species km<sup>-2</sup> for all plants (figure 2). The density of native plant species (robust ANOVA,  $F_{1,4} = 14.4$ ,  $p < 0.001$ ) and all plant species differed among realms (robust ANOVA,  $F_{1,4} = 17.3$ ,  $p < 0.001$ ), with cities in Indo-Malaya and Australasia having the lowest densities, probably owing to urban development histories [49].

Although our analyses thus far are positive indicators of the ability of cities to support diverse biotas, we found extensive decreases in the density of species for each city when compared with estimates of non-urban density of species. A median of 8% of non-urban density of bird species is currently found in these cities. This differed among realms (robust ANOVA,  $F_{1,5} = 6.0$ ,  $p = 0.013$ ), with the highest values occurring in the Palearctic and lowest in the Nearctic (figure 2). Cities currently support 36% of non-urban density of plant species, but this was reduced to 25% of non-urban density of plant species when only native plants were included. These values differed among realms for all plants (robust ANOVA,

**Table 1.** Robust regression models contrasting anthropogenic and non-anthropogenic correlates of bird and plant species density in cities worldwide. Change in model  $AIC_c$  ( $\Delta_i$ ) represents the difference between model  $i$  and the model with the lowest  $AIC_c$  score;  $AIC_c$  weight ( $w_i$ ) is the level of evidence for model  $i$  based on the entire set of models; the model with the minimum  $AIC_c$  is shown in italics. Density was log-transformed before analysis.

model	bird density				plant density				native plant density			
	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$AIC_c$	$\Delta_i$	$w_i$	$R^2$
full	205.4	33.8	0.00	0.24	312.4	22.8	0.00	0.30	337.5	52.4	0.00	0.26
anthropogenic	173.8	2.3	0.23	0.17	<i>289.6</i>	<i>0.0</i>	<i>0.94</i>	<i>0.16</i>	<i>285.1</i>	<i>0.0</i>	<i>0.96</i>	<i>0.19</i>
city age	246.8	75.3	0.00	0.00	295.3	5.7	0.05	0.06	291.3	6.2	0.04	0.08
landcover	<i>171.5</i>	<i>0.0</i>	<i>0.74</i>	<i>0.15</i>	302.6	13.0	0.00	0.11	298.2	13.0	0.00	0.11
non-anthropogenic	189.4	17.8	0.00	0.12	340.6	51.0	0.00	0.11	334.5	49.4	0.00	0.11
geography	179.9	8.4	0.01	0.00	308.1	18.5	0.00	0.01	305.2	20.1	0.00	0.01
climate	183.3	11.7	0.00	0.07	301.4	11.8	0.00	0.08	300.4	15.3	0.00	0.09
topography	179.4	7.8	0.01	0.07	308.1	18.5	0.00	0.01	305.4	20.3	0.00	0.02

**Table 2.** Robust regression models contrasting anthropogenic and non-anthropogenic correlates of the proportion of non-urban bird and plant species density retained in cities worldwide. Change in model  $AIC_c$  ( $\Delta_i$ ) represents the difference between model  $i$  and the model with the lowest  $AIC_c$  score;  $AIC_c$  weight ( $w_i$ ) is the level of evidence for model  $i$  based on the entire set of models; the model with the minimum  $AIC_c$  is shown in italics. Percentage predicted density was log-transformed before analysis.

model	bird density				plant density				native plant density			
	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$AIC_c$	$\Delta_i$	$w_i$	$R^2$
full	225.3	49.6	0.00	0.30	<i>290.0</i>	<i>0.0</i>	<i>1.00</i>	<i>0.34</i>	307	9.3	0.01	0.36
anthropogenic	177.9	2.2	0.24	0.18	304.3	14.3	0.00	0.17	<i>297.7</i>	<i>0.0</i>	<i>0.90</i>	<i>0.18</i>
city age	270.7	95.0	0.00	0.00	308.7	18.7	0.00	0.06	302.7	5.0	0.07	0.07
landcover	<i>175.7</i>	<i>0.0</i>	<i>0.74</i>	<i>0.16</i>	317.7	27.7	0.00	0.10	311.4	13.7	0.00	0.12
non-anthropogenic	194.0	18.3	0.00	0.15	360.9	70.9	0.00	0.09	345.3	47.6	0.00	0.14
geography	184.3	8.6	0.01	0.02	318.6	28.6	0.00	0.04	314.3	16.6	0.00	0.03
climate	189.5	13.8	0.00	0.06	307.6	17.6	0.00	0.14	306.3	8.6	0.01	0.14
topography	184.2	8.5	0.01	0.09	321.3	31.3	0.00	0.01	316.6	18.9	0.00	0.01

$F_{1,4} = 15.5$ ,  $p < 0.001$ ) and native plants (robust ANOVA,  $F_{1,4} = 14.5$ ,  $p < 0.001$ ), with Indo-Malaya and Australasia experiencing the greatest loss in density of species compared with non-urban levels (figure 2). These regions are important biodiversity hotspots [50] and projected increases in urban land area in these regions [8] can be expected to have profound effects on the world's biodiversity.

In order to understand the factors that drive the density of species in cities, we examined anthropogenic and non-anthropogenic (environmental) correlates of the density of species and the change in the density of species from non-urban levels. The density of bird and plant species was best explained by anthropogenic features of the city (table 1). For birds, density of species was negatively associated with urban landcover. Thus, the greater the proportion of urban landcover in the city, the lower the density of bird species, indicating that vegetation structure is an important component of bird species conservation in cities, paralleling results from within-cities analyses [51]. For all plants (native and exotic) and only native plants, the density of species was positively associated with the cover of intact vegetation and city age

(see the electronic supplementary material, table S4). Not surprisingly, greater proportions of intact vegetation in cities, as found in older cities, preserve plant species. These results highlight the importance of including remnant vegetation and restoring natural areas in the design of cities [49].

The same anthropogenic factors were identified as key predictors of the loss in density of birds and plants from non-urban levels (table 2; and see the electronic supplementary material, table S5). As expected, the characteristics of the city primarily determined the loss in the density of bird and native plant species. However, the best combination of predictors for all plants included the full complement of anthropogenic and non-anthropogenic factors (table 2). In addition to anthropogenic associations, negative associations with temperature and precipitation seasonality were identified for all plants (see the electronic supplementary material, table S5). These results indicate that exotic plant species compensate more substantially for losses in the density of species in regions with colder temperatures and lower precipitation seasonality, characteristics of northern temperate regions. The loss of native species [49,52] and the

successful establishment of exotic species [53] is a dynamic process within urban plant communities that, when considered globally, is not exclusively related to human factors.

Here, we show that although cities support regional biodiversity and native species, the process of urbanization has had profound effects on biodiversity; cities worldwide contain substantially lower densities of species compared with non-urban levels. Efforts directed towards conservation and restoration of native vegetation within urban landscapes could support greater concentrations of both bird and plant species, ameliorating the projected declines of biodiversity with rapid urban growth [8]. Our study represents the largest urban global database of multiple taxa, but some realms are still under-represented, highlighting the lack and/or accessibility of systematic studies in these cities. There is an immediate need for better compilation and monitoring of urban biota in areas of high regional biodiversity, such as tropical cities and cities within biodiversity hotspots. Understanding the structure, composition and history of biodiversity in these regions is therefore paramount to reconciling human development with the maintenance of existing diversity and ecosystem services. The human experience is

increasingly defined within an urban context. Our results highlight that cities can support both biodiversity and people, but retaining these connections requires sustainable urban planning, conservation and education focused on each city's unique natural resources.

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**Data accessibility.** Species data are available in the electronic supplementary material and from the corresponding author. Sources of biotic, environmental and anthropogenic data are found in the electronic supplementary material.

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## References

- UN. 2011 *World population prospects: the 2010 revision*. New York, NY: UN.
- Schneider A, Friedl MA, Potere D. 2010 Mapping global urban areas using MODIS 500-m data: new methods and datasets. *Remote Sens. Environ.* **114**, 1733–1746. (doi:10.1016/j.rse.2010.03.003)
- Luck GW. 2007 A review of the relationships between human population density and biodiversity. *Biol. Rev.* **82**, 607–645. (doi:10.1111/j.1469-185X.2007.00028.x)
- Kühn I, Brandl R, Klotz S. 2004 The flora of German cities is naturally species rich. *Evol. Ecol. Res.* **6**, 749–764.
- Cincotta RP, Wisniewski J, Engelman R. 2000 Human population in the biodiversity hotspots. *Nature* **404**, 990–992. (doi:10.1038/35010105)
- Williams NSG *et al.* 2009 A conceptual framework for predicting the effects of urban environments on floras. *J. Ecol.* **97**, 4–9. (doi:10.1111/j.1365-2745.2008.01460.x)
- McKinney ML. 2002 Urbanization, biodiversity, and conservation. *Bioscience* **52**, 883–890. (doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- Seto KC, Guneralp B, Hutryra LR. 2012 Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl Acad. Sci. USA* **109**, 16 083–16 088. (doi:10.1073/pnas.1211658109)
- United Nations Environment Programme. 2007 Report of the cities and biodiversity: achieving the 2010 diversity target. Montreal, Canada: UNEP/CBD.
- Sukopp H. 2002 On the early history of urban ecology in Europe. *Preslia* **74**, 373–393. (doi:10.1007/978-0-387-73412-5\_6)
- Pickett STA *et al.* 2011 Urban ecological systems: scientific foundations and a decade of progress. *J. Environ. Manage.* **92**, 331–362. (doi:10.1016/j.jenvman.2010.08.022)
- McDonnell MJ, Hahs AK. 2009 Comparative ecology of cities and towns: past, present and future. In *Ecology of cities and towns: a comparative approach* (eds MJ McDonnell, AK Hahs, J Breuste), pp. 71–89. Cambridge, UK: Cambridge University Press.
- La Sorte FA, McKinney ML, Pyšek P. 2007 Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. *Glob. Change Biol.* **13**, 913–921. (doi:10.1111/j.1365-2486.2007.01329.x)
- Niemelä J, Kotze DJ, Venn S, Penev L, Stoyanov I, Spence J, Hartley D, Montes de Oco E. 2002 Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: an international comparison. *Landsc. Ecol.* **17**, 387–401. (doi:10.1023/A:1021270121630)
- Clergeau P, Savard JPL, Mennechez G, Falardeau G. 1998 Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. *Condor* **100**, 413–425. (doi:10.2307/1369707)
- Pautasso M *et al.* 2011 Global macroecology of bird assemblages in urbanized and semi-natural ecosystems. *Glob. Ecol. Biogeogr.* **20**, 426–436. (doi:10.1111/j.1466-8238.2010.00616.x)
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008 Global change and the ecology of cities. *Science* **319**, 756–760. (doi:10.1126/science.1150195)
- Hobbs RJ *et al.* 2006 Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.* **15**, 1–7. (doi:10.1111/j.1466-822X.2006.00212.x)
- Rebele F. 1994 Urban ecology and special features of urban ecosystems. *Glob. Ecol. Biogeogr. Lett.* **4**, 173–187. (doi:10.2307/2997649)
- Winter M *et al.* 2011 Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Natl Acad. Sci. USA* **106**, 21 721–21 725. (doi:10.1073/pnas.0907088106)
- BirdLife International and NatureServe. 2012 *Bird species distribution maps of the world*. Cambridge, UK: BirdLife International.
- IUCN. 2011 *IUCN red list of threatened species, version 2011.1*. See <http://www.iucnredlist.org>.
- BirdLife International. 2011 *The BirdLife checklist of the birds of the world, with conservation status and taxonomic sources, version 4.0*. Cambridge, UK: BirdLife International. See <http://www.birdlife.info/im/species/checklist.zip>.
- Taxonomic Name Resolution Service. 2011 *Taxonomic name resolution service*. iPlant Collaborative. See <http://tnrs.iplantcollaborative.org/index.html>.
- Kreft H, Jetz W. 2007 Global patterns and determinants of vascular plant diversity. *Proc. Natl Acad. Sci. USA* **104**, 5925–5930. (doi:10.1073/pnas.0608361104)
- Hurlbert AH, Jetz W. 2007 Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl Acad. Sci. USA* **104**, 13 384–13 389. (doi:10.1073/pnas.0704469104)
- Wilkstrom N, Kenrick P. 1997 Phylogeny of Lycopodiaceae (Lycopsidea) and the relationships of *Phylloglossum drummondii* Kunze based on rbcL sequences. *Int. J. Plant Sci.* **158**, 862–871. (doi:10.1086/297501)

28. Taylor WC, Hickey RJ. 1992 Habitat, evolution and speciation in *Isoetes*. *Ann. MO Bot. Gard.* **79**, 613–622. (doi:10.2307/2399755)
29. Korall P, Kenrick P. 2002 Phylogenetic relationships in Selaginellaceae based on RBCL sequences. *Am. J. Bot.* **89**, 506–517. (doi:10.3732/ajb.89.3.506)
30. Smith AR, Pryer KM, Schuettelpelz E, Korall P, Schneider H, Wolf PG. 2006 A classification for extant ferns. *Taxon* **55**, 705–731. (doi:10.2307/25065646)
31. Stevens PF. 2012 *Angiosperm phylogeny website, version 12*. St Louis, MO: Missouri Botanical Garden. See <http://www.mobot.org/mobot/research/apweb/welcome.html>.
32. Olson DM *et al.* 2001 Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience* **51**, 933–938. (doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
33. Koleff P, Gaston KJ, Lennon JJ. 2003 Measuring beta diversity for presence–absence data. *J. Anim. Ecol.* **72**, 367–382. (doi:10.1046/j.1365-2656.2003.00710.x)
34. Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ. 2001 The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J. Anim. Ecol.* **70**, 966–979. (doi:10.1046/j.0021-8790.2001.00563.x)
35. Langfelder P, Zhang B, Horvath S. 2008 Defining clusters from a hierarchical cluster tree: the dynamic tree cut package for R. *Bioinformatics* **24**, 719–720. (doi:10.1093/bioinformatics/btm563)
36. R Development Core Team. 2013 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org>.
37. Sushinsky JR, Rhodes JR, Possingham HP, Gill TK, Fuller RA. 2012 How should we grow cities to minimize their biodiversity impacts? *Glob. Change Biol.* **19**, 401–410. (doi:10.1111/gcb.12055)
38. Werner P. 2011 The ecology of urban areas and their functions for species diversity. *Landsc. Ecol. Eng.* **7**, 231–240. (doi:10.1007/s11355-011-0153-4)
39. Gaston KJ. 2000 Global patterns in biodiversity. *Nature* **405**, 220–227. (doi:10.1038/35012228)
40. Menard S. 1995 *Applied logistic regression analysis: Sage university series on quantitative applications in the social sciences*. Thousand Oaks, CA: Sage.
41. Burnham KP, Anderson RD. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
42. Yohai V, Stahel WA, Zamar RH. 1991 A procedure for robust estimation and inference in linear regression. In *Directions in robust statistics and diagnostics, part II* (eds WA Stahel, SW Weisberg), pp. 365–374. New York, NY: Springer.
43. Venables WN, Ripley BD. 2002 *Modern applied statistics with S*. New York, NY: Springer.
44. La Sorte FA, McKinney ML. 2007 Compositional changes over space and time along an occurrence–abundance continuum: anthropogenic homogenization of north American avifauna. *J. Biogeogr.* **34**, 2159–2167. (doi:10.1111/j.1365-2699.2007.01761.x)
45. Butchart SHM *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)
46. Atkinson IAE, Cameron EK. 1993 Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends Ecol. Evol.* **8**, 447–451. (doi:10.1016/0169-5347(93)90008-D)
47. Hulme PE *et al.* 2008 Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J. Appl. Ecol.* **45**, 403–414. (doi:10.1111/j.1365-2664.2007.01442.x)
48. La Sorte FA, Pyšek P. 2009 Extra-regional residence time as a correlate of plant invasiveness: European archaeophytes in North America. *Ecology* **90**, 2589–2597. (doi:10.1890/08-1528.1)
49. Hahs AK *et al.* 2009 A global synthesis of plant extinction rates in urban areas. *Ecol. Lett.* **12**, 1165–1173. (doi:10.1111/j.1461-0248.2009.01372.x)
50. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. (doi:10.1038/35002501)
51. Chace JF, Walsh JJ. 2006 Urban effects on native avifauna: a review. *Landsc. Urban Plan.* **74**, 46–69. (doi:10.1016/j.landurbplan.2004.08.007)
52. Duncan RP *et al.* 2011 Plant traits and extinction in urban areas: a meta-analysis of 11 cities. *Glob. Ecol. Biogeogr.* **20**, 509–519. (doi:10.1111/j.1466-8238.2010.00633.x)
53. Lonsdale WM. 1999 Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536. (doi:10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2)