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Urban areas have lower species richness, but maintain functional diversity: insights from the African Bird Atlas Project

Alan Tristram Kenneth Lee^{1,2*} , Ulf Ottosson³, Colin Jackson⁴ , Sidney Shema⁵ and Chevonne Reynolds^{2,6} 

¹ Centre for Functional Biodiversity, University of KwaZulu-Natal, Scottsville, South Africa

² FitzPatrick Institute of African Ornithology, DSI/NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

³ AP Leventis Ornithological Research Institute, University of Jos, Jos, Nigeria

⁴ A Rocha Kenya, Watamu, Kenya

⁵ Ornithology Section, National Museums of Kenya, Nairobi, Kenya

⁶ School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

*Correspondence: alan.tk.lee@googlemail.com

High human population growth and rapid urbanisation, particularly in Africa, have led to an increased interest in the impacts of this land-use change on bird communities. The African Bird Atlas Project, where species presence lists are collected in pentads, is a valuable source of data with which to explore the extent of these impacts. Here, for the first-time, we test for differences in species richness patterns across 50 matched pentad pairs from sub-Saharan Africa classified as either urban (or semi-urban) and rural. We found that species richness was lowest in pentads classified as urban (mean \pm SD: 132 ± 59 species), compared with rural (172 ± 54). However, species richness was similar, compared with rural pentads, when levels of urbanisation were maintained at intermediate levels (semi-urban: 141 ± 69). Surprisingly, we found no significant differences in functional diversity measures between any land-use categories. Across most major dietary guilds (carnivores, herbivores, insectivores, granivores) species richness was lower in urbanised pentads and species were often small. However, the overall biomass of these guilds was similar between urbanised and non-urbanised areas, indicating the presence of common urban exploiter species. This resulted in no differences in functional diversity overall. Pollinators and piscivores showed little difference in metrics between rural and urban pentads. According to a model of the functional traits we consider, an African urban exploiter species is best described by being a scavenger, and less likely to be a habitat specialist, but fill a variety of niches. The urban spatial planning implications are that rare and range-restricted species in proximity to cities, as well as large bird species, will require particular attention and conservation measures as African cities continue to expand. Species richness could be maintained with intermediate levels of urban infrastructure development.

Les zones urbanisées sont moins riches en espèces mais conservent une diversité fonctionnelle: un aperçu du projet d'Atlas des oiseaux d'Afrique

La forte croissance de la population humaine et l'urbanisation rapide, plus particulièrement en Afrique, ont suscité un intérêt accru sur les impacts de ce changement d'utilisation des terres sur les communautés aviaires. Le projet d'Atlas des oiseaux d'Afrique, qui collecte les données relatives à la présence des espèces au travers de pentades (groupe de cinq unités), est une source précieuse de données permettant d'explorer l'étendue de ces impacts. Au travers de cet article, et pour la première fois, nous testons les différences en termes de richesse d'espèces, au travers de modèles basés sur 50 paires de pentades appariées d'Afrique sub-saharienne et classées comme urbaines (ou semi-urbaines) ou rurales. Nous avons estimé que la richesse en espèces était la plus faible dans des pentades de catégorie urbaine (moyenne \pm σ : 132 ± 59 espèces) par comparaison aux groupes ruraux (172 ± 54 espèces). Néanmoins, il a été constaté que la richesse en espèces était similaire aux pentades rurales dès lors que le niveau d'urbanisation restait contenu à un niveau intermédiaire (semi-urbain: 141 ± 68). Pour ce qui concerne la diversité fonctionnelle, nous avons été surpris de ne pas trouver de différences significatives entre les catégories d'usage des terres. Quant aux régimes alimentaires des guildes principales (carnivores, herbivores, insectivores, granivores), la richesse en espèces était plus faible dans les pentades urbaines et les espèces étaient souvent de petite taille. Cependant, la biomasse globale de ces guildes était identique entre les zones urbanisées et non-urbanisées, ce qui indique la présence d'espèces communes exploitant ces zones. Ceci induit qu'il n'y a pas de différences dans la diversité fonctionnelle globale. Les pollinisateurs et les piscivores présentaient peu de différence de mesures entre les pentades rurales et urbaines. D'après un modèle des traits fonctionnels, nous considérons qu'une espèce africaine d'exploitation urbaine est mieux décrite comme étant un charognard, remplissant une variété de niches, et moins à même d'être un spécialiste de cet habitat. En matière d'aménagement urbain, cela implique que les espèces rares et à aire de restriction restreinte ainsi que les grandes espèces d'oiseaux se trouvant à proximité des villes, nécessiteront une attention particulière et des mesures de conservation tant que les villes africaines poursuivent leur expansion. La diversité des espèces pourrait être conservée avec des développements d'infrastructures urbaines maintenus à des niveaux intermédiaires.

Keywords: functional divergence, Kenya BirdMap, metropolitan, Nigeria BirdMap, Pied Crow, SABAP2, urban adapter, urban landscapes, urbanization

Supplementary material: available at <https://doi.org/10.2989/00306525.2021.1902876>

Introduction

The world has experienced a dramatic shift to urban living (Grimm et al. 2008). Concern surrounding the environmental impacts of this expanding urbanisation has led to a growing research interest in urban biodiversity (McKinney 2006; Faeth et al. 2011; Beninde et al. 2015). However, despite this increased focus we still lack foundational knowledge of how biodiversity is distributed in urban landscapes, especially in the developing world. Given that Africa's population is the fastest growing in the world and expected to increase from the current 1.2 billion people to >1.8 billion by 2035 (Institute for Security Studies 2020), there is growing need to focus on biodiversity in these rapidly urbanising African landscapes (Magle et al. 2012). Additionally, in Africa, which is characterised by developing countries with strong socio-economic gradients, as well as a more tropical climate and uniquely structured cityscapes, we expect that urban influences on biodiversity will be markedly different to what is known from cities of the Global North (Becker and Morrison 1988; Gupta 2002; Seto et al. 2010; McHale et al. 2013; Chamberlain et al. 2020).

Urban land cover is expected to triple from its current extent by 2030, with considerable loss of natural habitat in the biodiverse developing world, and especially in Africa (Seto et al. 2012). Typically for birds, increased urbanisation acts to reduce species richness (Batáry et al. 2018). At the same time, urbanisation can create new ecological niches and opportunities for birds, for instance stable food supplies (Stoffberg et al. 2019) and nesting opportunities (Martin et al. 2014; Reynolds et al. 2019), allowing certain species to thrive in cities. Furthermore, a study on the worldwide impact of urbanisation on avian functional diversity suggested highly urbanised environments have substantially different functional compositions and 20% less functional diversity on average than surrounding natural habitats (Sol et al. 2020). However, it is important to note Africa was poorly represented in that study (only three regions were considered). Similarly, a landmark study attempting to describe characteristics of the 'urban bird' essentially answers this question for only the United Kingdom (Evans et al. 2011). Therefore, despite a focus on urban ecological research and several key reviews emerging in recent years (Faeth et al. 2011; Beninde et al. 2015; Batáry et al. 2018; Chamberlain et al. 2020), information for African cities is still largely lacking and limits our ability to make informed decisions around how African avifauna respond to this rapid land transformation.

Across Africa, how bird species are responding to urbanisation and associated threats and opportunities, is very mixed: population declines for Hooded Vulture *Necrosyrtes monachus* (Mullié et al. 2017), dietary adaptation for Crowned Eagle *Stephanoaetus coronatus* (McPherson et al. 2015; van der Meer et al. 2018), earlier breeding for Marabou Stork *Leptoptilos crumenifer* (Pomeroy and Kibuule 2017) and Peregrine Falcon *Falco peregrinus* (Sumasgutner et al. 2020) and facilitation

of the alien urban invader the Indian House Crow *Corvus splendens* (Shimba and Jonah 2017), are some examples of the numerous varied responses. Additionally, Chamberlain et al. (2018) showed long-term changes in bird functional feeding guilds in response to an urban gradient in Kampala, Uganda, where insectivores and granivores were found to have declined, whereas the most common predators and scavengers benefitted from the inability of municipal waste management to keep pace with growth from the human population, hence providing more potential food resources.

If urban transformation restructures avian communities at local scales, it is important to establish whether these effects translate into landscape patterns that can later be used to assess regional functional resilience (as per Child et al. 2009). Here we provide a first step towards this goal by quantifying avian species and functional richness patterns in selected pairs of rural-urbanised sites across sub-Saharan Africa. Using a paired sampling design and data from the Africa Bird Atlas Project we explore species and functional richness in relation to urbanisation categories and aim to identify functional group differences at a continental scale for Africa's birds. Finally, we use the functional traits to predict what makes a bird species more likely to be classified as an African urban exploiter and to list a set of the most widespread species in our survey domain.

Materials and methods

Data and data selection

This analysis makes use of data from the African Bird Atlas Project (ABAP, hereon: atlas), which is based on the protocols developed for the second Southern African Bird Atlas Project (Underhill 2016). In South Africa, this project was initiated in 2007, to collect gridded data on bird species occurrence for the region and is ongoing, with the protocol then being extended to the surrounding countries in southern Africa. The protocol enlists citizen scientists to collect species lists for a minimum of a two hour or maximum five day sampling period at the spatial resolution of a pentad (5 × 5 minutes latitude and longitude and there are nine pentads in a quarter degree grid cell). Both the Kenya and Nigeria Bird Atlas projects use this same protocol and they were initiated in 2013 and 2015, respectively. These projects have galvanised local birdwatching communities to use this protocol and allow for important comparisons across sub-Saharan African countries. Where all accessible major habitats have been covered for the minimum of two hours lists qualify as 'full protocol' lists, otherwise lists are submitted as an 'ad hoc' protocol. Each list provides presence/absence data for the occurrence of a species in a pentad. An index of relative abundance, known as reporting rate, can be calculated using the full protocol lists, where the reporting rate is a proportion of the number of times a species has been reported across a set of lists. The reporting rate ranges then from 0, i.e. never recorded,

to 1, i.e. the species was recorded for all full protocol lists (for more details see Lee et al. 2017).

We used a paired sampling design across the available atlas survey domain, and selected a pentad situated on a major city or town (urban centres) and then paired this with a rural pentad <60 km away, but within the same biome classification. Only a single pentad was selected from each major urban centre based on maximum urban coverage, to minimise issues of spatial autocorrelation. We selected urban centres to compare with a nearby more rural pentad from across the atlas domain (Figure 1). It quickly became apparent that major urban centres were poorly covered by atlas efforts across the continent, and that pentads rarely fitted neatly over a town, necessitating a

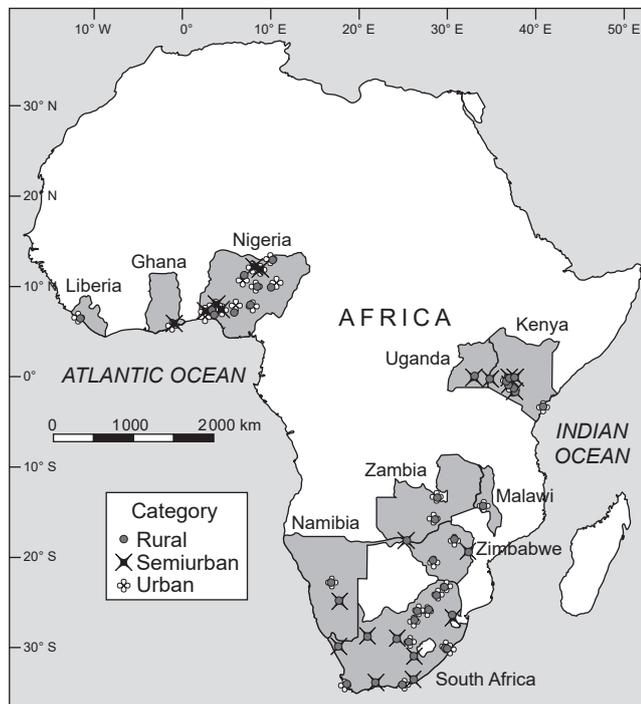


Figure 1: The location of paired pentads selected from the African Bird Atlas Project from across Africa. This pentad data was used to explore patterns of species richness and functional guild change between pentads dominated by either rural or urban land-use

‘semi-urban’ category centred on a rural town, but where urban land-use was between 15% and 50% cover. The final pairings were: 28 urban–rural; 6 urban–semi-urban and 16 semi-urban– rural pairs. Pentad selection criteria were based on visual inspection of pentads using the coverage maps and satellite imagery at <http://sabap2.birdmap.africa/> as follows: pentad pairs needed to contain equivalent available waterbodies (e.g. lakes, rivers), coastline was avoided wherever possible, and pentads needed to have a good sampling effort (>4 full protocol lists). In addition, urban pentads needed to be dominated by urban land-use, as identified by built infrastructure (including suburban, commercial and industrial land-use zones), preferably accounting for >60% of the pentad area (urban cover was rarely greater than this). Recreational areas were included e.g. urban parks and green belts. Rural pentads needed to be dominated by a rural land-use, e.g. agricultural, protected area or natural land-cover, preferably accounting for >80% of the pentad area, and importantly contain no commercial urban settlements. We also avoided pentads dominated by only a protected area. A protected area pentad category was considered and then rejected, because although protected areas are well covered by atlas efforts, there are relatively few pentads close to urban centres that are dominated by a protected area or protected area of the same habitat.

To ensure balanced list sampling between the pentad pairs we selected only lists marked as ‘full protocol’ and that were sampled for more than two hours. For each pair we then determined the pentad with the lower number of lists and randomly sampled the matching pentad for an equivalent number of lists. From the initial 5 870 lists and 325 935 records of 1 175 species, this resulted in a final dataset of 2 492 lists and 135 099 records, with median of 12 lists per pentad (interquartile range: 8–30) and 1 060 species. Supplementary Table 1 identifies the pentads included and the nearest city to which each pair was assigned, as well as the percentage urban cover and resulting urbanisation category, number of lists and species richness.

Analysis of species richness

Species richness was calculated as the accumulation of all species occurring in the selected lists for each pentad. Species richness was normally distributed, allowing for the use of linear models to predict species richness as a

Table 1: Summary statistics for species richness (observed as well as estimated by rarefaction), and Shannon–Wiener and Simpson’s diversity indices for the sets of rural, urban and semi-urban African pentads. Standard error (SE) as well as the lower and upper confidence limits (LCL, UCL) for the estimates are presented

Diversity	Site	Observed	Estimator	SE	LCL	UCL
Species richness	Rural	1 028	1 118.059	23.177	1 082.824	1 175.941
	Urban	786	910.617	30.948	863.151	987.286
	Semi-urban	769	855.247	22.515	821.142	911.658
Shannon diversity	Rural	401.928	405.253	1.5	402.312	408.193
	Semi-urban	331.205	337.396	2.207	333.7	341.723
	Urban	296.404	299.464	1.343	296.831	302.096
Simpson diversity	Rural	267.162	267.996	1.157	267.162	270.264
	Semi-urban	219.785	221.374	1.625	219.785	224.559
	Urban	199.255	199.916	1.042	199.255	201.958

function of urbanisation category. The number of cards was included in the models as an offset value, because species richness is influenced by sampling effort (linear model $\beta = 1.42 \pm 0.15$, $t = 9.2$, $p < 0.001$; i.e. on average one species is added to a pentad for each additional card). The number of hours spent atlasing in each category did not differ significantly (ANOVA: Sum sq = 8 475, $F = 0.37$, $p = 0.69$), and was thus not included in the models. We implemented a linear mixed effects model using the lme4 package (Bates et al. 2015) with atlasing region as a random effect (Western, Eastern and Southern Africa) to account for variation resulting from repeated observations from the same countries, but where we could not include country, because several were represented by only one city pair. Differences between the urbanisation categories were tested using estimated marginal means (also known as least squares means) using the emmeans function from the emmeans package (Lenth and Lenth 2018). Furthermore, a linear model was run predicting pentad species richness as a function of percentage urban cover, which was illustrated in a LOESS regression fit implemented using ggplot2 package (Wickham 2016).

To predict expected species richness for each urbanisation category (urban, semi-urban and rural) by rarefaction based on species-list data we used the iNEXT function from the iNEXT package version 2.0.20 (Chao et al. 2014). This also provides values for the Shannon–Wiener and Simpson’s diversity indices, measures of species diversity and dominance, respectively. A visual comparison of species restricted to urbanised or rural pentads was undertaken using density plots of mass in relation to habitat specialisation.

Analysis of functional guilds

Functional diversity is an increasingly used concept to address changes in biodiversity (Mason et al. 2005). Functional diversity summarises the key properties of ecosystems, and is useful for the evaluation of the effects of land use on the provision of ecosystems services for human wellbeing (Harris et al. 2006; Pla et al. 2011). The definition of functional diversity (from Mason et al. 2005) is the distribution of species and abundance of a community in niche space, including the amount of niche space filled by species in the community (functional richness). The evenness of abundance distribution in filled niche space (functional evenness) and the degree to which abundance distribution in niche space maximises divergence in functional characters within the community (functional divergence).

Each species was classified according to a set of 11 functional traits mostly related to diet, size and habitat specialization. Mass values were obtained from Rose et al. (2019) or author ringing records, or various internet sources. The dietary classes are based on Table 1 in Child et al. (2009), which the authors argue represent ecological services. For instance, the ecological service of species classed as scavengers is carcass and waste disposal, as well as disease control. The class defined as carnivores, where species are known to include vertebrate prey in their diet, can control rodent species and similarly for insectivores, which can control invertebrate pest species

(Whelan et al. 2015). Pollinating species are important for plant reproduction, and granivores for control of weed species. We also include piscivores, ecological engineers (e.g. woodpeckers and barbets), habitat specialization (including biome restricted species and primary forest specialists); and species foraging in aquatic environments as specialised classes. The classification in all cases was binary, and non-exclusive e.g. a species could belong to multiple dietary classes to account for omnivores. Our full list of species with assigned functional traits is available as Supplementary Information Table S2. We supplemented these traits with an additional set of morphological data and ecological niche assignments from Pigot et al. (2020) resulting in a final set of 26 traits for use in investigating functional diversity.

We then calculated the following standard measures of functional diversity: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Villéger et al. 2008), using reporting rate in pentads as proxies of abundance measures (Underhill 2016). The functional diversity measures were calculated using the dbFD function from the FD package for R (Laliberté and Legendre 2010; Laliberté et al. 2014), applying weightings for dietary guild and the trait and biometric data from Pigot et al. (2020). The number of Principal Coordinate Analyses (PCoA) axes to keep as ‘traits’ for calculating FRic was set to 9 to aid computation, with resulting quality of the reduced-space representation = 0.73. As per species richness, the functional diversity measures were tested between rural-urbanised categories using estimated marginal means, with the functional diversity measures for each pentad as the sampling units. Data from all pentads were used for these analyses.

Testing for differences in functional dietary guilds

Given differing results between species richness and functional diversity, there is a need for an intermediate scale analysis on how different guilds are responding to urbanisation. We identified that the ‘semi-urban’ pentad urbanisation category likely does not inform differences between rural and urban bird community species richness and confounds pairwise analysis (see results), so we removed data to include only the 28 urban–rural pairs (56 pentads), excluding pentad pairs where one or another pentad was classified as semi-urban. Differences in dietary functional guilds between rural and urban pentads were evaluated based on three measures: the total number of species; the mean mass of the bird community for each respective guild; and a log-transformed score of relative biomasses based on the relative abundance of each species (i.e. reporting rate) multiplied by species mass, which we call ‘projected biomass’. This last measure allows us to see whether a functional guild is represented by equivalent biomass regardless of species composition, i.e. where there is compensation within a guild for pentads with lower species richness occurring because of a higher abundance of certain species. Differences between these measures were tested using paired *t*-tests after testing for distribution assumptions using the Shapiro–Wilk test implemented using the shapiro.test and t.test functions in R 3.5.3 (R Core Team 2019).

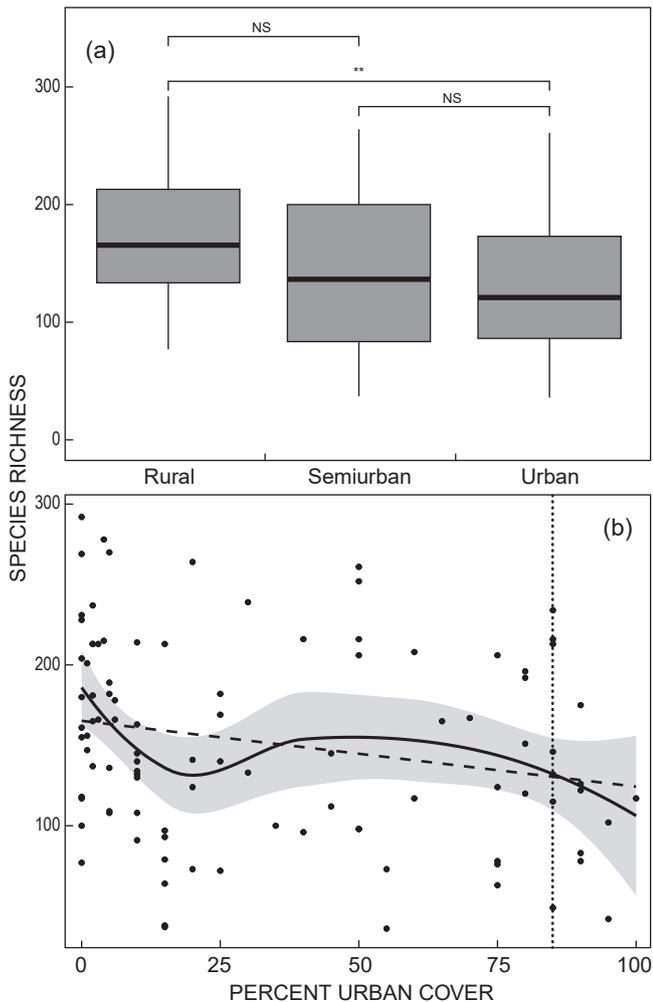


Figure 2: (a) Boxplots of avian species richness in a pentad across sub-Saharan Africa as a function of urban cover categories. Boxes indicate the inter-quartile range with horizontal bars the median species richness. There were significant differences between rural and urban classes, but neither differed from the semi-urban category. (b) A linear regression fit (dashed line) and LOESS smoothed fit (solid line) of total species richness of a pentad against the percent urban cover within a pentad. Standard error of the LOESS smooth fit is indicated with grey shading. A vertical dotted line indicates 85% urban cover, beyond which it is rare to have pentads with >150 species

Predicting the African urban exploiter bird species

Species were also scored on whether they were synanthropic, i.e. benefiting from the presence of human infrastructure or cityscapes, based on expert opinion and available literature (Hockey et al. 2005). We scored each species as synanthropic ('urban exploiter') based on our understanding of whether or not a species was benefiting from the presence of human infrastructure and modification that is characteristic of urbanisation. Clear examples of these in Europe include House Martin *Delichon urbica* and Barn Swallows *Hirundo rustica* that nest on buildings and in Africa the Hadeda Ibis *Bostrychia hagedash*, range expansion of which

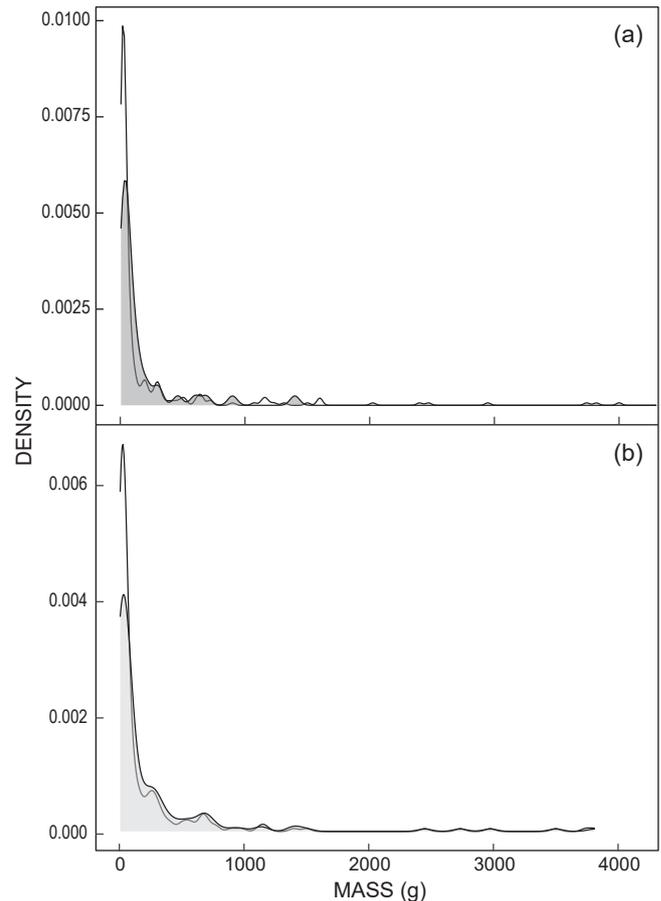


Figure 3: (a) Density plots of mass profiles of bird species recorded only from rural pentads (white) and those recorded from urban pentads only (grey) for the set of birds from 100 pentads from across sub-Saharan Africa. (b) Density plot of habitat specialist mass profiles for species found in rural (white) and urban (grey) pentads: the difference in peaks indicates the loss of habitat specialists in urban pentads

is often associated with watered lawns in suburban areas (Duckworth and Altwegg 2014). However, not all species are strictly synanthropic: Barn Swallows are not preferentially associated with urban regions in Africa, so this species was not scored as an urban exploiter in our list. We predicted the probability of a species being classified as an urban exploiter using a generalised linear mixed effects model (logistic regression), based on the following functional traits and guild membership: mass (log-transformed), carnivore, scavenger, insectivore, herbivore, pollinator, granivore, piscivore and habitat specialist, with family as random effect as a control for phylogeny, implemented using the lme4 package (Bates et al. 2015). We used information theoretic model selection to find the best models by Akaike's Information Criteria (AIC). Finally, we characterise a habitat specialist species by range and abundance using a similar modelling approach. Summary values are presented as mean \pm standard deviation, unless stated otherwise.

Results

Species richness patterns

Based on 100 pentads across sub-Saharan Africa, species richness was highest in pentads classified as rural (172 ± 54 species), followed by semi-urban pentads (141 ± 69), and lowest for urban pentads (132 ± 59) (Figure 2a). There was a significant difference in species richness between the rural and urban pentads ($\beta: 23.96 \pm 8.49$, $t = 2.82$, $p = 0.016$), but not between the rural and semi-urban ($\beta: 19.26 \pm 9.46$, $t = 2.3$, $p = 0.11$) or urban and semi-urban ($\beta: 4.71 \pm 10$, $t = 0.47$, $p = 0.89$) categories. Using percentage urban cover as a predictor allowed us to predict the loss of approximately one species per 2.7% increase in urban cover. However, the fit of the data is not exactly linear, with a slow decline in species richness until very high urban cover percentage (>85%) when the decrease is marked (illustrated in Figure 2b by the fitting of a LOESS smooth curve). For predicted species richness by rarefaction the set of rural pentads was the highest (Table 1), with expected totals of 1 118, 910 and 855 species for rural, urban and semi-urban categories, respectively. This trend was also seen for the Shannon–Wiener and Simpson’s diversity indices. The diversity index values are all significantly different from each other between categories (confidence intervals do not overlap, see Table 1).

We recorded 48 bird species unique to urban pentads (i.e. these species were not recorded in other pentad categories), but 292 species unique to rural pentads. An examination of the density plots of the mass profiles shows a large number of small species that are not recorded from the urban pentad partner, as well as the potential exclusion of several larger species (Figure 3a), with the difference accounted for mostly by habitat specialists (Figure 3b).

Functional guild patterns

There were no significant differences between categories for any of the functional diversity metrics (FRic, FEve, FDiv; Appendix Table A1). However, this effect was marginal for functional richness, which trended to be higher for rural pentads, compared with urban pentads (Figure 4a). The opposite pattern was seen for functional divergence, i.e. this measure trended to be higher in urban pentads and is interpreted as that the most abundant species tended to occur at extremities of the functional character range (Figure 4b). To explore where this divergence might be happening requires an individual examination of the results of the dietary guilds.

Dietary guild patterns

The dietary guild that showed the greatest differences between rural and urban pentads was the carnivore guild (Figure 5, Table 2). Species richness was lower in urban pentads ($t = -3.32$, $df = 27$, $p = 0.003$) and the community of species representing this guild was heavier in the rural pentads ($t = -4.89$, $p < 0.1$), but the projected biomass (based on abundance), although lower for the urban pentads, was not significantly different ($t = -1.62$, $p = 0.12$); i.e. there was some compensation for species loss by increased abundance of the available smaller,

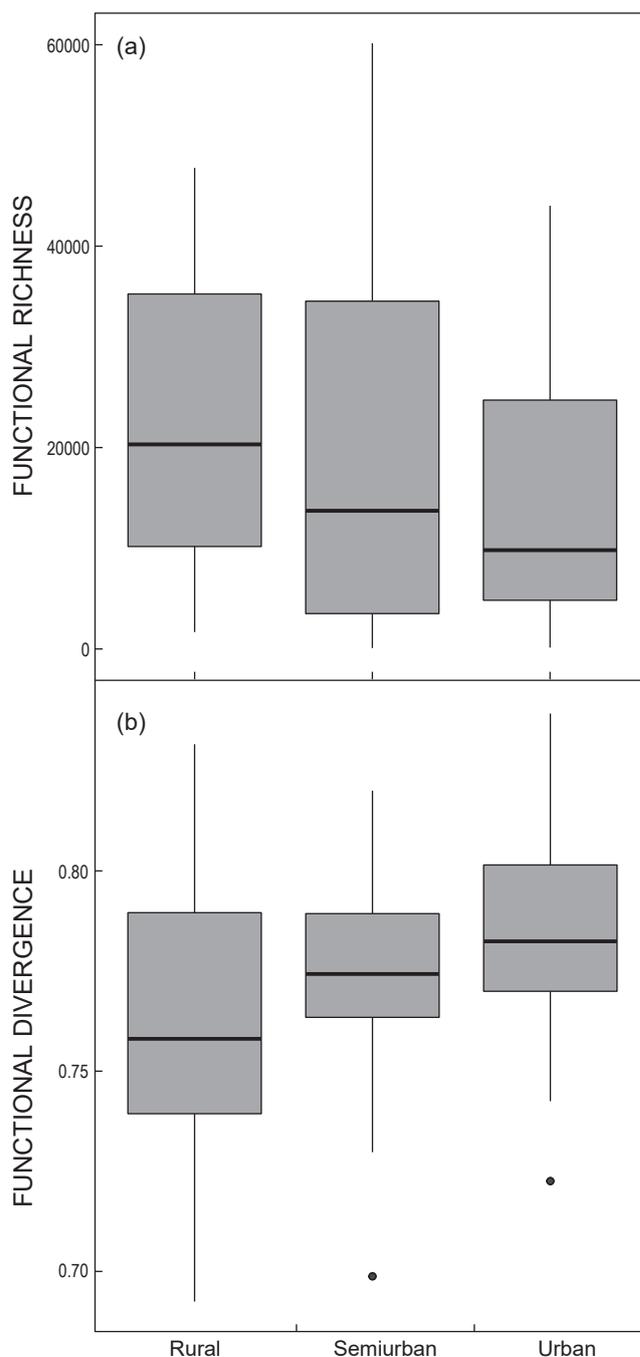


Figure 4: Functional diversity of avifaunal communities in the context of the African urban landscape, represented by functional richness and functional divergence: there were no significant differences, but these charts suggest an emerging trend. Functional evenness is not illustrated as results were homogenous between categories (see Appendix Table A1 for statistical details)

common species. The Shapiro–Wilk tests suggested this analysis was not suitable for scavengers, although an inspection of mass and biomass charts suggests a similar pattern to the carnivores with the loss of large species from urban environments again compensated for by higher abundance of remaining scavengers (Appendix Figures).

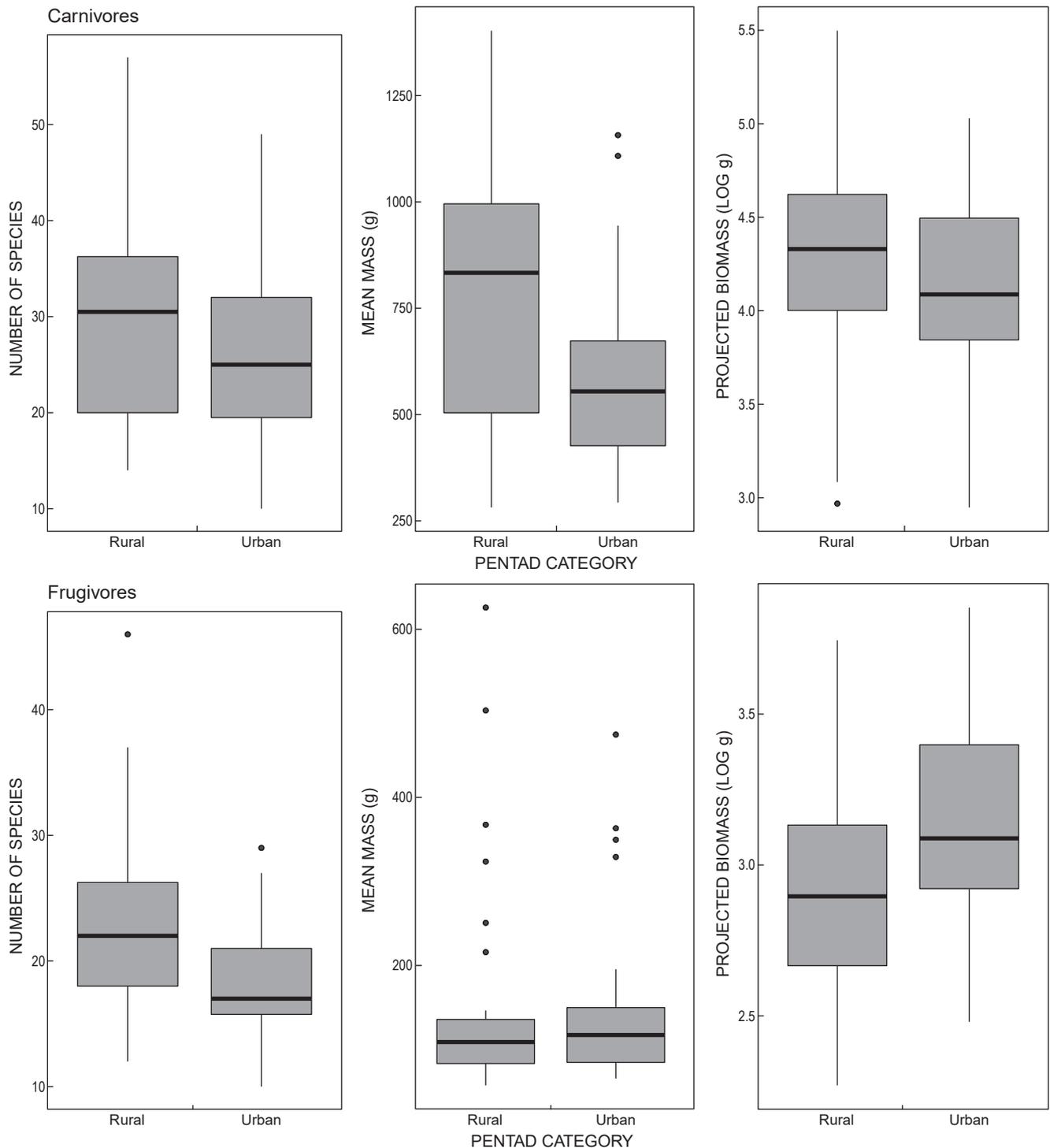


Figure 5: Boxplots of differences in three metrics of the carnivorous and frugivorous bird guilds between urban and rural paired pentads based on summaries from 56 pentads from across sub-Saharan Africa. The number of recorded species is lower for the set of urban pentads in each case, and those species tend to be smaller (lower mean mass) in the case of carnivores. Projected biomass (log of mass × reporting rate) trended lower for urban pentads for carnivores, but was significantly higher for frugivores; this contrasted with other dietary guilds where values were similar

The prominence of Pied Crow *Corvus albus* across this set of pentads (Table 3) is noteworthy in this regard. Interestingly for frugivores, despite generally lower species richness in urban pentads, the relative biomass values were significantly higher in the urban pentads for this guild,

suggesting there are some very common members of these guilds in African cities. Insectivores, herbivores and granivores were also represented by fewer species in urban pentads, but had equivalent biomass resulting in no change in functional diversity. There were no marked patterns in

Table 2: Avian dietary guild comparison between 28 urban and rural pentad pairs. Species richness is the mean number of species representing a guild found in a pentad. Mass is the mean of the set of the previous species (g or log g). Projected biomass (Biomass) is the mass value multiplied by the relative abundance (reporting rate). Statistical results (*t*-tests) are provided where conditions for this test were satisfied (by Shapiro–Wilk’s tests). Lower and upper 95% confidence intervals (LCL, UCL) are also provided, *df* = 27 in all cases

Guild	Metric	Rural	Urban	<i>t</i>	LCL	UCL	<i>p</i>
Carnivores	Species richness	27 ± 10	22 ± 8	-3.2	-7.63	-1.80	0.003
	Mass (g)	812 ± 319	619 ± 228	-4.89	-273	-111	< 0.001
	Biomass	4.3 ± 0.6	4.2 ± 0.5	-1.62	-0.29	0.3	0.117
Scavengers	Species richness	3.1 ± 1.7	3.2 ± 1.8				
	Mass (g)	1254 ± 1090	874 ± 633				
	Biomass	5.1 ± 0.65	5.1 ± 0.84				
Herbivores	Species richness	9.6 ± 6.7	7.8 ± 6.5	-2.78	-3.16	-0.48	0.009
	Mass (log g)	5.8 ± 1.5	5.8 ± 1.2				
	Biomass	4.3 ± 1.2	4.3 ± 1.2	0.37	-0.43	0.61	0.72
Insectivores	Species richness	99 ± 36	79 ± 31	-4.33	-29.25	-10.39	< 0.001
	Mass (g)	194 ± 75	177 ± 62	-0.99	-51.35	17.78	0.33
	Biomass	2.55 ± 0.41	2.59 ± 0.4	0.44	-0.16	0.24	0.66
Frugivores	Species richness	21.1 ± 5.8	17.2 ± 4.6	-2.63	-7.5	-0.87	0.1
	Mass (g)	173 ± 140	160 ± 112				
	Biomass	2.91 ± 0.32	3.13 ± 0.36	2.49	0.4	0.39	0.2
Granivores	Species richness	37.2 ± 14.2	29.5 ± 12.8	-4.15	-11.52	-3.90	< 0.001
	Mass (log g)	3.75 ± 0.32	3.76 ± 0.31	0.15	-0.14	0.16	0.89
	Biomass	2.52 ± 0.33	2.59 ± 0.40	0.85	-0.11	0.26	0.40
Pollinators	Species richness	5.0 ± 2.34	4.5 ± 2.25	-0.86	-1.69	0.69	0.39
	Mass (g)	14.78 ± 6.97	14.3 ± 6.83				
	Biomass	1.45 ± 0.46	1.44 ± 0.26	-0.9	-0.20	0.18	0.93
Piscivores	Species richness	13.0 ± 6.34	13.0 ± 7.47	0.4	-3.11	3.25	0.96
	Mass (g)	922 ± 406	756 ± 339	-2.45	-306	-27	0.2
	Biomass	4.7 ± 0.73	4.8 ± 0.56	0.7	-0.30	0.32	0.94

Table 3: Coefficients of the logistic regression model best predicting probability of being classified as an African urban exploiter bird species based on functional guild characteristics, based on a dataset of 1 060 bird species. Models are ranked by AIC

Term	Estimate	SE	<i>t</i>	<i>p</i>
AIC = 403				
(Intercept)	-2.919	0.227	-12.853	0.000
Scavenger	2.370	0.643	3.686	0.000
Habitat specialist	-2.108	0.732	-2.881	0.004
AIC = 404				
(Intercept)	-2.992	0.235	-12.741	0.000
Scavenger	2.332	0.630	3.703	0.000
Habitat specialist	-2.065	0.732	-2.822	0.005
Granivore	0.401	0.360	1.114	0.265
AIC = 405				
(Intercept)	-3.050	0.241	-12.636	0.000
Scavenger	2.310	0.626	3.689	0.000
Habitat specialist	-2.035	0.732	-2.780	0.005
Granivore	0.412	0.351	1.173	0.241
Frugivore	0.348	0.363	0.959	0.338

the remaining guilds (piscivores, aquatic specialists and ecological engineers; Table 2; Appendix Figures).

Predictors of urban exploiters

Of the functional guilds used to predict whether we thought that a species was an urban exploiter or not, for the set of three models within two AIC of the top model, the scavenger guild was retained as a positive predictor variable for

all three models. Habitat specialist was retained as a significant negative predictor for all three of the top models and the top model retained only these two predictors (Table 3). The granivore and frugivore guilds were retained as non-significant predictors for two and one models, respectively (Table 3). Habitat specialists for this set of birds were best described as species with low abundance in restricted ranges (binomial glm: abundance × range interaction $\beta = -6.45e^{-3} \pm 2.1e^{-3}$; $Z = -3.078$, $p = 0.002$).

The top 20 most widely recorded species (Table 4) included several urban adaptor species in the top five most widely distributed species, but were represented by a range of sizes and foraging guilds. The urban scavenger, Pied Crow, was the most widespread and was frequently recorded (52% reporting rate). Red-eyed Dove *Streptopelia semitorquata* and Laughing Dove *Streptopelia senegalensis* are common frugivore/granivore species also considered abundant in suburban landscapes. Cattle Egret heronries can be found in urban parklands. The Little Swift *Apus affinis* nests in the eaves of buildings, and African Palm-swifts *Cypsiurus parvus* (which we did not classify as urban exploiters, although some researchers do so) also benefit from the planting of palm trees in urban environments.

Discussion

Our broad-scale analysis revealed that African urban landscapes still hold value for African birds, and that high bird diversity persists in these landscapes to some extent;

Table 4: Top 20 most widely distributed species across 100 pentads from sub-Saharan Africa: Range indicates the number of pentads a species was recorded from. Reporting rate is the percentage of times that a species was recorded for a set of cards within its range. Range here can be a maximum of 100. * = urban exploiters

Common name	Scientific name	Mass	Reporting rate	Range
Crow, Pied*	<i>Corvus albus</i>	438.0	52%	99
Egret, Cattle*	<i>Bubulcus ibis</i>	345.0	56%	93
Dove, Red-eyed*	<i>Streptopelia semitorquata</i>	233.1	68%	90
Dove, Laughing*	<i>Streptopelia senegalensis</i>	96.4	64%	90
Swift, Little*	<i>Apus affinis</i>	27.1	34%	87
Palm-swift, African	<i>Cypsiurus parvus</i>	15.3	48%	85
Cuckoo, Diderick	<i>Chrysococcyx caprius</i>	33.6	24%	81
Kite, Black-shouldered	<i>Elanus caeruleus</i>	244.4	30%	80
Heron, Grey	<i>Ardea cinerea</i>	1334.4	34%	79
Heron, Black-headed	<i>Ardea melanocephala</i>	1165.9	36%	78
Prinia, Tawny-flanked	<i>Prinia subflava</i>	9.2	51%	78
Whydah, Pin-tailed	<i>Vidua macroura</i>	15.1	27%	78
Paradise-flycatcher, African	<i>Terpsiphone viridis</i>	15.0	28%	75
Cormorant, Reed	<i>Phalacrocorax africanus</i>	473.0	38%	74
Hamerkop, Hamerkop	<i>Scopus umbrette</i>	453.8	28%	73
Drongo, Fork-tailed	<i>Dicrurus adsimilis</i>	48.8	50%	72
Kite, Yellow-billed*	<i>Milvus milvus</i>	689.7	37%	70
Kingfisher, Pied	<i>Ceryle rudis</i>	79.9	25%	70
Swallow, Barn	<i>Hirundo rustica</i>	20.0	34%	70
Mannikin, Bronze	<i>Lonchura cucullata</i>	10.1	45%	70

but overall rural species richness remained higher. There were only some cases where our species diversity metrics differed significantly between the urbanised-rural pentad-pairs and there was no compelling evidence for loss of functional diversity. This suggests a high resilience of African avifauna to current levels of urbanisation. However, as is the case with urban studies from the Global North, high levels of urbanisation do seem to have a filtering effect on species in the carnivore guild (Kettel et al. 2018), which is of concern given the globally high rates of decline amongst raptor species (Garbett et al. 2018). Crucially, pentads classified as semi-urban, i.e. those with urban infrastructure maintained at below 50%, might offer a unique development opportunity for African cities moving forward as a potential threshold at which one can maintain biodiversity, but also allow for the expansion of urban infrastructure. Higher levels of infrastructure development were associated with lower species richness, and this was especially pronounced for pentads with urban cover greater than 85%.

Species richness and diversity

Our analysis of the African Bird Atlas Project database indicates that pentads dominated by urban infrastructure have lower cumulative species richness, compared with nearby rural pentads, whereas pentads with lower levels of human infrastructure (semi-urban) had intermediate species richness. The same trends were obvious when comparing the Shannon–Wiener and Simpson’s diversity indices across the gradient. The high Simpson’s diversity index suggests that the high diversity associated with pentads that are more rural is also dominated by certain species, although these dominant species vary across the continent. This feeds into the globally observed trend of a decline in species diversity as the amount of urban land cover increases across landscapes (Batáry

et al. 2018). This general pattern is also seen in bird communities of developing countries (van Rensburg et al. 2009; MacGregor-Fors and Schondube 2011; Silva et al. 2015; Chamberlain et al. 2018), although some notable exceptions arise depending on the quality of the surrounding natural (rural) vegetation type and water availability (Dures and Cumming 2010; Chamberlain et al. 2020). Unfortunately, it is difficult to ascribe causality to the variety of different ecological and environmental factors that are affecting bird diversity across our urban–rural gradient. However, previous studies have shown that vegetation heterogeneity, landscape connectivity, urban green spaces, waterbodies, exotic ornamental plants etc., can all have a positive effect on species richness and diversity in cities (e.g. Faeth et al. 2011; Suri et al. 2017; Rodrigues et al. 2018).

An analysis of body size did reveal one potential mechanism for the difference in species richness and diversity between urbanised and rural pentads. Density plots showed the loss of a few large bird species, as well as many small habitat specialists, from pentads classified as urban. An example of the loss of a large-bodied habitat specialist is the Saddle-billed Stork *Ephippiorhynchus senegalensis*, which is now largely restricted to protected areas across Africa, despite an increase in waterbodies; their preferred habitat (Gula et al. 2019). Similarly, we found little evidence that larger-sized raptors, with the exception of the two *Milvus* kite species, were benefitting from city environments, although McPherson et al. (2021) report higher densities of four raptor species in African urban, rather than rural environments, namely the Black Sparrowhawk *Accipiter melanoleucus*, African Crowned Eagle *Stephanoaetus coronatus*, Lanner Falcon *Falco biarmicus* and Peregrine Falcon *Falco peregrinus*. In general, raptors appear to be highly susceptible to different types of land-use

change: for example, Childs et al. (2009) showed a decline in raptor species across an agricultural-protected area gradient and Little and Navarro (2019) used atlas data to show changes in raptor abundance with time attributable to anthropogenic alteration around Cape Town. The loss of raptors from urban ecosystems can have disproportionate ecological and ecosystem service consequences, because these species are important for maintaining pest populations (Amar et al. 2018). Therefore, the ongoing global raptor decline and specific loss across cities is a concern (Buechley et al. 2019). Finally, whereas the number of habitat specialists was lower for the urbanised pentads, it is notable that many still were recorded from this category, and once again suggests a level of resilience amongst the birdlife of African cities at current urbanisation levels.

Functional diversity and dietary guilds

Urbanisation typically acts as a filter on functional traits, with knock-on effects for ecological function and ecosystem service delivery in cities (Croci et al. 2008). Studies from Global North cities suggest that we should have expected a large shift to bird communities consisting of small-bodied habitat generalists (Evans et al. 2011). We were therefore surprised to find that currently there are no differences in functional diversity measures across the urban gradient. This is also surprising given the 20% decrease in global functional diversity recently reported by Sol et al. (2020). However, Hagen et al. (2017) observed functional diversity of urban avian assemblages was not consistently different from that of non-urban assemblages, and was higher when accounting for species richness. For our dataset, there was a slight trend, albeit non-significant, towards higher functional divergence in urban environments. Despite this, our results offer a glimmer of hope for African cities and suggest that ecological function and ecosystem service delivery are being maintained here.

Our examination within dietary guilds indicated lower species richness of several guilds, notably carnivores and possibly scavengers, although lower species richness and smaller body size was offset by increased abundance of common species. This is most obvious in the scavenger guild, where almost all vultures (except the Hooded Vulture) are rarely recorded in urban environments, but these species have been replaced by large numbers of a few common scavenger species: Pied Crow and Marabou Stork, and Sacred Ibis *Threskiornis aethiopicus* to a lesser degree. Similar to the findings of Chamberlain et al. (2018) from Uganda, generalist scavengers appear to be benefiting across the continent, whereas some insectivores are declining, although notable exceptions appear to include Fork-tailed Drongo *Dicrurus adsimilis* and Little Swift. However, for all of these guilds, as well as frugivores, there are large numbers of common species, such as Laughing Dove and Red-eyed Dove, making up for loss of specialists.

What makes an African urban bird?

Our findings generally conform to earlier results suggesting that urban exploiting birds are generalists (Evans et al. 2011), with the implication that habitat specialists in proximity to expanding cities will require conservation attention. However, of note is that the African urban bird

is more likely to be described by scavenging dietary habits, revealing the unique foraging niche available across the African continent and commented on before by Chamberlain et al. (2018). McPherson et al. (2021) also noted that urban raptors are best described by a scavenging diet. Accordingly, some birds are providing a valuable ecological service across sub-Saharan Africa in the role of waste disposal.

Implications for spatial planning

Urban green infrastructure (e.g. parks, reserves, riparian zones, gardens) is important for biodiversity in urbanising landscapes (MacGregor-Fors and Schondube 2011; Swamy et al. 2019). In addition, there is a growing consensus of the value of this biodiversity for the quality of life of urban dwellers (Cox et al. 2017). Given the many benefits of urban green infrastructure and the associated biodiversity, it is important to foster these elements in cities. Our analysis revealed that maintaining urban land-cover at intermediate levels in the landscape could present a win-win scenario for both biodiversity and human development, including human health and well-being, and promoting urban green infrastructure in cityscapes is a possible mechanism to achieve this. Such interventions will benefit rare, range-restricted and large-bodied species, considered losers in the face of urbanisation, providing buffer for biodiversity against the continued expansion of African cities.

Comments on BirdMap coverage and caveats

Citizen science datasets provide valuable data, but this data can be subject to unusual additional aspects of variation that may depend on observers and region (Kelling et al. 2015; Gelmann et al. 2016). Despite the value of the bird atlas data, there are still notable gaps in the atlas spatial coverage of African urban centres, even in southern Africa. Gaborone and Francistown (Botswana) had fewer than four full protocol cards; likewise, Maputo and Beira (Mozambique) could not be included, although there are pentads in these countries in more natural landscapes with good coverage. Other potential towns had to be excluded, because their centres fall on pentad corners, i.e. towns were spread over four pentads, resulting in only marginal urban classification of any associated pentads (e.g. Maun). The only country where coverage in cities tends to be higher than adjacent rural pentads is South Africa. Outside South Africa, atlasing hotspots tend to centre on protected areas and there is a need to extend atlasing efforts to more African countries and cities worldwide to monitor and better inform changes happening to avifaunal communities on this unique continent.

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ORCID

ATK Lee: <https://orcid.org/0000-0002-5858-9351>

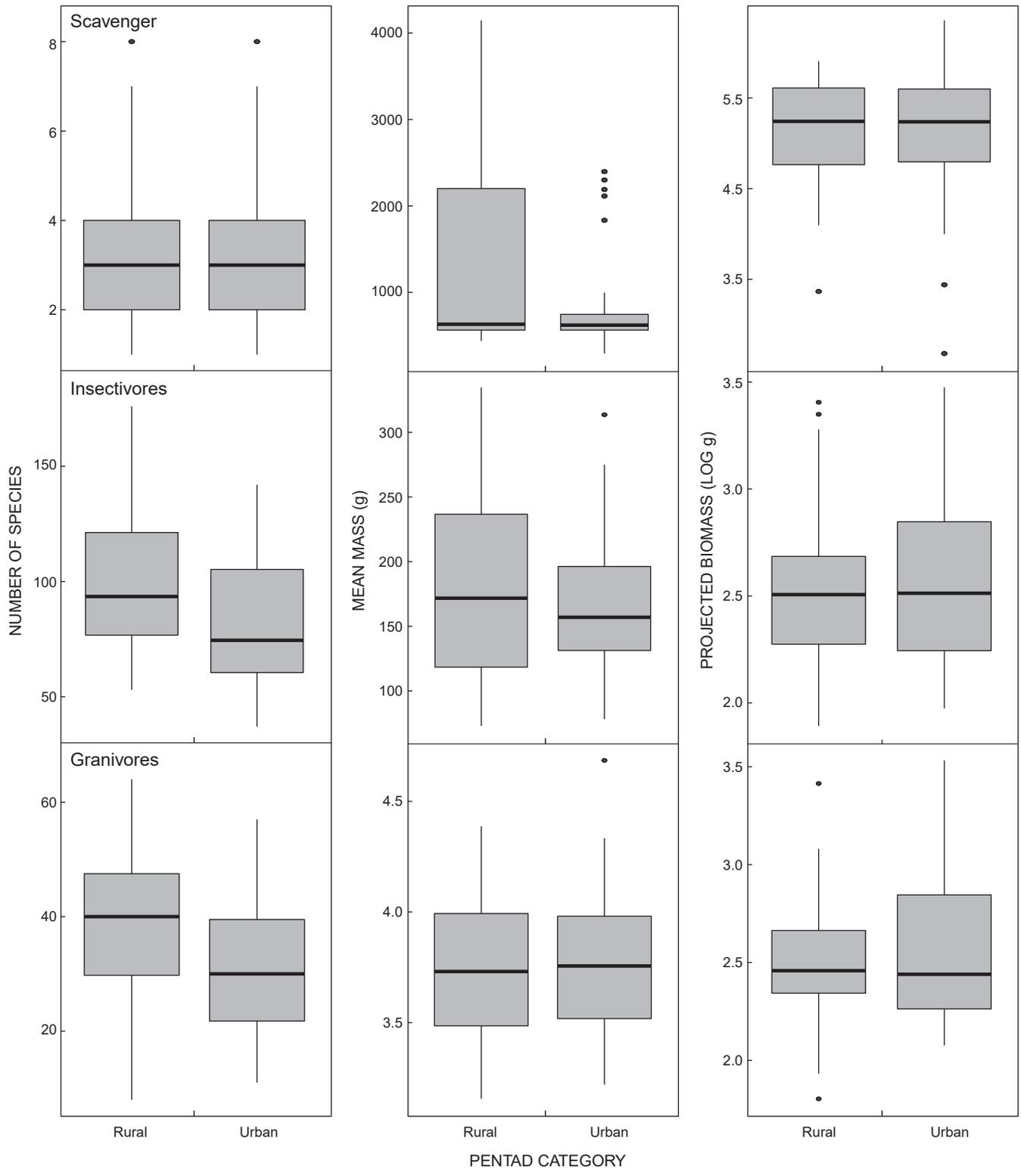
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Chevonne Reynolds: <https://orcid.org/0000-0002-2345-7017>

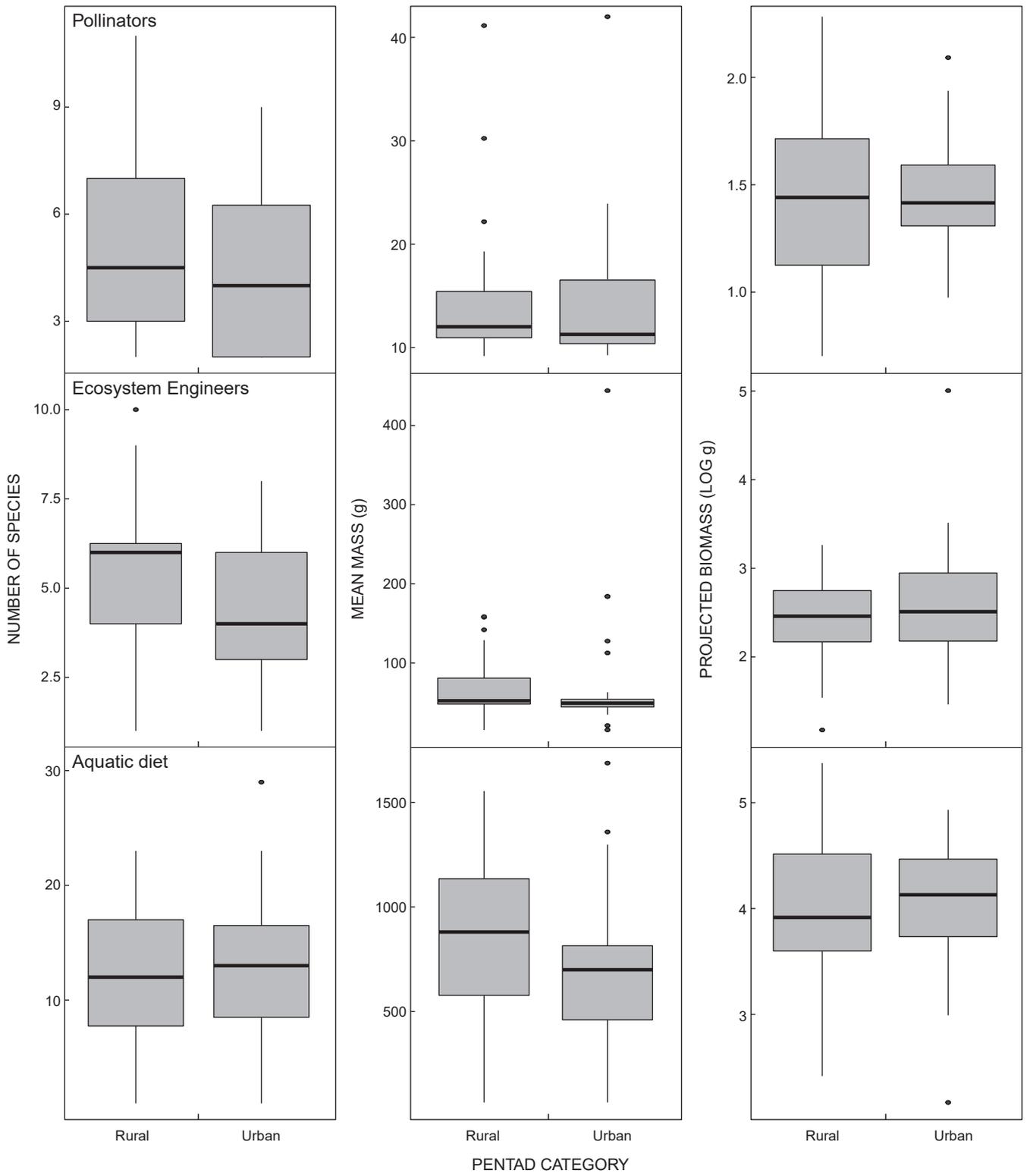
References

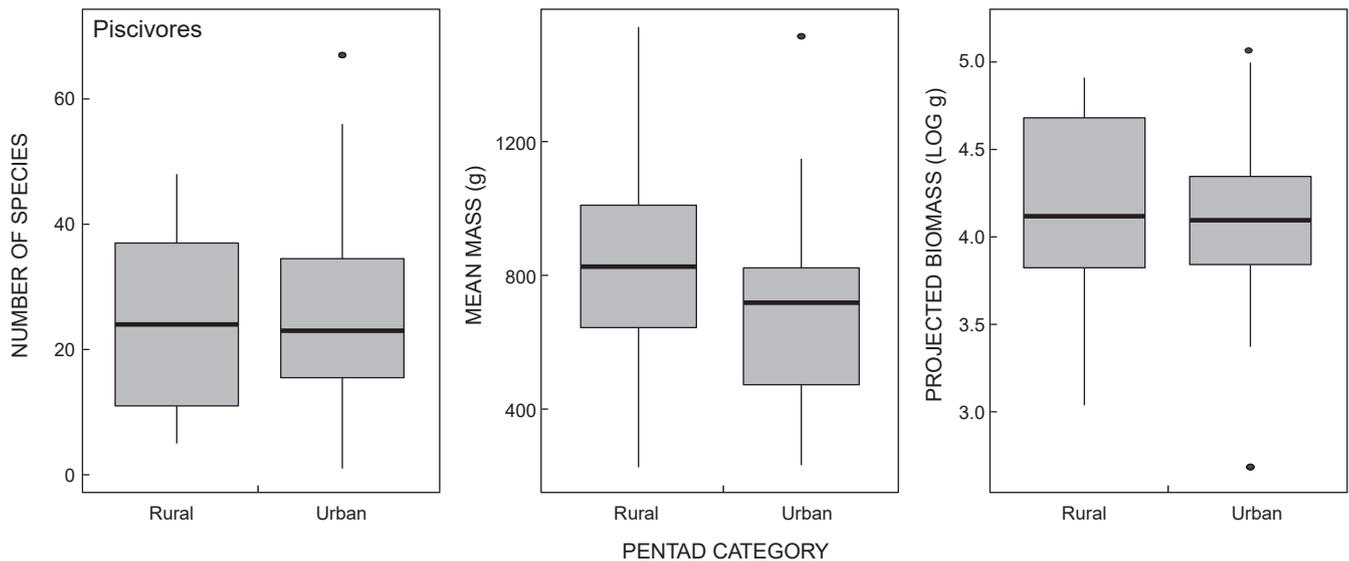
- Amar A, Buij R, Suri J, Sumasgutner P, Virani MZ. 2018. Conservation and ecology of African raptors. In: Sarasola J, Grande J, Negro J (Eds). *Birds of Prey*. pp 419–455.
- Batáry P, Kurucz K, Suarez-Rubio M, Chamberlain DE. 2018. Non-linearities in bird responses across urbanization gradients: a meta-analysis. *Global Change Biology* 24: 1046–1054. <https://doi.org/10.1111/gcb.13964>.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Becker CM, Morrison AR. 1988. The determinants of urban population growth in Sub-Saharan Africa. *Economic Development and Cultural Change* 36: 259–278. <https://doi.org/10.1086/451651>.
- Beninde J, Veith M, Hochkirch A. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology letters* 18: 581–592. <https://doi.org/10.1111/ele.12427>.
- Buechley ER, Santangeli A, Girardello M, Neate-Clegg MHC, Oleyar D, McClure CJW, Şekercioğlu ÇH. 2019. Global raptor research and conservation priorities: Tropical raptors fall prey to knowledge gaps. *Diversity & Distributions* 25: 856–869. <https://doi.org/10.1111/ddi.12901>.
- Chamberlain D, Kibuule M, Skeen RQ, Pomeroy D. 2018. Urban bird trends in a rapidly growing tropical city. *Ostrich* 89: 275–280. <https://doi.org/10.2989/00306525.2018.1489908>.
- Chamberlain D, Reynolds C, Amar A, Henry D, Caprio E, Batáry P. 2020. Wealth, water and wildlife: landscape aridity intensifies the urban luxury effect. *Global Ecology and Biogeography* 29: 1595–1605. <https://doi.org/10.1111/geb.13122>.
- Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84: 45–67. <https://doi.org/10.1890/13-0133.1>.
- Child MF, Cumming GS, Amano T. 2009. Assessing the broad-scale impact of agriculturally transformed and protected area landscapes on avian taxonomic and functional richness. *Biological Conservation* 142: 2593–2601. <https://doi.org/10.1016/j.biocon.2009.06.007>.
- Cox DTC, Shanahan DF, Hudson HL, Plummer KE, Siriwardena GM, Fuller RA, Anderson K, Hancock S, Gaston KJ. 2017. Doses of neighborhood nature: the benefits for mental health of living with nature. *Bioscience* 67: 147–155. <https://doi.org/10.1093/biosci/biw173>.
- Croci S, Butet A, Clergeau P. 2008. Does urbanization filter birds on the basis of their biological traits. *The Condor* 110: 223–240. <https://doi.org/10.1525/cond.2008.8409>.
- Duckworth GD, Altwegg R. 2014. Environmental drivers of an urban hadeda ibis population. *Ardea* 102: 21–29. <https://doi.org/10.5253/078.102.0104>.
- Dures SG, Cumming GS. 2010. The confounding influence of homogenising invasive species in a globally endangered and largely urban biome: does habitat quality dominate avian biodiversity? *Biological Conservation* 143: 768–777. <https://doi.org/10.1016/j.biocon.2009.12.019>.
- Evans KL, Chamberlain DANE, Hatchwell BENJ, Gregory RD, Gaston KJ. 2011. What makes an urban bird? *Global Change Biology* 17: 32–44. <https://doi.org/10.1111/j.1365-2486.2010.02247.x>.
- Faeth SH, Bang C, Saari S. 2011. Urban biodiversity: patterns and mechanisms. *Annals of the New York Academy of Sciences* 1223: 69–81. <https://doi.org/10.1111/j.1749-6632.2010.05925.x>.
- Garbett R, Herremans M, Maude G, Reading RP, Amar A. 2018. Raptor population trends in northern Botswana: a re-survey of road transects after 20 years. *Biological Conservation* 224: 87–99. <https://doi.org/10.1016/j.biocon.2018.05.020>.
- Geldmann J, Heilmann-Clausen J, Holm TE, Levinsky I, Markussen B, Olsen K, Rahbek C, Tøttrup AP. 2016. What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity & Distributions* 22: 1139–1149. <https://doi.org/10.1111/ddi.12477>.
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global Change and the Ecology of Cities. *Science* 319: 756–760. <https://doi.org/10.1126/science.1150195>.
- Gula J, Weckerly F, Sundar KG. 2019. The first range-wide assessment of Saddle-billed Stork *Ephippiorhynchus senegalensis* distribution. *Ostrich* 90: 347–357. <https://doi.org/10.2989/00306525.2019.1696900>.
- Gupta A. 2002. Geoindicators for tropical urbanization. *Environmental Geology* 42: 736–742. <https://doi.org/10.1007/s00254-002-0551-x>.
- Harris JA., Hobbs RJ, Higgs E, Aronson J. 2006. Ecological Restoration and Global Climate Change. *Restoration Ecology* 14: 170–176. <https://doi.org/10.1111/j.1526-100X.2006.00136.x>.
- Hockey PAR, Dean WRJ, Ryan PG. 2005. *Roberts' Birds of Southern Africa* (7th edn). Institute for Security Studies. 2020. Africa's population boom: burden or opportunity?
- Reynolds JS, Ibáñez-Álamo JD, Sumasgutner P, Mainwaring MC. 2019. Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology* 160: 841–860.
- Kelling S, Johnston A, Hochachka WM, Iliff M, Fink D, Gerbracht J, Lagoze C, La Sorte FA, Moore T, Wiggins A, et al. 2015. Can observation skills of citizen scientists be estimated using species accumulation curves? *PLoS ONE* 10: e0139600. <https://doi.org/10.1371/journal.pone.0139600>.
- Kettel EF, Gentle LK, Quinn JL, Yarnell RW. 2018. The breeding performance of raptors in urban landscapes: a review and meta-analysis. *Journal of Ornithology* 159: 1–18. <https://doi.org/10.1007/s10336-017-1497-9>.
- Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305. <https://doi.org/10.1890/08-2244.1>.
- Laliberté E, Legendre P, Shipley B, Laliberté ME. 2014. Package 'FD': Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Lee ATK, Altwegg R, Barnard P. 2017. Estimating conservation metrics from atlas data: the case of southern African endemic birds. *Bird Conservation International* 27: 323–336. <https://doi.org/10.1017/S0959270916000307>.
- Lenth R, Lenth MR. 2018. Package 'lsmeans'. *The American Statistician* 34: 216–221.
- Little RM, Navarro RA. 2019. Implications of geographical range changes and resultant sympatry for three Accipiter Hawks on the Cape Peninsula, South Africa. *Ostrich* 90: 139–143. <https://doi.org/10.2989/00306525.2019.1613270>.
- MacGregor-Fors I, Schondube JE. 2011. Gray vs. green urbanization: relative importance of urban features for urban bird communities. *Basic and Applied Ecology* 12: 372–381. <https://doi.org/10.1016/j.baae.2011.04.003>.
- Magle SB, Hunt VM, Vernon M, Crooks KR. 2012. Urban wildlife research: past, present, and future. *Biological Conservation* 155: 23–32. <https://doi.org/10.1016/j.biocon.2012.06.018>.
- Martin RO, Sebele L, Koeslag A, Curtis O, Abadi F, Amar A. 2014. Phenological shifts assist colonisation of a novel environment in a range-expanding raptor. *Oikos* 123: 1457–1468. <https://doi.org/10.1111/oik.01058>.
- Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111: 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- McHale MR, Bunn DN, Pickett STA, Twine W. 2013. Urban ecology in a developing world: why advanced socioecological theory

- needs Africa. *Frontiers in Ecology and the Environment* 11: 556–564. <https://doi.org/10.1890/120157>.
- McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>.
- McPherson SC, Brown M, Downs CT. 2015. Diet of the Crowned Eagle (*Stephanoaetus coronatus*) in an urban landscape: potential for human-wildlife conflict? *Urban Ecosystems* 19: 383–396. <https://doi.org/10.1007/s11252-015-0500-6>.
- McPherson SC, Sumasgutner P, Downs CT. 2021. South African raptors in urban landscapes: a review. *Ostrich* 92: xxx–xxx. <https://doi.org/10.2989/00306525.2021.1900942>.
- Mullié WC, Couzi F-X, Diop MS, Piot B, Peters T, Reynaud PA, Thiollay J-M. 2017. The decline of an urban Hooded Vulture *Necrosyrtes monachus* population in Dakar, Senegal, over 50 years. *Ostrich* 88: 131–138. <https://doi.org/10.2989/00306525.2017.1333538>.
- Oliveira Hagen E, Hagen O, Ibáñez-Álamo JD, Petchey OL, Evans KL. 2017. Impacts of urban areas and their characteristics on avian functional diversity. *Frontiers in Ecology and Evolution* 5: 84. <https://doi.org/10.3389/fevo.2017.00084>.
- Pigot AL, Sheard C, Miller ET, Bregman TP, Freeman BG, Roll U, Seddon N, Trisos CH, Weeks BC, Tobias JA. 2020. Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution* 4: 230–239. <https://doi.org/10.1038/s41559-019-1070-4>.
- Pla L, Casanoves F, Di Rienzo J. 2011. *Quantifying functional biodiversity*. London: Springer.
- Pomeroy D, Kibuule M. 2017. Increasingly urban Marabou Storks start breeding four months early in Kampala, Uganda. *Ostrich* 88: 261–266. <https://doi.org/10.2989/00306525.2017.1308443>.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- van Rensburg BJ, Peacock DS, Robertson MP. 2009. Biotic homogenization and alien bird species along an urban gradient in South Africa. *Landscape and Urban Planning* 92: 233–241. <https://doi.org/10.1016/j.landurbplan.2009.05.002>.
- Rodrigues AG, Borges-Martins M, Zilio F. 2018. Bird diversity in an urban ecosystem: the role of local habitats in understanding the effects of urbanization. *Iheringia. Série Zoologia* 108: e2018017. <https://doi.org/10.1590/1678-4766e2018017>.
- Rose S, Thomson RL, Oschadleus H-D, Lee ATK. 2019. Summarising biometrics from the SAFRING database for southern African birds. *Ostrich* 91: 169–173. <https://doi.org/10.2989/00306525.2019.1645054>.
- Seto KC, Güneralp B, Hutyra LR. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America* 109: 16083–16088. <https://doi.org/10.1073/pnas.1211658109>.
- Seto KC, Sánchez-Rodríguez R, Fragkias M. 2010. The new geography of contemporary urbanization and the environment. *Annual Review of Environment and Resources* 35: 167–194. <https://doi.org/10.1146/annurev-environ-100809-125336>.
- Shimba MJ, Jonah FE. 2017. Nest success of the Indian House Crow *Corvus splendens*: an urban invasive bird species in Dar es Salaam, Tanzania. *Ostrich* 88: 27–31. <https://doi.org/10.2989/00306525.2016.1223766>.
- Silva CP, García CE, Estay SA, Barbosa O. 2015. Bird richness and abundance in response to urban form in a Latin American city: Valdivia, Chile as a case study. *PLoS ONE* 10: e0138120. <https://doi.org/10.1371/journal.pone.0138120>.
- Sol D, Trisos C, Múrria C, Jeliakov A, González-Lagos C, Pigot AL, Ricotta C, Swan CM, Tobias JA, Pavoine S. 2020. The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters* 23: 962–972. <https://doi.org/10.1111/ele.13495>.
- Stofberg M, Cunningham SJ, Sumasgutner P, Amar A. 2019. Juggling a “junk-food” diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosystems* 22: 1019–1026. <https://doi.org/10.1007/s11252-019-00885-3>.
- Sumasgutner P, Jenkins A, Amar A, Altwegg, R. 2020. Nest boxes buffer the effects of climate on breeding performance in an African urban raptor. *PLoS ONE* 15: e0234503. <https://doi.org/10.1371/journal.pone.0234503>.
- Suri J, Sumasgutner P, Hellard É, Koeslag A, Amar A. 2017. Stability in prey abundance may buffer Black Sparrowhawks *Accipiter melanoleucus* from health impacts of urbanization. *Ibis* 159: 38–54. <https://doi.org/10.1111/ibi.12422>.
- Swamy S, Nagendra H, Devy S. 2019. Building biodiversity in neighbourhood parks in Bangalore city, India: ordinary yet essential. *PLoS ONE* 14: e0215525. <https://doi.org/10.1371/journal.pone.0215525>.
- Underhill LG. 2016. The fundamentals of the SABAP2 protocol. *Biodiversity Observations*: 1–12.
- van der Meer T, McPherson S, Downs C. 2018. Temporal changes in prey composition and biomass delivery to African Crowned Eagle nestlings in urban areas of KwaZulu-Natal, South Africa. *Ostrich* 89: 241–250. <https://doi.org/10.2989/00306525.2018.1449027>.
- Villéger S, Mason NWH, Moullot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301. <https://doi.org/10.1890/07-1206.1>.
- Whelan CJ, Şekercioğlu ÇH, Wenny DG. 2015. Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology* 156: 227–238. <https://doi.org/10.1007/s10336-015-1229-y>.
- Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.



Appendix Figures: Figures of dietary guild comparisons between rural and urban pentads (28 pairs). Number of species is the indication of species richness; mean mass an indication of the relative size of the members of the guild for each rural-urban category; and projected biomass are the values of mass (log-transformed) multiplied by reporting rate (abundance)





Appendix Table A1: Measures of functional diversity across African pentads characterised by their urbanisation (rural, semi-urban, urban). For each measure (Functional richness, evenness and divergence) the results of estimated means are provided with significance values for each pair. DF was 97 in each case. There were no significant differences between any groups

Level 1	Level 2	Estimate	SE	<i>t</i>	<i>p</i>
Functional richness					
rural	semi-urban	1 561.54	2 936.10	0.532	0.856
rural	urban	1 867.10	2 631.48	0.710	0.758
semi-urban	urban	305.56	3 112.48	0.098	0.995
Functional evenness					
rural	semi-urban	-4.37	6.81	-0.641	0.798
rural	urban	1.33	6.11	0.218	0.974
semi-urban	urban	5.70	7.22	0.788	0.711
Functional divergence					
rural	semi-urban	-4.36	6.80	-0.641	0.798
rural	urban	1.31	6.10	0.216	0.975
semi-urban	urban	5.67	7.21	0.787	0.712

Supplementary table legends (csv files available at <https://doi.org/10.2989/00306525.2021.1902876>):

Supplementary Table 1: A table of the 100 pentads from the African Bird Atlas Project used to examine patterns of species richness across Africa. Pentad = survey block; cat_urban_rural = urbanisation category (urban, rural or semi-urban), city = city pair including name of the associated city and a nearby rural or semi-urban pentad; Region = three broad atlassing regions used to control variation in modelling; percent_urban = a percentage of a pentad covered by urban infrastructure; lists: the number of atlas cards (bird lists) for the pentad; SpR = the number of species recorded for the pentad according to the atlas project; Fric = Functional Richness; Feve = Functional evenness; Fdivergence = Functional divergence (these three being measures of functional diversity as determined using the FD package).

Supplementary Table 2: A table of the traits associated with 1060 species recorded in the 100 sub-Saharan pentads considered for the analysis of patterns of species richness and functional diversity of urban and non-urban bird communities. Spp = A species identifier number used by the African Birdmap Project; species are scored as belonging to a dietary guild (1) or not (0), as well as if we considered the species to be habitat specialists or urban exploiters (adapters).