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LETTER

The worldwide impact of urbanisation on avian functional diversity

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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.

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INTRODUCTION

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 (Dıaz & 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

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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—that is 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 are 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; Sekercioglu *et al.* 2016; Pigot *et al.* 2016a). Importantly, the functional traits underpinning these processes have recently been comprehensively measured in birds (Pigot et al., 2020; 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 where the diversity inside each city is 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. 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 regions. 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.

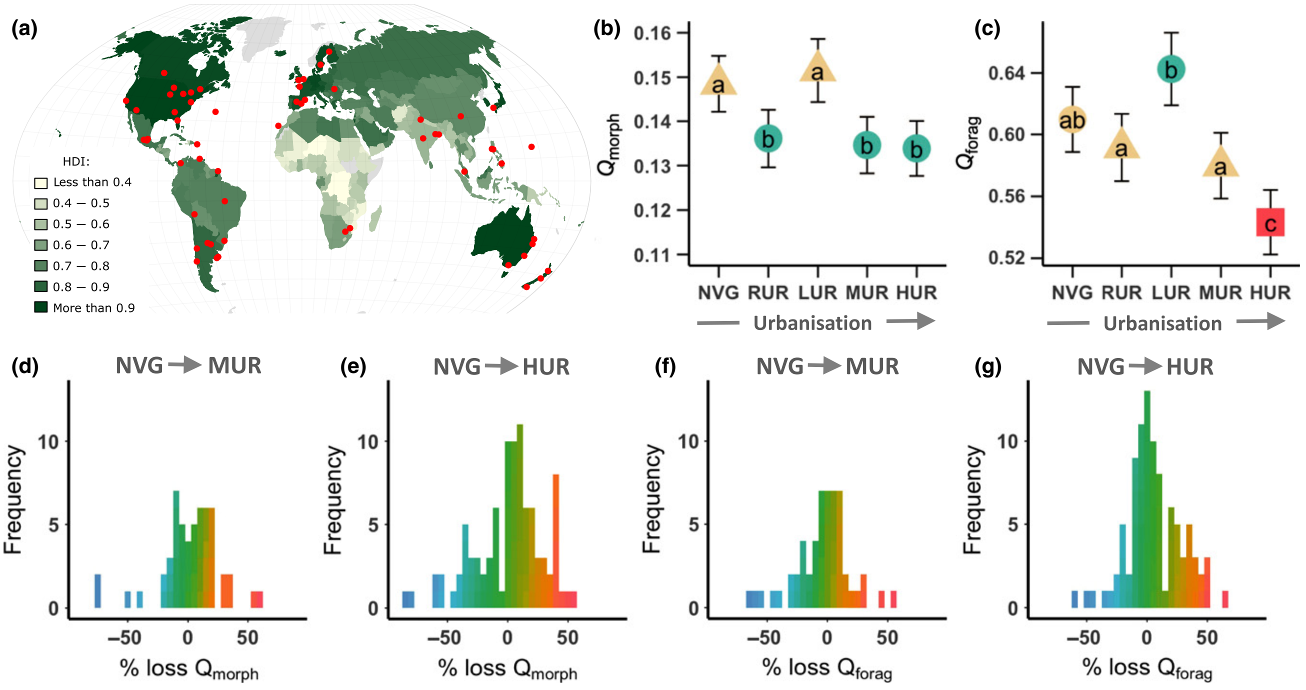

Figure 1 Changes in functional diversity across urbanisation gradients worldwide. (a) Geographic location of 50 study regions in relation to United Nations human development index (HDI). (b and c) Effects of urbanisation on functional diversity (quadratic entropy, Q), based on morphological traits (b) 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 regions, 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 and e) morphological diversity (Q_{morph}) and (f and g) foraging niche diversity (Q_{forag}) in moderately urbanised (d and f) and highly urbanised (e and g) areas relative to natural vegetation across assemblages within study regions. Colour scales in panels d–g illustrate the progression from low (blue) to high (red) loss of functional diversity.

Functional traits

To describe major axes of niche variation across our sample of bird species, we compiled comprehensive datasets of two types of traits (Table S2). First, we used data from Pigot et al. (2020) 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., 2020). 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., 2020; Appendix 3). We did this because although morphology accounts for substantial variation in the avian niche (Pigot et al. 2016b, 2020), 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.

We used Rao's quadratic entropy (Q) to estimate functional diversity for each assemblage. Mathematically, this is expressed as follows:

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

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 $meanD = \left(\sum_{ij} d_{ij}\right)/(S \times (S-1))$, 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 $Q = H_{GS}{*}mean\ D + BC$. 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 $I_e = H_{GS}{*}S/(S\text{-}1)$; (5) community-level functional redundancies as $1\text{-}Q/H_{GS}$ (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 biodiversity 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 effects 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

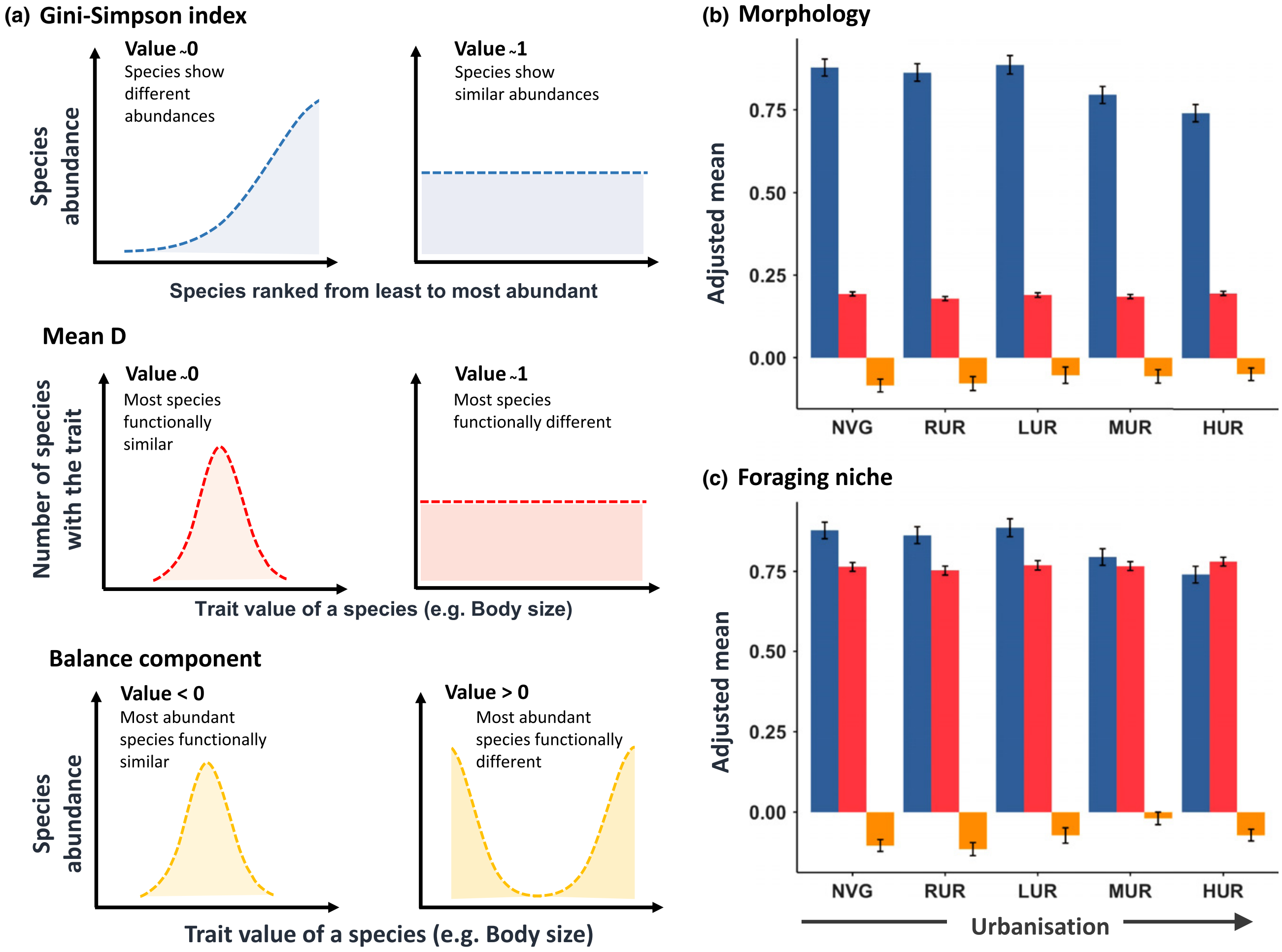

Figure 2 Decomposition of functional diversity across urbanisation gradients. Panel a illustrates the decomposition of functional quadratic entropy into the Gini-Simpson index (blue), unweighted mean functional dissimilarity (*mean D*, red) and balance component (orange). Panels b and c show variation 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).

highly 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 and e).

Although morphology accounts for substantial variation in the avian niche (Pigot et al. 2016b, 2020), 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,

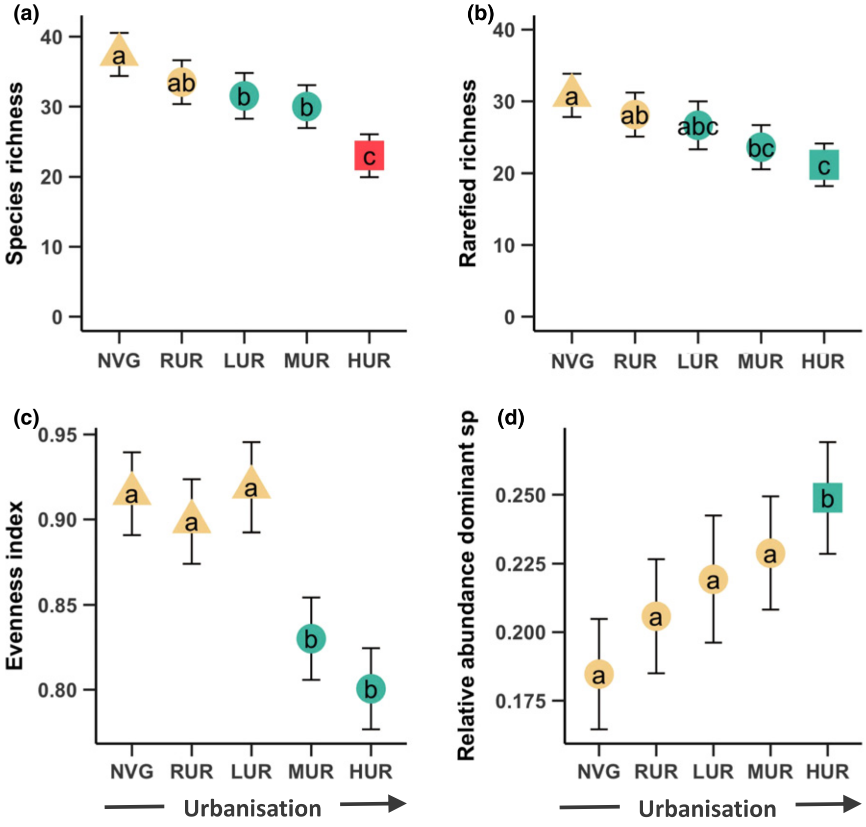

Figure 3 Changes in species richness and abundance along urbanisation gradients based on species richness (a), rarefied species richness (b), index of abundance evenness among species (c) and relative abundance of the single most abundant species (d). Values are adjusted means and standard errors derived from models. Plots c and 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.

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 and 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

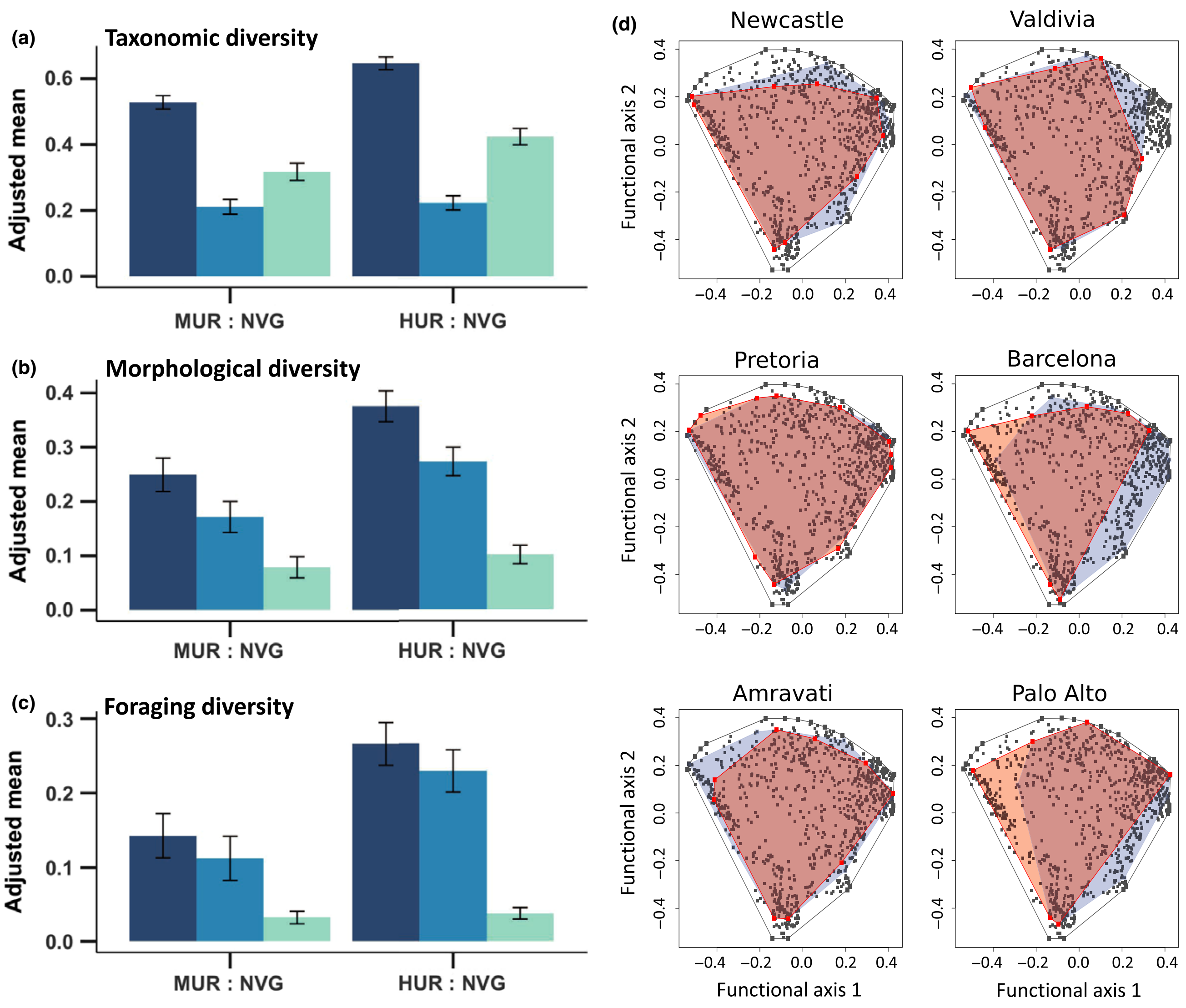

Figure 4 Changes in taxonomic and functional ß-diversity across urbanisation gradients. Estimates of taxonomic (a), morphological (b) and foraging (c) ß-diversity between urban and non-urban habitats (MUR: moderately urbanised; HUR: highly urbanised; NVG: natural vegetation). Overall ß-diversity (dark 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.

functional dissimilarity between species (Fig. 2b andc). 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 and 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 and 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

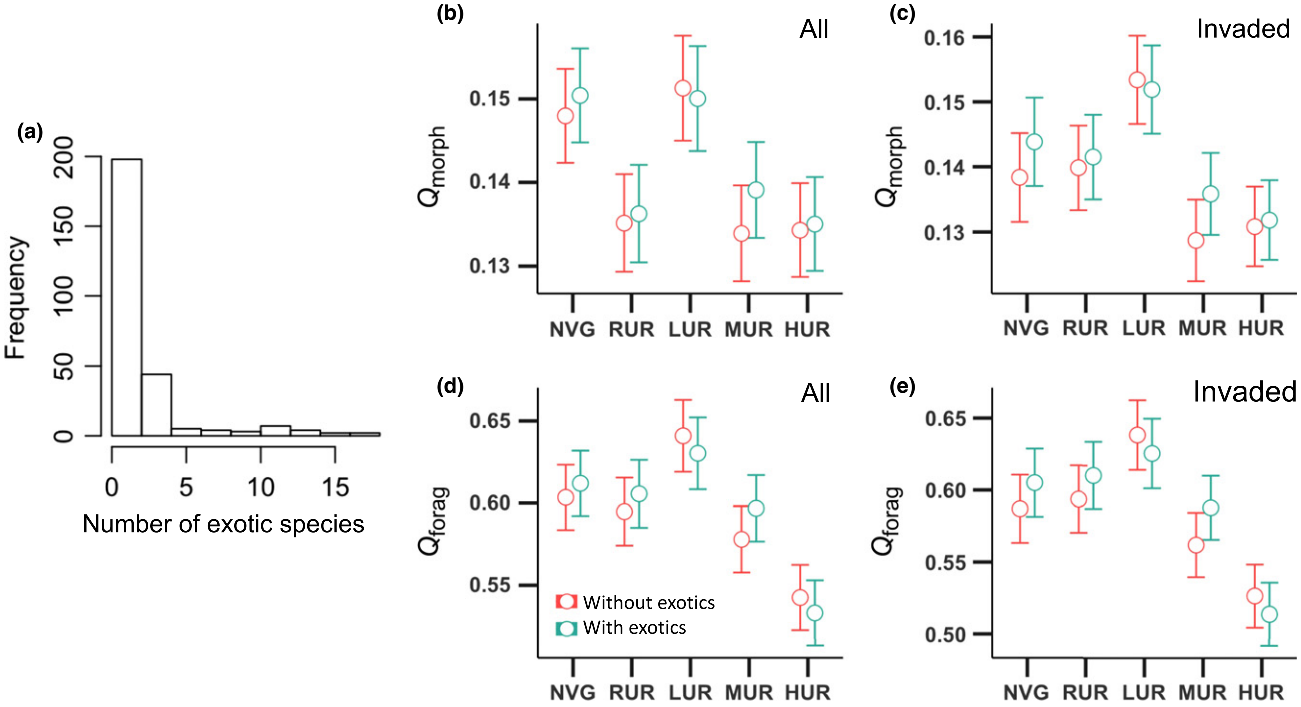

Figure 5 Influence of exotic species on changes in functional diversity (quadratic entropy, *Q*) across urbanization gradients. Frequency distribution (a) of the number of exotic species per assemblage. Changes in *Q* based on morphological traits (b and c) and foraging niche (d and e), with exotic species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

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 and 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–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 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 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 find 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 (Fig. 1a) and hence our findings may not apply to less industrialized (Fig. 1a) 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, 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 invertebrates (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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AUTHOR CONTRIBUTIONS

D.S., C.T., A.J. and S.P. conceived and designed the study; D.S., C.T., C.GL., A.L.P. and J.A.T. collected data; D.S., C.T., S.P. and C.R. designed the analyses, and D.S. and C.M. conducted the analyses; DS wrote the manuscript and all authors edited and approved it.

DATA AVAILABILITY STATEMENT

The data supporting the results are available on Dryad (https://doi.org/10.5061/dryad.2rbnzs7jf).

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

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