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Daniel Sol[1,2]*, Christopher Trisos[3,4]*, Cesc Múrria[5], Alienor Jeliazkov[6,7], Cesar González-Lagos[8,9], Alex L. Pigot[10], Carlo Ricotta[11], Christopher M. Swan[12], Joseph A. Tobias[13*], Sandrine Pavoine[14]*

Affiliations:

[1]CSIC, Spanish National Research Council, CREAF-UAB, Catalonia 08193, Spain.
[2]CREAF, Centre for Ecological Research and Applied Forestries, Catalonia 08193, Spain.
[3]African Climate and Development Initiative (ACDI), University of Cape Town, South Africa.
[4]National Socio-Environmental Synthesis Center (SESYNC), University of Maryland, Annapolis, MD, USA.
[5]Grup de Recerca Freshwater Ecology, Hydrology and Management (FEHM) and Institut de Recerca de la Biodiversitat (IRBio), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Catalonia, Spain.
[6]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.
[7]Department of Computer Science, Martin Luther University Halle-Wittenberg, 06099 Halle (Salle), Germany
[8]Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Santiago, Chile.
[9]Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile.
[10]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, WC1E 6BT, UK.
[11]Department of Environmental Biology, University of Rome 'La Sapienza', 00185 Roma, Italy.
[12]University of Maryland Baltimore County, Baltimore, Maryland, USA.
[13]Department of Life Sciences, Imperial College London, Berkshire SL5 7PY, UK.
[14]Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, 75005 Paris, France.

*To whom correspondence should be addressed: Daniel Sol: d.sol@creaf.uab.cat; Christopher Trisos: christophertrisos@gmail.com; Joseph A. Tobias: j.tobias@imperial.ac.uk; Sandrine Pavoine: sandrine.pavoine@mnhn.fr

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Name and complete mailing address of the person to whom correspondence should be sent: Daniel Sol, CREAF-CSIC, Cerdanyola del Vallès, Catalonia E-08193, Spain. TEL: +34 93-5814678. E-MAIL: d.sol@creaf.uab.cat

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Abstract. Urbanisation is driving rapid declines in species richness and abundance worldwide, but the general implications for ecosystem function and services remain poorly understood. Here, we integrate global data on bird communities with comprehensive information on traits associated with ecological processes to show that assemblages in highly urbanised environments have substantially different functional composition and 20% less functional diversity on average than surrounding natural habitats. These changes occur without significant decreases in functional dissimilarity between species; instead, they are caused by a decrease in species richness and abundance evenness, leading to declines in functional redundancy. The reconfiguration and decline of native functional diversity in cities are not compensated by the presence of exotic species but are less severe under moderate levels of urbanisation. Thus, urbanisation has substantial negative impacts on functional diversity, potentially resulting in impaired provision of ecosystem services, but these impacts can be reduced by less intensive urbanisation practices.

Urban expansion is a major driver of land-use change, with a projected increase in urban land cover of 1.2 million km^2 by 2030 (Seto *et al.* 2012). The process of urbanisation is an extreme form of land-use intensification causing a reduction and fragmentation of natural habitats, along with profound changes in human disturbance and resource availability (McKinney 2002). Because such rapid and extreme environmental alterations can cause local extinction (Bell 2017), it follows that species richness in cities is often lower than in surrounding natural habitats (Aronson *et al.* 2014; Sol *et al.* 2014; Ibáñez-Álamo *et al.* 2017). Species loss is a concern because it can alter the stability and functioning of ecosystems (Oliver *et al.* 2015), with negative consequences for ecosystem services and human wellbeing (Díaz *et al.* 2006; Cardinale *et al.* 2012). However, previous global analyses of the consequences of urbanisation have focused primarily on quantifying species loss rather than estimating its broader impacts on ecosystem functions (Díaz & Cabido 2001; Díaz *et al.* 2011). With over half the human population currently living in urban areas (United Nations 2018) and benefiting directly from urban nature (Millenium Ecosystem Assessment 2010; Cardinale *et*

al. 2012), there is an urgent need for improved understanding of how urbanisation affects components of biodiversity linked to ecosystem functions and services.

A major obstacle in addressing this challenge arises because the functional effects of species loss are difficult to quantify in natural systems, particularly at large scales (Winfree *et al.* 2015). Several factors complicate the issue, including species niche overlap**,** non-random species extinctions, and the tendency for a few abundant species to dominate the community (Flynn *et al.* 2009; Winfree *et al.* 2015). High overlap among niches increases functional redundancy, theoretically reducing the impact of species loss on ecosystem function, whereas the extinction of even a few species disproportionately contributing to function can substantially alter ecosystem functioning in communities with low functional redundancy (Flynn *et al.* 2009; Winfree *et al.* 2015). Asymmetries in abundance can also weaken the effect of extinctions because the loss of rare species may have little immediate impact on ecosystem functions and services (Winfree *et al.* 2015).

Perhaps the most tractable way of quantifying ecosystem functions delivered by biodiversity at global scales is to look beyond species loss and to focus instead on functional diversity—i.e. the identity, variety and relative abundance of phenotypic traits of organisms that influence key ecosystem processes (Tilman 2001; Petchey & Gaston 2002; Díaz *et al.* 2007). Evidence is accumulating that species richness provides at best a crude estimate of ecosystem function, resilience and stability, which are instead more closely related to metrics of functional diversity (Hooper et al. 2005; Díaz et al. 2006; Flynn et al. 2011). Recent studies applying these metrics have taken significant steps forward in assessing the ecosystem consequences of urbanisation (Oliveira Hagen *et al.* 2017; La Sorte *et al.* 2018). However, progress has been limited because data on functional traits related to ecosystem roles is often highly incomplete at global scales (Tobias & Pigot 2019). Widespread gaps in data, and the use of broad categorical traits (e.g. diet), weaken previous analyses by reducing sample sizes, introducing biases, and over-estimating functional redundancy. In addition, the use of geographical range polygons to estimate local communities tends to underestimate changes in functional diversity with urbanisation (Oliveira Hagen *et al.* 2017) and, more importantly, offers little insight into the drivers and wider implications of those impacts.

Here, we present a worldwide assessment of changes in avian functional diversity across the urban–wildland gradient. Birds—the largest class of tetrapod vertebrates—are a useful system for assessing impacts of environmental change on ecosystem function because they are relatively easy to survey and offer a suite of measurable traits (e.g. wing and beak shape) with an established link to ecological or trophic processes (Pigot *et al.* 2016a, 2019). In addition, birds are a conspicuous component of biodiversity in most regions and play an essential role in key ecological processes, including seed dispersal, pollination, pest control, nutrient cycling and scavenging (Lundberg & Moberg 2003; Sekercioglu 2006; Pigot *et al.* 2016a; Sekercioglu *et al.* 2016). Importantly, the functional traits underpinning these processes have recently been comprehensively measured in birds (Pigot *et al.* 2019; Tobias & Pigot 2019), enabling the characterisation of entire assemblages at unparalleled scope and resolution.

Following previous studies (Newbold et al. 2015; Oliveira Hagen et al. 2017; Sol et al. 2017), we adopt a space-for-time substitution approach with the diversity inside each city compared with the diversity in the surrounding non-urbanised habitats. The space-for-time approach provides a standard alternative when time-series data are unavailable (Winfree *et al.* 2011; Blois *et al.* 2013; Oliveira Hagen *et al.* 2017; but see Damgaard 2019). Within cities, we distinguish three levels of land-use intensity: highly urbanised environments (e.g. city centres), moderately urbanised environments (e.g. suburbs), and little urbanised environments (e.g. urban parks). Outside cities, we classify habitats as either rural (i.e. human-modified) or natural vegetation. Finally, we combine habitat-specific bird community data with complete species-level ecological trait data. For each species we use a set of 47 traits, including morphological measurements and foraging behaviour, to capture variation in how species interact with and contribute to ecosystem functioning (see Materials and Methods).

To evaluate changes in functional diversity across the urban–wildland gradient, we use Rao's quadratic entropy framework (Shimatani 2001; Zoltan 2005; Pavoine 2012; Ricotta *et al.* 2016). Functional quadratic entropy (Q_f) represents the expected dissimilarity between two individuals randomly drawn from the community. The quadratic entropy framework represents an advance from previous studies of urbanisation in that it captures the different facets of

functional diversity—trait identity, variety and abundance—while accounting for the confounding effect of species richness (Ricotta *et al.* 2016). Furthermore, by effectively partitioning the contribution of these different components to functional diversity (Shimatani 2001), the framework enables a more detailed exploration of how and why functional diversity changes with urbanisation.

Materials and Methods

Survey data. We gathered presence/absence and abundance data from published studies and reports for well-characterized assemblages spanning cities and surrounding habitats from Africa, Australia, Europe, North America and South America (**Fig. 1a**). We restricted the analyses to cases where comparable local survey data were available within urban habitats and in nearby rural and/or natural habitats. The final dataset contained almost 10,000 records of bird species from 319 local assemblages distributed across 50 regions. Species abundance per unit area or unit time were available for 269 of these assemblages, spanning 42 cities. Of the 1507 bird species detected during the surveys, 66 were exotic (invasive or non-native species) in at least one study region (**Appendix 1**). Following Newbold et al. (2015), we used published habitat descriptions to classify each assemblage into three categories reflecting the intensity of human use in urban habitats **(Table S1)**: (1) highly urbanised environments (HUR) mainly contain densely packed buildings with vegetation scarce or absent; (2) moderately urbanised environments (MUR) are residential areas with single-family houses and associated gardens (Marzluff 2001); and (3) little-urbanised environments (LUR) have few buildings and abundant vegetation (e.g. urban parks). The habitats outside the city were assigned to either natural vegetation (NVG) or rural habitat (RUR) based on the description of the habitat given in the source paper (for justification see Sol *et al.* 2014, 2017). Standardised survey methods were used across habitats within each region, although not always with the same sampling effort **(Table S1)**. Some abundance metrics—those not reported as densities per unit time, distance, area or volume sampled—were sensitive to sampling effort (Newbold *et al.* 2015). In these cases, we estimated effort-corrected abundance values by dividing the abundance measurement by sampling

effort (Newbold *et al.* 2015). To ensure that communities were accurately sampled and unbiased across land use types, we used sample-size-based rarefaction curves and estimated species richness after rarefaction to the median observed community size.

Functional traits. To describe major axes of niche variation across our sample of 1488 bird species, we compiled comprehensive datasets of two types of traits **(Table S2)**. First, we used data from Pigot et al. (2019) on eight morphological traits measured with callipers from museum specimens (**Appendix 2**). The traits include beak length, depth and width (to describe major axes of variation in beak morphology, the primary resource related trait in birds), wing length and first secondary feather length (to describe variation in wing shape, related to flight strength and dispersal ability), tarsus length and tail length (related to microhabitat and foraging substrate) and body size (related to energetic constraints, competitive ability and pace of life)(Cannon *et al.* 2019). In addition, we used the length of the wing and first secondary feather to estimate the hand-wing index (Claramunt *et al.* 2012). Together, these traits have previously been shown to provide an accurate index of avian trophic niches (Pigot *et al.* 2019). All morphological variables were log-transformed before analyses. Second, we compiled published data describing both foraging niche and dietary niche for all study species (Pigot *et al.* 2019; **Appendix 3**). We did this because although morphology accounts for substantial variation in the avian niche (Pigot *et al.* 2016b, 2019), the functional role of a species in an ecosystem may be more directly inferred by how the species uses resources (Petchey & Gaston 2006; Oliveira Hagen *et al.* 2017). For instance, species that primarily rely on fruits are expected to play roles in seed dispersal whereas those that eat insects should contribute to invertebrate control (Chan *et al.* 2016). Extending the simplified behavioural classification presented for all birds by Tobias & Pigot (2019), we classified species according to the proportional use of 30 different foraging behaviours across eight dietary categories (**Table S2**), providing insights into the trophic structure of communities at an unprecedented resolution. To further interpret some of the results, we used a simplified version focused on the dietary niche (**Table S2**). To describe major axes of variation in morphology, we used the two-step principal component analysis (PCA) process proposed by Trisos et al.

(2014), while variation in dietary and foraging niches were obtained by means of a Principal Coordinates Analysis (PCoA), based on Manly distances (Manly 1986). Results of these ordination analyses are shown in **Table S3.**

Functional diversity. We compared avian diversity across land-use categories with a space-for-time substitution approach using Rao's quadratic entropy (*Q*) to estimate functional diversity for each assemblage. Mathematically, this is expressed as:

$$Q_f = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j$$

where d_{ij} is the functional dissimilarity between the *i*-th and *j*-th species bounded between 0 and 1, p_i and p_j are their respective relative abundances, and *s* is the number of species. Our functional diversity metrics were based on Euclidean distances for morphology and Manly distances for foraging niche, in both cases standardised by dividing by the maximum distance across the whole species dataset. Rao's quadratic entropy was estimated on relative abundance data. We obtained relative abundance by dividing the abundance of a species in an assemblage by the sum of all individuals in the assemblage, including exotic species when present.

Decomposition of *Q*. Following Shimatani (2001), quadratic entropy was decomposed into three components (**Fig. 2a**): (1) the Gini-Simpson index $H_{GS} = 1 - \sum_i p_i^2$, where p_i is the relative abundance of species *i*; (2) the average dissimilarity between two species $meanD = \left(\sum_{ij} d_{ij}\right) / \left(S \times (S-1)\right)$, where *S* is the number of species and d_{ij} the functional difference between species *i* and *j*; and (3) a balance component describing the covariance between species' abundance and the functional dissimilarities between species (BC), such as $Q = H_{GS} * meanD + BC$. To facilitate interpretation, we transformed BC to a correlation coefficient. To further interpret the results, we also estimated: (4) the abundance evenness index (I_e) independent of species richness (*N*) as $I_e = H_{GS} * S/(S-1)$; (5) community-level functional redundancies as $1 - Q/H_{GS}$ (Ricotta *et al.* 2016); and (6) species-level functional uniqueness, as the mean functional dissimilarity of a species from the

rest of the species in the region (Ricotta *et al.* 2016; Pavoine *et al.* 2017). These metrics were estimated with the R-package adiv (Pavoine 2018) and our own R code, available upon request.

Functional ß-diversity. Functional ß-diversity was estimated using the decomposition of Rao's quadratic entropy index (following Ricotta & Szeidl 2009) and the betaQmult function developed by Villéger et al. (2012). To estimate the influence of species identities (taxonomy) and the contribution of the turnover and nestedness components on the overall functional ß-diversity, we also estimated a multidimensional functional space for the morphological and foraging traits using, respectively, the PCA and PCoA axes (Villéger *et al.* 2012). The pairwise ß-diversity in functional composition between communities was estimated using Jaccard's dissimilarity index which can be decomposed into the functional turnover and nestedness, as implemented in 'betapart' (Baselga & Orme 2012). Strict turnover corresponds to replacement of trait composition while the functional richness remains constant, whereas nestedness corresponds to subsetting in trait composition due to a non-random gain or loss of traits (Baselga 2010).

Analysis of biodiversity changes across land use gradients. Variation in *Q* and the suite of metrics were modelled as a function of habitat by means of linear mixed models, using the R-packages 'nlme' (Pinheiro *et al.* 2014) and 'lme4' (Bates *et al.* 2015). The response variables were continuous and normally distributed so we used models with a Gaussian structure of errors. To cope with spatial autocorrelation, we used a model selection approach based on AIC to define the best structure of random factors and spatial correlation (i.e. spherical, exponential, gaussian, linear, and rational derived from geographic coordinates) for all linear mixed-effects models. The variance component parameters were estimated by restricted maximum likelihood (REML) with habitat as a fixed effect. We built the final models using the best structures, including either region or region nested within country as random factors, which adequately removed spatial autocorrelation of all response variables (see examples in **Fig. S1**). We conducted multiple statistical tests across habitat categories within each model, so we adjusted p-values for false discovery rates (Benjamini & Hochberg 1995).

Because we fitted different random intercepts for each study region, the results presented in figures are adjusted means and standard errors (ES) derived from the models.

Model checking. All models were checked for normality and homogeneity of variance by visual inspection of residuals. The main models were further validated by excluding potential outliers. To identify outliers, we used the Tukey method based on interquartile range. With some exceptions (<10% of data), the observed values of species richness and Gini-Simpson index were close to the extrapolated asymptotic value (see above), indicating good accuracy.

Functional uniqueness and tolerance to urbanisation. Following Sol et al. (2014, 2017), we used Gaussian phylogenetic mixed model to assess how functional uniqueness of species—measured either as morphological or foraging niche originality (Ricotta *et al.* 2016)—affects their tolerance to urbanisation (response variable). Tolerance to urbanisation was measured as the log-log difference in the number of individuals of a species recorded between the most intensively modified habitat and nearby natural habitat (Sol *et al.* 2017). Negative values indicate low species tolerance to urbanisation. We included phylogeny (extracted from www.BirdTree.org; Jetz *et al.* 2012) and region as random factors in the models. Fixed and random effects were estimated by means of a Bayesian approximation, as implemented in the R-package 'MCMCglmm' (Hadfield 2010). To facilitate model convergence, we used inverse-Gamma distribution priors for random effects, and ran the model twice with different starting values, sampling 1000 iterations from a total of 101000.

Functional traits and tolerance to urbanisation. We assessed the extent to which functional traits predict the tolerance of species to urbanisation with a Random Forests (RF) approach using the package randomForest (Liaw & Wiener 2002). RF is a machine-learning algorithm that can efficiently analyse many predictors simultaneously and account for interactions (Brieuc *et al.* 2018). In addition, we also modelled presence/absence of species in the intensively

urbanised environment and, if present, their relative abundance in the assemblage. Species were considered to occur in intensively urbanised habitat if detected there in at least one study region. We used regression-based trees for tolerance and abundance, calculating mean abundance when a species was present in more than one city. We included relative abundance and all functional traits as predictors in the model, either independently or as part of axes derived from PCAs (morphological traits) or PCoAs (foraging traits). We assessed the predictive power of models by estimating the proportion of variance in the out-of-bag response variable explained by the model (PVE). We used a similar approach to model the presence/absence of species in highly urbanised habitat, except that in this case we used classification-based trees instead of regression trees. We assessed the predictive power of this model by estimating the misclassification of out-of-bag samples (error rate) when using the model (OOB-ER). Following the randomForest protocol suggested by Brieuc et al. (2018), we first optimized the mtry parameter (number of predictors to be randomly sampled at each node in a tree). We then used the optima of each metric to run 2000 trees twice, and compared the stability of the results (correlation > 0.97 in all cases). Following model convergence, PVE and OOB-ER were taken from last tree in the forest.

Results and Discussion

We found that morphological diversity—quantified as the functional quadratic entropy of morphology (Q_m)—is significantly lower in moderate and highly urbanised habitats than in natural vegetation, but is maintained in rural areas and little urbanised habitats such as urban parks (**Fig. 1b)**. The mean reduction in Q_m compared to surrounding natural vegetation is 12% for moderate and 20% for highly urbanised habitats, with losses as high as 60% in extreme cases (**Fig. 1d,e)**.

Although morphology accounts for substantial variation in the avian niche (Pigot *et al.* 2016b, 2019), the functional role of a species might be more directly inferred by how species use resources (Petchey & Gaston 2006; Oliveira Hagen *et al.* 2017). We therefore repeated the analyses with our comprehensive dietary and behavioural classifications of species, which enabled the characterisation of their foraging niches at an unprecedented resolution. We found that functional quadratic entropy of foraging niches (Q_{forag}) is maintained in rural and moderately urbanised habitat compared to surrounding natural vegetation and even increases

in little urbanised habitat (**Fig. 1c**). In contrast, Q_{forag} tends to be lower in highly urbanised habitats than in natural vegetation, with a mean decline of 19% (**Fig. 1c,f,g**). Thus, both morphological and behavioural components of diversity show a clear trend of greater losses of functional diversity in highly urbanised areas.

The loss of functional diversity in response to urbanisation may reflect the local extinction of functionally unique species, particularly those occupying foraging niches that are not available in highly altered urban habitats. This explanation, however, appears unlikely for two reasons. First, we find no evidence that tolerance to urbanisation, measured as change in abundance between highly urbanised habitat and surrounding natural vegetation in each region (Evans et al. 2011; Sol et al. 2017), is lower in functionally unique species (**Table S4)**. Second, highly urbanised habitats —and, to a lesser extent, moderately urbanised areas— are characterised by lower community-level functional redundancy (i.e., they contain fewer individuals with similar functional traits) compared to natural habitats (**Fig. S2**), a pattern particularly noticeably when using high resolution data (i.e. foraging niche information). Thus, the loss of functional diversity in highly urbanised habitats occurs despite a decrease in functional redundancy.

To explain these seemingly contrasting results, we decomposed functional quadratic entropy for morphology and foraging niche into its three components (Shimatani 2001): The Gini-Simpson index (probability that two individuals randomly selected from an assemblage belong to different species), the *mean D* (unweighted mean functional dissimilarity between species), and the balance component (covariance between species' abundance and their functional dissimilarities). The decomposition of Q_f into these underlying components allowed us to pinpoint why functional diversity declines in urbanised habitats (**Fig. 2a**). If the declines reflected environmental filtering, whereby species with particular traits decline or are lost first when an area is urbanised (Díaz & Cabido 2001; Oliveira Hagen *et al.* 2017; La Sorte *et al.* 2018), we would expect a significant decrease in functional dissimilarity between species across the urbanisation gradient. Instead, we found that decreases of functional diversity in highly urbanised areas occur without significant decreases in functional dissimilarity between species (**Fig. 2b,c**). In fact, the mean functional dissimilarity between species (*mean D*) in highly urbanised habitats is even higher than in rural areas (**Fig. S3**; see also Oliveira Hagen *et al.* 2017). These results do

not contradict the existence of adaptive traits that provide tolerance to urbanisation (Evans *et al.* 2011; Sol *et al.* 2014) because the functional traits we use were selected primarily to reflect species functional roles in ecosystems rather than their responses to environmental change (Suding *et al.* 2008). Indeed, we find that species tolerance to urbanisation is only weakly related to their position in morphological and behavioural space (**Fig. S4**). This implies that species with similar ecosystem functions may differ in their responses to urbanisation (Flynn *et al.* 2009). A dissociation between effect and response traits is an important ecosystem property because it decouples species responses to environmental change from their effects on function, which increases ecosystem resilience (Lawton & Brown 1994; Oliver *et al.* 2015). However, the decrease in functional redundancy we detect in urbanised areas suggests that this 'insurance effect' is impaired, potentially reducing the stability of intensively urbanised ecosystems.

Rather than a decrease in functional dissimilarity between species, the low Q_f of urbanised areas is better explained by a decrease in the Gini-Simpson index (**Figs. 2b-c**, **S3, S5**). On average, the probability of observing two individuals from different species by chance is 17% lower in highly urbanised areas than in the surrounding natural vegetation and rural habitats. One reason is that urbanised areas contain fewer species (**Fig. 3a,b**), a pattern well documented in previous studies (Sol *et al.* 2014). However, species loss alone does not account for the decline in the Gini-Simpson index. Abundance evenness among species—another component of this index—also decreases with urbanisation (**Fig. 3c**), indicating that highly urbanised regions (and those moderately urbanised, to a lesser extent) are frequently dominated by a small number of highly abundant species (**Fig. 3d**). These dominant species tend not to be functionally unique, as indicated by the low values of the balance components (**Fig. 2b,c**), so their relative contribution to functional diversity is generally low. Thus, the loss of functional diversity in moderately and highly urbanised environments relative to surrounding natural and rural habitats reflects a decrease in both species richness and abundance evenness. However, decreases in species richness are lower in moderately urbanised areas (Fig.1c; Fig. 3), which help to explain the less pronounced loss of functional diversity. In little urbanised habitats, the decrease in species richness is similar to that observed for moderately urbanised habitats, but abundance evenness is maintained compared to surrounding rural and natural vegetation. Thus,

functional diversity is highly preserved compared to highly and moderately urbanised areas.

In addition to causing net changes in functional diversity, urbanisation has the potential to reconfigure the functional composition of communities if species with particular sets of traits are replaced by species with different sets of traits more tolerant to the new environmental conditions (Loreau *et al.* 2001). There is substantial turnover in species composition between natural vegetation and urbanised habitats (**Fig. 4a)**, with urban species representing a subset of adaptable lineages drawn from a variety of natural and artificial habitats (Shochat *et al.* 2006; Sol *et al.* 2017). Functional ß-diversity is also particularly high between natural and highly urbanised habitats (**Fig. S6**) but, unlike species composition, this is mainly driven by functional nestedness rather than turnover (**Fig. 4b,c,d**). The contrasting patterns between taxonomic and functional ß-diversities suggest that urban specialists generally play similar functional roles to species that they replace, implying again that the higher functional uniqueness of urban habitats compared to natural habitats primarily arises from the loss of functionally redundant species.

The analysis of multiple morphological and foraging niche features also reveals shifts in the abundance-weighted mean community value of key functional traits (**Fig. S7**). For instance, compared to natural areas, highly urbanised areas exhibit a small but significant tendency to be dominated by larger bodied individuals. This makes sense given that small-bodied species tend to be more abundant in natural habitats than larger species (White *et al.* 2007), whereas in highly urbanised environments the trend is reversed due to the relative abundance of a few large-bodied birds such as pigeons, gulls and crows (**Fig. S8**). Our analysis also reveals changes in highly urbanised assemblages along a number of other functional dimensions, with an over-representation of individuals from species with higher tarsus-to-tail-length ratio, more pointed wings, and more granivorous diets, as well as a marked decline of individuals foraging on fruits or invertebrates, particularly within specific foraging strategies (**Fig. S7**). Similar changes are also observed in little and moderately urbanised habitats, most notably in body size and shape, although these changes tend to be less frequent and of lower magnitude for other functional dimensions compared with highly urbanised habitats (**Fig. S7**). Again, these functional shifts are not only caused by

the loss of species but also by domination of urban environments by a small number of highly abundant species (**Fig. S8**). We also show that functional shifts are remarkably consistent across regions, likely because the species that best tolerate urbanisation—and hence become dominant in the community—tend to belong to a few avian lineages (Sol *et al.* 2014, 2017).

Our conclusion that functional diversity declines in highly urbanised areas contrasts with the observation by Oliveira Hagen et al. (2017) that functional diversity of urban avian assemblages is not consistently different from that of non-urban assemblages. These discrepancies probably reflect methodological differences in the scale of analysis and the metrics used to estimate functional diversity. Oliveira Hagen et al. (2017) used global data of species occurrence in urban and non-urban avian assemblages located across the globe. While this analysis provides realistic assessments of the overall importance of cities as reservoirs of biodiversity, cities are in fact mosaics of habitats reflecting different degrees of urbanisation. Greater habitat diversity within cities compared to semi-natural areas dominated by a single habitat may thus under-estimate the real impact of urbanisation, particularly in its most intensive forms. In addition, the decline of functional diversity that we detected in highly urbanised areas was mainly driven by changes in species abundance. This suggests that restricting the analyses to species occurrences may be insufficient to detect changes in functional diversity across urbanisation gradients.

Nevertheless, one possible caveat to our analyses is that we ignored the potential impact of exotic species, which tend to be more successful in human-altered habitats (Case 1996; Aronson *et al.* 2014; Cadotte *et al.* 2017) and thus could partially compensate for the loss of native biodiversity in delivering ecosystem functions (Hobbs & Mooney 1998; Sax & Gaines 2008). Exotics could even enhance functional diversity if they play functional roles that are unique in the ecosystem (Oliveira Hagen *et al.* 2017). However, when we re-ran our analyses with exotic species included, this did not alter the conclusion that urban areas generally support lower functional diversity than natural habitats (**Fig. 5**). Therefore, the tendency of exotic species to proliferate in cities does not compensate for the loss of native functional diversity in most urban environments.

A separate potential limitation of our analyses is that sampling is mostly based on highly industrialised regions and hence our findings may not apply to

less industrialized contexts. We tackled this limitation using spatially explicit analyses (**Fig. S1**), which do not alter our general conclusions about the impacts of urbanisation on functional diversity. Nonetheless, given the current geographical bias in studies of urbanisation (**Fig. 1**), there is particular need for more research in developing countries.

Conclusions

Current human population projections estimate that 68% of people will live in urban areas by 2050 (United Nations 2018), making the functioning and stability of urban ecosystems ever more central to human well-being. As functional diversity is crucial for the long-term provisioning of ecosystem services (Díaz & Cabido 2001; Cardinale *et al.* 2012; Pigot *et al.* 2016a), our finding that urbanisation significantly reduces functional diversity—with declines up to 60% in the worst cases—should raise considerable concern.

A potential risk is that the loss of avian functional diversity and redundancy may impair and destabilise certain ecosystem functions and the delivery of ecosystem services in urbanised areas, with more idiosyncratic outcomes dependent on the features of each particular city (Bregman et al. 2916; Oliveira Hagen et al. 2017). For instance, avian predation has been identified as a dominant force controlling arthropods on plants in some urban areas (Kozlov et al. 2017). Thus, an environment with fewer avian insectivores is unlikely to be able to deliver pest control services in case of pest outbreak or invasion/infestation by different types of invertebrate (Sekercioglu et al. 2016). Likewise, loss of diversity of seed dispersers means that seed dispersal efficiency across and into urban environments may be impaired (Caughlin et al. 2012). The absence of animal pollinators in urban areas have indeed been shown to favour wind-pollinated plants, potentially leading to declines in many endozoochrous (animal-dispersed) plant species (Lososová et al., 2006). However, the exact implications of changes in functional diversity for human well-being in cities requires further understanding of how functional traits relate to both ecosystem functions and the needs of different sectors of society (Díaz et al. 2011). The loss of certain ecosystem services such as seed dispersal, pest control, or carrion removal may not be so critical if they can be sourced from near-by surrounding

habitats or replaced by humans—although this can be costly (Hougner *et al.* 2006).

Although the relationship between changes in avian functional diversity and the delivery of ecosystem services in urban areas is complex, our analyses highlight that the consequences should be lower in less intensively urbanised habitats, such as those containing urban parkland, where functional diversity appears to be maintained at close to natural levels. Our findings thus align with recent claims (Frishkoff *et al.* 2014; Oliveira Hagen *et al.* 2017) suggesting that the maintenance of avian functional diversity and thus critical ecosystem functions and services is achievable with forward-looking policies and concerted actions to reduce the intensity of urbanisation.

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References

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., *et al.* (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc R Soc B*, 281, 20133330.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr*, 19, 134–143.

Baselga, A. & Orme, C.D.L. (2012). Betapart: an R package for the study of beta diversity. *Methods Ecol Evol*, 3, 808–812.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects

Models Using lme4. *J Stat Softw*, 67: 1-48.
Bell, G. (2017). Evolutionary Rescue. *Annu Rev Ecol Evol Syst*, 48, 605–627.
Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc B*, 57, 289–300.
Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T. & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proc Natl Acad Sci*, 110, 9374–9379.
Bregman, T.P., Lees, A.C., MacGregor, H.E.A., Darski, B., de Moura, N.G., Aleixo, A., *et al.* (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc R Soc B Biol Sci*, 283, 20161289.
Brieuc, M.S.O.O., Waters, C.D., Drinan, D.P. & Naish, K.A. (2018). A practical introduction to random forest for genetic association studies in ecology and evolution. *Mol Ecol Resour*, 18, 755–766.
Cadotte, M.W., Yasui, S.L.E., Livingstone, S. & MacIvor, J.S. (2017). Are urban systems beneficial, detrimental, or indifferent for biological invasion? *Biol Invasions*, 19, 3489–3503.
Cannon, P.G., Gilroy, J.J., Tobias, J.A., Anderson, A., Haugaasen, T. & Edwards, D.P. (2019). Land-sparing agriculture sustains higher levels of avian functional diversity than land sharing. *Glob Chang Biol*. 25, 1576–1590.
Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
Case, T.J. (1996). Global patterns in the establishment and distribution of exotic birds. *Biol Conserv*, 78, 69–96.
Caughlin, T., Wheeler, J.H., Jankowski, J. & Lichstein, J.W. (2012). Urbanized landscapes favored by fig-eating birds increase invasive but not native juvenile strangler fig abundance. *Ecology*, 93, 1571–1580.
Chan, K.M.A., Balvanera, P., Benessaiah, K., Chapman, M., Díaz, S., Gómez-Baggethun, E., *et al.* (2016). Why protect nature? Rethinking values and the environment. *Proc Natl Acad Sci USA*, 113, 1462–1465.
Claramunt, S., Derryberry, E.P., Remsen, J. V. & Brumfield, R.T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc R Soc B Biol Sci*, 279, 1567–1574.
Damgaard, C. (2019). A Critique of the Space-for-Time Substitution Practice in Community Ecology. *Trends Ecol Evol*, 34, 416–421.
Díaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol*, 16, 646–655.
Díaz, S., Fargione, J., Chapin, F.S. & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biol*, 4, 1300–1305.
Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci USA*, 104, 20684–20689.
Díaz, S., Quetier, F., Caceres, D.M., Trainor, S.F., Perez-Harguindeguy, N., Bret-Harte, M.S., *et al.* (2011). Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. *Proc Natl Acad Sci USA*, 108, 895–902.
Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D. & Gaston, K.J. (2011). What makes an urban bird? *Glob Chang Biol*, 17, 32–44.
Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., *et al.* (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecol Lett*, 12, 22–33.
Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity--ecosystem-function relationships. *Ecology*, 92, 1573–1581.

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Hadly, E.A., Daily, G.C., Mendenhall, C.D., *et al.* (2014). Loss of avian phylogenetic diversity in neotropical agricutural systems. *Science*, 345, 1343–1346.

Hadfield, J.D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *J Stat Softw*, 33, 1–22.

Hobbs, R.J. & Mooney, H.A. (1998). Broadening the Extinction Debate: Population Deletions and Additions in California and Western Australia. *Conserv Biol*. 12, 271–283.

Hooper, D.U., Chapin III, F.S. & Ewel, J.J. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr*, 75, 3–35.

Hougner, C., Colding, J. & Söderqvist, T. (2006). Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. *Ecol Econ*, 59, 364–374.

Ibáñez-Álamo, J.D., Rubio, E., Benedetti, Y. & Morelli, F. (2017). Global loss of avian evolutionary uniqueness in urban areas. *Glob Chang Biol*, 23, 2990–2998.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 542, 344-347.

Kozlov, M.V., Lanta, V., Zverev, V., Rainio, K., Kunavin, M.A. & Zvereva, E.L. (2017). Decreased losses of woody plant foliage to insects in large urban areas are explained by bird predation. Glob Change Biol, 23, 4354–64.

Lawton, J.H. & Brown, V.K. (1994). Redundancy in Ecosystems. In: *Biodiversity and Ecosystem Function* (eds. Schulze, E.-D. & Mooney, H.A.). Springer-Verlag, Berlin, pp. 255–270.

Liaw, A. & Wiener, M. (2002). Classification and Regression by randomForest. *R News*, 2, 18–22.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.* (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294, 804–808.

Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horáková, V., Pyšek, P., and Tichý, L. (2006). Patterns of plant traits in annual vegetation of man-made habitats in central Europe. Perspect. Plant Ecol. Evol. Syst., 8, 69–81.

Lundberg, J. & Moberg, F. (2003). Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management. *Ecosystems*, 6, 0087–0098.

Manly, B.F.J. (1986). *Multivariate Statistical Methods. A Primer. Chapman Hall London, New York.*

Marzluff, J.M. (2001). Worldwide urbanization and its effects on birds. In: *Avian Ecology and Conservation in an Urbanizing World (Marzluff J.M., Bowman R., Donnelly R., eds)*. Springer US, Boston, MA, pp. 19–47.

McKinney, M. (2002). Urbanization, biodiversity, and conservation. *Bioscience*, 52, 883–890.

Millenium Ecosystem Assessment. (2010). *Ecosystems and Human Well-Being: Biodiversity Synthesis*. Island Press, Washington.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

Oliveira Hagen, E., Hagen, O., Ibáñez-Álamo, J.D., Petchey, O.L. & Evans, K.L. (2017). Impacts of Urban Areas and Their Characteristics on Avian Functional Diversity. *Front Ecol Evol*, 5, 1–15.

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., *et al.* (2015). Biodiversity and resilience of ecosystem functions. *Trends Ecol Evol*, 30, 673–684.

Pavoine, S. (2012). Clarifying and developing analyses of biodiversity: towards a generalisation of current approaches. *Methods Ecol Evol*, 3, 509–518.

Pavoine, S. (2018). adiv: Analysis of Diversity. R package version 1.2. *https://CRAN.R-project.org/package=adiv*.

Pavoine, S., Bonsall, M.B., Dupaix, A., Jacob, U. & Ricotta, C. (2017). From phylogenetic to functional originality: Guide through indices and new developments. *Ecol Indic*, 82, 196–205.
Petchey, O.L. & Gaston, K.J. (2002). Extinction and the loss of functional diversity. *Proc R Soc B*, 269, 1721–1727.
Petchey, O.L. & Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecol Lett*, 9, 741–758.
Pigot, A.L., Bregman, T., Sheard, C., Daly, B., Etienne, R.S. & Tobias, J.A. (2016a). Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Proc R Soc B*, 283, 20161597.
Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T., Freeman, B., Seddon, N., et al. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. Nat Ecol Evol, 4, 230–239.
Pigot, A.L., Trisos, C.H. & Tobias, J.A. (2016b). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proc R Soc B*, 283, 1–9.
Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2014). *Package "nlme." R vignette*.
Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L. & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: a quantitative guide. *Methods Ecol Evol*, 7, 1386–1395.
Ricotta, C. & Szeidl, L. (2009). Diversity partitioning of Rao's quadratic entropy. *Theor Popul Biol*. 76, 299-302.
Sax, D.F. & Gaines, S.D. (2008). Species invasions and extinction: The future of native biodiversity on islands. *Proc Natl Acad Sci*, 105, 11490–11497.
Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol Evol*, 21, 464–471.
Sekercioglu, C.H., Wenny, D. & Whelan, C.J. (2016). *Why birds matter: Avian ecological function and ecosystem services*. University of Chicago Press, Chicago, USA.
Seto, K.C., Guneralp, B. & Hutyra, L.R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci USA*, 109, 16083–16088.
Shimatani, K. (2001). On the measurement of species diversity incorporating species differences. *Oikos*, 93, 135–147.
Shochat, E., Warren, P., Faeth, S., McIntyre, N. & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol*, 21, 186–191.
Sol, D., Bartomeus, I., González-Lagos, C. & Pavoine, S. (2017). Urbanisation and the loss of phylogenetic diversity in birds. *Ecol Lett*, 20, 721–729.
Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecol Lett*, 17, 942–950.
La Sorte, F.A., Lepczyk, C.A., Aronson, M.F.J., Goddard, M.A., Hedblom, M., Katti, M., *et al.* (2018). The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. *Divers Distrib*, 24, 928–938.
Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., *et al.* (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Glob Chang Biol*, 14, 1125–1140.
Tilman, D. (2001). Functional Diversity. *Encyclopedia of biodiversity*. Academic Press, San Diego.
Tobias, J.A. & Pigot, A.L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. *Phil Trans R Soc B*, 374, 20190012.
Trisos, C.H., Petchey, O.L. & Tobias, J.A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *Am Nat*, 184, 593–608.

United Nations. (2018). *World Urbanizaton Prospects*. New York, USA.
Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2012). Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. *PLoS One*, 7, e40679.
White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends Ecol Evol*, 22, 323–330.
Winfree, R., Bartomeus, I. & Cariveau, D.P. (2011). Native Pollinators in Anthropogenic Habitats. *Annu Rev Ecol Evol Syst*, 42, 1–22.
Winfree, R., Fox, J., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol Lett*, 18, 626–635.
Zoltan, B.-D. (2005). Rao' s quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci*, 16, 533–540.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure 1 Changes in functional diversity across urbanisation gradients worldwide. a, Geographic location of 50 focal cities in relation to United Nations human development index (HDI). b-c, Effects of urbanisation on functional diversity (quadratic entropy, Q), based on morphological traits (b) and foraging niche (c), expressed as effect size (mean ± SE). Habitat categories are arranged left-to-right with increasing intensity of urbanisation (NVG: natural vegetation; RUR: rural habitat; LUR: little-urbanised habitat; MUR: moderately urbanised habitat; HUR: highly urbanised habitat). Quadratic entropy was only calculated for surveys with information on species abundance (269 assemblages from 42 cities, comprising 1332 native species). Significant pairwise differences ($P < 0.05$) across habitats are indicated by different colours, shapes and letters on data points. Lower panels show frequency distribution of the percentage change of (d-e) morphological diversity (Q_{morph}) and (f-g) foraging niche diversity (Q_{forag}) in moderately urbanised (d, f) and highly urbanised (e, g) areas relative to natural vegetation across assemblages within study sites. Colour scales in panels d-g illustrate the progression from low (blue) to high (red) loss of functional diversity.

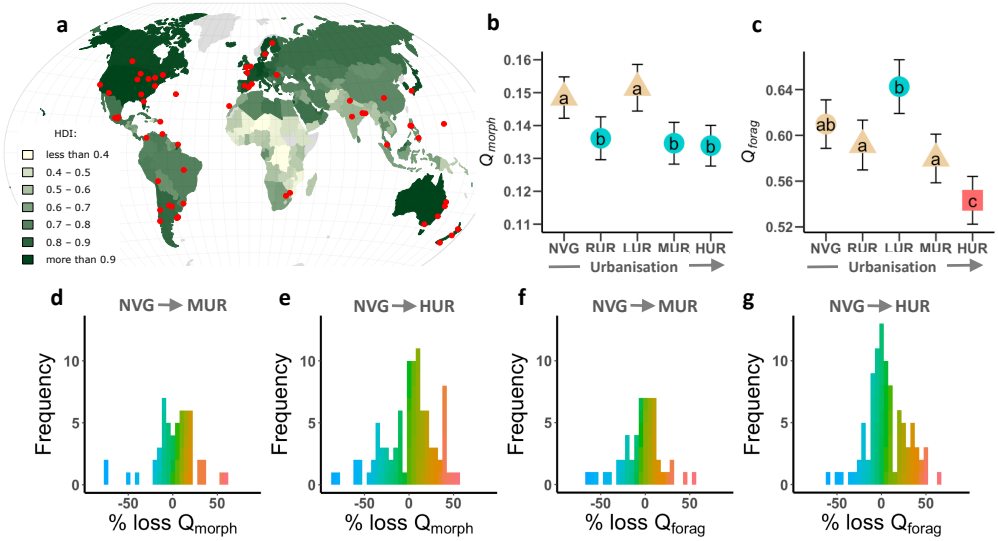


Figure 2 Decomposition of functional diversity across urbanisation gradients. Panel a illustrates the decomposition of functional quadratic entropy into the Gini-Simpson index (blue), unweighted mean functional dissimilarity (*mean D*, red) and balance component (orange). Panels b and c show variation across habitat types in Gini-Simpson index (blue bars), *mean D* (red bars), and the balance component (orange bars) for morphological traits (b) and foraging niche (c). Values represent adjusted means ± SE of the models shown in Fig. 1; habitats are coded as in Fig. 1. The Gini-Simpson index provides the best explanation for the loss of functional diversity in highly urbanised habitats (to assess habitat differences, see Fig. S3 in the Supporting Information section).

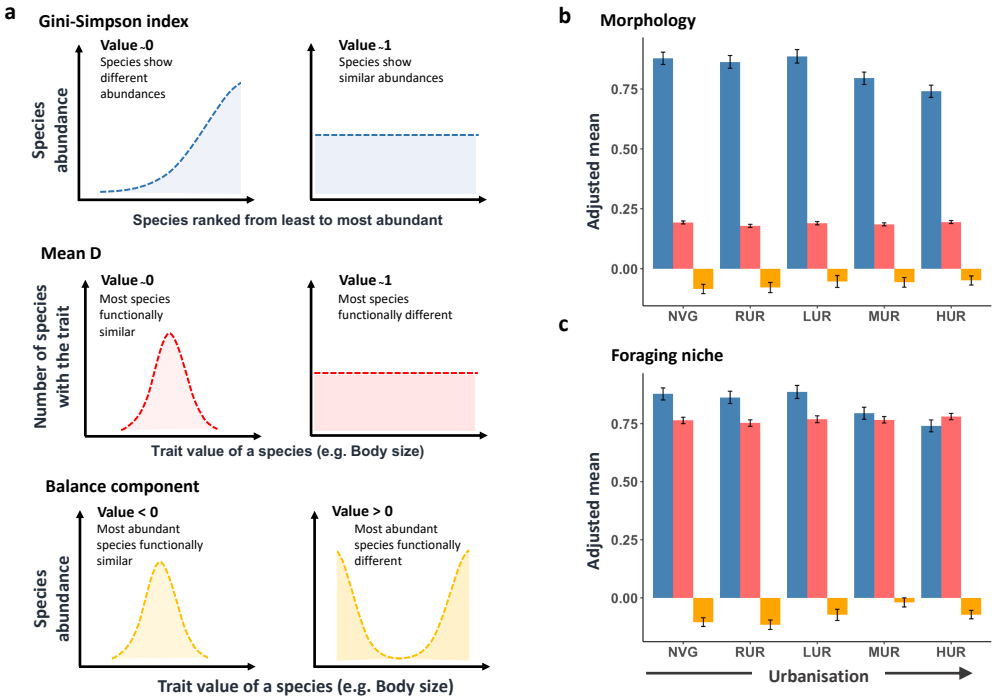


Figure 3 Changes in species richness and abundance along urbanisation gradients based on species richness (a), rarefied species richness (b), index of abundance evenness among species (c) and relative abundance of the single most abundant species (d). Values are adjusted means and standard errors derived from models. Plots c-d are based on the restricted dataset with information on species abundance (see Fig. 1), whereas data for plot b is further restricted to surveys with available information on the total number of individuals detected. Pairwise differences across habitats are indicated by differences in colours, shapes and letters, as in Fig. 1. NVG: natural vegetation; RUR: rural habitats; LUR: little-urbanised habitat; MUR: moderately urbanised habitats; HUR: highly urbanised habitat.

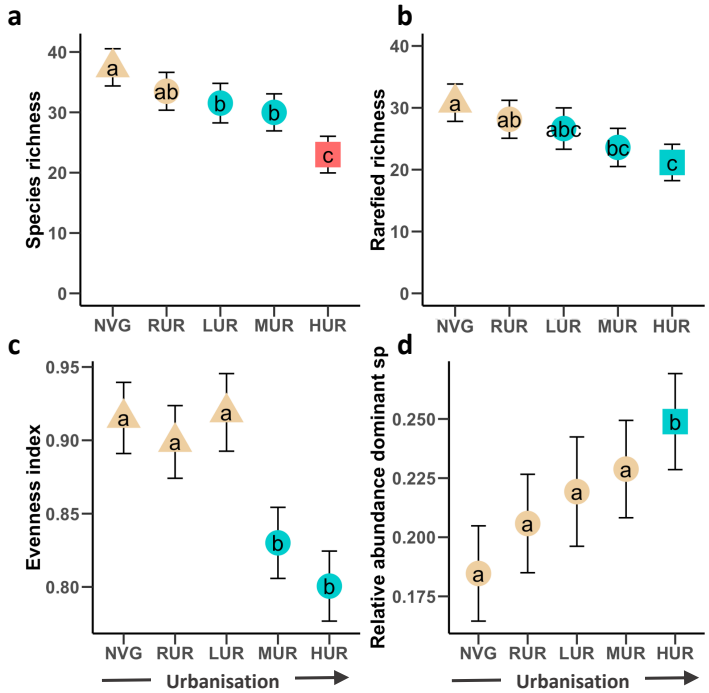


Figure 4 Changes in taxonomic and functional ß-diversity across urbanisation gradients. Estimates of taxonomic (a), morphological (b) and foraging (c) ß-diversity between urban and non-urban habitats (MUR: moderately urbanised; HUR: highly urbanised; NVG: natural vegetation. Overall ß-diversity (dark blue bars) are separated into nestedness (sky blue bars) and turn-over (light blue bars) based on Jaccard pair-wise dissimilarity. Values are adjusted means and standard errors derived from models. Panel d shows overlap in the functional space (represented by the first two axes of variation in foraging niche) for natural vegetation (blue) and highly urbanised (red) habitats in six representative study regions.

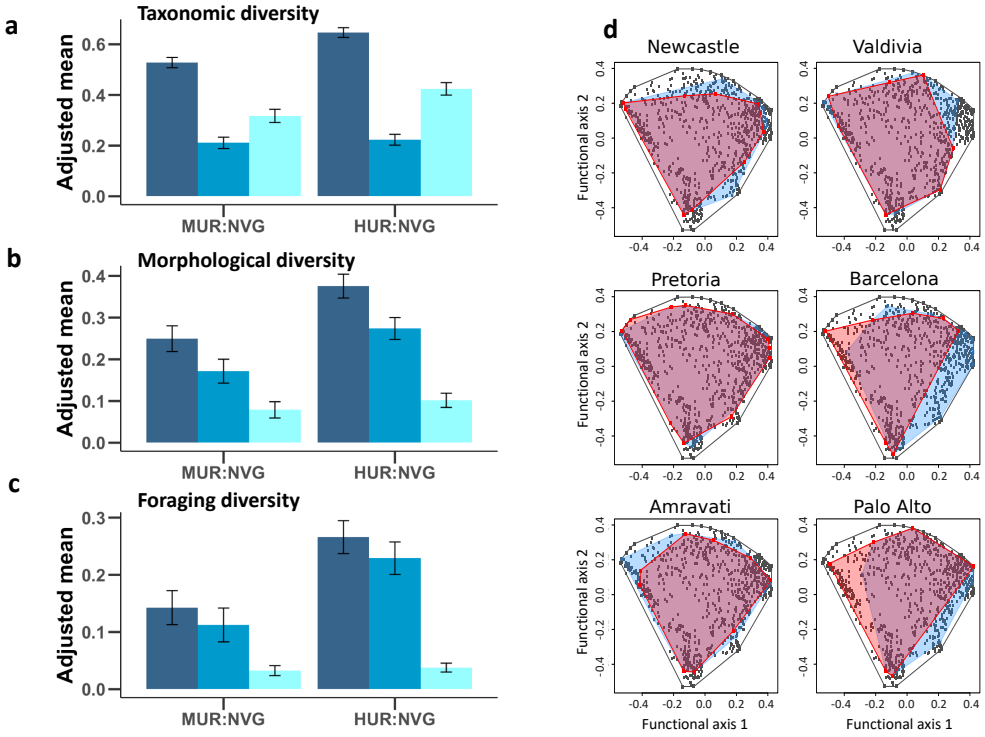
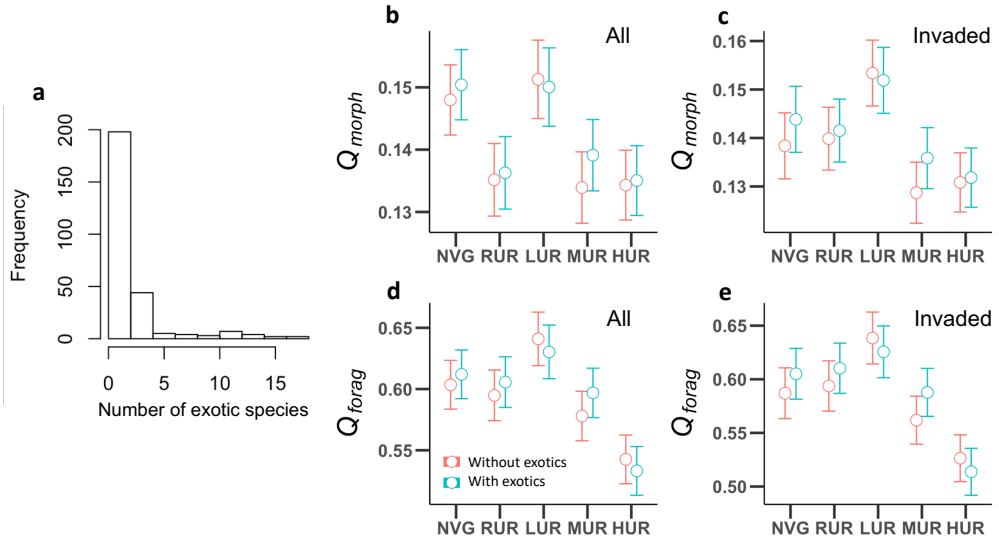


Figure 5 Influence of exotic species on changes in functional diversity (quadratic entropy, *Q*) across urbanization gradients. Frequency distribution (a) of the number of exotic species per assemblage. Changes in *Q* based on morphological traits (b-c) and foraging niche (d-e), with exotic species included (blue line) and excluded (red line), expressed as effect size (means ± standard errors). Panels include either all assemblages (b-c) or only invaded assemblages (i.e. those with more exotics species) (d-e).



Supporting Information for:

The worldwide impact of urbanisation on avian functional diversity

Daniel Sol[1,2]*, Christopher Trisos[3,4]*, Cesc Múrria[5], Alienor Jeliazkov[6,7], Cesar González-Lagos[8,9], Alex L. Pigot[10], Carlo Ricotta[11], Christopher M. Swan[12], Joseph A. Tobias[13]*, Sandrine Pavoine[14]*

[1]CSIC, Spanish National Research Council, CREAF-UAB, Catalonia 08193, Spain.
[2]CREAF, Centre for Ecological Research and Applied Forestries, Catalonia 08193, Spain.
[3]African Climate and Development Initiative (ACDI), University of Cape Town, South Africa.
[4]National Socio-Environmental Synthesis Center (SESYNC), University of Maryland, Annapolis, MD, USA.
[5]Grup de Recerca Freshwater Ecology, Hydrology and Management (FEHM) and Institut de Recerca de la Biodiversitat (IRBio), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Catalonia, Spain.
[6]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.
[7]Department of Computer Science, Martin Luther University Halle-Wittenberg, 06099 Halle (Salle), Germany
[8]Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Santiago, Chile.
[9]Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile.
[10]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, WC1E 6BT, UK.
[11]Department of Environmental Biology, University of Rome 'La Sapienza', 00185 Roma, Italy.
[12]University of Maryland Baltimore County, Baltimore, Maryland, USA.
[13]Department of Life Sciences, Imperial College London, Berkshire SL5 7PY, UK.
[14]Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, 75005 Paris, France.

*To whom correspondence should be addressed: Daniel Sol: d.sol@creaf.uab.cat; Christopher Trisos: christophertrisos@gmail.com; Joseph A. Tobias: j.tobias@imperial.ac.uk; Sandrine Pavoine: sandrine.pavoine@mnhn.fr

Number of Figures: 8
Number of Tables: 4

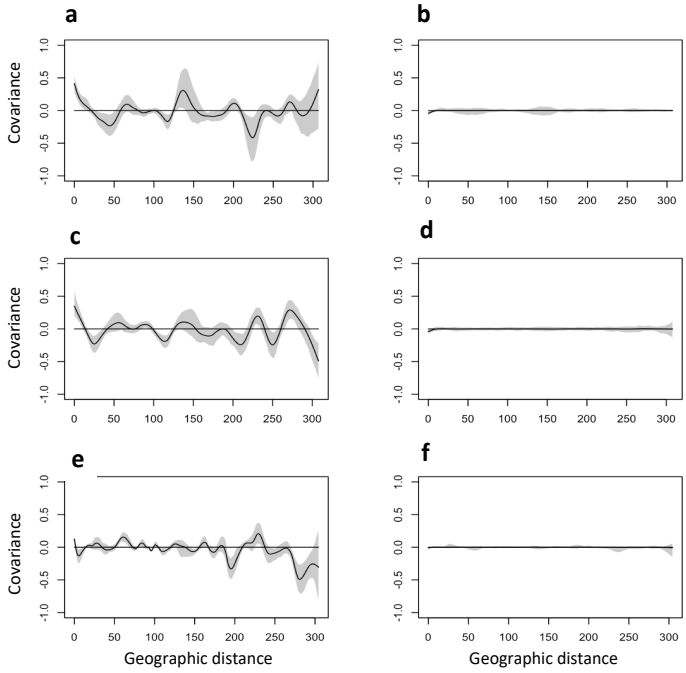


Figure S1. Analyses of spatial autocorrelation. a-f, Spline correlograms of the Pearson residuals of several illustrative models before and after accounting for spatial autocorrelation: species richness (**a,b**), morphological quadratic entropy (**c,d**) and ß foraging niche entropy (**e,f**) before (left plots) and after (right plots) accounting for spatial autocorrelation. The grey band represents the 95% confidence envelope. All the other response variables exhibited similar behaviours. Details on the structure of the models is provided in the main text.

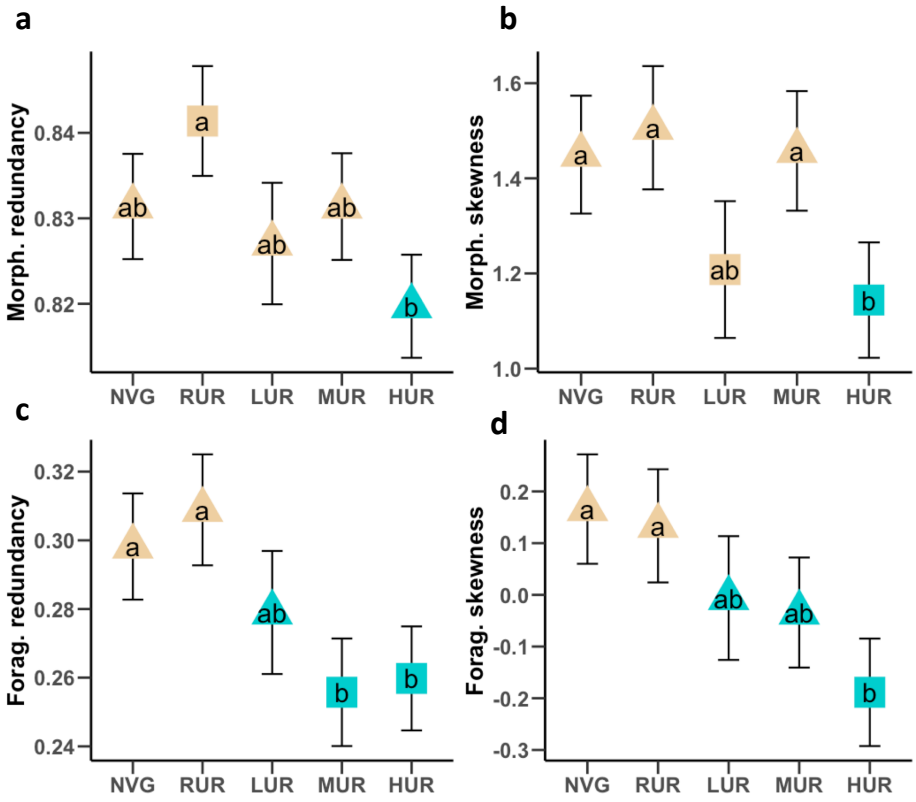


Figure S2. Changes in functional redundancy and distribution of functional uniqueness along urbanization gradients. a-c, Functional redundancies for morphology (**a**) and foraging niche (**c**) from natural vegetation (NVG) to highly urbanized habitat (HUR). **b-d**, Degree of skewness in the distribution of species' functional uniqueness (i.e., the mean of functional dissimilarity of each species from the rest of the species assemblage), for morphology (**b**) and foraging niche (**d**). Positive skewness indicates lower functional uniqueness within assemblages. Habitats and statistical differences are coded as in Fig. 1.

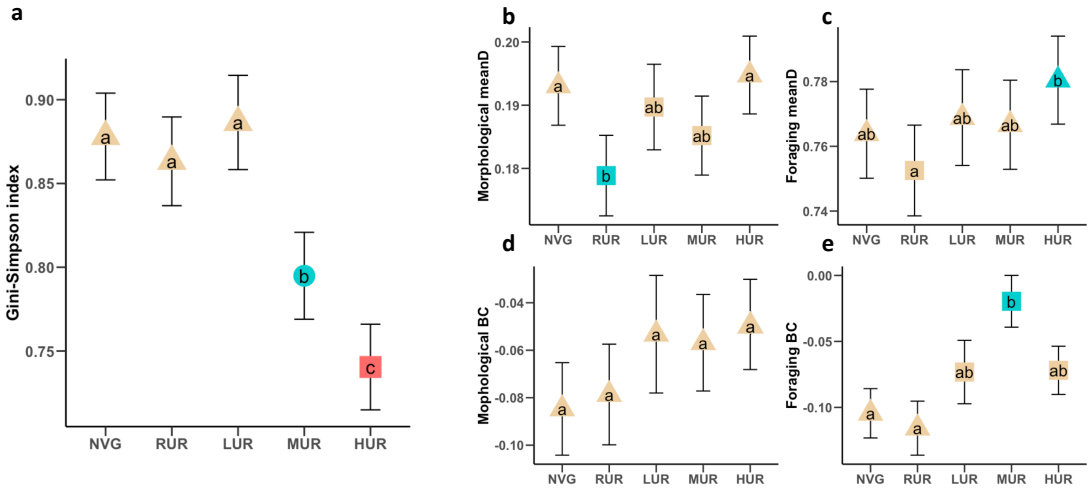


Figure S3. Variation along the urbanization gradients of the three main components of functional quadratic entropy along urbanization gradients. a, Gini-Simpson index **(a). b-c,** *Mean D* estimates for morphology (**b**) and foraging niche (**c**). **d-e,** Balance component estimates for morphology (**d**) and foraging niche (**e**). Values are mean effect size ± SE. Habitats and statistical differences are coded as in Fig. 1.

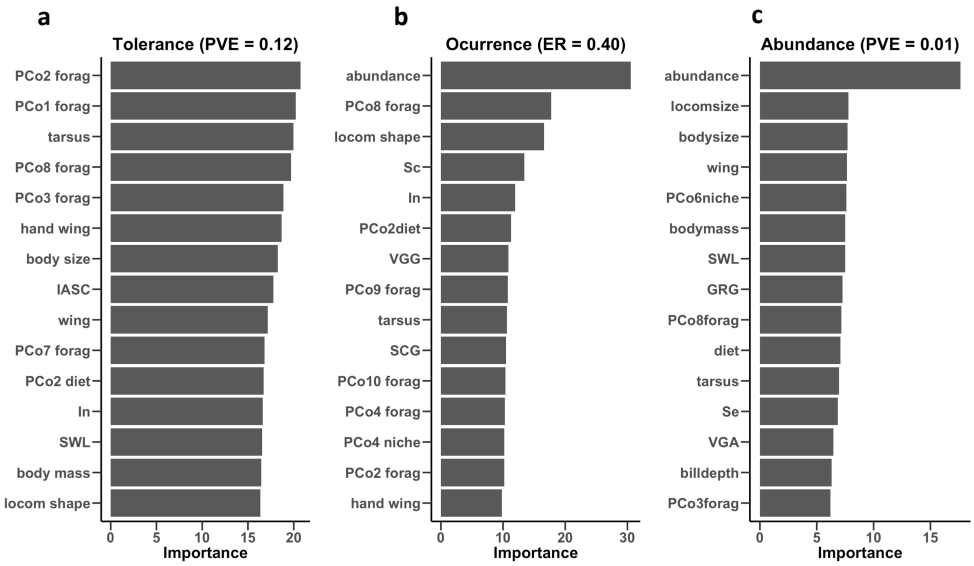


Figure S4. Predictive power of functional traits. a-c, Random forests describing the power of functional traits to predict tolerance of species to urbanization, measured as the change in abundance between the intensively urbanized habitat and surrounding natural vegetation (**a**), their presence/absence in the most intensively urbanized habitat (**b**) and, for those present, the relative abundance of species (**c**). The functional traits are poor predictors of the sensitivity of species to urbanization (≈ 12% of variance explained). They are also poorly associated with the occurrence and dominance of species in the most intensively urbanized environment, which were instead better explained by the relative abundance of the species in the surrounding natural vegetation. PVE is proportion of variance in the out-of-bag response variable that is explained by the model and ER the misclassification of out-of-bag samples (see Methods for details). Abbreviations are presented in the Supplementary Table 1.

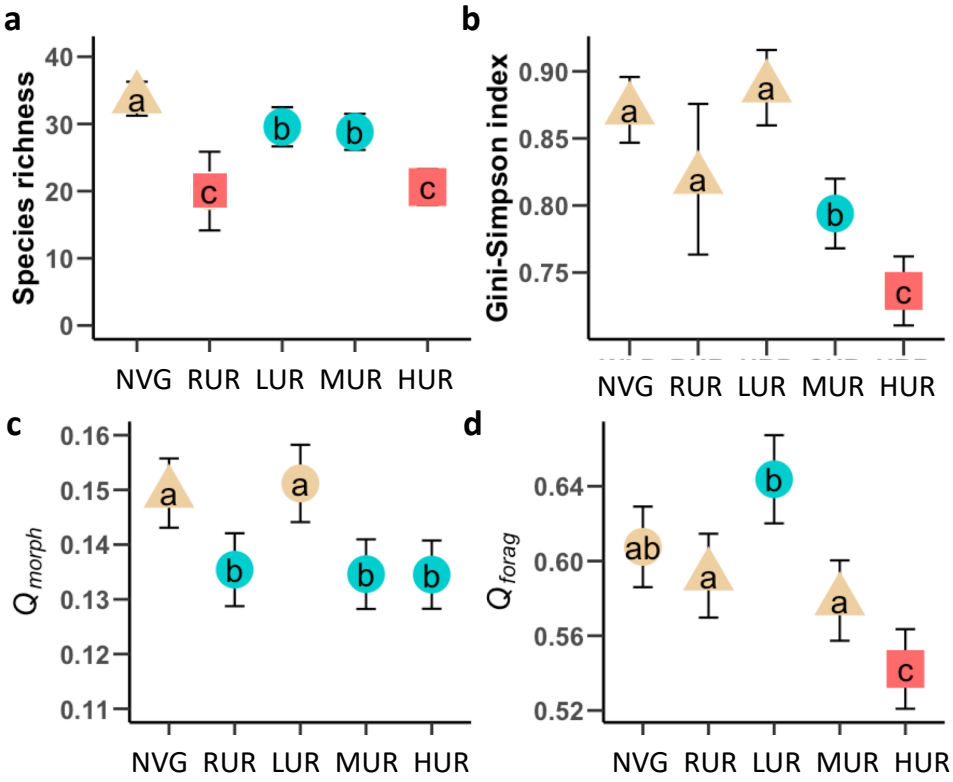


Figure S5. Loss of biodiversity along urbanization gradients, once 22 assemblages (14 of which were from a single city) identified as potential outliers are removed. a-d, Species richness (**a**), Gini-Simpson index (**b**), morphological diversity (*Q morph*) (**c**) and foraging diversity (*Q forag*) (**d**) along the urbanization gradients, expressed as effect size (means ± SE). Habitats and statistical differences are coded as in Fig. 1.

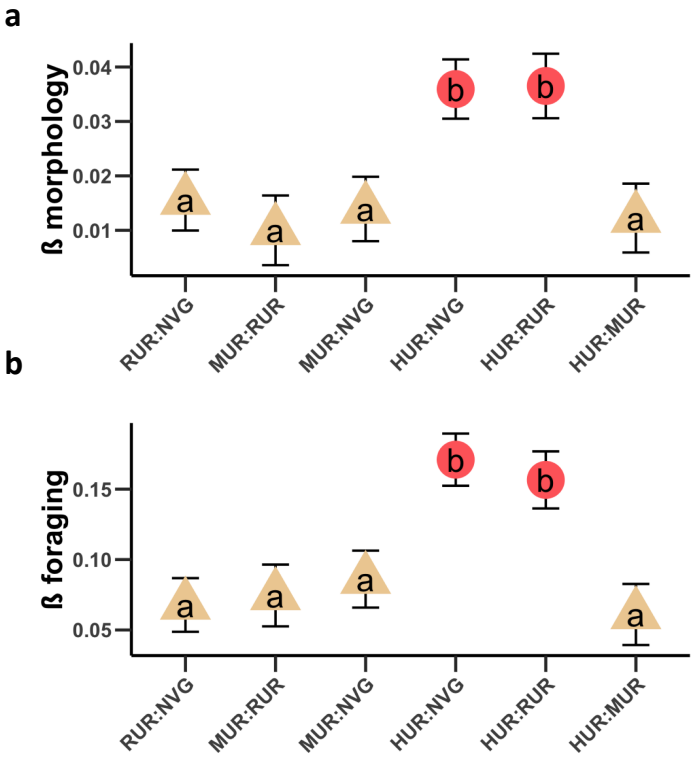


Figure S6. Functional quadratic ß entropy across urbanized and non-urbanized habitats. a-b, Quadratic ß entropy for morphology (**a**) and foraging niche (**b**). Habitats and statistical differences are coded as in Fig. 1.

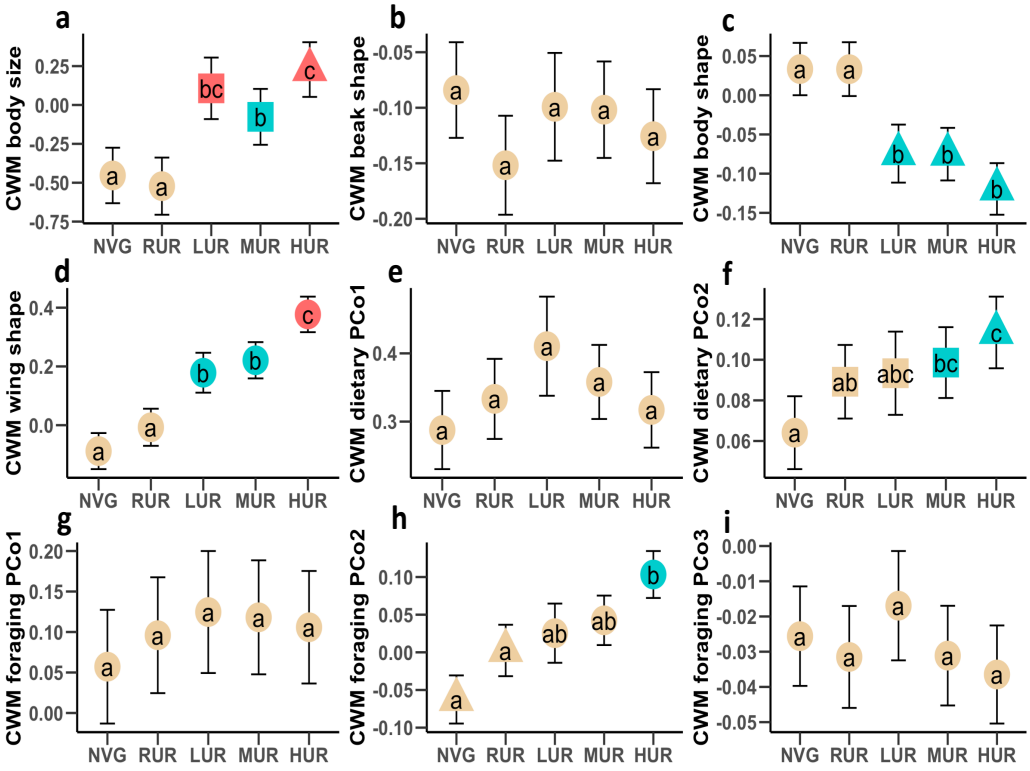


Figure S7. Community-weighted means (CWM) for the main morphological, resource use and foraging niche axes of variation across habitats. a-c, Community weighted means for morphological axes, derived from PCAs. **d-f,** Community weighted means for dietary niche axes, derived from a PCoA. **g-i,** Community weighted means for foraging niche axes, derived from a PCoA. Habitats and statistical differences are coded as in Fig. 1. Details on the morphological and niche axes provided in the Supporting Table 2.

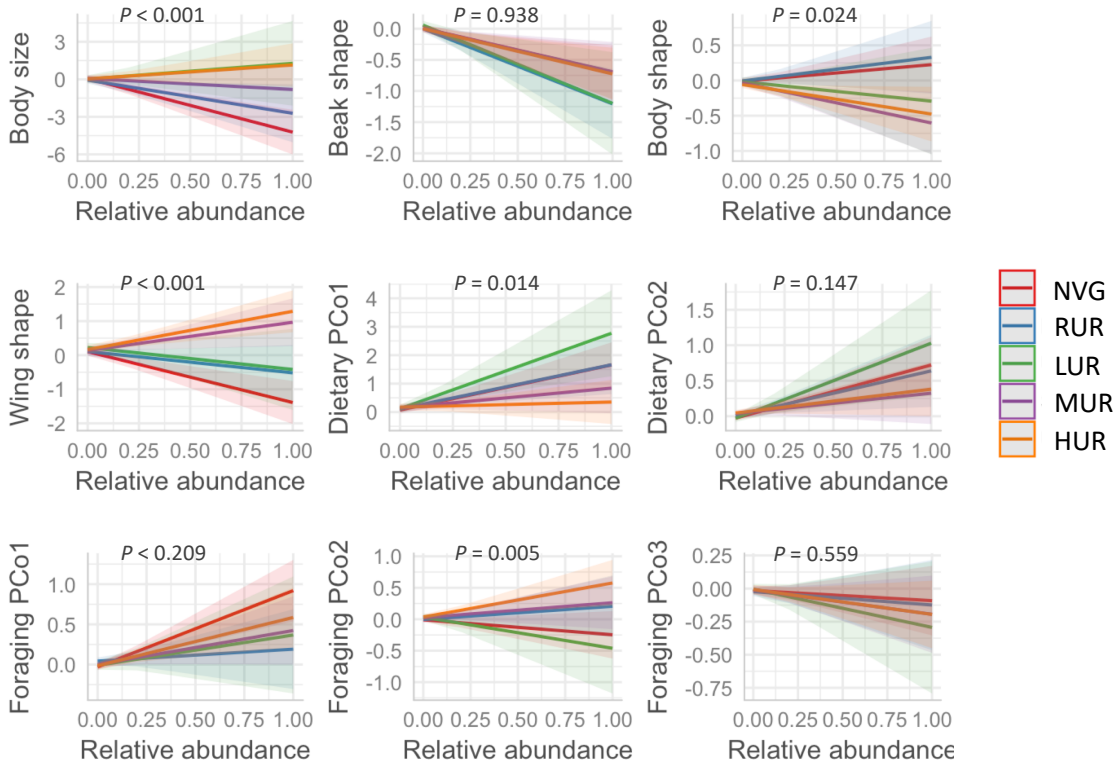


Figure S8. Relationship between relative abundance and the main morphological, resource use and foraging niche axes of variation across habitats. P values indicate the significance in slope between NVG and HUR. Habitats are coded as in Fig. 1.

Table S1. Number of assemblages in habitats within and outside each city.
NVG=natural vegetation, RUR=rural habitats, LUR= little urbanized habitat (specifically urban parks), MUR= moderately urbanized habitats and HUR= highly urbanized habitat.

City	Country	NVG	RUR	LUR	MUR	HUR	Source
Amravati	India	1	1	0	1	1	[1]
Barcelona	Spain	2	0	0	0	4	[2]
Brisbane	Australia	4	2	0	6	0	[3]
Bristol	United Kindom	0	1	1	1	0	[4]
Cameron Highlands	Malaysia	5	3	0	0	1	[5]
Cayenne	French Guiana	3	2	2	0	1	[6]
Ciudad de Mexico	Mexico	0	0	1	1	2	[7]
Cluj-Napoca	Romania	0	0	2	2	2	[8]
Dunedin	New Zealand	3	2	0	2	2	[9]
Fukuoka	Japan	1	0	0	1	1	[10]
Gainesville	USA	2	0	1	0	2	[11]
Hamilton	New Zealand	0	0	5	5	0	[12]
Harwich	United Kindom	2	2	4	6	4	[13]
Iowa	USA	1	0	1	2	2	[14]
Jamshedpur	India	1	0	0	1	1	[15]
Jerusalem	Israel	0	1	1	1	1	[16]
Kolkata	India	0	3	0	0	3	[17]
La Paz	Bolivia	1	1	1	1	2	[18]
Lansing	USA	0	1	1	2	1	[19]
Las Palmas	Spain	7	2	0	1	1	[20]
Madrid	Spain	4	0	0	1	2	[21]
Mar del Plata	Argentina	0	3	3	4	2	[22]
Margarita Island	Venezuela	1	0	1	1	1	[23]
Melbourne	Australia	1	0	0	2	1	[24]
Mindanao	Phillipines	0	2	0	0	1	[25]
Minneapolis Saint Paul	USA	8	9	0	0	4	[26]
Monteria	Colombia	1	2	0	0	1	[27]
Montreal	Canada	1	1	2	1	0	[28]
Morelia	Mexico	1	0	1	1	2	[29]
Newcastle	Australia	1	0	0	1	1	[30]
Olongapo	Phillipines	2	1	0	1	1	[31]
Orebro	Sweden	0	2	2	2	2	[32]
Oxford	USA	2	0	1	1	2	[33]
Palmas	Brazil	3	0	0	2	0	[34]
Palo Alto	USA	1	0	2	1	2	[35]

Pauri	India	3	0	0	0	3	36
Phalaborwa	South Africa	2	1	0	1	0	37
Phoenix	USA	0	2	0	1	1	38
Pretoria	South Africa	1	0	0	1	1	39
Puerto Rico	USA	1	0	1	1	1	40
Quezon City	Phillipines	0	0	3	0	1	41
Rennes	France	0	2	0	4	1	42
Santa Fe	Argentina	1	0	2	1	1	43
Santiago	Chile	0	2	2	0	2	44
Saskatoon	Canada	0	3	0	0	3	45
Tornio	Finland	1	0	0	1	1	46
Toronto	Canada	0	2	0	4	1	47
Valdivia	Chile	1	1	0	1	1	48
Valencia	Spain	4	6	1	2	2	49
Washington, DC	USA	0	0	1	1	3	50

1. Kale, M., Dudhe, N., Kasambe, R., Chakane, S., & Bhattacharya, P. (2012). Impact of urbanization on avian population and its status in Maharashtra state, India. International Journal of Applied Environmental Sciences, 7(1), 59–76.

2. Herrando, S., Ferrer X. Informe del seguiment d`ocells a la ciutat de barcelona (2004), 50 pp.

3. Sewell, C., Catterall, C. Bushland modification and styles of urban development: their effects on birds in south-east Queensland, Wildlife Res. 25, 41–63 (1998).

4. Baker, P., Thomas, R., Newson, S. Habitat associations and breeding bird community composition within the city of Bristol, UK, Bird Study (2010).

5. Soh, M. C. K., Sodhi, N. S., Lim, S. L. H. High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia, Biol. Conserv. 129, 149–166 (2006).

6. Reynaud, P. Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis, J. Enviro. Manage. 59, 121–140 (2000).

7. Ortega-Álvarez R, MacGregor-Fors I (2009) Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. Landsc Urban Plan 90(3–4):189–195.

8. Máthé, O. and P. Batáry (2015). "Insectivorous and open-cup nester bird species suffer the most from urbanization." Bird Study 62(1): 78-86.

9. Vanheezik, Y., Smyth, A., Mathieu, R. Diversity of native and eotic birds across an urban gradient in a New Zealand city, Landscape Urban Plan. 87, 223–232 (2008).

10. Mikami OK, Mikami K. Structure of the Japanese avian community from city centers to natural habitats exhibits a globally observed pattern. Landsc Ecol Eng. 2014;10: 355–360.

11. Stracey, C. M., and S. K. Robinson. 2012. Does nest predation shape urban bird communities? Pp. 49–70 in C. A. Lepczyk and P. S. Warren (editors). Urban bird ecology and conservation. Studies in Avian Biology (no. 45), University of California Press, Berkeley, CA.

12. http://www.hamilton.govt.nz/our-services/environment-and-health/biodiversity/Documents/Landcare%20Hamilton%20bird%20survey.pdf

13. Mason, C.F. 2006. Avian species richness and numbers in the built environment: can new housing developments be good for birds? Biodiversity and Conservation 15:2365–2378

14. McCurdy, Jason D. "The effects of human development on avian diversity along an urban-rural gradient in Iowa City, Iowa." MA (Master of Arts) thesis, University of Iowa, 2016.

15. Verma SK, Murmu T Das. Impact of environmental and disturbance variables on avian community structure along a gradient of urbanization in Jamshedpur, India. PLoS One. 2015;10: e0133383.

16. Bino G, et al. (2008) Accurate prediction of bird species richness patterns in an urban environment using Landsat-derived NDVI and spectral unmixing. Int J Remote Sens 29(13):3675–3700.

17. Sengupta S, Mondal M, Basu P (2014) Bird species assemblages across a rural urban gradient around Kolkata, India. Urban Ecosyst. doi:10.1007/s11252-013-0335-y.

18. Villegas, M., Garitano-Zavala, Á. Bird community responses to different urban conditions in La Paz, Bolivia, Urban Ecosystems 13, 375–391 (2010).

19. Joo W, Gage SH, Kasten EP. Analysis and interpretation of variability in soundscapes along an urban–rural gradient. Landsc Urban Plan. 2011;103: 259–276.

20. Carrascal, L., Palomino, D., Polo, V. Patrones de distribución, abundancia y riqueza de especies de la avifauna terrestre de la isla de La Palma (islas Canarias), Graellsia 64, 209–232 (2008).

21. Palomino, D., Carrascal, L. M.Urban influence on birds at a regional scale : A case study with the avifauna of northern Madrid province, Landscape Urban Plan 77, 276–290 (2006).

22. Leveau Bird traits in urban–rural gradients: how many functional groups are there? J Ornithol (2013) 154:655–662

23. Sanz V, Caula S. Assessing bird assemblages along an urban gradient in a Caribbean island (Margarita, Venezuela). Urban Ecosyst. 2015;18: 729–746.

24. White, J. G., et al. (2005). "Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation." Landscape and Urban Planning 71(2-4): 123-135.

25. Bird Diversity and Structure in Different Land-use Types in Lowland South- Central Mindanao, Philippines. Tropical Life Sciences Research, 26(2), 85–103, 2015

26. Chapman KA, Reich PB (2007) Land use and habitat gradients determine bird community diversity and abundance in suburban, rural and reserve landscapes of Minnesota, USA. Biol Conserv. doi:10.1016/j.biocon.2006.10.050.

27. Domínguez-López ME, Ortega-Álvarez R. The importance of riparian habitats for avian communities in a highly human-modified Neotropical landscape. Rev Mex Biodivers. 2014;85: 1217–1227.

28. Barrie, C. 2013. Birds and insect diversity along an urban disturbance gradient, PhD Thesis

29. López López, Silvia. Efecto de la urbanización sobre las comunidades de aves y lepidopteros de la ciudad de Morelia. PhD Thesis, Universidad Michoacana de San Nicolás de Hidalgo, 2010

30. Sol, D., Bartomeus, I., Griffin, A. C. The paradox of invasion in birds: competitive superiority or ecological opportunism? Oecologia 169(2), 553-564 (2012)

31. Posa, M., Sodhi, N. Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines, Biol Conserv 129, 256–270 (2006).

32. Sandstrom, U., Angelstam, P., Mikusinski, G. Ecological diversity of birds in relation to the structure of urban green space, Landscape Urban Plan. 77, 39–53 (2006).

33. Crosby, N. A., Blair, R. B. in Avian Ecology and Conservation in an Urbanizing World, (2001), pp. 523–541.

34. Reisa E., López-Iborrab GM & Torres Pinheiroa R. 2012. Changes in bird species richness through different levels of urbanization: Implications for biodiversity conservation and garden design in Central Brazil. Landscape and Urban Planning 107 (2012) 31–42

35. Blair, R. B. Land use and avian species diversity along an urban gradient, Ecol. Appl. 6, 506–519 (1996).

36. Naithani & Dinesh Bhatt. Bird community structure in natural and urbanized habitats along an altitudinal gradient in Pauri district (Garhwal Himalaya) of Uttarakhand state, India. Biologia 67/4: 800—808, 2012

37. Coetzee BWT, Chown SL (2016) Land-use change promotes avian diversity at the expense of species with unique traits. Ecol Evol 6(21):7610–7622.

38. Green, D., Baker, M. Urbanization impacts on habitat and bird communities in a Sonoran desert ecosystem, Landscape Urban Plan. 63, 225–239 (2003).

39. Van Rensburg, B. J., Peacock, D. S., Robertson, M. P., van Rensburg, B. J. Biotic homogenization and alien bird species along an urban gradient in South Africa, Landscape Urban Plan. 92, 233–241 (2009).

40. Edgar O. Vázquez Plass and Joseph M. Wunderle Jr (2013) Avian distribution along a gradient of urbanization in northeastern Puerto Rico. Ecological Bulletins 54: 141–156, 2013

41. Vallejo B.J., Aloya A.B, Ong P.S. 2009 The distribution, abundance and diversity of birds in Manila's last greenspaces. Landscape and Urban Planning 89: 75–85

42. Clergeau, P., Mennechez, G., Sauvage, A. Lemoine, A. in Avian Ecology and Conservation in an Urbanizing World, J. Marzluff, R. Bowman, R. Donnelly, Eds. (Springer US, 2001), pp. 69–88.

43. Maximiliano A. Cristaldi, Alejandro R. Giraudo, Vanesa Arzamendia, Gisela P. Bellini & Juan Claus (2017) Urbanization impacts on the trophic guild composition of bird communities, Journal of Natural History, 51:39-40, 2385-2404, DOI: 10.1080/00222933.2017.1371803

44. Díaz, I., Meynard, C., Sharon, R., and Armesto, J. J. (Unpublished) Linking habitat structure and avian conservation in urban areas: Birds in Santiago de Chile.

45. Sodhi, N.S. 1992. Comparison between urban and rual bird communities in praire Saskatchewan: Urbanization and short-term population trends. Canadian Field-Naturalist 106:2010-2015

46. Huhtalo, H. & Järvinen, O. 1977. Quantitative composition of urban bird community in Tornio, Northern Finland. Bird Study, 24:3, 179-185

47. Savard, J. P. Falls, J. B. in Avian Ecology and Conservation in an Urbanizing World, J. Marzluff, R. Bowman, R. Donnelly, Eds. (Springer US, 2001), pp. 543–568.

48. Sol, D., González-Lagos, C., Moreira, D., Maspons, J., & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. Ecology Letters, 17, 942–95. http://doi.org/10.1111/ele.12297

49. Murgui, E. Influencia de la estructura del paisaje a diferentes escalas espaciales sobre las comunidades y poblaciones de aves urbanas. PhD thesis, (2006).

50. Hadidian J, et al. 1997 A citywide breeding bird survey for Washington, DC. Urban Ecosyst 1, 87–102. http://www.pwrc.usgs.gov/birdscap/birdscap.html#Data

Table S2. Description of functional traits.

Morphological traits

1. **Wing length (WL)**
2. **Second wing length (SWL)**
3. **Hand-wing index (HWI)**
4. **Tail length (TIL)**
5. **Tarsus length (TSL)**
6. **Bill length (BL)**
7. **Bill width (BW)**
8. **Bill depth (BD)**
9. **Body mass (BM)**

Dietary traits

1. **Invertivore (In) -** invertebrates in air or terrestrial habitats.
2. **Aquatic predator (Aq) -** invertebrates and vertebrates in aquatic habitats.
3. **Frugivore (Fr) -** fruit.
4. **Nectarivore (Ne) -** nectar and plan exudates.
5. **Granivore (Gr) -** seeds.
6. **Herbivore (Pl) -** vegetation (not including seeds, nectar or fruit).
7. **Vertivore (Vt) -** terrestrial vertebrates.
8. **Scavenger (Sc) -** carrion and human waste

Foraging niche traits

1. **Invertivore aerial screen (IASC)** – species capturing flying invertebrates on the wing (e.g. swallows, swifts). Often described as 'hawking'. In contrast to ISA, IASC is characterized by continuous and extended flight with multiple items captured before landing.

2. **Invertivore aerial sally (ISA)** – species capturing flying invertebrates in mid-air, with the attack starting from a perch (i.e. branch, rock, fence post, telegraph wire, etc.) and then returning to a perch (e.g. Jacamars, kingbirds, etc). 'Hawking' will sometimes refer to this category, but the key distinguishing feature is that only a single prey item is captured before returning to a perch.

3. **Invertivore sally to substrate (ISS)** – species capturing invertebrates (including arachnids, worms, molluscs, etc.) attached to the substrate (e.g. leaves, twigs, branches, rock faces, etc) following an aerial attack maneuver (e.g. flight, pounce, jump, hover).

4. **Invertivore sally to ground (ISG)** – species capturing invertebrates on the ground following an aerial attack maneuver (e.g. flying, gliding, dropping or pouncing) (e.g. Chats, shrikes, kiskadee etc). The aerial maneuver may be followed by brief hopping toward prey (e.g. terns).

5. **Invertivore glean arboreal (IGA)** – species capturing invertebrates attached to the substrate (e.g. leaves, twigs, branches, grass, bamboo, stems, hanging dead-leaves [not dead leaves on the ground] etc). No aerial attack maneuver is involved.

6. **Invertivore glean bark (IGB)** – species capturing invertebrates attached to or concealed within large branches and trunks of trees (e.g. Woodpeckers, treecreepers, woodcreepers, wallcreepers, nuthatches, sitellas, nuthatch vanga, etc. Includes honeyguides). This is distinguished from IGA by at least one criteria. First, the species employs specialized methods for moving over surfaces which are often, but not always vertical, vertical and too large to be gripped by the closed foot (including creeping, climbing or scaling). Second, the species extracts prey from in/under the bark using specialized methods (including hammering, probing or chiseling). Also includes species capturing insects from rock and cliff-faces (though not just on boulders [see IGG]), habitually perching on or clinging to large mammals and species that feed on honey and beeswax.

7. **Invertivore glean ground (IGG)** – species capturing invertebrates on the ground. In contrast to ISG, the search and attack manouvers take place on the ground (e.g. Thrushes). This includes species standing on the ground and gleaning insects from vegetation (e.g. tinamous or larks) but excludes species that jump or sally upwards to capture prey from vegetation (ISS) or the air (ISA). The ground is dry and thus excludes aquatic habitats (including beaches, estuaries, wetlands and marshes [see AQGR]).

8. **Aquatic predator ground (AQGR)** – species capturing invertebrates or vertebrates while standing in aquatic habitats (including beaches, estuaries, wetlands and marshes) (e.g. storks, herons, shorebirds). Prey may be captured on the ground or on/under water. This category includes species capturing aquatic prey (e.g. fish) or terrestrial prey in aquatic habitats (e.g. grasshopper).

9. **Aquatic predator perch (AQPE)** – species capturing invertebrates or vertebrates on/under water following a direct attack flight from a perch (e.g. kingfisher).

10. **Aquatic predator air (AQAI) -** species capturing invertebrates or vertebrates on/under water during continuous flight (including dipping, hovering, pattering, snatching). In contrast to AQPE, prey item is identified while flying (not from perch). The predators body may partially submerge but does not plunge beneath the surface (AQPL). Includes kleptoparasitic species capturing fish by chasing other piscivores and forcing them to regurgitate (e.g. skuas, frigatebirds).

11. **Aquatic predator plunge (AQPL) -** species capturing invertebrates or vertebrates by plunging under water following continuous flight. The predators body submerges entirely beneath the surface, with the prey captured either by the momentum of the plunge or following propelled swimming.

12. **Aquatic predator surface (AQSU) -** species capturing invertebrates or vertebrates on/under water whilst swimming on the waters surface. In contrast to AQPE or AQAI there is no direct attack flight. The species may dip under the water but, in contrast to AQDI, contact with the surface is maintained.

13. **Aquatic predator dive (AQDI) -** species capturing invertebrates or vertebrates under water by diving from the surface (not the air, see AQPE and AQPL).

14. **Frugivore aerial (FAE)** – species foraging on fruits in flight, including those that hover to pluck fruit from bushes and trees (e.g. oilbird, some manakins).

15. **Frugivore glean (FGL)** – species foraging on fruits while perched (not in flight) above ground and plucking fruits from vegetation (e.g. toucans, hornbills).

16. **Frugivore ground (FGR)** – species foraging on fruits lying on the ground (e.g. thrushes, trumpeters).

17. **Nectarivore aerial (NAE)** – species feeding on nectar or other plant exudates (e.g. sap) while in flight (e.g. hummingbirds).

18. **Nectarivore glean (NGL)** – species feeding on nectar or other plant exudates (e.g. sap) while perched, including nectar predators that pierce corollas (e.g. sunbirds, flowerpiercers). Species feeding on honey (e.g. honeyguides) are included under IGB.

19. **Granivore above-ground (GRA)** – species foraging on seeds, grains and nuts taken from vegetation (e.g. trees, grass stems) while perched (e.g. seedeaters, finches).

20. **Granivore ground (GRG)** – species foraging on fallen seeds, grains and nuts collected from the ground. Including birds that eat grains by, on, and under water (e.g. partridges, pheasants, finches).

21. **Herbivore above-ground (PA)**– species foraging on leaves, buds, blossom, or other vegetation (except fruit and nectar). The food is taken from above ground, generally while the species is perching on branches or other stems. Generally, a small part of diet, except for the Hoatzin.

22. **Herbivore ground (PG)** – species foraging on leaves, buds, blossom, or other vegetation (except fruit) taken while the species is on the ground. The vegetation may itself be off the ground, so long as the species forages terrestrially.

23. **Herbivore aquatic (PA)** – species foraging on aquatic vegetation either below or above the water surface (algae, pondweed, waterside vegetation). The species collects vegetation while under water, sitting on the waters surface or wading.

24. **Vertivore aerial screening (VASC)** – species captures vertebrate prey during flight. Both predator and prey are in flight (e.g. peregrine, hobby, falcon)

25. **Vertivore aerial to substrate (VAS)** – species captures prey on branches or the ground by diving from the air, usually after circling or hovering in flight. Includes quartering flight (e.g. kestrels, kites, some owls).

26. **Vertivore sally to substrate (VSS)** – species captures prey on branches or the ground by diving from a perch (e.g. many owls, eagles).

27. **Vertivore glean ground (VGG)** – species capturing prey on the ground, including eggs in ground nests, while they themselves are also walking or running on the ground (e.g. secretary bird, seriemas, ground hornbills).

28. **Vertivore glean arboreal (VGA)** – species capturing prey from foliage, branches, epiphytes, cavities, bark or other arboreal substrate while perched on the substrate. There is no flight attack involved. This includes eating bird chicks from arboreal nests and drinking blood while perched on mammals (e.g. oxpeckers).

29. **Scavenger aquatic (SCA)** – species eating carrion (dead animal or fish remains) from water (e.g. petrels, albatrosses).

30. **Scavenger ground (SCG)** – species eating carrion (dead animal or fish remains) on the ground (e.g. vultures).

Table S3. Main axes of variation in morphology, foraging niche and dietary niche. The axes have been extracted from either a Principal Component Analyses (morphology) or a Principal Coordinate Analysis (rest). Values are either Pearson's (morphology) or Spearman's (rest) coefficient of correlation of the traits with the axes.

Morphology

	PC1 (Body size)	PC2 (Beak shape)	PC3 (Body shape)
BM	0.96	0.11	0.04
BL	0.84	0.51	0.03
BW	0.87	-0.25	-0.1
BD	0.88	-0.21	-0.05
TSL	0.83	0.14	0.45
SWL	0.97	0.05	0.05
WL	0.94	0.13	-0.12
HWI	0.17	0.11	-0.36
TIL	0.84	0.01	-0.38

Foraging niche

	PCo1	PCo2	PCo3	PCo4	PCo5	PCo6	PCo7
Pl	0.09	-0.04	0.07	-0.32	-0.19	-0.08	-0.03
Vt	0.09	0.22	0.37	-0.17	-0.39	-0.37	0.4
Sc	0.1	0.15	0.2	-0.06	-0.2	-0.2	0.2
IASC	-0.28	0.45	0.17	0.32	0.18	0.1	-0.07
ISA	-0.18	-0.1	-0.04	0.02	0.1	0.15	-0.05
ISS	-0.21	-0.05	0	0.08	0.11	0.14	-0.04
ISG	-0.01	0.16	0.22	-0.03	-0.12	-0.13	0.16
IGB	-0.09	-0.06	0	-0.09	0.03	0.1	-0.04
IGA	-0.47	**-0.79**	-0.76	0.27	0.39	0.39	-0.34
IGG	0.75	0.1	0.1	-0.32	-0.33	-0.31	0.13
AQGR	0.27	0.2	0.26	-0.13	-0.36	-0.35	0.32
AQPE	0.03	0.12	0.15	0.02	-0.11	-0.11	0.13
AQAI	0.1	0.18	0.21	0.04	-0.15	-0.16	0.16
AQPL	0.07	0.16	0.17	0.05	-0.1	-0.12	0.12
AQSU	0.12	0.16	0.18	0.01	-0.15	-0.15	0.13
AQDI	0.06	0.12	0.14	0.04	-0.09	-0.09	0.09

FAE	-0.03	0.01	0.03	0	0.01	0.02	-0.01
FGL	-0.37	**-0.64**	-0.41	-0.51	0.5	0.52	-0.39
FGR	0.22	0.08	0.12	-0.17	-0.23	-0.21	0.16
NAE	-0.23	0.19	0.26	0.27	0.21	0.19	-0.11
NGL	-0.2	-0.25	-0.16	-0.14	0.16	0.36	0.02
GRA	-0.07	-0.37	-0.23	-0.37	0.06	0.24	-0.61
GRG	0.63	0.22	0.15	-0.17	-0.28	-0.25	0.04
PA	-0.08	-0.16	-0.07	-0.28	-0.01	0.1	-0.18
PG	0.23	0.09	0.15	-0.2	-0.26	-0.23	0.14
PAQ	0.11	0.11	0.13	-0.02	-0.13	-0.12	0.08
VASC	0.02	0.14	0.18	0.03	-0.13	-0.13	0.15
VAS	0.03	0.2	0.25	0.04	-0.18	-0.18	0.21
VSS	0	0.21	0.31	-0.02	-0.23	-0.23	0.27
VGA	-0.06	-0.06	-0.01	-0.11	-0.07	-0.04	0.04
VGG	0.18	0.11	0.22	-0.23	-0.32	-0.3	0.29
SCA	0.05	0.1	0.13	0.01	-0.1	-0.1	0.1
SCG	0.1	0.14	0.19	-0.07	-0.2	-0.19	0.2

Dietary niche

	PCo1	PCo2	PCo3	PCo4	PCo5	PCo6	PCo7
In	-0.82	-0.89	0.14	-0.77	-0.46	0.13	-0.21
Aq	0.13	0.3	0.06	0.28	0.35	-0.43	-0.5
Fr	0.33	-0.02	-0.23	0.11	-0.12	-0.18	0.45
Ne	0.09	0.14	0.32	-0.19	-0.26	-0.01	0.05
Se	0.41	0.49	-0.54	0.58	0.13	0.55	0.56
Pl	0.24	0.24	-0.07	0.29	0.15	0.08	0.19
Vt	-0.02	0.11	-0.04	0.07	-0.01	-0.4	-0.41
Sc	0.04	0.12	0.06	0.11	0.1	-0.17	-0.15

Table S4. Gaussian phylogenetic mixed model testing how functional uniqueness of species affects their tolerance to urbanization. Tolerance is measured as change in abundance (corrected for sampling effort, when necessary) between highly urbanised habitat and surrounding natural vegetation in each region[1,2]. Species-level functional uniqueness is the mean functional dissimilarity of each species from the rest of the species from a same region. Fixed and random effects were estimated by means of a Bayesian approximation[3]. Abbreviations: l-95% CI = Inferior 95% credibility interval; U-95% CI = Upper 95% credibility interval; eff. Samp = Effect sample.

	Morphology				
Random effects	post.mean	l-95% CI	u-95% CI	eff. samp	
Phylogeny	4.738	3.082	6.517	1000	-
Region	4.603	2.318	7.400	1000	-
Residual	5.19	4.712	5.714	1000	-
	-	-	-	-	-
Fixed effects	post.mean	l-95% CI	u-95% CI	eff. samp	pMCMC
(Intercept)	-1.024	-3.333	1.197	1000	0.37
Morphological uniqueness	-0.694	-4.008	2.854	1000	0.7
	Foraging niche				
Random effects	post.mean	l-95% CI	u-95% CI	eff. samp	
Phylogeny	4.652	2.866	6.364	1000	-
Region	4.766	2.336	8.031	1000	-
Residual	5.198	4.678	5.717	1000	-
	-	-	-	-	-
Fixed effects	post.mean	l-95% CI	u-95% CI	eff. samp	pMCMC
(Intercept)	-2.235	-4.833	-0.221	1138	0.06
Foraging niche uniqueness	1.409	-0.322	2.931	1095	0.076