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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 km²) has declined substantially:

Urbanization
for 110 cities. The lists encompass 36 countries on six continents

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species owing to habitat alteration and destruction may
biotic interchange and extinctions of indigenous native
of a similar suite of exotic species owing to human-mediated
systems [18], characterized by fragmented and disturbed
over time, across the world’s cities [13]. Cities are novel eco-
homogenization, or an increase in compositional similarity
biotic interchange, have been hypothesized to result in biotic
biodiversity at the global scale are lacking.

Despite recognition by the Convention on Biological Diver-
sity [9] of the importance of biodiversity in cities and a history
of urban ecology research [10–11], global-scale synthesises of
urban biodiversity are lacking [12]. A few studies have com-
pared the diversity of single taxa within cities across contin-
ents [13–16], but the majority of urban biodiversity research has focused on compositional patterns within individ-
ual cities. Generalities made on the effects of urbanization on
the patterns and drivers of species diversity have been primar-
ily based on studies of individual cities [17]. While it is clear
that urbanization changes the local biota, comprehensive ana-
lyses 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 eco-
systems [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 bio-
diversity and analyse the global consequences of urbanization
on biodiversity, we compiled urban bird species lists for 54

cities and city-wide florlas 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
1.8 \times 10^8), geographical areas (15–2787 km^2) and establish-
ment 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.

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 pre-
sent 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 Diver-
sity [9] of the importance of biodiversity in cities and a history
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for 110 cities. The lists encompass 36 countries on six continents

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) col-
lected 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 compre-
ensive 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 classi-
fied 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 km² for
each city using estimates of city area (see the electronic supple-
mental 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 elec-
tronic 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
cell area of 3091 km². 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 for 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 km². The density of non-urban plant and bird 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

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.
species of birds and plants within cities were examined by bio-

graphic realm [32] using Student’s t-tests. We examined

compositional similarity among cities using a hierarchical cluster

analysis and the β-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-anthropo-
genic 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 collinear-
ity [40]. We retained 10 predictors for analysis (see the electronic
supplementary material, tables S4 and S5) after they were
depicted in 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 ≤ 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 maxi-
mum 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 cor-
rection for small sample size (AICc) scores [41] were averaged
across runs. We ranked the eight models based on their AICc,
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 anthro-
pogenic 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 sfsmisc.

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 supplemen-
tary 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 bioge-
ographic 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 homog-
egenized 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 analise patterns of species abun-
dance, 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 simi-
lar 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 Zea-
land 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 commu-
nities 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 medula (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
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$^{-2}$ (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$^{-2}$ was found in these cities for native plants and 4.7 species km$^{-2}$ 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, which 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, $F_{1,4} = 14.4$, $p < 0.001$) and for native plant species (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].

![Figure 2](https://example.com/figure2.png)

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

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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, \( \Delta_i \) represents the difference between model \( i \) and the model with the lowest AIC score; AIC weight (\( w_i \)) is the level of evidence for model \( i \) based on the entire set of models; the model with the minimum AIC is shown in italics. Percentage predicted density was log-transformed before analysis.

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\( F_{1,4} = 15.5, p < 0.001 \) 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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