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Dan Chamberlain[1*], Micheal Kibuule[2], Roger Skeen[2] and Derek Pomeroy[2]

[1] *University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy*

[2] *Makerere University, P.O.Box 7298, Kampala, Uganda*

*Corresponding author, email dan.chamberlain99@gmail.com, tel. +39 011 6704534

Abstract Impacts of urbanization on biodiversity are commonly studied using urbanization gradients which provide a space-for-time substitution in estimating consequences of urban expansion. Rates of urbanization and human population growth are high in tropical countries of the developing world, which also hold most of the world's biodiversity hot-spots, yet few studies have considered biodiversity trends along urban gradients in these regions. Bird communities across a gradient of nine sites in Uganda, from the city centre of Kampala to outlying rural locations, were studied over a six year period. These sites were ordered along an urbanization gradient using Principle Components Analysis based on habitat variables estimated at each site. Bird species richness showed a decrease from rural to urban sites, a trend especially evident in forest birds. There was no clear pattern in total abundance, total biomass or biomass per individual along the gradient. However, this latter result was heavily influenced by a colony of Marabou Storks at one site. When this species was omitted, there was evidence of a positive trend with urbanization, showing that as species richness decreased, the bird community was increasingly dominated by larger species with increasing urbanization, which were mainly scavengers able to exploit human refuse. These results provide further support for the negative impacts of urbanization on species richness, but also demonstrate trends in abundance and biomass are variable across different regions. In particular, the increasing dominance of larger species in urban areas may be relevant to certain geographic and/or socioeconomic contexts.

Introduction

Rates of urbanization are increasing globally (Cohen 2006; Seto et al. 2011). Urbanization is one of the most severe and irreversible forms of human impact, having far-reaching consequences for land cover, hydrology, biogeochemistry and climate (Grimm et al. 2008). It also has major impacts on biodiversity, typically by replacing natural or semi-natural habitats with relatively high biodiversity with non-natural habitats that can be exploited by only a relatively few, often alien, species (McKinney 2002). Even those species that are able to adapt to urban environments show striking differences from populations in natural habitats in many aspects of their ecology (e.g. Cowie and Hinsley 1988; Hõrak 1993; Chace and Walsh 2006; Chamberlain et al. 2009). Generalist species are better able to exploit urban environments (e.g. Evans et al. 2010), and urban communities tend to be dominated by the same or similar species, even in widely geographically separated areas, hence it is a process that seemingly promotes biotic homogenization (McKinney 2006). As a consequence, there is a general (but by no means universal) pattern of lower animal and plant species richness with increasing urbanization (Faeth et al. 2011), although those species that are able exploit urban environments may often occur at higher densities than their counterparts in (semi-)natural habitats, in particular, birds and arthropods (Faeth et al. 2011). Indeed, Chace and Walsh (2006) reviewed the published literature on birds and found a general intermediate peak in species richness along the urban gradient. The relatively few studies that have considered total bird biomass variations in relation to urban-rural gradients have found inconsistent trends – some studies have found that biomass shows a similar general trend to species richness, typically with an intermediate peak along the gradient (Blair 1996; Jokimäki et al. 2002; Pautasso et al. 2011), whilst others have found negative correlations, with the highest biomass being in urban areas where species richness is lowest (e.g. Chace and Walsh 2006; Mikami and Mikami 2014).

Gradients of land-use, from urban centres to natural or semi-natural habitats, are often used to assess impacts of urbanization on biodiversity as they provide a space-for-time substitution in estimating consequences of urban expansion (McDonnel and Pickett 1990). There are many examples of such studies,

particularly from Europe and North America (e.g. Blair 1996; Clergeau et al. 1998; Niemela et al. 2009; Bergerot et al. 2011; Fatel et al. 2014). However, studies from the tropics are scarce, and for birds at least, there are few from developing countries (Marzluff et al. 2001; Pautasso et al. 2011), yet the developing world shows the highest rates of human population growth (United Nations Population Fund 2014), the highest rates of expected future urbanization of the human population (Cohen 2006), and most biodiversity hot-spots are in the developing world (Myers et al. 2000). There is therefore the expectation that impacts on biodiversity due to urbanization are likely to be most marked in developing tropical countries (Filloy et al. 2015), hence further studies in the developing world are essential in order to understand potential consequences of urbanization (Trimble and van Aarde 2014), and also to begin to formulate strategies that may allow increasing urbanization in a more sustainable way (e.g. Stott et al. 2015).

We considered trends in bird communities across a gradient of nine sites in southern Uganda, from the city centre of Kampala to outlying rural locations characterized by agricultural land interspersed with forest fragments. Kampala is one of the fastest growing African cities, having shown a rapid expansion in area and in its human population (Vermeiren et al. 2012), a pattern common in Africa, which has amongst the highest rates of urban land expansion globally (Seto et al. 2011). Nevertheless, suburban and rural habitats surrounding Kampala, even if anthropogenic, may hold highly rich bird communities, including some species of conservation concern (Allen and Fripp 1964; Carswell 1986; Carswell et al. 2005; Ssemmanda and Pomeroy 2010). Studying gradients in the bird community will therefore enable an assessment of the potential impacts of increasing urban development on the avifauna. Furthermore, we define species into habitat groups (e.g. Bennun et al. 1996) in order to determine if overall trends in relation to the gradient are being driven by differential responses of species with different broad habitat requirements.

We considered three community-level measures to describe variations in biodiversity along the urban-rural gradient, species richness, total abundance and total biomass (the latter two based on individuals of all species). Field observations of birds in city centres of Kampala and other African cities suggest that large birds are quite common even in very built-up areas (pers. obs.). In Kampala, larger

scavenging species are certainly widespread in highly urbanized areas (Ssemmanda and Pomeroy 2010). We therefore also analysed the mean biomass of individual birds (i.e. total biomass/total abundance) to assess whether these observations were supported by the data.

Methods and materials

Study sites

The original vegetation of the part of Uganda where Kampala lies was rain forest (the mean annual rainfall being about 1100mm), with papyrus swamps filling many of the valleys, and some rocky hilltops having grassland savannas (Langdale-Brown et al 1964). The first clearances for cultivation were about a thousand years ago, and this gradually spread so that in the 1800s, when Kampala was only a small settlement, most of the area currently built-up will have been small-holder farms, whose main crops were bananas and coffee. It seems likely that some of the original forest trees remained, as they do to this day. Modern Kampala extends some 10km from the centre in all directions, except in some southern parts where it reaches Lake Victoria. Apart from the central area, most houses and other buildings are single storey, and many have gardens, although there are increasingly blocks of flats and other larger buildings, usually not exceeding five storeys.

Nine sites were surveyed in areas chosen to be generally representative of different land uses in and around Kampala, from the city centre to the surrounding rural areas. As a set, they reflected the main types of habitat found in Kampala; thus, each included some open spaces, and all except for the Commercial area and Makerere University campus included some wetter areas in a valley, although none retains typical swamp vegetation. However, they represented a wide range of green spaces and of tree numbers (Table 1). Sites were visited a variable number of times between 2010 and 2015, from between 8 (Mpanga) and 38 visits (Lusanja).

Transect surveys

For each site, a transect of 2km length was surveyed. The transects form part of a set (currently 79 in number) covering much of Uganda and administered nationally by NatureUganda. Each transect had to be readily accessible to facilitate continuing monitoring into the future and therefore used public roads and well-established footpaths, with no issues of access. Each transect was walked slowly, each count taking around 90 minutes to complete. Most visits were made between 0700 and 1100. The presence of all birds detected was noted irrespective of distance from the transect (i.e. it was unbounded, following standard monitoring protocols of NatureUganda). Each transect was divided into 200m sections, and the following habitat data were also collected from each section on the first visit: number of large (>8m) native trees, number of small (3-8m) native trees, number of large exotic trees, number of small exotic trees, number of 'house-sized' buildings, number of large buildings (commercial, apartments, industrial), index of cover of bushland or fallow habitats (rank score from 0 to 3, where 0 = absent, 1 = present in small amounts, 2 = present, covering up to 50% of the section, 3 = covering more than 50% of the section), cover of wetland habitats (as for bushland/fallow). There was very little change in habitat on the transects during the course of the surveys.

There were two different bird data sets available for analysis. Data for the number of species and total number of individuals were available for the whole sample at the transect section level, when most counts were made in January and July. There was also a more detailed data set comprising six of the sites which were visited every month from September 2010 to August 2011, from which the abundance of individual species (needed for the calculation of biomass) at the transect level was available. For the latter, species were also defined into broad groups based on their main habitat types. Following Bennun et al. (1996), species were defined as: forest specialists, characteristic of and mostly confined to undisturbed forest; forest generalists that breed in forests, but which can be commonly found in secondary forests, including edge habitats; forest visitors, birds that are commonly found in forests, but are not dependent on it and usually breed in other habitats (these three groups were classed as, respectively, FF, F and f

according to Bennun et al. 1996). In addition, we defined: generalists as species that occur in a range of

usually open habitats that can tolerate anthropogenic landscapes to some degree (there were also some

savanna species in this group), or that are found across a range of habitats (e.g. several raptor species);

wetland species that are strictly dependent on the presence of water bodies; and, Palearctic migrants that

breed in Europe or Asia and do not breed in sub-Saharan Africa.

Data analysis

Habitat variables typically vary along urbanization gradients in a more-or-less predictable way, for example

a decrease in tree cover and an increase in hard surfaces along the gradient from rural to urban sites.

Therefore, there tends to be a high degree of inter-correlation among habitat variables, which presents a

challenge to statistical analysis, as high levels of collinearity amongst predictor variables are undesirable

(Zuur et al. 2009). Gradients in habitat were analysed initially using Principal Components Analysis (PCA),

which describes general trends in the data set by quantifying axes that are linear combinations of habitat

variables that represent broad environmental gradients (James and McCulloch 1990). In other words, the

approach enables the quantification of variations in habitat along the urbanization gradient in terms of a

few axes, instead of a larger number of inter-correlated variables. PCA axes were derived at the section

level, based on the correlation matrix between variables. The mean value of axis 1 was then used to

quantify an objectively defined gradient at the transect level.

Species richness and total abundance were analysed at the section level using GLMMs with the

package lme4 (Bates et al. 2013), specifying transect section as a random effect to account for repeated

sampling, and also year (as a factor variable) to account for annual variation. Site was specified as a fixed

effect. Many species show strong seasonal patterns related to wet and dry seasons (Carswell et al. 2005),

in terms of breeding activity and migration (both intra-African migrants and Palearctic migrants wintering in

Africa). Season was therefore also included as a fixed effect, defined as the early dry season (January and

February), the late dry season (July to September), the early wet season (March to May) and the late wet

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season (October to December). Initial models assuming Poisson errors showed a high level of overdispersion for both richness and abundance, therefore models were run specifying a negative binomial error distribution using the glmmADMB package (Bolker et al. 2012).

A similar approach was used considering PCA scores from axis 1 at the section level as fixed effects, instead of site. The relationship between individual habitat variables at the section level and richness and abundance was assessed by running a model for each variable as a fixed effect, and as previously, transect section and year as random effects. In addition, the effect of total trees, total native trees and total exotic trees was considered, giving a total of 11 models for each of species richness and abundance. The best performing model was assessed according AIC in order to identify the variable which was most closely related to richness and abundance.

Analyses of biomass were from the more detailed dataset and hence considered a shorter gradient of 6 sites over a 12 month period. This data was balanced in that there was a count for each site in each month, hence ANOVA-type models (or a non-parametric equivalent) were used. Biomass was calculated by taking the mean mass for a given species as reported in the *Birds of Africa* series of books (e.g. Brown et al. 1982; Urban et al. 1986), multiplying it by the abundance of that species per transect, and then summing the total mass across all species for a given transect and visit, and calculating the mass per individual by dividing total mass by total abundance. Total biomass was log-transformed and analysed using a two-way analysis of variance in relation to site and month. Individual biomass showed a bimodal distribution which could not be approximated to a normal distribution using transformations. These data were therefore analysed using a non-parametric Friedman test, considering a matrix of sites by months. Further analyses omitting Marabou Stork *Leptoptilus crumeniferus* (see Results) resulted in normal distributions for both total biomass and individual biomass, so analysis of variance was used in both cases.

The four measures, species richness, total abundance, total biomass and individual biomass, were also extracted per site per visit from the above 6 sites according to the six defined habitat groups (forest specialists, forest generalists, forest visitors, generalists, waterbirds and Palearctic migrants). The initial goal of the analysis was to assess whether linear trends across the gradient were consistent across sites.

For this, models were constructed that tested for the interaction between site-level PCA scores and group as a factor variable. As repeated monthly counts were taken from each site, site was fitted as a random factor in each model. As above, species richness and abundance were analysed using a mixed model specifying negative binomial errors. At the group level, log-transformations resulted in approximately normal distributions for both total mass and individual mass. These were analysed using a linear mixed model with normal errors.

Results

Habitat gradients

The first axis explained 34% of variation in the data and was characterised by positive correlations with the abundance of trees of all types, and a negative correlation with the number of large buildings (Table 2), and hence represented a gradient from built-up to well-vegetated sections. Lower axes explained much less variation (e.g. 18% for axis 2) and were less easy to interpret and were not considered further. Mean PCA score on axis 1 was calculated per site to define the urbanization gradient (Table 3).

Species richness and abundance

A total of 156 species was recorded during the six years of the survey, the maximum richness per section on any single visit being 36, and per whole transect 78 (both at Kiweebwa). There was a highly significant difference in species richness between sites ($\chi^2_8 = 235.91$, P < 0.001), and a tendency for wet seasons to have higher species richness than dry seasons, though the difference was not quite significant ($\chi^2_3 = 7.40$, P = 0.060). When sites were ordered according to mean PCA score, there was a general increase in richness from the commercial city centre through to rural sites just outside the city, and there was a significant correlation between estimated richness per site and the rank order of the site according to the gradient (r_s

= 0.80, n = 9, P = 0.014), although the average species richness in the most rural site, Kifu, actually showed a marked drop compared to the other rural sites (Fig. 1). When considering habitat gradients using PCA axis scores derived at the section level, there were significant positive effects of PCA1 (χ^2_1 = 55.81, P < 0.001). When models were run separately on individual habitat variables, the rank score for bushland and fallow cover had the best performing models in terms of AIC (ΔAIC = -9.80 compared to the next best model), species richness being significantly positively associated with higher ranked sections (χ^2_1 = 49.84, P <0.001, parameter estimate = 0.34 ± 0.05).

Estimating species richness at the site level from section-level data could have led to underestimates if there was a high turnover between sections (hypothetically, a transect could have, say, ten unique species per section, which would lead to a species richness estimate based on section-level models of ten, whereas the true site-level richness would be 100). To address this, the species richness was determined at the transect level, and correlated with the estimates from the section-level model. There was an almost perfect matching (r_s = 0.98, n = 9, P < 0.001), therefore estimates were not confounded by species turnover between sections.

There was a highly significant difference in total abundance between sites (χ^2_8 = 33.33, P < 0.001), although there was no particular pattern in relation to the urbanization gradient (Fig. 2), and there was no overall correlation with the rank order of sites (r_s = 0.47, n = 9, P = 0.21). There was a highly significant effect of season (χ^2_3 = 56.61, P < 0.001), where abundance was higher in the wet seasons when many species breed (hence there will be many young birds in the environment). There was a significant positive effect of PCA1 (χ^2_1 = 10.14, P = 0.001).

Biomass

The total biomass, whilst showing significant differences between sites ($F_{5,55}$ = 111.23, P < 0.001), did not show a particular pattern along the gradient, the highest estimate of log(mass) being 14.03 ± 0.14 at Makerere and lowest at Muyenga (10.20 ± 0.14), i.e. two sites adjacent on the gradient. Similarly, there

was a significant difference between sites (Friedman χ^2_5 = 50.67, P < 0.001), but no pattern with respect to the gradient, for individual mass (Fig. 3A). However, both these results are likely to have been affected by a single species, the Marabou Stork, which has a large nesting colony at Makerere (832 pairs in 2015-16, c. 80% of the entire Kampala nesting population; M Kibuule, unpubl. data). When this species was removed, there was still no pattern in terms of the gradient in total biomass, but there was a significant difference in individual mass between sites ($F_{5,55}$ = 27.91, P < 0.001), showing a clearer pattern of increasing mean mass per individual bird from rural to urban sites (Fig. 3B).

Species groups

There were only two forest specialists species recorded (Grey Parrot *Psittacus erithacus* and Black Cuckoo *Cuculus clamosus*, although records of the latter may have included both the resident forest specialist *C.c. gabonensis*, and the intra-Africa migrant nominate race, which occurs across a greater range of habitats – Carswell et al. 2005), so these were combined with forest generalists to make a single forest group. There were significant interactions between group and PCA score for each of the four measures (P < 0.001 in each case). Subsequently therefore, each group was analysed separately. Species richness showed significant positive associations with PCA score (i.e. it increased from urban to rural sites) for the forest (χ^2_1 = 73.58, P < 0.001), forest visitor (χ^2_1 = 59.19, P < 0.001) and generalist groups (χ^2_1 = 12.50 P < 0.001; Fig. 4a). Generalist species showed a more-or-less linear increase in species richness along the gradient, whereas both forest species and forest visitors showed an increasing rate of increase towards more rural sites, showing that generalists were dominant in more urban sites, but that the community was more balanced between these groups in more rural sites. Indeed, 72% of species were generalists in the most urban site on the gradient, whereas 2% and 19% were forest species and forest visitors respectively. In the most rural site on the gradient, the respective figures were 18%, 38% and 42%. Similarly, there were significant positive associations between total abundance and PCA score for forest (χ^2_1 = 61.41, P < 0.001) and forest visitor groups (χ^2_1 = 29.34, P < 0.001; Fig. 4b). Total biomass and individual biomass showed significant

positive associations with PCA score only for the forest group (respectively $\chi^2_1 = 29.73$, $P < 0.001$ and $\chi^2_1 = 6.92$, $P < 0.01$; Fig 4c). The two measures were very similar in the most urbanized sites, because there were only a few individuals of forest species in urban sites, but the two trends diverged as sites became more rural. There was a weak suggestion of a negative trend with individual biomass and PCA score for the generalist group ($\chi^2_1 = 2.96$, $P = 0.085$) when omitting Marabou Storks, but otherwise removing this species made very little difference to the overall patterns.

Discussion

There was a general increase in species richness along the gradient from urban to rural sites, in common with many other studies (e.g. Chace and Walsh 2006; Clergeau et al. 2006; Faeth et al. 2011; Mikami and Mikami 2014; Sanz and Caula 2015), suggesting that fewer species are able to exploit increasingly urbanized habitats. For birds, several studies have also found that species richness peaks at an intermediate level of urbanization (Chace and Walsh 2006), presumably because these are relatively diverse habitats that are effectively ecotones where different habitats overlap. There was no clear peak in this study, but there was a drop in species richness in the most rural site on the gradient, Kifu. This may suggest that a longer gradient that included sites with even lower levels of urbanization could have revealed such an intermediate peak. However, this seems unlikely if a full gradient is considered from urban centres to the natural climax vegetation of the region, tropical forest, which has a high species richness. Although we do not have directly comparable data using the same methodology, point counts from Mpanga forest reserve showed a maximum species richness of 79 for a single visit, compared to 58 for the adjacent rural site at Mpanga considered here. Surveys in other forest reserves within the region show higher richness estimates (e.g. 108 species in Mabira – Chamberlain et al. 2008). Therefore, we suspect that the lower species richness at Kifu was caused by particular site-level factors, or it was not well-characterised along the urban-rural gradient, rather than being evidence of an intermediate peak in species richness.

The urbanization gradient derived from PCA explained 34% of variation in the habitat data. It is possible to derive informative gradients from this level of variation which is comparable with other studies which may interpret meaningful axes with much lower level of explained variation (e.g. Janžekovič & Novak 2012). Nevertheless, the analysis suggests that there was still much unexplained variation. Further research should consider collecting additional data, such as vegetation structure or levels of disturbance, which may result in a more precise characterization of sites long the gradient.

Unlike trends in species richness, there was no particular pattern evident in relation to the urbanization gradient for either total abundance or total biomass. Furthermore, there was no matching of general trends at the site level between any of the four variables considered (Spearman rank correlation, not significant in each pairwise comparison), the closest correlation being between species richness and abundance (r_s = 0.63, P = 0.076). The trend in total abundance therefore did not match the increase seen in more urbanized areas reported in many other studies, including in East Africa (Njorge et al. 2015). Similarly, total biomass trends did not accord with other studies, where variations matched those for species richness, i.e. a general decrease towards urbanised sites (Blair 1996; Jokimäki et al. 2002; Pautasso et al. 2011). Whilst there have been some studies that have found evidence of an increase in total biomass towards more urbanised sites (Chace and Walsh 2006; Mikami and Mikami 2014), this was also not the case here. In these studies, biomass typically correlated with the abundance of individual species, suggesting that urbanized sites have more individuals of fewer species (Chace and Walsh 2006).

The lack of correlation in Kampala may be due to the finding that larger species dominated in more urbanized sites, at least when omitting Marabou Stork, hence the most urbanized sites had relatively few species, but those species tended to be relatively large. Indeed, species such as Yellow-billed Kite *Milvus aegyptius*, Hooded Vulture *Necrosyrtes monachus*, African Openbill *Anastomas lamelligerus*, Hamerkop *Scopus umbretta* and Hadada Ibis *Bostrychia hagedash* are all commonly seen in urban Kampala. These species are typically scavengers, and therefore their presence in urbanized sites may simply be a reflection of the availability of food resources through refuse, and hence may be an indicator of the efficiency of municipal waste management. There may also be cultural aspects to the presence of these species in

densely populated areas, where levels of persecution are low or non-existent, which itself may be related to an appreciation of the ecosystem service provided in terms of removing carrion and other waste.

When considered according to main breeding habitat, forest species, as expected, showed a decline in species richness and abundance with increasing urbanization. This pattern was also evident in generalist species, but it was not as marked (Fig. 4). The decline in species richness was therefore mostly driven by loss of forest species, concurring with Lim and Sodhi (2004) that tropical forest birds are poor colonisers of urban habitats. Given that the PCA gradient was defined largely on the abundance of trees, this is not surprising, though it does suggest that planning for urban development that incorporates more trees is likely to be beneficial. Moreover, in terms of total species richness, the variable which had the best fitting univariate model was the cover of bushland and fallow. These results together therefore suggest that in order to promote sustainable urban development for birds in Kampala, some semi-natural habitat should be maintained within the urban matrix.

These data were collected using standard monitoring methods whose goal is to determine the general avifauna of particular areas for the purposes of long-term monitoring, rather than to produce estimates of population size or density. The survey transects were therefore unbounded. There is thus an implicit assumption in the analysis that detectability was equal across sites. It seems likely that habitats with greater cover of trees, especially mature trees, are likely to have been compromised in terms of detecting certain species, especially smaller passerines that spend much time in the canopy. To this extent, the estimate of species richness may have been biased towards lower estimates in more rural sites. Equally, however, large buildings are also likely to reduce detectability in a similar manner in more urban sites, where there will also likely be an effect of urban noise on the detection of birds by song and calls. So, there is an argument that detectability could be compromised towards both ends of the gradient. The general trends in species richness and the abundance of large birds (and hence individual biomass) generally match with other studies (Chamberlain et al. 2008; Carswell et al. 2005), and we do not believe that variations in detectability will have had a great influence on the observed trends. Nevertheless, the extent to which changes in detectability vary across the gradient, and whether this variation changes the

conclusions drawn from this study, would be possible to assess with further more detailed transect surveys that measured the distance of detected birds from the transect and so could account for detectability across habitats (e.g. Buckland et al. 1993).

Community measures such as species richness and abundance provide the basis for important initial analyses in assessing impacts of urbanization on avifaunas. Here, we have further refined this approach by considering these variables according to the species main (natural) habitat type in order to define species groups that are particularly sensitive to urbanization. However, a greater understanding of the avian community's reaction to urbanisation could be achieved by analysing avian functional and biologically distinct communities through an analysis of species traits (e.g. Croci et al. 2008; Evans et al. 2010), which could include the species' dietary and foraging strategies, nesting requirements and body size. Such an analysis of trends in persistence of functional communities across the urbanisation gradient should be considered a future research priority for Afrotropical birds.

This paper has added to the large scientific literature that has considered bird community trends across urban-rural gradients, but it is one of the few that has been carried out in the developing world. The findings in terms of species richness show commonalities with several other studies in that species richness declines with increasing urbanization (e.g. Blair 1996; Jokimäki et al. 2002; Pautasso et al. 2011), including in tropical countries in Africa (van Renseburg et al. 2009; Njoroge et al. 2014) and elsewhere (e.g. Bhatt and Joshi 2011; Soh et al. 2006). However, unlike other studies, there were no trends in abundance or total biomass. Moreover, there was evidence that the bird community became increasingly dominated by larger, typically scavenging species with increasing urbanization. Considering the gradient as a space-for-time substitution, this suggests that continuing the rate of urbanization in the Kampala area (Vermeiren et al. 2012) will lead to a further loss of species, especially forest-associated species.

Whether the observed patterns are peculiar to Kampala, or whether they are more widespread in Africa, or in the tropics in general, is worthy of further research. Field observations certainly suggest that large scavengers dominate in several other African cities (e.g. Nairobi, Accra, Dakar, Harare), but there is marked regional variation in species composition. Of the four main scavenger species, Pied Crows and

Yellow-billed Kites are common in most tropical African cities. Marabou Storks are more restricted; they occur in all the main towns of Uganda, and in recent years have also invaded Nairobi, Kenya (pers. obs) and are common in Harare, Zimbabwe (J. Pierini pers. comm.). However, they are unknown, for example in Accra and Dakar (J. Roberts, P. Robinson, pers. comm.). Hooded Vultures, likewise, are present in many Ugandan towns, but are absent from those above about 1500m, such as Fort Portal and Kabale, and also Nairobi in Kenya (L. Bennun, pers. comm.). Hooded Vultures are also fairly common in Accra and Dakar, but they are declining in both cities (J. Roberts, P. Robinson, pers. comm.).

The extent to which a high abundance of large scavengers is due to climatic or biogeographic influences, socioeconomic factors (e.g. investment in waste management and refuse collection), or cultural perceptions (e.g. an appreciation of the ecosystem services that such birds provide) could be assessed by carrying out similar surveys across urban-rural gradients in several African cities spanning a range of climatic and socioeconomic conditions. This study has provided the basis for just such a wider consideration of urban biodiversity trends in the developing world, which needs to include human-modified alongside natural habitats (Trimble and van Aarde 2014).

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Table 1. Mean ± se values of habitat variables recorded at each site, calculated across each 200m section of a transect (n = 10). Values represent counts of either individual trees or individual buildings, with the exception of Bush/Fallow and Wetland, which were scored as an index from 0 (not present) to 3 (covering the majority of the section) for each transect section. Sites are ordered according to the PCA gradient (see Table 3). Location is given in UTM coordinates.

| Site	Location (easting/northing)	Native trees (small)	Native trees (large)	Exotic trees (small)	Exotic trees (large)	Buildings (house-sized)	Buildings (large)	Bush/Fallow	Wetland
Industrial	36N 455672/35069	0.20 ± 0.20	0.20 ± 0.13	3.20 ± 0.65	1.00 ± 0.60	4.80 ± 1.26	9.70 ± 1.68	0.00	0.20 ± 0.13
Commercial	36N 453703/34607	2.00 ± 0.98	1.30 ± 0.37	14.60 ± 2.39	2.60 ± 0.73	1.90 ± 0.67	10.10 ± 2.81	0.00	0.00
Kikoni	36N 451332/36674	0.60± 0.31	1.50 ± 1.50	3.10 ± 1.06	1.70 ± 1.05	14.10 ± 4.45	2.20 ± 0.66	0.20 ± 0.13	0.10 ± 0.10
Muyenga	36N 457356/33356	0.80 ± 0.59	0.90 ± 0.41	8.00 ± 1.24	7.40 ± 1.85	3.30 ± 1.00	4.70 ± 1.23	1.00 ± 0.26	0.10 ± 0.10
Makerere	36N 451720/37151	7.10 ± 1.82	9.50 ± 2.44	11.60 ± 3.15	1.80 ± 0.84	2.20 ± 0.98	2.20 ± 0.53	0.60 ± 0.27	0.90 ± 0.90
Lusanja	36N 451903/44834	12.20 ± 2.24	0.80 ± 0.39	14.60 ± 3.51	1.60 ± 1.10	8.60 ± 3.21	0.30 ± 0.30	1.60 ± 0.27	0.30 ± 0.21
Mpanga	36N 422425/22399	7.10 ± 1.47	8.10 ± 1.39	89.40 ± 16.40	23.10 ± 4.99	9.00 ± 2.07	0.00	0.50 ± 0.17	0.00
Kifu	36N 474406/57954	38.20 ± 7.21	16.80 ± 3.82	86.20 ±13.33	19.80 ± 3.51	8.70 ± 2.07	0.20 ± 0.20	1.30 ± 0.15	0.00
Kiweebwa	36N 469516/50365	26.40 ± 5.70	20.00 ± 3.92	34.90 ± 7.94	13.90 ± 3.14	2.10 ± 0.86	0.90 ± 0.90	1.00 ± 0.21	0.30 ± 0.15

Table 2. Eigenvectors for the first principal component (PC1) describing habitat gradients in transects across an urban rural gradient based on 9 sites. The analysis was carried out at the section level (n = 90).

Variable	PC1
Small native trees	0.42
Large native trees	0.42
Small exotic trees	0.45
Large exotic trees	0.45
House	0.06
Large building	-0.39
Bushland/Fallow	0.30
Wetland	0.02

Table 3. Mean ± SE PC1 score for each site (n = 10 for each), in ascending order (i.e. from most to least urbanized) for the full sample (n = 9 sites).

Site	PC1 score
Industrial	-1.87 ± 0.13
Commercial	-1.63 ± 0.23
Kikoni	-1.08 ± 0.09
Muyenga	-0.78 ± 0.14
Makerere	-0.35 ± 0.17
Lusanja	-0.06 ± 0.21
Mpanga	1.44 ± 0.38
Kiweebwa	1.55 ± 0.36
Kifu	2.74 ± 0.18
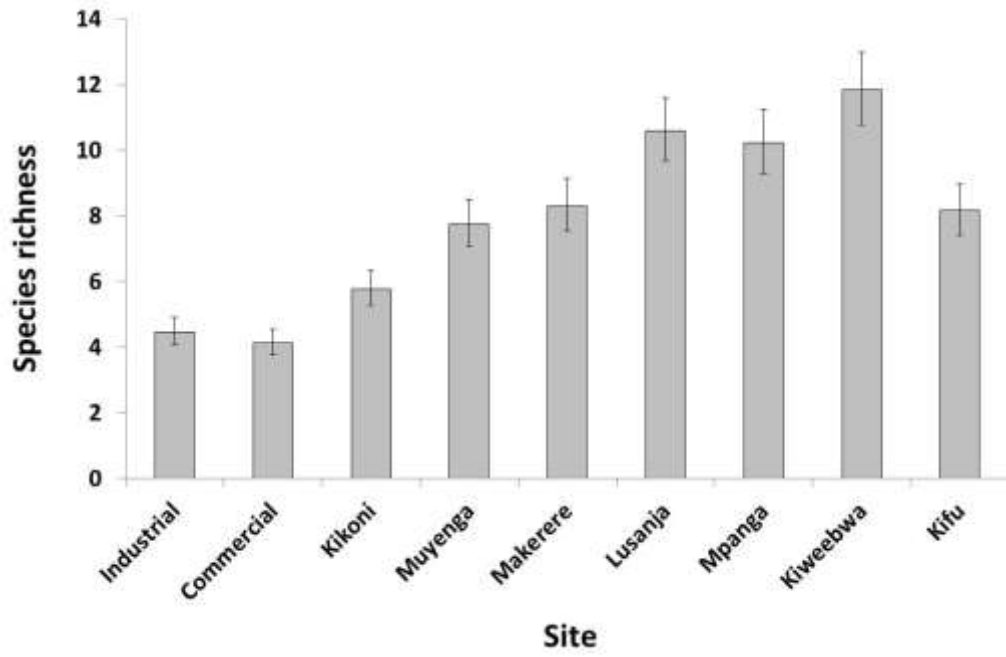
Fig. 1 Estimated species richness (± SE) per 200m section per site, ordered according to a gradient of urbanization (see Table 3). Estimates are derived from a GLMM which included year and month as random effects
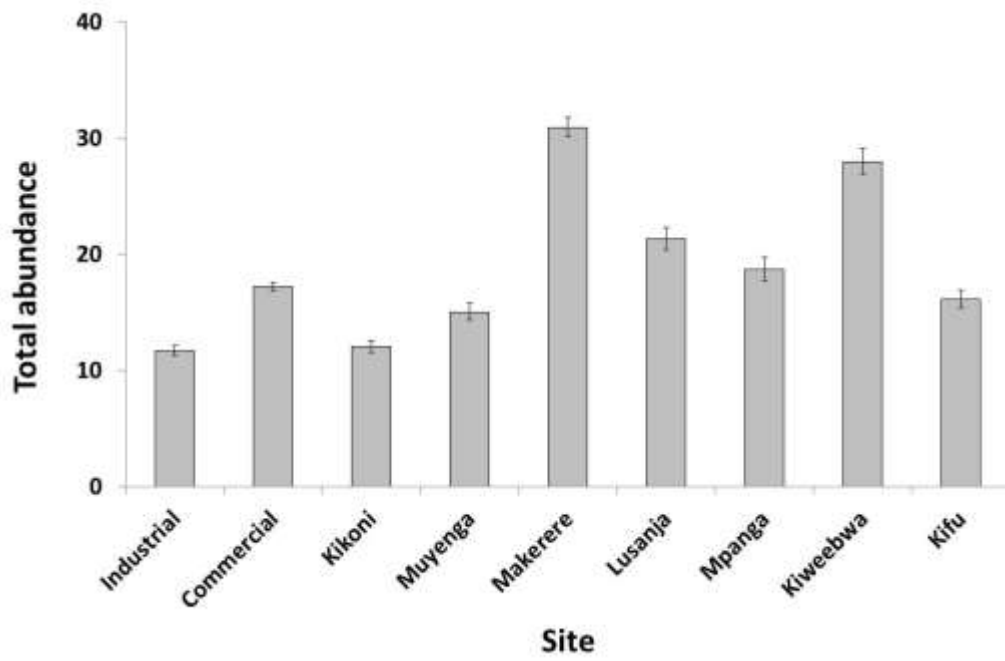
Fig. 2 Estimated total abundance (± SE) per 200m section per site, ordered according to a gradient of urbanization (see Table 3). Estimates are derived from a GLMM which included year and month as random effects
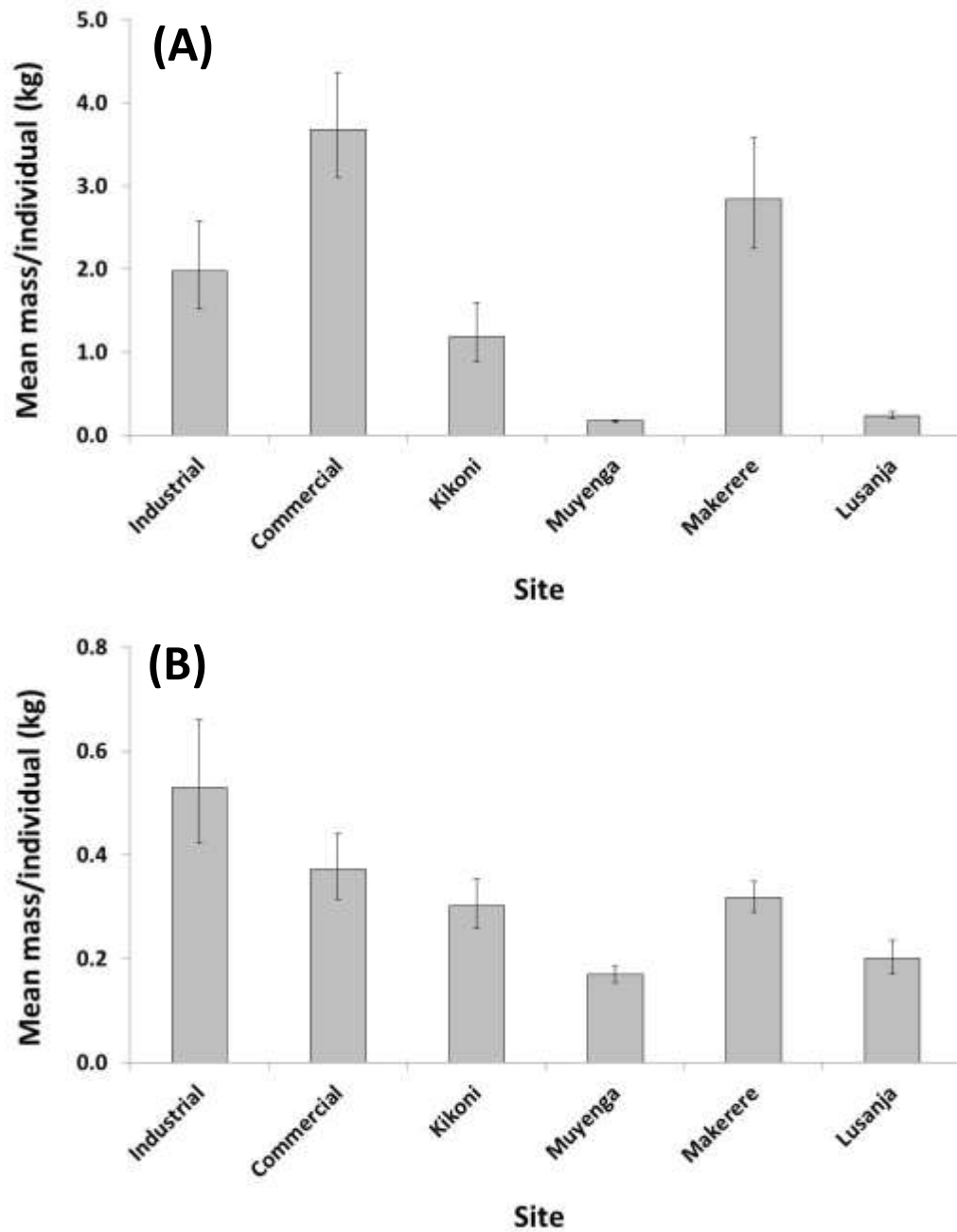
Fig. 3 Estimated mean mass per individual bird (± SE) per site, ordered according to a gradient of urbanization (see Table 3). Estimates are derived from a GLMM which included month as a random effect. (A) All species, (B) mean mass not including Marabou Stork
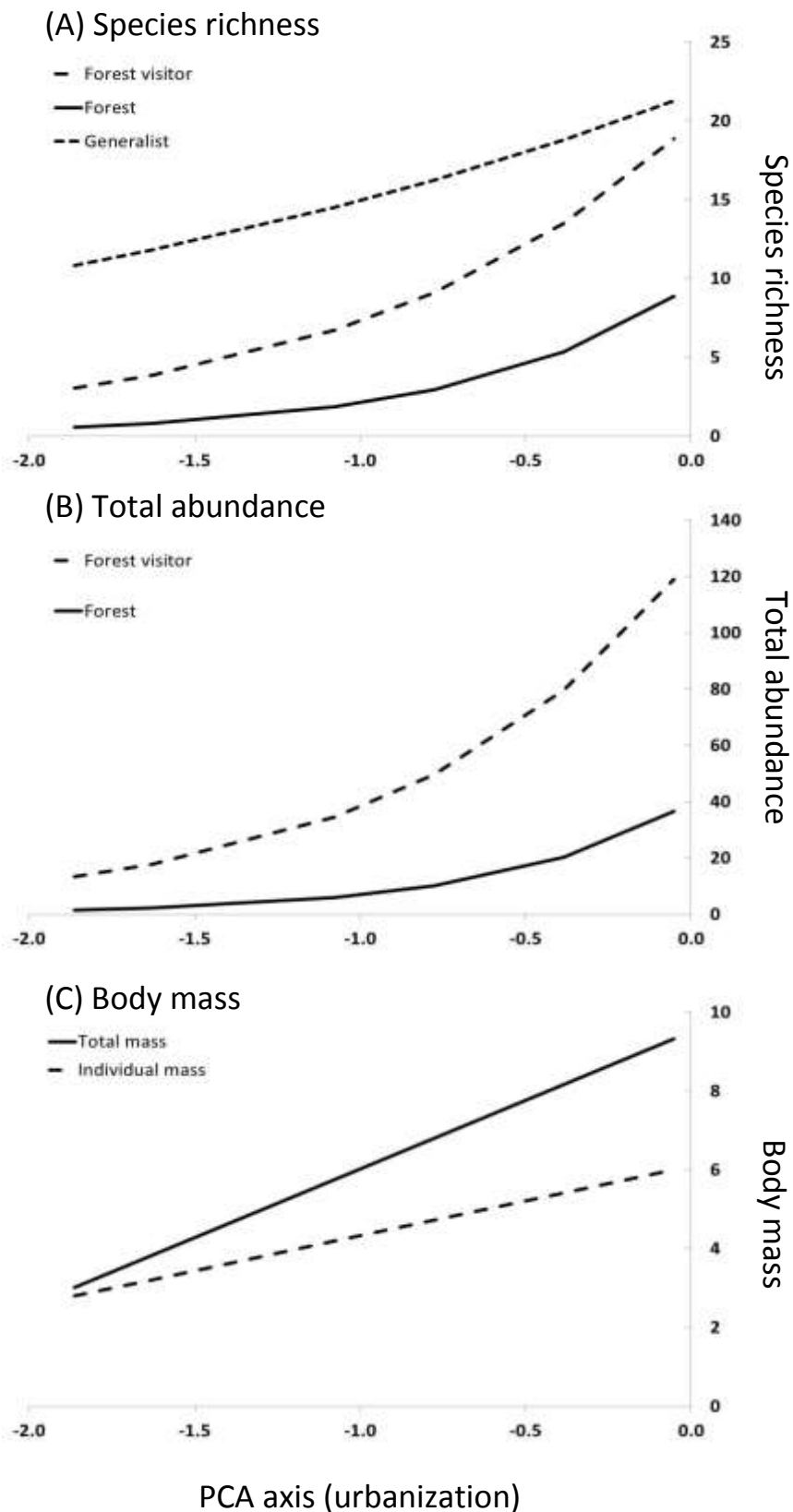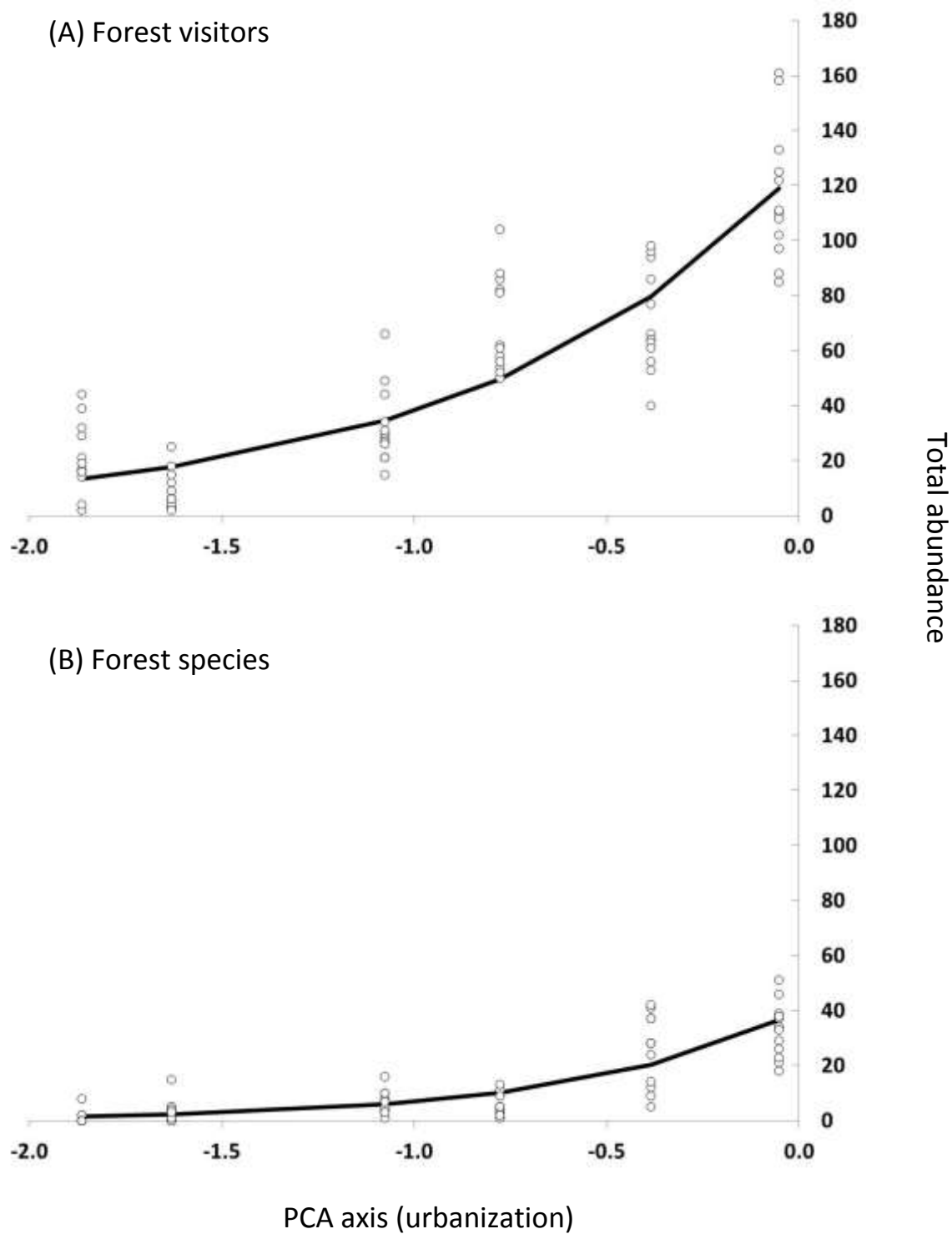
Fig. 4 Trends in (A) species richness, (B) total abundance and (C) mass in relation to a PCA axis describing a gradient from urbanized (more negative values) to rural (values close to 0) sites. Figures A and B show trends for different groups of species. Figure C shows trends in total body mass, expressed as log(x+1), and mean mass per individual, for forest species. Trends were fitted from generalised linear models. Figures including observed values are presented in the Supplementary Material

Online Supplementary Material

Detailed presentation of trends in richness (Fig. S1), abundance (Fig. S2) and body mass (Fig. S3), including both fitted trends and observed values.
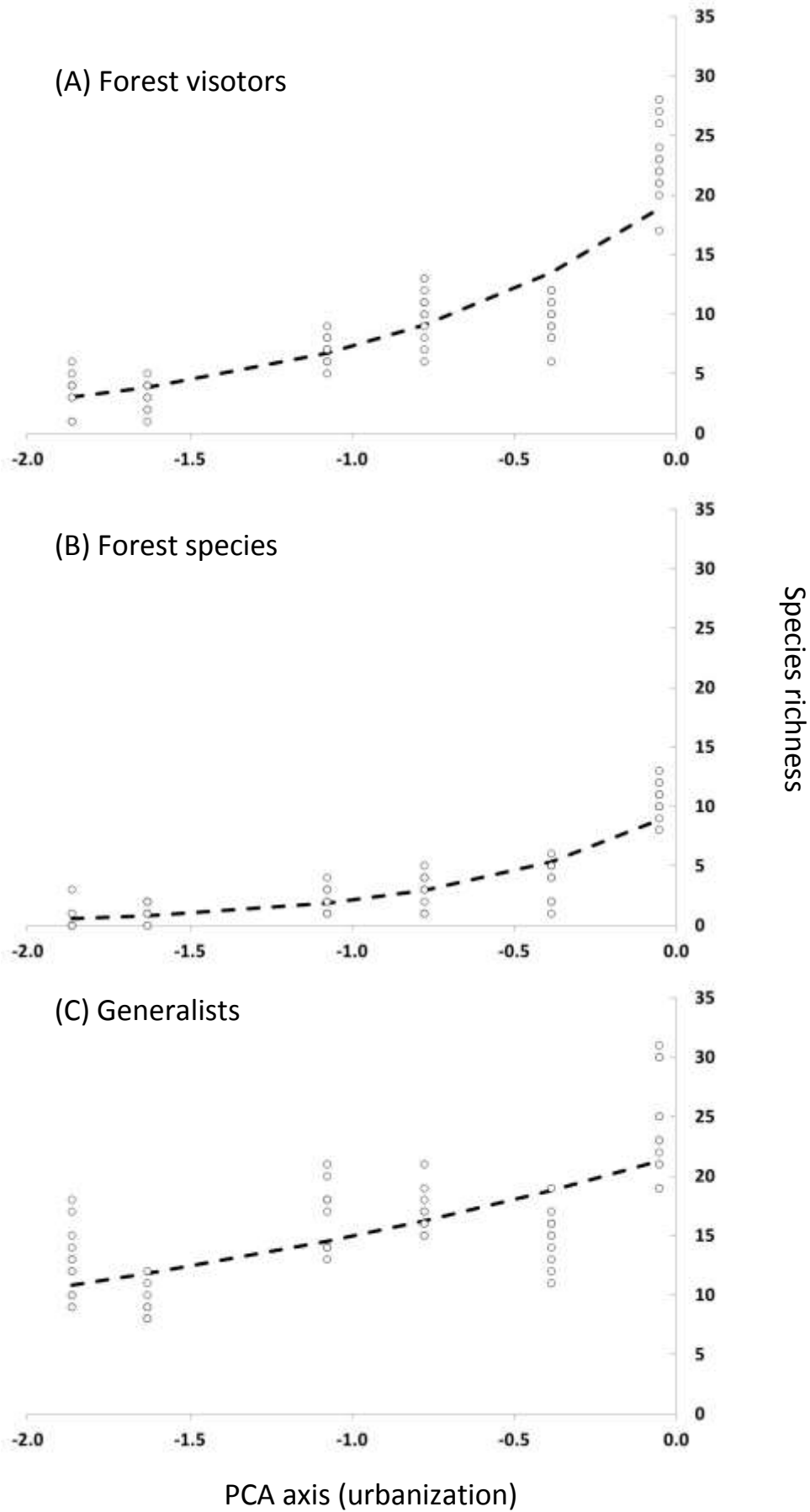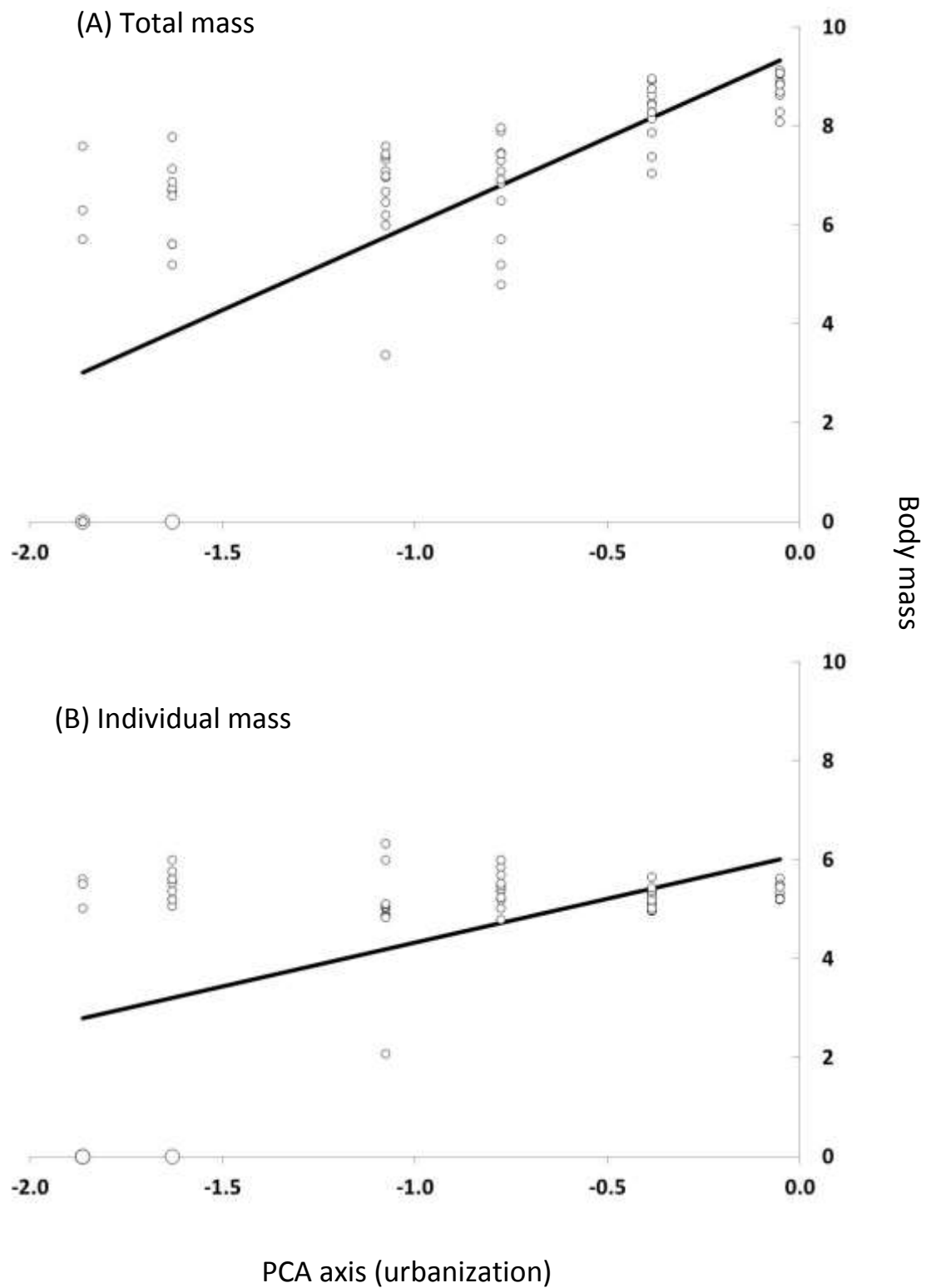
Fig. S1. Trends in species richness in relation to a PCA axis describing a gradient from urbanized (more negative values) to rural (values close to 0) sites for different groups of species defined according to habitat. Trends were fitted from generalised linear models.

(A) Forest visitors

(B) Forest species

PCA axis (urbanization)

Total abundance

Fig. S2. Trends in total abundance in relation to a PCA axis describing a gradient from urbanized (more negative values) to rural (values close to 0) sites for different groups of species defined according to habitat. Trends were fitted from generalised linear models.

Fig. S3. Trends in body mass for forest species in relation to a PCA axis describing a gradient from urbanized (more negative values) to rural (values close to 0) sites. Trends in total body mass, expressed as log(x+1), and mean mass per individual, for forest species are shown. Trends were fitted from generalised linear models.