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Global macroecology of bird assemblages in urbanized and semi-natural ecosystems

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ABSTRACT

Aim Despite the increasing pace of urbanization, little is known about how this process affects biodiversity globally. We investigate macroecological patterns of bird assemblages in urbanized areas relative to semi-natural ecosystems.

Location World-wide.

Methods We use a database of quantitative bird surveys to compare key assemblage structure parameters for plots in urbanized and semi-natural ecosystems controlling for spatial autocorrelation and survey methodology. We use the term 'urbanized' instead of 'urban' ecosystems as many of the plots were not located in the centre of towns but in remnant habitat patches within conurbations.

Results Some macroecological relationships were conserved in urbanized landscapes. Species–area, species–abundance and species–biomass relationships did not differ significantly between urbanized and non-urbanized environments. However, there were differences in the relationships between productivity and assemblage structure. In forests, species richness increased with productivity; in both forests and open habitats, the evenness of species abundances declined as productivity increased. Among urbanized plots, instead, both species richness and the evenness of species abundances were independent of variation in productivity.

Main conclusions Remnant habitats within urbanized areas are subject to many ecological alterations, yet key macroecological patterns differ remarkably little in urbanized versus non-urbanized plots. Our results support the need for increased conservation activities in urbanized landscapes, particularly given the additional benefits of local experiences of biodiversity for the human population. With increasing urbanization world-wide, broad-scale efforts are needed to understand and manage the effects of this driver of change on biodiversity.

Keywords

Birds, conservation biogeography, environmental impacts, habitat heterogeneity, more-individuals hypothesis, rarity, scale, species–energy relationship, species–people coexistence, urban ecology.

INTRODUCTION

Urbanized areas are characterized by high human population densities. They are a dynamic patchwork of remnant semi-natural habitats in a matrix of residential, commercial and industrial infrastructure. Urbanized landscapes cover less than 5% of the global land area, but are inhabited by roughly half of the world's human population (Cohen, 2004; McDonald, 2008). The proportion of people living in urbanized areas continues to grow, due to human population increase, economic development and social trends (Grimm *et al.*, 2008; Sodhi, 2008).

There is a perception that ecologists focus their investigations on pristine ecosystems and neglect those heavily influenced by humankind (for birds, e.g. McDonnell & Pickett, 1990; Blair, 1996; Miller & Hobbs, 2002). However, such a criticism, at least in absolute terms and for birds, is no longer warranted, as many studies of avian assemblages have been carried out in urbanized areas (Jones & Wieneke, 2000; Marzluff *et al.*, 2001; Lim & Sodhi, 2004). This provides great opportunities to understand broad patterns in the assemblage structure of birds in urbanized ecosystems.

To date, the majority of comparative studies of the structure of urbanized avian assemblages have been relatively restricted in their geographic scope. They have included comparisons of avian assemblages before and after urbanization (e.g. Aldrich & Coffin, 1980; Idzelis, 1992), in urban and in neighbouring non-developed areas (e.g. Lussenhop, 1977; Natuhara & Imai, 1996) or in ecosystems at differing levels of urbanization (e.g. Guthrie, 1974; Crooks *et al.*, 2004). A few intra-continental (Jokimäki *et al.*, 1996, Jokimäki & Kaisanlahti-Jokimäki, 2003) and pair-wise inter-continental (Clergeau *et al.*, 1998, 2001; Jokimäki *et al.*, 2002) comparisons of urbanized avian assemblages have also been made. However, it remains unclear whether urbanized bird assemblages exhibit systematic macroecological patterns, and whether these are similar to those exhibited in other land-use types. Asking this question is important as it can provide deeper insights into the nature of bird community organization and how this is affected by today's pervasive human activities. We believe it is important to investigate this issue globally, as urbanization is now accelerating in countries outside the well-studied North American and European regions.

At a local scale, many ecological effects of urbanization have long been recognized, including alteration of resource flows, disturbance regimes, habitat distribution and species composition, and a frequently impoverished experience of nature by the human population (Turner *et al.*, 2004; Alberti, 2005; Miller, 2005). Whereas local case studies have reported decreases, increases or more complex changes in species richness, abundance and biomass in response to urban development (Hohtola, 1978; Lancaster & Rees, 1979; Blair, 1996; McKinney, 2002), at a broader grain and extent of analysis there is a general spatial co-occurrence of biodiversity and human population density (Luck, 2007; Pautasso, 2007; Fjeldså & Burgess, 2008).

The scale dependence of the spatial correlation between biodiversity and human population prompts the question of what form this relationship takes over a global extent, but using data from local plots. Given the pace of urban sprawl and the densification of existing urban areas (Breheny, 1997; Brueckner, 2000; Zimmermann *et al.*, 2010), it is of concern that little is known about the general effects of urbanization on local biodiversity (Clergeau *et al.*, 1998, 2006; Jokimäki & Kaisanlahti-Jokimäki, 2003; La Sorte, 2006). Thus, although there have been numerous local studies of how urbanization affects bird assemblage structure, a comprehensive analysis of the available data is lacking.

In this study, we compare fundamental macroecological patterns in urbanized versus more natural ecosystems (open and forest habitats). Natural and semi-natural ecosystems generally show positive species–area, species–abundance, species–biomass, abundance–area and species–productivity relationships (for birds, e.g. Currie *et al.*, 2004; Pautasso & Gaston, 2005, 2006; Mönkkönen *et al.*, 2006; Lepczyk *et al.*, 2008). Here we investigate whether these relationships persist in urbanized ecosystems.

Urban habitats have been reported to be relatively species poor (e.g. Hohtola, 1978; Blair, 1996), so it can be expected that the intercept of the species–area relationship is lower for urbanized compared with semi-natural habitats. A similar expectation holds for the species richness–productivity relationship. Conversely, as assemblage abundances have been reported to be higher in urban areas (e.g. Nuorteva, 1971; Lancaster & Rees, 1979; Cam *et al.*, 2000), the intercept of the assemblage abundance–plot area relationship is expected to be higher for urbanized than semi-natural ecosystems. Since urban areas have been reported to exhibit lower species richness but higher assemblage abundance (Chiari *et al.*, 2010), the species richness–abundance relationship is predicted to have either a lower intercept or a steeper slope in urbanized than in semi-natural ecosystems. We also inquire whether the proportion of exotic species varies with increasing species richness in urbanized areas.

The analysis allows a test of the more-individuals hypothesis as a broad-scale explanation of patterns in species richness in urbanized ecosystems. The more-individuals hypothesis assumes that species-rich communities have larger populations, thereby reducing the chances of local extinctions (e.g. Srivastava & Lawton, 1998). Whilst such hypothesis is supported by the evidence in semi-natural ecosystems (e.g. Hurlbert, 2004; Yee & Juliano, 2007), the hypothesis has been little tested in ecosystems strongly modified by humans and over comprehensive geographic scales (Rowhani *et al.*, 2008; Chiari *et al.*, 2010). For the relationship between evenness of species abundances and productivity, we expect a lower intercept in urbanized than in semi-natural ecosystems because urban assemblages have been reported to show a higher dominance of the most abundant species (e.g. Tomiałojć, 1970; Nuorteva, 1971; Beissinger & Osborne, 1982).

Birds were chosen as the taxon of study as they are relatively well studied, are frequently used to assess the conservation value of native habitats and can be useful surrogates for other components of biodiversity (e.g. Sodhi *et al.*, 1999; Hurlbert & Haskell, 2003; Kent, 2005). Making use of a growing number of

studies investigating urbanized avian assemblages and comparing them with nearby assemblages in non-urbanized habitats, we aim at a globally coherent investigation of the impact of urbanization on avian assemblage structure.

MATERIALS AND METHODS

Analyses were based on a new global database of quantitative bird surveys (see Appendix S1 in Supporting Information). We assembled data from the literature (1930–2003) on breeding bird assemblages in forest (557 plots), open (308 plots) and urbanized (184 plots) habitats across the planet (Fig. 1a,b). Plots were categorized as urbanized even if they were located in green areas within towns or in suburbia. Data retrieval from the published literature and the analytical methods used are described with more detail in previous studies focusing, respectively, on patterns in territory mapped forest plots and on the generalized individuals–area relationship (Pautasso & Gaston, 2005, 2006).

In the analyses reported here, habitat types were grouped into an urbanized subset (any habitat type in the presence of urbanization), an open habitat subset (cropland, pasture, tundra, grassland/steppe, hot desert) and a forest subset (wooded tundra, boreal forest, cool conifer forest, temperate mixed forest, temperate deciduous forest, warm mixed forest, tropical woodland, tropical forest). All the reported patterns for open habitats are qualitatively similar including and excluding cropland and pasture, and quantitative differences do not affect any of the conclusions drawn. Surveys were included in the analyses irrespective of their methodology (territory mapping, line transects and point counts) but its potential confounding effect was controlled for in models by including survey method as a categorical variable. Variable distance surveys were excluded because plot area is not fixed in such designs. Surveys with fewer than eight visits were excluded to minimize the confounding effect of variation in survey effort among plots.

Productivity data were matched to plots with a spatial join in a GIS environment at a 0.5° resolution. As a measure of productivity, we used the Fourier-adjusted, sensor and solar zenith angle corrected, interpolated, reconstructed (FASIR) adjusted normalized difference vegetation index (NDVI). The NDVI dataset used provides a 17-year, satellite record of monthly changes in the photosynthetic activity of land vegetation (Los *et al.*, 2000). Using mean annual net primary productivity (NPP) data instead of NDVI did not change results qualitatively, and quantitative differences did not affect any conclusions. Also including survey year in models did not affect parameter estimates for the other factors, as survey year was not a significant factor in the models studied. Explanatory variables recorded for each plot included: plot area (range for forest, open habitat and urbanized plots: 0.002–13, 0.005–14.7, 0.009–15.3 km^2), latitude (43° S–66° N, 40° S–71° N, 37° S–59° N), longitude (148° W–173° E, 157° W–153° E, 123° W–175° E), survey year (1940–98, 1924–99, 1953–97), NPP (0.2–11.4, 0.4–11.6, 0.2–11.3 kg C year^{-1} m^{-2}) and NDVI (0.20–0.81, 0.04–0.75, 0.33–0.77).

Derived variables include number of species at the plot with indication of density (4–319, 1–92, 2–67), assemblage abundance (2–10,402, 2–5533, 1–3549 individuals plot^{-1}), assemblage biomass (0.1–1386, 0.03–3196, 0.1–510 kg plot^{-1}) and evenness of species abundances [Bulla's O (Bulla, 1994) = 0.058–0.889, 0.154–1, 0.219–1]. Bulla's O is a measure of evenness which is expected to be independent of variations in species richness amongst assemblages (Bulla, 1994). All these derived variables do not include species present at such small numbers as to seriously thwart their detection or a meaningful estimation of
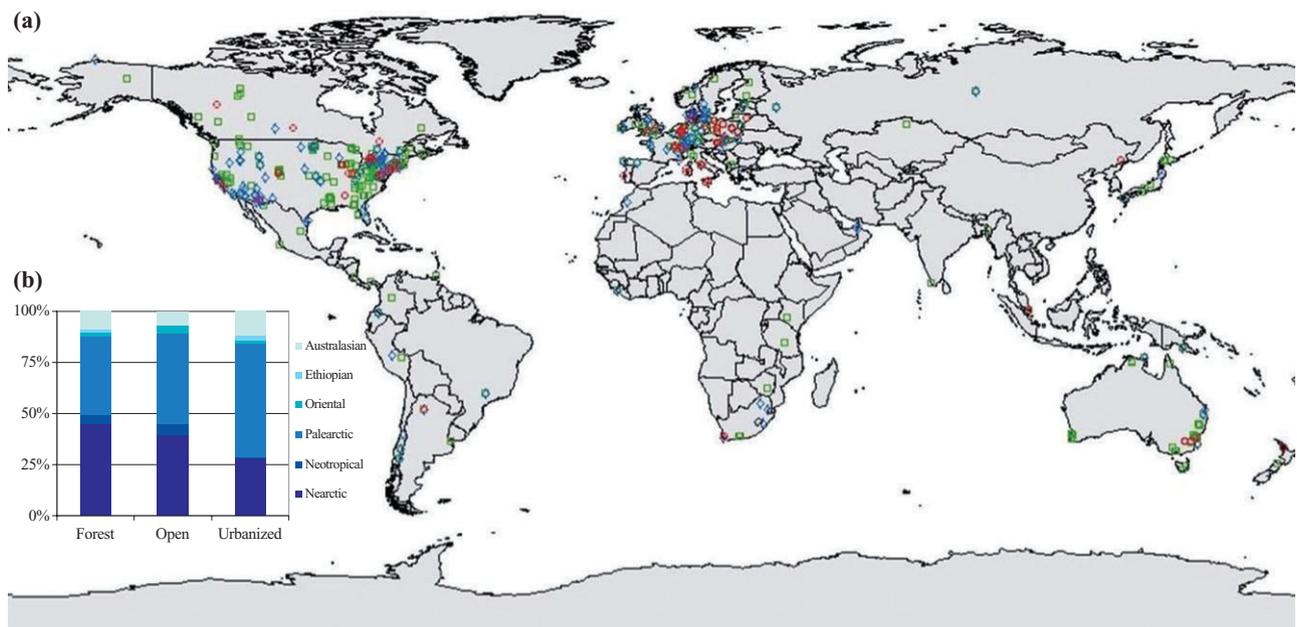

Figure 1 (a) Geographic distribution of survey plots analysed (symbols: green squares = forest, blue diamonds = open habitats, red triangles = urbanized habitats). (b) Proportional representation of different biogeographic regions in the studies analysed.

their abundance, whereas the species richness used in models is the total number of species counted in a plot. However, results of models using for species richness the number of species with an abundance entry are consistent with those using total species richness. Abundances are expressed in per plot terms and not per unit area to avoid spurious correlations in models controlling for plot area, for relationships of the form x/y as a function of y (Brett, 2004). Body masses for 90% of the bird species with an abundance entry in the whole database were retrieved from published monographs or existing compilations; for the remaining species generic means were assigned. Native versus exotic status was assigned on the basis of whether the plot in which a certain species occurred was located within or outside the historical distributional range of the same species.

All variables were log-transformed prior to analysis, except for NPP, NDVI and evenness of species abundances, which were already approximately normally distributed. Differences in the slopes and, in case of non-significantly different slopes, in the intercept of linear regressions of data from urbanized versus forest and versus open habitats were assessed on the basis of 84% confidence intervals (not 95% intervals because both regression parameters are estimated with an error; Payton *et al.*, 2003). A sequential Bonferroni correction of significance values was used to account for multiple tests (Rice, 1989). Throughout our analyses, we controlled for the potentially confounding effect of spatial autocorrelation by fitting a spatial covariance matrix to the data and using this to adjust statistical tests accordingly (Littell *et al.*, 1996). Mixed models were run in SAS 8.2. using an exponential covariance structure, after having ascertained its better fit (in terms of both the Akaike and Bayesian information criteria) to the null model for all independent variables compared with spherical, Gaussian, linear, linear-logarithm and power structures. A nugget parameter was added to the two governing the converging process because of marked variations in the response variable at a small scale hindering convergence. Convergence was sought with no more than 50 iterations of the mixed model at a significance level of 10^{-5}. We used absolute distances after reprojection of latitudes and longitudes of plots to Lambert conical coordinates for each biogeographic region.

RESULTS

Despite considerable statistical power, the species–area relationship did not differ significantly among the three habitat types in slope or intercept (Fig. 2a, Table 1a). Likewise, the intercept and slope of the assemblage abundance–plot area relationship were not significantly different for urbanized versus non-urbanized habitats (Fig. 2b, Table 1b). Also, there were no significant differences in the species richness–assemblage abundance relationship in urbanized compared with forest and open habitats (Table 1c). These results show remarkable robustness of avian macroecological patterns to urbanization.

Positive species richness–assemblage biomass relationships were found in both urbanized areas and in the other habitat types, with no significant difference in intercept and slope of these relationships (Table 1d). However, there were some differences in the relationships involving productivity, although there were no significant differences in a comparison of slopes and intercepts of the relationships. On the one hand, species richness increased with productivity in forests (Fig. 3a, Table 1e) and the evenness of species abundances declined as productivity increased in both forests and open habitats (Fig. 3b; Table 1f). On the other hand, amongst urbanized plots both species richness and the evenness of species abundances did not vary significantly with variation in productivity (Fig. 3a,b, Table 1e,f).

As a greater proportion of urbanized plots was studied in the Palaearctic (Fig. 1b), a biogeographic region which is not particularly species rich, the absence of significant differences in the species richness of urbanized plots compared with other habitats is probably not a consequence of differences in geographic representations between habitat types (geographic realm was in fact not a significant factor in all models analysed). Given that only species-poor urbanized assemblages showed a high proportion of exotic species (Fig. 4), there was a decrease in the proportion of exotic species with increasing species richness in urbanized areas.

Results were confirmed when analysing the data overlapping in their range for the x variable, i.e. leaving out of the analysis forest and open habitat plots outside of the range in the x variable (area, abundance, biomass and productivity) for the urbanized dataset (Table 2). An analysis of all data pooled together with habitat as a categorical factor confirmed the robustness of the investigated relationships to including main habitat as an explanatory factor (Table 3). Moreover, more variance was explained by main habitat when distinguishing between forest, open and urbanized habitat, rather than the distinction between urbanized and non-urbanized habitat (Table 3), which was often a non-significant factor in the model.

DISCUSSION

The quantitative similarities in species richness of urbanized and less perturbed habitats at a global scale (no significant differences in the species–area, –abundance and –biomass relationships) are remarkable given the array of changes in biotic and abiotic conditions accompanying urbanization (Baccini, 1997; Marzluff & Ewing, 2001; Foley *et al.*, 2005). These results underline the biodiversity value of urbanized landscapes in the face of the trend for local infilling and densification in currently undeveloped remnant natural areas.

In addition, the surprisingly high numbers of species in urbanized ecosystems reported here can be part of the daily experience of nature and environmental education of people living in densely populated regions around the world (Fernández-Juricic & Jokimäki, 2001; Fuller *et al.*, 2007; Pautasso & McKinney, 2007). This educational role is important in spite of the generally lower conservation value of the species composition of urbanized assemblages (McKinney, 2006). Moreover, the slope of the species–area relationship in urbanized ecosystems is, at least in absolute terms, the greatest
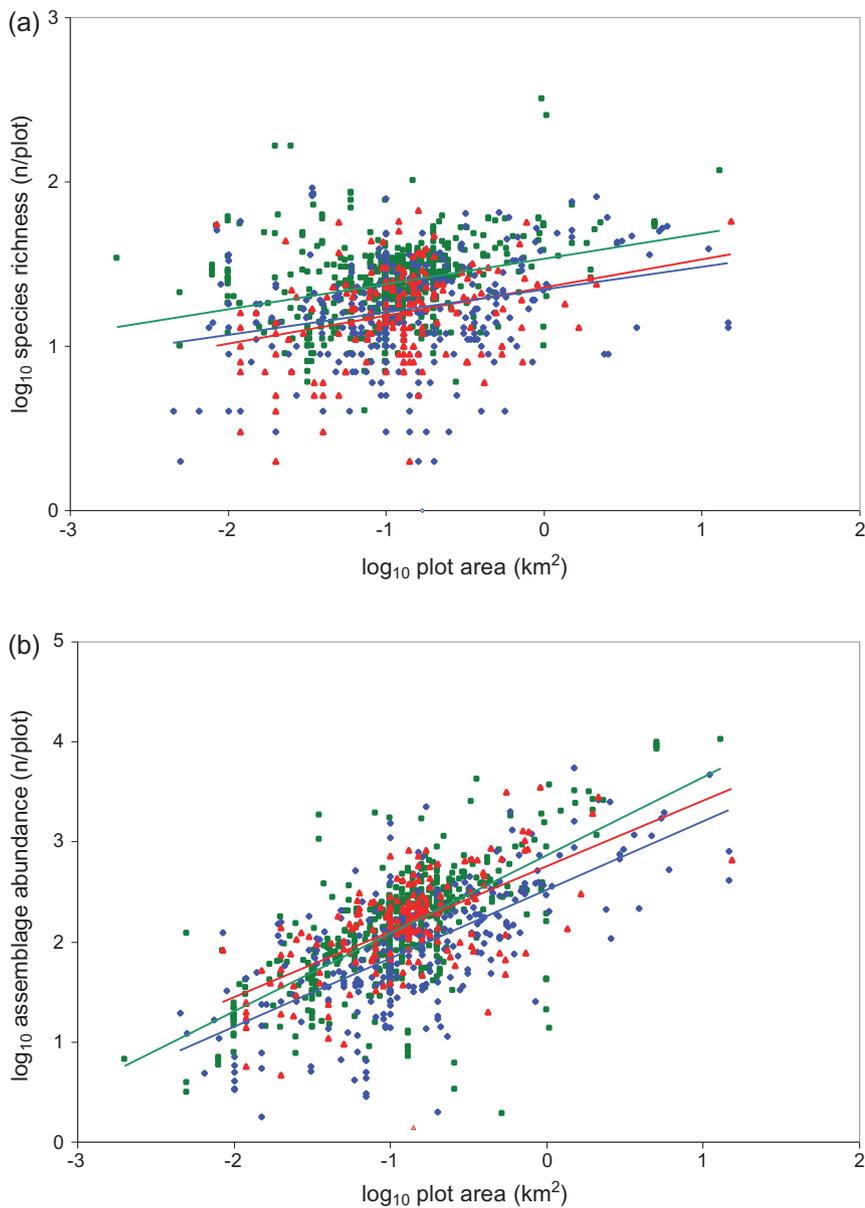
(a)

(b)

Figure 2 (a) Species richness–plot area relationship and (b) assemblage abundance–plot area relationship (see Table 1 for parameter estimates and *P* values controlling for spatial autocorrelation, and survey methodology) (symbols: green squares = forest, blue diamonds = open habitats; red triangles = urbanized habitats).

amongst the three datasets, suggesting a high spatial turnover of species and habitat heterogeneity with increasing plot area in urbanized landscapes.

Our results are not likely to simply be explained by a high richness of exotic species in urbanized assemblages, since the vast majority of species in most urbanized plots were native, and only species-poor urbanized assemblages showed a high proportion of exotic species. Possible explanations for this pattern, clearly deserving further investigation, are that: (1) unsaturated avian urbanized assemblages are more prone to invasion by exotic species, (2) invasion by exotic species impoverishes urbanized assemblages, and/or (3) a few exotic species are best able to cope with highly urbanized areas – hence the frequent presence of feral pigeons (*Columba livia*), common mynas (*Acridotheres tristis*) and house sparrows (*Passer domesticus*) in the most highly urbanized locations.

The lack of variation in the species–area relationship between urbanized and more natural ecosystems could be a consequence of the positive large-scale association between alpha diversity and human population density. Areas suitable for urban development often coincide with regions of high biodiversity, as both tend to have high productivity (Pidgeon *et al.*, 2007; Cantarello *et al.*, 2010). Urbanization might also directly increase energy availability, thus enabling the colonization and coexistence of more species. This effect may be common in arid ecosystems, where urbanization is associated with increased water availability, irrigated vegetation and greater vertical habitat stratification (Crooks *et al.*, 2004). A further, non-mutually exclusive explanation for the surprising diversity of bird communities in urbanized landscapes is the high habitat heterogeneity of these regions (Barbosa *et al.*, 2010; Pecher *et al.*, 2010).

Table 1 Mixed models of avian assemblage parameters in forests (f), open (o) and urbanized (u) habitats.

	Model	Habitat	Model R^2	Slope	Diff. sl.	Intercept	Diff. int.
a	Species richness versus plot area	f	0.14	+0.19 ± 0.02***	n.s.	1.68 ± 0.07	n.s.
		o	0.15	+0.18 ± 0.03***	n.s.	1.36 ± 0.06	n.s.
		u	0.10	+0.27 ± 0.04***		1.48 ± 0.05	
b	Abundance versus plot area	f	0.48	+0.81 ± 0.03***	n.s.	2.86 ± 0.06	n.s.
		o	0.47	+0.72 ± 0.05***	n.s.	2.62 ± 0.05	n.s.
		u	0.43	+0.68 ± 0.05***		2.90 ± 0.07	
c	Species richness versus abundance	f	0.31	+0.29 ± 0.02***	n.s.	0.83 ± 0.08	n.s.
		o	0.41	+0.35 ± 0.03***	n.s.	0.44 ± 0.09	n.s.
		u	0.35	+0.36 ± 0.05***		0.47 ± 0.15	
d	Species richness versus biomass	f	0.42	+0.26 ± 0.02***	n.s.	1.26 ± 0.08	n.s.
		o	0.37	+0.26 ± 0.02***	n.s.	0.96 ± 0.11	n.s.
		u	0.33	+0.26 ± 0.04***		1.07 ± 0.20	
e	Species richness versus NDVI	f	0.15	+0.35 ± 0.14*	n.s.	1.50 ± 0.10	n.s.
		o	0.18	+0.40 ± 0.22 n.s.	n.s.	1.18 ± 0.11	n.s.
		u	0.17	+0.50 ± 0.46 n.s.		1.26 ± 0.23	
f	Evenness of abundances versus NDVI	f	0.27	−0.16 ± 0.02***	n.s.	0.78 ± 0.04	n.s.
		o	0.16	−0.12 ± 0.02***	n.s.	0.71 ± 0.04	n.s.
		u	0.21	−0.06 ± 0.04 n.s.		0.52 ± 0.06	

Apart from model R^2, results are given controlling for spatial autocorrelation; n.s. $P > 0.05$, *$P < 0.05$, ***$P < 0.001$ (Bonferroni correction). All models also control for survey methodology by including it as a categorical variable, and for plot area where not used as an independent variable. Parameter estimates are given together with their standard errors. Slope (Diff. sl.) and intercept (Diff. int.) of the relationships in forest and open habitats are compared with those of urbanized areas. The following variables were transformed prior to analysis: plot area ($\log_{10}$ plot area), species richness ($\log_{10}$ no. of species plot^{-1}), abundance ($\log_{10}$ no. of individuals plot^{-1}), biomass ($\log_{10}$ kg plot^{-1}). Evenness of species abundances is expressed as Bulla's O. NDVI, normalized difference vegetation index.

Studies from natural habitats commonly report an increase in species richness with increasing energy availability (e.g. Currie *et al.*, 2004; Pautasso & Gaston, 2005; Mönkkönen *et al.*, 2006). This does not appear to be the case for the urbanized ecosystems of this analysis, suggesting energy inputs (more food, higher predictability of food, irrigation, a more complex vegetation structure, higher temperature or a combination of these factors) deriving from human activities that are more important than elsewhere (Decker *et al.*, 2000). According to the more-individuals hypothesis, higher energy availability sustains populations at a greater number of individuals, which in turn enables the coexistence of more species (Srivastava & Lawton, 1998). However, if these energy inputs were translating into species in a similar way across the range of pre-existing environmental energy availability, then a positive species–energy relationship would also be found for urbanized plots. That this is not the case may suggest an effect of anthropogenic energy sources.

However, Fig. 3(b) shows that few studies of urbanized bird assemblages have been carried out at the lower end of the environmental productivity range. Whether this lack of data is causing the absence of a significant slope in the species–energy relationship for urbanized plots is an open question. It could just as well be argued that the lack of a significant increase in the relationship is caused by the low species richness values in the urbanized data points at the upper end of the environmental productivity range. Our results are confirmed when analysing the data that overlap in the productivity range. Nonetheless, further standardized (bird) survey work is needed at both ends

of the environmental productivity range (boreal and tropical towns) to resolve this issue. There are some data from tropical towns and cities, e.g. Jamaica (Oelke, 1968), Havana, Cuba (de las Pozas & Balát, 1981), Singapore (Sodhi *et al.*, 1999), Townsville, Australia (Jones & Wieneke, 2000), French Guyana (Reynaud & Thioulouse, 2000), but additional quantitative and comparative censuses from the tropics are needed, especially in view of the much higher biodiversity at stake in these regions compared with North America and Europe.

The absence of a positive species–energy relationship for urbanized birds is consistent with the finding that the evenness of species abundances in forest and open habitats decreases with increasing productivity, whereas that of urbanized assemblages does not vary significantly. At higher levels of energy availability there is no significant increase in rare species in urbanized assemblages as happens in natural habitats. This might be expected given that urbanized ecosystems are: (1) recently established and so not enough time may have elapsed for colonization by rare species, (2) fragmented and disconnected and thus often not able to sustain meta-populations of rare species, and (3) frequently colonized by generalist organisms which tend to appropriate the majority of artificial energy inputs to the detriment of rare species (Fernández-Juricic, 2000; Chace & Walsh, 2006; Schochat *et al.*, 2006; Fuller *et al.*, 2008).

Given that we have used data from bird surveys carried out for a wide range of purposes, some degree of noise will be inevitable. That many of the well-known macroecological relationships have been found, however, suggests that statistical power
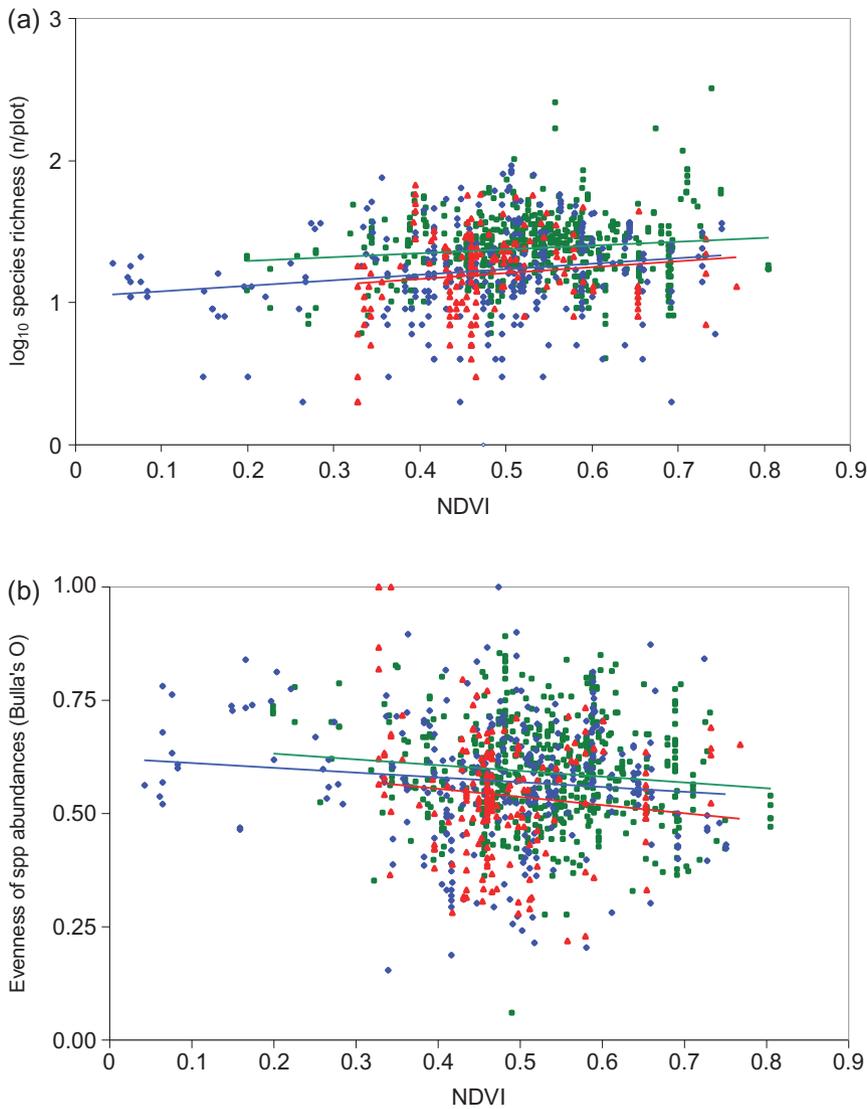
Figure 3 (a) Species richness–normalized difference vegetation index (NDVI) relationship and (b) evenness of species abundance–NDVI relationship. See Table 1 for parameter estimates and *P* values controlling for spatial autocorrelation, plot area and survey methodology (symbols: green squares = forest, blue diamonds = open habitats; red triangles = urbanized habitats).
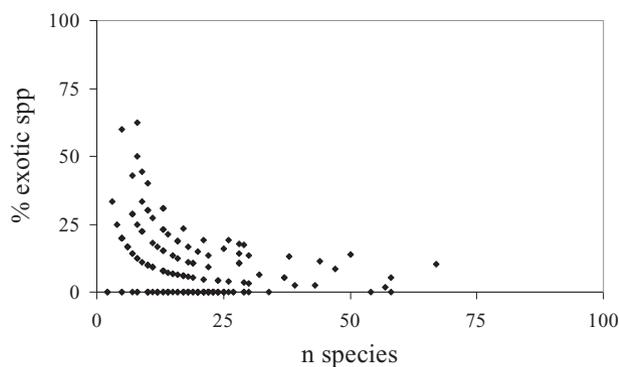

Figure 4 Proportion of exotic species as a function of total number of species in urbanized assemblages.

sent the three main habitats studied, some sampling bias towards green areas in urbanized ecosystems and the presence of pervasive human influences on bird communities also in non-urbanized plots. Clearly, robust and widespread standardized surveys would be required to confirm our results, though these would be difficult to achieve in practice for bird communities of the past decades.

Overall, our results suggest that urbanized landscapes support surprisingly diverse bird assemblages and therefore add importance to efforts aimed at the preservation of the remaining patches and greenways of semi-natural vegetation in areas of high human population density.

ACKNOWLEDGEMENTS

was sufficient. This said, the urbanized data used include plots from towns varying in age, size, human population density and proportion of built-up area. Furthermore, there will be differences in how accurately the sampled bird communities repre-

Table 2 Mixed models of avian assemblage parameters in forests (f), open (o) and urbanized (u) habitats, without data outside the urban range of the x variable for the forest and open dataset.

	Model	Habitat (*n* plots)	Model R^2	Slope	Diff. sl.	Intercept	Diff. int.
a	Species richness versus plot area	f (550)	0.14	$+0.19 \pm 0.02$***	n.s.	1.68 ± 0.07	n.s.
		o (304)	0.12	$+0.17 \pm 0.03$***	n.s.	1.36 ± 0.07	n.s.
		u (185)	0.10	$+0.27 \pm 0.04$***		1.48 ± 0.05	
b	Abundance versus plot area	f (550)	0.45	$+0.82 \pm 0.04$***	n.s.	2.87 ± 0.06	n.s.
		o (304)	0.46	$+0.72 \pm 0.05$***	n.s.	2.62 ± 0.06	n.s.
		u (185)	0.43	$+0.68 \pm 0.05$***		2.90 ± 0.07	
c	Species richness versus abundance	f (549)	0.31	$+0.32 \pm 0.02$***	n.s.	0.76 ± 0.08	n.s.
		o (305)	0.40	$+0.36 \pm 0.03$***	n.s.	0.40 ± 0.09	n.s.
		u (185)	0.35	$+0.36 \pm 0.05$***		0.47 ± 0.15	
d	Species richness versus biomass	f (552)	0.41	$+0.27 \pm 0.02$***	n.s.	1.24 ± 0.05	n.s.
		o (307)	0.36	$+0.25 \pm 0.03$***	n.s.	0.99 ± 0.06	n.s.
		u (185)	0.33	$+0.26 \pm 0.04$***		1.07 ± 0.20	
e	Species richness versus NDVI	f (539)	0.15	$+0.35 \pm 0.16$*	n.s.	1.52 ± 0.11	n.s.
		o (280)	0.18	$+0.09 \pm 0.32$ n.s.	n.s.	1.44 ± 0.17	n.s.
		u (185)	0.17	$+0.50 \pm 0.46$ n.s.		1.26 ± 0.23	
f	Evenness of abundances versus NDVI	f (539)	0.17	-0.39 ± 0.15**	n.s.	0.67 ± 0.07	n.s.
		o (280)	0.09	$+0.02 \pm 0.12$ n.s.	n.s.	0.53 ± 0.06	n.s.
		u (185)	0.21	-0.06 ± 0.04 n.s.		0.52 ± 0.06	

Apart from model R^2, results are given controlling for spatial autocorrelation; n.s. $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ (Bonferroni correction). All models also control for survey methodology by including it as a categorical variable, and for plot area where not used as an independent variable. Parameter estimates are given together with their standard errors. Slope (Diff. sl.) and intercept (Diff. int.) of the relationships in forest and open habitats are compared with those of urbanized areas. The following variables were transformed prior to analysis: plot area ($\log_{10}$ plot area), species richness ($\log_{10}$ no. of species plot^{-1}), abundance ($\log_{10}$ no. of individuals plot^{-1}), biomass ($\log_{10}$ kg plot^{-1}). Evenness of species abundances is expressed as Bulla's O. NDVI, normalized difference vegetation index.

Table 3 Mixed models of avian assemblage parameters: (i) for forest and open habitat plots together (without urbanized plots, $n = 866$), and for forest, open and urbanized data together ($n = 1051$), (ii) without habitat as a variable, and with main habitat (iii, forest, open or urbanized; iv, urbanized versus non-urbanized) as a categorical variable.

	Model		Model R^2	Slope	Intercept	Habitat	R^2 (hab.)
a	Species richness versus plot area	i	0.10	$+0.18 \pm 0.02$***	1.55 ± 0.05		
		ii	0.08	$+0.19 \pm 0.02$***	1.54 ± 0.04		
		iii	0.19	$+0.21 \pm 0.01$***	1.52 ± 0.05	**	0.11
		iv	0.11	$+0.19 \pm 0.02$***	1.50 ± 0.05	n.s.	0.03
b	Abundance versus plot area	i	0.44	$+0.73 \pm 0.03$***	2.73 ± 0.04		
		ii	0.44	$+0.72 \pm 0.03$***	2.74 ± 0.04		
		iii	0.48	$+0.73 \pm 0.03$***	2.91 ± 0.05	*	0.04
		iv	0.44	$+0.72 \pm 0.03$***	2.90 ± 0.05	n.s.	0.00
c	Species richness versus abundance	i	0.36	$+0.35 \pm 0.02$***	0.59 ± 0.06		
		ii	0.32	$+0.33 \pm 0.02$***	0.59 ± 0.05		
		iii	0.39	$+0.31 \pm 0.02$***	0.61 ± 0.06	**	0.07
		iv	0.37	$+0.34 \pm 0.02$***	0.49 ± 0.06	*	0.05
d	Species richness versus biomass	i	0.35	$+0.29 \pm 0.02$***	1.05 ± 0.03		
		ii	0.27	$+0.27 \pm 0.01$***	1.11 ± 0.03		
		iii	0.41	$+0.26 \pm 0.01$***	0.96 ± 0.05	**	0.14
		iv	0.36	$+0.27 \pm 0.01$***	0.95 ± 0.05	*	0.09
e	Species richness versus NDVI	i	0.14	$+0.53 \pm 0.14$**	1.29 ± 0.08		
		ii	0.12	$+0.54 \pm 0.14$**	1.27 ± 0.07		
		iii	0.20	$+0.37 \pm 0.13$**	1.34 ± 0.08	**	0.08
		iv	0.15	$+0.52 \pm 0.14$**	1.23 ± 0.08	n.s.	0.03
f	Evenness of abundances versus NDVI	i	0.14	-0.10 ± 0.05*	0.59 ± 0.02		
		ii	0.12	-0.09 ± 0.05 n.s.	0.57 ± 0.02		
		iii	0.14	-0.10 ± 0.05*	0.53 ± 0.03	n.s.	0.02
		iv	0.13	-0.10 ± 0.05*	0.53 ± 0.02	n.s.	0.01

R^2 (hab.) = R^2 explained by habitat. Apart from model R^2, results are given controlling for spatial autocorrelation; n.s. $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ (Bonferroni correction). All models also control for survey methodology by including it as a categorical variable, and for plot area where not used as an independent variable. Parameter estimates are given together with their standard errors. The following variables were transformed prior to analysis: plot area ($\log_{10}$ plot area), species richness ($\log_{10}$ no. of species plot^{-1}), abundance ($\log_{10}$ *n* of individuals plot^{-1}), biomass ($\log_{10}$ kg plot^{-1}). Evenness of species abundances is expressed as Bulla's O. NDVI, normalized difference vegetation index.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of references from which bird abundance data were obtained.

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BIOSKETCH

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