

1 **The worldwide impact of urbanisation on avian functional** 2 **diversity**

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4 Daniel Sol^{1,2*}, Christopher Trisos^{3,4*}, Cesc Múrria⁵, Alienor Jeliaskov^{6,7}, Cesar
5 González-Lagos^{8,9}, Alex L. Pigot¹⁰, Carlo Ricotta¹¹, Christopher M. Swan¹²,
6 Joseph A. Tobias^{13*}, Sandrine Pavoine^{14*}

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8 **Affiliations:**

9 ¹CSIC, Spanish National Research Council, CREAf-UAB, Catalonia 08193, Spain.

10 ²CREAF, Centre for Ecological Research and Applied Forestries, Catalonia 08193, Spain.

11 ³African Climate and Development Initiative (ACDI), University of Cape Town, South
12 Africa.

13 ⁴National Socio-Environmental Synthesis Center (SESYNC), University of Maryland,
14 Annapolis, MD, USA.

15 ⁵Grup de Recerca Freshwater Ecology, Hydrology and Management (FEHM) and Institut
16 de Recerca de la Biodiversitat (IRBio), Departament de Biologia Evolutiva,
17 Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona
18 (UB), Catalonia, Spain.

19 ⁶German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig,
20 Germany.

21 ⁷Department of Computer Science, Martin Luther University Halle-Wittenberg, 06099
22 Halle (Salle), Germany

23 ⁸Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS),
24 Universidad Bernardo O'Higgins, Santiago, Chile.

25 ⁹Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica
26 de Chile, Santiago, Chile.

27 ¹⁰Centre for Biodiversity and Environment Research, Department of Genetics, Evolution
28 and Environment, University College London, London, WC1E 6BT, UK.

29 ¹¹Department of Environmental Biology, University of Rome 'La Sapienza', 00185 Roma,
30 Italy.

31 ¹²University of Maryland Baltimore County, Baltimore, Maryland, USA.

32 ¹³Department of Life Sciences, Imperial College London, Berkshire SL5 7PY, UK.

33 ¹⁴Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national
34 d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne
35 Université, 75005 Paris, France.

36

37 *To whom correspondence should be addressed: Daniel Sol: d.sol@creaf.uab.cat;

38 Christopher Trisos: christophertrisos@gmail.com; Joseph A. Tobias:

39 j.tobias@imperial.ac.uk; Sandrine Pavoine: sandrine.pavoine@mnhn.fr

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46
47 Name and complete mailing address of the person to whom correspondence should be
48 sent: Daniel Sol, CREA-FC, Cerdanyola del Vallès, Catalonia E-08193, Spain. TEL:
49 +34 93-5814678. E-MAIL: d.sol@creaf.uab.cat
50

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52 C.T., C.G.L., A.L.P. and J.A.T. collected data; D.S., C.T., S.P. and C.R. designed the
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55

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58 Figshare or Hal) and the data DOI will be included at the end of the article.
59

60 **Abstract. Urbanisation is driving rapid declines in species richness and**
61 **abundance worldwide, but the general implications for ecosystem function**
62 **and services remain poorly understood. Here, we integrate global data on**
63 **bird communities with comprehensive information on traits associated with**
64 **ecological processes to show that assemblages in highly**
65 **urbanised environments have substantially different functional composition**
66 **and 20% less functional diversity on average than surrounding natural**
67 **habitats. These changes occur without significant decreases in functional**
68 **dissimilarity between species; instead, they are caused by a decrease in**
69 **species richness and abundance evenness, leading to declines in functional**
70 **redundancy. The reconfiguration and decline of native functional diversity in**
71 **cities are not compensated by the presence of exotic species but are less**
72 **severe under moderate levels of urbanisation. Thus, urbanisation has**
73 **substantial negative impacts on functional diversity, potentially resulting in**
74 **impaired provision of ecosystem services, but these impacts can be reduced**
75 **by less intensive urbanisation practices.**
76

77 Urban expansion is a major driver of land-use change, with a projected increase in
78 urban land cover of 1.2 million km² by 2030 (Seto *et al.* 2012). The process of
79 urbanisation is an extreme form of land-use intensification causing a reduction
80 and fragmentation of natural habitats, along with profound changes in human
81 disturbance and resource availability (McKinney 2002). Because such rapid and
82 extreme environmental alterations can cause local extinction (Bell 2017), it
83 follows that species richness in cities is often lower than in surrounding natural
84 habitats (Aronson *et al.* 2014; Sol *et al.* 2014; Ibáñez-Álamo *et al.* 2017). Species
85 loss is a concern because it can alter the stability and functioning of ecosystems
86 (Oliver *et al.* 2015), with negative consequences for ecosystem services and
87 human wellbeing (Díaz *et al.* 2006; Cardinale *et al.* 2012). However, previous
88 global analyses of the consequences of urbanisation have focused primarily on
89 quantifying species loss rather than estimating its broader impacts on ecosystem
90 functions (Díaz & Cabido 2001; Díaz *et al.* 2011). With over half the human
91 population currently living in urban areas (United Nations 2018) and benefiting
92 directly from urban nature (Millenium Ecosystem Assessment 2010; Cardinale *et*
93 *al.* 2012), there is an urgent need for improved understanding of how urbanisation
94 affects components of biodiversity linked to ecosystem functions and services.

95 A major obstacle in addressing this challenge arises because the functional
96 effects of species loss are difficult to quantify in natural systems, particularly at
97 large scales (Winfree *et al.* 2015). Several factors complicate the issue, including
98 species niche overlap, non-random species extinctions, and the tendency for a few
99 abundant species to dominate the community (Flynn *et al.* 2009; Winfree *et al.*
100 2015). High overlap among niches increases functional redundancy, theoretically
101 reducing the impact of species loss on ecosystem function, whereas the extinction
102 of even a few species disproportionately contributing to function can substantially
103 alter ecosystem functioning in communities with low functional redundancy
104 (Flynn *et al.* 2009; Winfree *et al.* 2015). Asymmetries in abundance can also
105 weaken the effect of extinctions because the loss of rare species may have little
106 immediate impact on ecosystem functions and services (Winfree *et al.* 2015).

107 Perhaps the most tractable way of quantifying ecosystem functions
108 delivered by biodiversity at global scales is to look beyond species loss and to
109 focus instead on functional diversity—i.e. the identity, variety and relative
110 abundance of phenotypic traits of organisms that influence key ecosystem

111 processes (Tilman 2001; Petchey & Gaston 2002; Díaz *et al.* 2007). Evidence is
112 accumulating that species richness provides at best a crude estimate of ecosystem
113 function, resilience and stability, which are instead more closely related to metrics
114 of functional diversity (Hooper *et al.* 2005; Díaz *et al.* 2006; Flynn *et al.* 2011).
115 Recent studies applying these metrics have taken significant steps forward in
116 assessing the ecosystem consequences of urbanisation (Oliveira Hagen *et al.*
117 2017; La Sorte *et al.* 2018). However, progress has been limited because data on
118 functional traits related to ecosystem roles is often highly incomplete at global
119 scales (Tobias & Pigot 2019). Widespread gaps in data, and the use of broad
120 categorical traits (e.g. diet), weaken previous analyses by reducing sample sizes,
121 introducing biases, and over-estimating functional redundancy. In addition, the
122 use of geographical range polygons to estimate local communities tends to
123 underestimate changes in functional diversity with urbanisation (Oliveira Hagen
124 *et al.* 2017) and, more importantly, offers little insight into the drivers and wider
125 implications of those impacts.

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

139 Following previous studies (Newbold *et al.* 2015; Oliveira Hagen *et al.*
140 2017; Sol *et al.* 2017), we adopt a space-for-time substitution approach with the
141 diversity inside each city compared with the diversity in the surrounding non-
142 urbanised habitats. The space-for-time approach provides a standard alternative
143 when time-series data are unavailable (Winfree *et al.* 2011; Blois *et al.* 2013;

144 Oliveira Hagen *et al.* 2017; but see Damgaard 2019). Within cities, we distinguish
145 three levels of land-use intensity: highly urbanised environments (e.g. city
146 centres), moderately urbanised environments (e.g. suburbs), and little urbanised
147 environments (e.g. urban parks). Outside cities, we classify habitats as either rural
148 (i.e. human-modified) or natural vegetation. Finally, we combine habitat-specific
149 bird community data with complete species-level ecological trait data. For each
150 species we use a set of 47 traits, including morphological measurements and
151 foraging behaviour, to capture variation in how species interact with and
152 contribute to ecosystem functioning (see Materials and Methods).

153 To evaluate changes in functional diversity across the urban–wildland
154 gradient, we use Rao’s quadratic entropy framework (Shimatani 2001; Zoltan
155 2005; Pavoine 2012; Ricotta *et al.* 2016). Functional quadratic entropy (Q_f)
156 represents the expected dissimilarity between two individuals randomly drawn
157 from the community. The quadratic entropy framework represents an advance
158 from previous studies of urbanisation in that it captures the different facets of
159 functional diversity—trait identity, variety and abundance—while accounting for
160 the confounding effect of species richness (Ricotta *et al.* 2016). Furthermore, by
161 effectively partitioning the contribution of these different components to
162 functional diversity (Shimatani 2001), the framework enables a more detailed
163 exploration of how and why functional diversity changes with urbanisation.

164

165 **Materials and Methods**

166 **Survey data.** We gathered presence/absence and abundance data from published
167 studies and reports for well-characterized assemblages spanning cities and
168 surrounding habitats from Africa, Australia, Europe, North America and South
169 America (**Fig. 1a**). We restricted the analyses to cases where comparable local
170 survey data were available within urban habitats and in nearby rural and/or natural
171 habitats. The final dataset contained almost 10,000 records of bird species from
172 319 local assemblages distributed across 50 regions. Species abundance per unit
173 area or unit time were available for 269 of these assemblages, spanning 42 cities.
174 Of the 1507 bird species detected during the surveys, 66 were exotic (invasive or
175 non-native species) in at least one study region (**Appendix 1**). Following

176 Newbold *et al.* (2015), we used published habitat descriptions to classify each
 177 assemblage into three categories reflecting the intensity of human use in urban
 178 habitats (**Table S1**): (1) highly urbanised environments (HUR) mainly contain
 179 densely packed buildings with vegetation scarce or absent; (2) moderately
 180 urbanised environments (MUR) are residential areas with single-family houses
 181 and associated gardens (Marzluff 2001); and (3) little-urbanised environments
 182 (LUR) have few buildings and abundant vegetation (e.g. urban parks). The
 183 habitats outside the city were assigned to either natural vegetation (NVG) or rural
 184 habitat (RUR) based on the description of the habitat given in the source paper
 185 (for justification see Sol *et al.* 2014, 2017). Standardised survey methods were
 186 used across habitats within each region, although not always with the same
 187 sampling effort (**Table S1**). Some abundance metrics—those not reported as
 188 densities per unit time, distance, area or volume sampled—were sensitive to
 189 sampling effort (Newbold *et al.* 2015). In these cases, we estimated effort-
 190 corrected abundance values by dividing the abundance measurement by sampling
 191 effort (Newbold *et al.* 2015). To ensure that communities were accurately
 192 sampled and unbiased across land use types, we used sample-size-based
 193 rarefaction curves and estimated species richness after rarefaction to the median
 194 observed community size.

195 **Functional traits.** To describe major axes of niche variation across our sample of
 196 1488 bird species, we compiled comprehensive datasets of two types of traits
 197 (**Table S2**). First, we used data from Pigot *et al.* (2019) on eight morphological
 198 traits measured with callipers from museum specimens (**Appendix 2**). The traits
 199 include beak length, depth and width (to describe major axes of variation in beak
 200 morphology, the primary resource related trait in birds), wing length and first
 201 secondary feather length (to describe variation in wing shape, related to flight
 202 strength and dispersal ability), tarsus length and tail length (related to
 203 microhabitat and foraging substrate) and body size (related to energetic
 204 constraints, competitive ability and pace of life)(Cannon *et al.* 2019). In addition,
 205 we used the length of the wing and first secondary feather to estimate the hand-
 206 wing index (Claramunt *et al.* 2012). Together, these traits have previously been
 207 shown to provide an accurate index of avian trophic niches (Pigot *et al.* 2019). All
 208 morphological variables were log-transformed before analyses. Second, we

209 compiled published data describing both foraging niche and dietary niche for all
 210 study species (Pigot *et al.* 2019; **Appendix 3**). We did this because although
 211 morphology accounts for substantial variation in the avian niche (Pigot *et al.*
 212 2016b, 2019), the functional role of a species in an ecosystem may be more
 213 directly inferred by how the species uses resources (Petchey & Gaston 2006;
 214 Oliveira Hagen *et al.* 2017). For instance, species that primarily rely on fruits are
 215 expected to play roles in seed dispersal whereas those that eat insects should
 216 contribute to invertebrate control (Chan *et al.* 2016). Extending the simplified
 217 behavioural classification presented for all birds by Tobias & Pigot (2019), we
 218 classified species according to the proportional use of 30 different foraging
 219 behaviours across eight dietary categories (**Table S2**), providing insights into the
 220 trophic structure of communities at an unprecedented resolution. To further
 221 interpret some of the results, we used a simplified version focused on the dietary
 222 niche (**Table S2**). To describe major axes of variation in morphology, we used the
 223 two-step principal component analysis (PCA) process proposed by Trisos *et al.*
 224 (2014), while variation in dietary and foraging niches were obtained by means of
 225 a Principal Coordinates Analysis (PCoA), based on Manly distances (Manly
 226 1986). Results of these ordination analyses are shown in **Table S3**.

227

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

$$232 \quad Q_f = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j$$

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

240 assemblage by the sum of all individuals in the assemblage, including exotic
 241 species when present.
 242
 243 **Decomposition of Q .** Following Shimatani (2001), quadratic entropy was
 244 decomposed into three components (**Fig. 2a**): (1) the Gini-Simpson index , where
 245 p_i is the relative abundance of species i ; (2) the average dissimilarity between two
 246 species , where S is the number of species and d_{ij} the functional difference
 247 between species i and j ; and (3) a balance component describing the covariance
 248 between species' abundance and the functional dissimilarities between species
 249 (BC), such as $Q = H_{GS} * meanD + BC$. To facilitate interpretation, we transformed
 250 BC to a correlation coefficient. To further interpret the results, we also estimated:
 251 (4) the abundance evenness index (I_e) independent of species richness (N) as $I_e =$
 252 $H_{GS} * S / (S - 1)$; (5) community-level functional redundancies as $1 - Q / H_{GS}$ (Ricotta *et*
 253 *al.* 2016); and (6) species-level functional uniqueness, as the mean functional
 254 dissimilarity of a species from the rest of the species in the region (Ricotta *et al.*
 255 2016; Pavoine *et al.* 2017). These metrics were estimated with the R-package adiv
 256 (Pavoine 2018) and our own R code, available upon request.

257
 258 **Functional β -diversity.** Functional β -diversity was estimated using the
 259 decomposition of Rao's quadratic entropy index (following Ricotta & Szeidl
 260 2009) and the betaQmult function developed by Vill  ger *et al.* (2012). To estimate
 261 the influence of species identities (taxonomy) and the contribution of the turnover
 262 and nestedness components on the overall functional β -diversity, we also
 263 estimated a multidimensional functional space for the morphological and foraging
 264 traits using, respectively, the PCA and PCoA axes (Vill  ger *et al.* 2012). The
 265 pairwise β -diversity in functional composition between communities was
 266 estimated using Jaccard's dissimilarity index which can be decomposed into the
 267 functional turnover and nestedness, as implemented in 'betapart' (Baselga &
 268 Orme 2012). Strict turnover corresponds to replacement of trait composition while
 269 the functional richness remains constant, whereas nestedness corresponds to
 270 subsetting in trait composition due to a non-random gain or loss of traits (Baselga
 271 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 species intolerance 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.

313

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 (Briec *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 Briec *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.

338

339 Results and Discussion

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

346 Although morphology accounts for substantial variation in the avian niche
347 (Pigot *et al.* 2016b, 2019), the functional role of a species might be more directly
348 inferred by how species use resources (Petchey & Gaston 2006; Oliveira Hagen *et*
349 *al.* 2017). We therefore repeated the analyses with our comprehensive dietary and
350 behavioural classifications of species, which enabled the characterisation of their
351 foraging niches at an unprecedented resolution. We found that functional
352 quadratic entropy of foraging niches (Q_{forag}) is maintained in rural and moderately
353 urbanised habitat compared to surrounding natural vegetation and even increases
354 in little urbanised habitat (**Fig. 1c**). In contrast, Q_{forag} tends to be lower in highly
355 urbanised habitats than in natural vegetation, with a mean decline of 19% (**Fig.**
356 **1c,f,g**). Thus, both morphological and behavioural components of diversity show
357 a clear trend of greater losses of functional diversity in highly urbanised areas.

358 The loss of functional diversity in response to urbanisation may reflect the
359 local extinction of functionally unique species, particularly those occupying
360 foraging niches that are not available in highly altered urban habitats. This
361 explanation, however, appears unlikely for two reasons. First, we find no evidence
362 that tolerance to urbanisation, measured as change in abundance between highly
363 urbanised habitat and surrounding natural vegetation in each region (Evans *et al.*
364 2011; Sol *et al.* 2017), is lower in functionally unique species (**Table S4**). Second,
365 highly urbanised habitats—and, to a lesser extent, moderately urbanised areas—
366 are characterised by lower community-level functional redundancy (i.e., they
367 contain fewer individuals with similar functional traits) compared to natural
368 habitats (**Fig. S2**), a pattern particularly noticeably when using high resolution
369 data (i.e. foraging niche information). Thus, the loss of functional diversity in
370 highly urbanised habitats occurs despite a decrease in functional redundancy.

371 To explain these seemingly contrasting results, we decomposed functional
372 quadratic entropy for morphology and foraging niche into its three components

(Shimatzu 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

407 studies (Sol *et al.* 2014). However, species loss alone does not account for the
408 decline in the Gini-Simpson index. Abundance evenness among species—another
409 component of this index—also decreases with urbanisation (**Fig. 3c**), indicating
410 that highly urbanised regions (and those moderately urbanised, to a lesser extent)
411 are frequently dominated by a small number of highly abundant species (**Fig. 3d**).
412 These dominant species tend not to be functionally unique, as indicated by the
413 low values of the balance components (**Fig. 2b,c**), so their relative contribution to
414 functional diversity is generally low. Thus, the loss of functional diversity in
415 moderately and highly urbanised environments relative to surrounding natural and
416 rural habitats reflects a decrease in both species richness and abundance evenness.
417 However, decreases in species richness are lower in moderately urbanised areas
418 (Fig. 1c; Fig. 3), which help to explain the less pronounced loss of functional
419 diversity. In little urbanised habitats, the decrease in species richness is similar to
420 that observed for moderately urbanised habitats, but abundance evenness is
421 maintained compared to surrounding rural and natural vegetation. Thus,
422 functional diversity is highly preserved compared to highly and moderately
423 urbanised areas.

424 In addition to causing net changes in functional diversity, urbanisation has
425 the potential to reconfigure the functional composition of communities if species
426 with particular sets of traits are replaced by species with different sets of traits
427 more tolerant to the new environmental conditions (Loreau *et al.* 2001). There is
428 substantial turnover in species composition between natural vegetation and
429 urbanised habitats (**Fig. 4a**), with urban species representing a subset of adaptable
430 lineages drawn from a variety of natural and artificial habitats (Shochat *et al.*
431 2006; Sol *et al.* 2017). Functional β -diversity is also particularly high between
432 natural and highly urbanised habitats (**Fig. S6**) but, unlike species composition,
433 this is mainly driven by functional nestedness rather than turnover (**Fig. 4b,c,d**).
434 The contrasting patterns between taxonomic and functional β -diversities suggest
435 that urban specialists generally play similar functional roles to species that they
436 replace, implying again that the higher functional uniqueness of urban habitats
437 compared to natural habitats primarily arises from the loss of functionally
438 redundant species.

439 The analysis of multiple morphological and foraging niche features also
440 reveals shifts in the abundance-weighted mean community value of key functional

441 traits (**Fig. S7**). For instance, compared to natural areas, highly urbanised areas
442 exhibit a small but significant tendency to be dominated by larger bodied
443 individuals. This makes sense given that small-bodied species tend to be more
444 abundant in natural habitats than larger species (White *et al.* 2007), whereas in
445 highly urbanised environments the trend is reversed due to the relative abundance
446 of a few large-bodied birds such as pigeons, gulls and crows (**Fig. S8**). Our
447 analysis also reveals changes in highly urbanised assemblages along a number of
448 other functional dimensions, with an over-representation of individuals from
449 species with higher tarsus-to-tail-length ratio, more pointed wings, and more
450 granivorous diets, as well as a marked decline of individuals foraging on fruits or
451 invertebrates, particularly within specific foraging strategies (**Fig. S7**). Similar
452 changes are also observed in little and moderately urbanised habitats, most
453 notably in body size and shape, although these changes tend to be less frequent
454 and of lower magnitude for other functional dimensions compared with highly
455 urbanised habitats (**Fig. S7**). Again, these functional shifts are not only caused by
456 the loss of species but also by domination of urban environments by a small
457 number of highly abundant species (**Fig. S8**). We also show that functional shifts
458 are remarkably consistent across regions, likely because the species that best
459 tolerate urbanisation—and hence become dominant in the community—tend to
460 belong to a few avian lineages (Sol *et al.* 2014, 2017).

461 Our conclusion that functional diversity declines in highly urbanised areas
462 contrasts with the observation by Oliveira Hagen *et al.* (2017) that functional
463 diversity of urban avian assemblages is not consistently different from that of
464 non-urban assemblages. These discrepancies probably reflect methodological
465 differences in the scale of analysis and the metrics used to estimate functional
466 diversity. Oliveira Hagen *et al.* (2017) used global data of species occurrence in
467 urban and non-urban avian assemblages located across the globe. While this
468 analysis provides realistic assessments of the overall importance of cities as
469 reservoirs of biodiversity, cities are in fact mosaics of habitats reflecting different
470 degrees of urbanisation. Greater habitat diversity within cities compared to semi-
471 natural areas dominated by a single habitat may thus under-estimate the real
472 impact of urbanisation, particularly in its most intensive forms. In addition, the
473 decline of functional diversity that we detected in highly urbanised areas was
474 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 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 (Oliveira Hagen *et al.* 2017). The observed local decline of many bird species in cities may have important

consequences for ecosystem resilience and human wellbeing (Bregman et al. 2016). For instance, 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). Avian predation has been identified as a dominant force controlling arthropods on plants in some urban areas (Kozlov et al. 2017). Likewise, loss of diversity in functional traits of seed dispersers means that seed dispersal efficiency across and into urban environments is 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 (Hougnier *et al.* 2006).

Although the relationship between changes in avian functional diversity and the delivery of ecosystem services in urban areas is complex, our findings 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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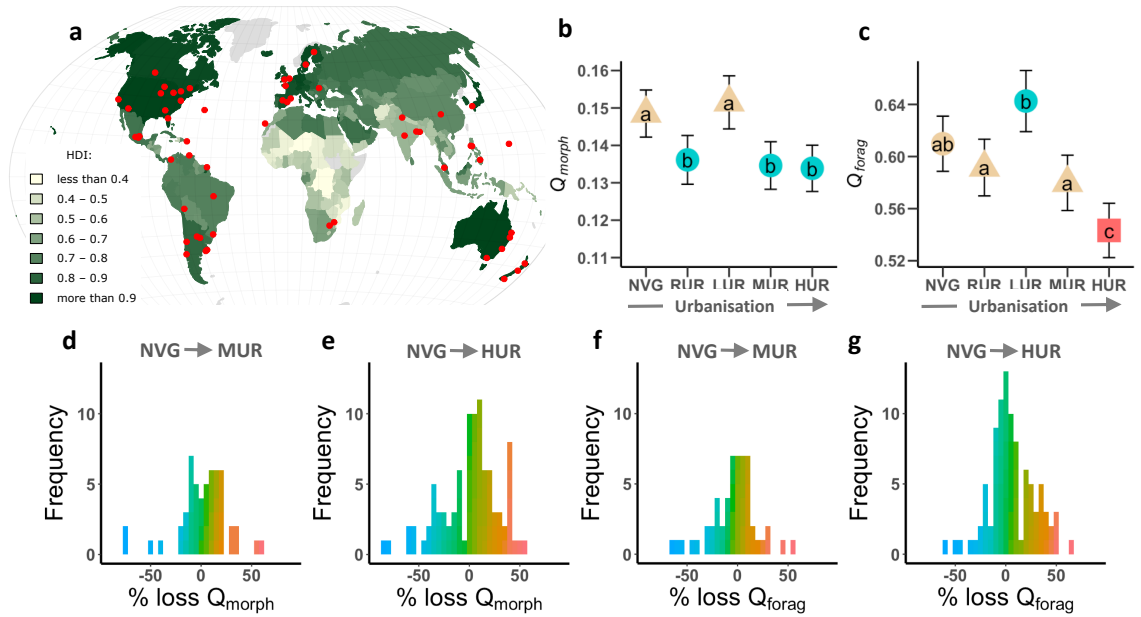


Figure 1 Changes in functional diversity across urbanisation gradients worldwide. a, Geographic location of 50 focal cities in relation to United Nations human development index (HDI). b-c, Effects of urbanisation on functional diversity (quadratic entropy, Q), based on morphological traits (b) and foraging niche (c), expressed as effect size (mean $\pm$ 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.

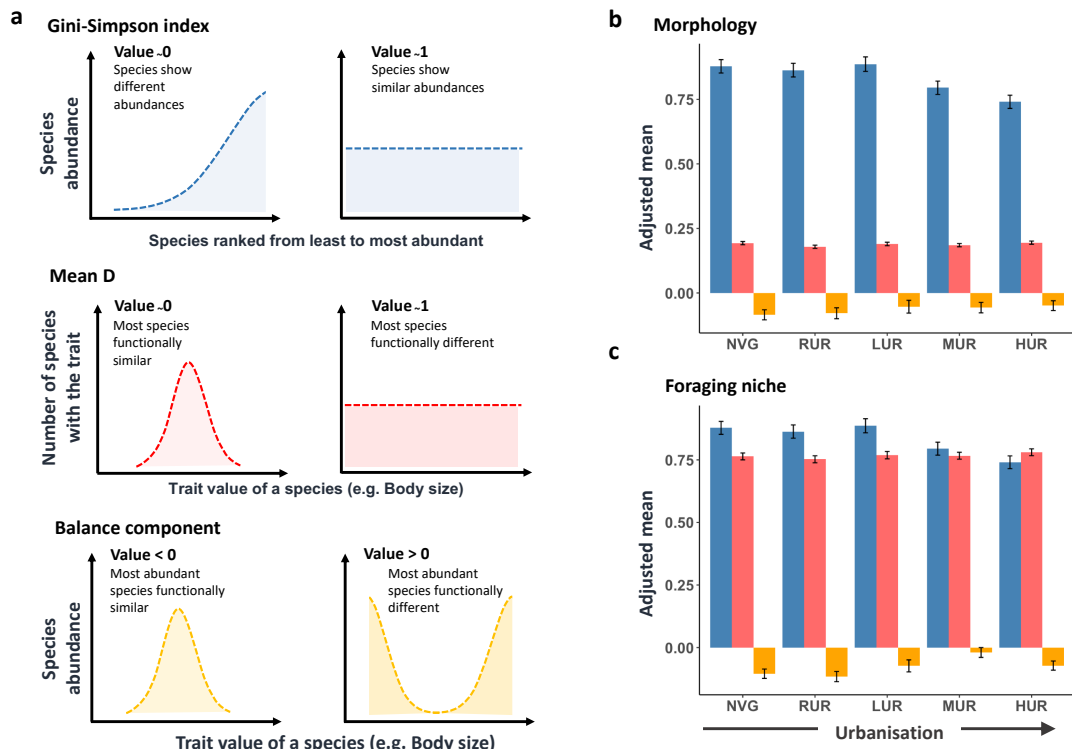
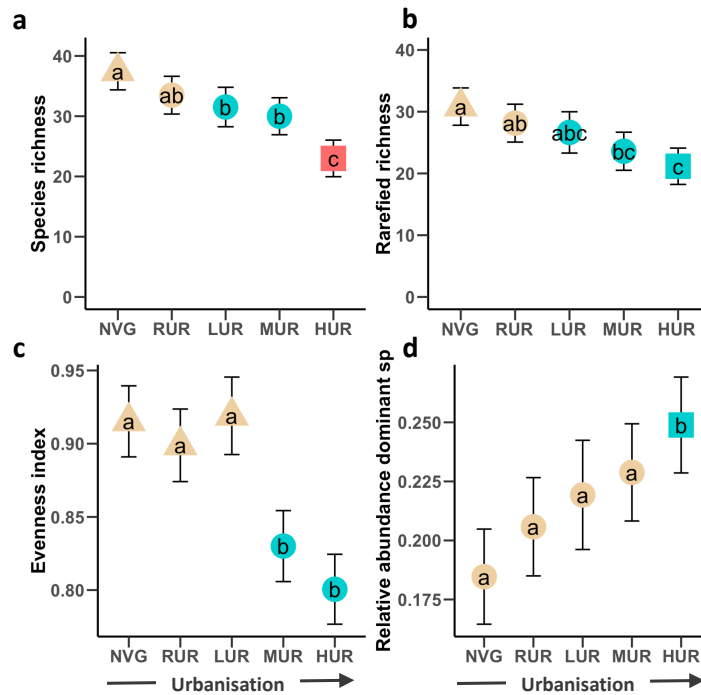


Figure 2 Decomposition of functional diversity across urbanisation gradients. Panel a illustrates the decomposition of functional quadratic entropy into the Gini-Simpson index (blue), unweighted mean functional dissimilarity (*mean D*, red) and balance component (orange). Panels b and c show variation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

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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.

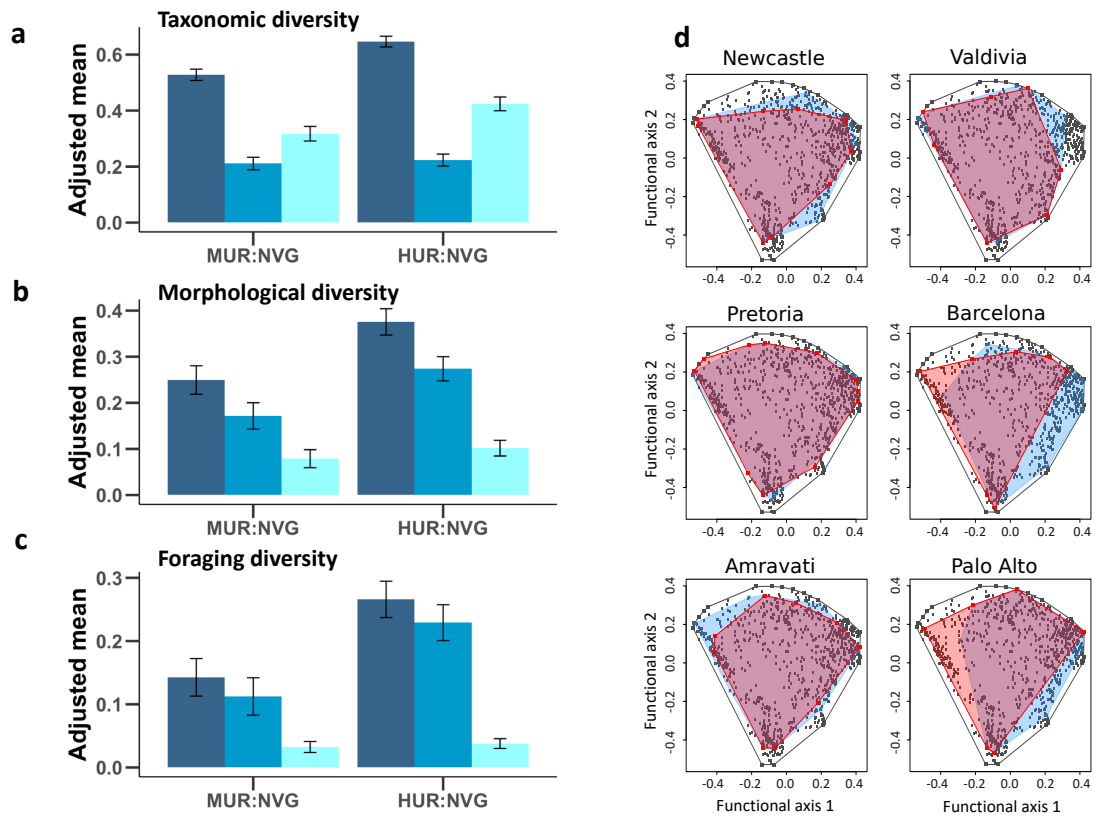
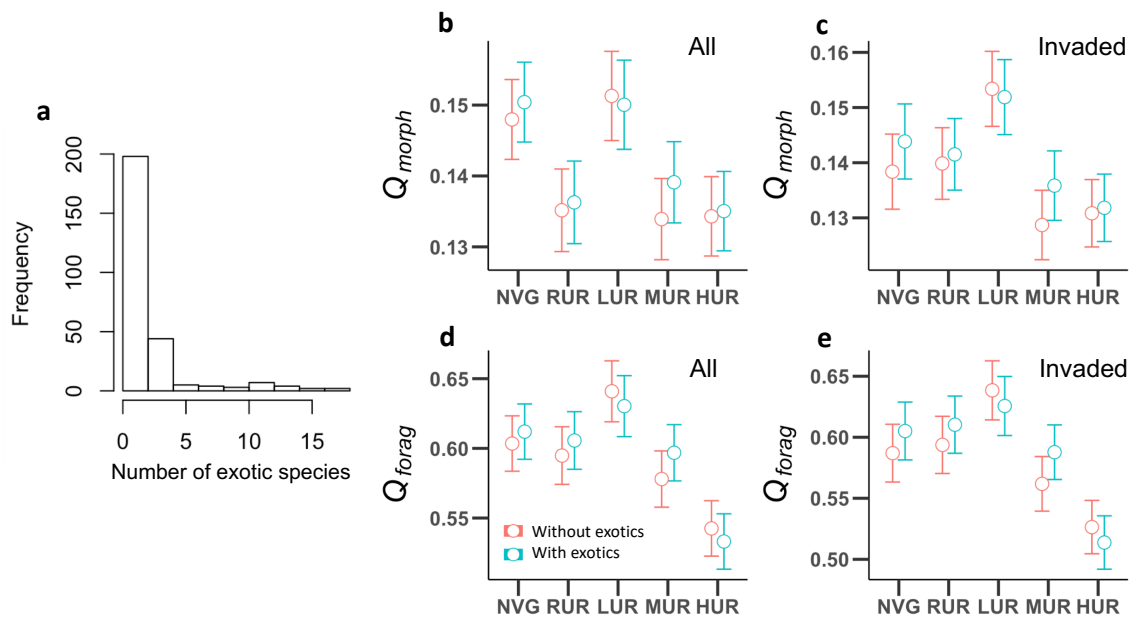


Figure 4 Changes in taxonomic and functional β -diversity across urbanisation gradients. Estimates of taxonomic (a), morphological (b) and foraging (c) β -diversity between urban and non-urban habitats (MUR: moderately urbanised; HUR: highly urbanised; NVG: natural vegetation). Overall β -diversity (dark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

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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 $\pm$ standard errors). Panels include either all assemblages (b-c) or only invaded assemblages (i.e. those with more exotics species) (d-e).