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LETTER

Avian diversity and function across the world's most populous cities

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Abstract

Understanding the composition of urban wildlife communities is crucial to promote biodiversity, ecosystem function and links between nature and people. Using crowdsourced data from over five million eBird checklists, we examined the influence of urban characteristics on avian richness and function at 8443 sites within and across 137 global cities. Under half of the species from regional pools were recorded in cities, and we found a significant phylogenetic signal for urban tolerance. Site-level avian richness was positively influenced by the extent of open forest, cultivation and wetlands and avian functional diversity by wetlands. Functional diversity co-declined with richness, but groups including granivores and aquatic birds occurred even at species-poor sites. Cities in arid areas held a higher percentage of regional species richness. Our results indicate commonalities in the influence of habitat on richness and function, as well as lower niche availability, and phylogenetic diversity across the world's cities.

KEYWORDS

avian, citizen science, eBird, habitat heterogeneity, latitudinal diversity gradient, phenotypic variation, urban ecology, urban tolerance, urbanization

INTRODUCTION

Biodiversity is threatened worldwide by land-use change, such as agricultural expansion and urbanization, which results in the loss (Fournier et al., 2020; Spotswood et al., 2021), fragmentation (Uchida et al., 2020) and degradation (McKinney, 2006) of remaining primary habitats. Urban expansion often puts pressure on high biodiversity areas (Aronson et al., 2014) and is currently most severe in tropical and subtropical savannas and grasslands (Brondizio et al., 2019). Urban ecosystems are novel habitats, and their community structure has no natural analogues (Uchida et al., 2020; Werner, 2011), involving major shifts in taxonomic (Beninde et al., 2015; Matuoka et al., 2020), functional (La Sorte et al., 2018; Swan et al., 2020) and phylogenetic structure away from the original communities of primary habitats that they replace (Uchida et al., 2020). These novel communities are often created from the loss of evolutionary distinctive species (Morelli et al., 2016) and biotic homogenization associated with urbanization (McKinney & Lockwood, 1999). Mitigating the impacts of urbanization by enhancing the biodiversity and ecosystem service value of cities is in keeping with the United Nations Sustainable Development Goals 11 ‘Sustainable Cities and Communities’ and 15 ‘Life on Land’ (United Nations, 2015).

While urbanization can lead to a predictable homogenization of habitats in places with very different natural geographies (Grimm et al., 2008; Uchida et al., 2020), the transformation tends to leave patches of heterogeneric greenspace differing in size, habitat type and spatial composition, often including small remnants of primary habitats (Crooks et al., 2004; Leveau, 2021). Although this is highly variable among individual cities (Aronson et al., 2014; Callaghan et al., 2019; Uchida et al., 2020). The communities of species that persist in individual patches are filtered by attributes such as patch size (Beninde et al., 2015), position on the urban–rural gradient (Lepczyk et al., 2017) and connection to other patches (Werner, 2011). The permeability and habitability of cities for wildlife also varies depending on factors

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such as socio-economic inequality (Baldock et al., 2019; Sultana et al., 2022), pollution (Batáry et al., 2018), habitat management (Spotswood et al., 2021), human population size and/or density (Oliveira Hagen et al., 2017), city size (Beninde et al., 2015; Uchida et al., 2020) and biogeography (Grimm et al., 2008; McKinney, 2002; Uchida et al., 2020). Biogeography also affects assemblage structure with variation across the latitudinal diversity gradient (Hillebrand, 2004) in turn mediated by environmental filters governed by the frequency of natural disturbances (Betts et al., 2019). These forces filter species from regional species pools that are not resilient to change and thus may leave these regional pools more resilient to future changes (Aronson et al., 2014; Betts et al., 2019; Filloy et al., 2019).

The ability of a species to persist in a city may be mediated by both resource availability (Jokimäki et al., 2016; Shochat et al., 2006; Spotswood et al., 2021) and interspecific competition (Lees, 2018). Overall, urban communities tend to be simpler than their non-urban counterparts, with loss of species often occurring without an associated loss of functional or phylogenetic diversity (Curtis et al., 2022; Kurucz et al., 2021). Urban species tend to exhibit broader environmental tolerance and increased behavioural flexibility (Shochat et al., 2006; Sol et al., 2014), have smaller body sizes (La Sorte et al., 2018), and are often granivorous, feed terrestrially and nest arboreally (Pinho et al., 2016). Species with very similar traits and morphologies are likely to play comparable roles in ecosystems (Dehling et al., 2016; Pigot et al., 2020) and may explain clustering in trait space (Mouillot et al., 2021). The loss of a species from an environment either reduces redundancy in a niche or removes a niche and thus reduces niche packing. Closely related species are likely to respond to urbanization in a similar way (Sol et al., 2014; Swan et al., 2020), but see Martin and Bonier (2018), and so we should expect a reduction in niche packing, with the remaining niches containing plenty of redundancy (Pagani-Núñez et al., 2019). It is likely that functionally rich communities with more redundant species have a higher resilience to disturbance, with redundant species able to compensate for natural population fluctuations when functionally similar species decline (Biggs et al., 2020).

The species that occupy a city are thus determined by three separate filters (1) a stochastic historical biogeographic filter that dictates the regional pool of species available to populate the urban environment, (2) a city-wide filter that allows species to spread into the urban environment via habitat availability and configuration, and (3) a local filter, via processes such as species interactions, that allow species to persist in the urban environment (Fournier et al., 2020; Lees, 2018; Lequerica Tamara et al., 2021). While these processes are beginning to be understood, few studies have compared multiple urban areas (Uchida et al., 2020) and those studies that have are largely focused on urban areas in the Global North (Filloy et al., 2019; Knapp et al., 2021), preventing generalizations of many observed patterns (Ibáñez-Álamo et al., 2017) especially to highly biodiverse regions in the Global South.

Here, we aim to understand patterns of avian diversity and function across the world's largest cities. We measure the biodiversity of urban avian communities as a proportion of the richness of the regional pool and investigate how this measure changes with respect to the local landscape. We then explore why some cities outperform others based on their landscape, historical geological processes and governance. Then we examine how functional diversity is impacted within our urban avian communities with respect to the local landscape. Finally, we look at how niche space is lost as biodiversity declines.

METHODS

We derived our urban communities from data submitted to eBird (Sullivan et al., 2014) (version EBD_relAug-2020), a large avian citizen science project which includes a submission protocol based around shared locations, called hotspots, where birders log their observations as checklists. Each of our urban communities were sited at one of these hotspots occurring in a city (calculated using city vector contains within QGIS (QGIS Development Team, 2022)). We selected cities with a population of at least two million from the GHS Settlement Model from the GHSL Data Package 2019 (Pesaresi et al., 2019) and included all cities that contained at least one urban hotspot. eBird hotspots can be any public location and are exposed as a coordinate in the eBird data set; however, they may attract observations from the surrounding area and may involve observations collected while travelling. While most urban hotspots encompass green and blue spaces, they may also include districts, or other urban features such as landfill sites (Arnold et al., 2021). Our communities were assembled using presence-only data and we followed a protocol developed by Callaghan et al. (2017) that gives us some certainty of recording 80%–90% of all species recorded at a hotspot, eliminating rare transient and vagrant species. We only included species in an urban community if they were also present in the regional pool and if they appeared on at least 10% of checklists at an urban hotspot.

We calculated our regional pools using BirdLife International's species distribution maps (BirdLife International and Handbook of the Birds of the World, 2020). We added each species to a city's regional pool when the species distribution vector intersected with the city vector using QGIS (QGIS Development Team, 2022). The BirdLife taxonomy (HBW & BirdLife International, 2020) was mapped to eBird using the BirdLife alternative names and Avibase (Lepage, 2011).

A second set of regional pools was created using eBird data with the full analysis repeated to ensure our results were robust and not biased by regional pool construction (Appendices S1 and S2). In Appendix S3 we present alternative analyses addressing potential biases associated with clustering of hotspots within certain cities, and the effect of excluding from the analyses those realms with few contributing cities. The effects of urbanization can be studied by comparing the species present therein with those potentially present as defined by a regional species pool. This replaces the temporal effect of urbanization with a spatial effect of urban versus non-urban (La Sorte et al., 2018). Using regional pools is a co-occurrence approach where a species that co-occurs in the regional pool with a species already present in the city has the potential to occupy the city itself (Fournier et al., 2020; Lessard et al., 2012; Srivastava, 1999). Using regional pools also permits comparison between cities in very different areas of the globe. For example, Belo-Horizonte, Brazil which sits in a biodiversity hotspot with over 500 regional bird species can be compared with Moscow with closer to 200 species (Werner, 2011).

All data were imported into BigQuery (Google, 2022) for modelling using dbt™ (DBT Labs, 2022). Final data sets were extracted in R using bigrquery (Edmondson, 2019) and analysis was performed in RStudio (RStudio Team, 2022). Further details of our approach can be found in Appendix S4.

Species richness within and between cities

We measured species richness as the percentage of the regional pool present at a hotspot. We sought to explain this response based on the surrounding landscape, elevation and biogeographic realm. To derive the species richness at each urban site we sampled groups of 15 checklists 100 times and took the average species richness. We measured habitat availability and extent using landcover metrics taken from the Copernicus Global Land Operations 'Vegetation and Energy' raster (Buchhorn et al., 2020) and elevation metrics derived from a global digital elevation model (European Environment Agency, 2016). The latitude and longitude of each urban hotspot were imported into Google Earth Engine (Gorelick et al., 2017) and we created a 5 km buffer around each hotspot (to cover a 10 km linear walk for a checklist; the maximum distance covered in any one of our checklists). We measured the proportion of each landcover within the buffer, the average elevation and the difference between the highest and lowest elevation (scaled 0–1). The city vectors were imported into Google Earth Engine (Gorelick et al., 2017) to create an intersection with the Ecoregions data set and we assigned each city to one of eight realms following RESOLVE (2017); areas of distinct evolutionary history that are collections of geographically close biomes, based on which realm covered the largest area of the city. Our urban hotspot explanatory variables were thus realm, mean elevation scaled, elevation range scaled, alongside proportion of land covered by: closed forest, cultivated, herbaceous vegetation (non-woody vegetation), herbaceous wetland, open forest, permanent water, shrubs (woody vegetation) and urban. As these environmental predictors are proportion of area covered, there is some collinearity among them, with the highest measure between open and closed forest as 0.37 and then urban and closed forest as −0.31. We included the city as a random effect and the log of the number of checklists at a hotspot as a covariate. To verify the variance explained by the city random effect, we used the best model selected by the dredge for each regional pool. We fitted the best model with the random effects and used the r.squaredGLMM in the MuMIn R package (Bartoń, 2021) to state the amount of variance explained by the whole model and the amount of variance explained by just the fixed effects. We then used an ANOVA to test whether the models with and without the random effect were significantly different.

We recorded the intercepts of the city random effect for each city from the best models from above—these represent a standardized species richness response that is comparable across cities. We sought to explain these responses using 47 variables that describe local landscape, physical geography and governance (Appendix S4). We imputed missing values for variables that were not available for all cities using the random forest package (Liaw & Wiener, 2018). Variables describing the surroundings of the city were measured in circular buffers at three scales: 25, 50, and 100 km. The regional vectors were created using Google Earth Engine. We used a variable selection technique based on random forests (Breiman, 2001) originally developed by Genuer et al. (2010). This method performs well in an ecological setting (Fox et al., 2017; Richardson et al., 2022). It is also robust to a high predictor-to-data point ratio and to autocorrelation among predictors (Genuer et al., 2010). We then built a set of GLM models using the selected variables and the best model using LOOCV backward-step selection (James et al., 2017). Finally, we explored the latitudinal diversity gradient effect by fitting a quadratic GLM for the intercepts of the city random effect explained by latitude.

Phylogenetic signal for urban adaptability

We calculated a bird-family response variable for family-specific *urban tolerance* by dividing the number of cities within which a family was present (at any hotspot) by the number of regional pools a family was present in. Thus, a family with an *urban tolerance* of 1 is always present in a city when present in a regional pool. This shows how likely a family is to be present in a city when it is found in the city's regional pool. We only included families that contain 10 or more species in our data set and occur in more than 2 regional pools. We used the phylogenetic maximum clade tree based on a set of trees from Jetz et al. (2012) which use the Hackett et al. (2008) backbone. The family-level tree was created from the species-level tree, by pruning to keep one representative per family and replacing the remaining tip names with the representative family names. We mapped family to the slightly altered BirdLife taxonomy and then calculated the phylogenetic signal based on Pagel's (1999) lambda, using the phytools R package (Revell, 2012).

Functional richness within urban hotspots

We used the first four trait axes from the PCA from Pigot et al. (2020). These are: PC1—body size (84% of variation); PC2—beak size (6%); PC3—species with short tails and pointed beaks to species with long tails and stubby beaks (4%); PC4—species with long tails and pointed beaks to species with short tails and stubby beaks (3%). We also used foraging niche ($n=33$) and trophic niche ($n=10$) of each species from the Pigot et al. (2020) data set. We added nocturnality from Wilman et al. (2014). We created niches by clustering species by morphology and splitting these clusters by foraging niche, trophic niche and nocturnality. We identified morphological clusters of species using the first four PCA axes with a density clustering algorithm (densityClust R package: Pedersen et al., 2017). We used a peak cluster threshold (delta) of 0.5, and a local density threshold (rho) between clusters of 0.2. We repeated the analysis for two niche configurations with different numbers of niches to confirm that the number of niches does not affect the result. This yielded 263 niches in the regional pools with a median of three species per niche (minimum: 1, 25th percentile: 1, 75th percentile: 7 and maximum: 1145). We repeated the analysis using 38 clusters (delta = 0.6, creating 188 niches) and 204 clusters (delta = 0.4, creating 401 niches) to examine whether results were sensitive to the number of clusters.

We define a well-performing urban ecosystem as one which has many niches for its given species richness. We calculated the number of niches present in the regional pool for each city, and the number of these niches represented in each of our samples at each of our hotspots to create an average per hotspot. From this, we calculated the proportion of niches present at each hotspot. To calculate the proportion of niches for the given proportion of richness, we first sought to find the best model for explaining niche richness at a hotspot given its species richness. Thus, hotspots with positive residuals from fitting this model are over-performing in terms of niche richness per species richness, whereas hotspots with negative residuals are under-performing. To find the best model, we fitted linear, quadratic and cubic models using the proportion of regional richness calculated earlier. We used an ANOVA to test if these were different and then chose the best model using AIC (James et al., 2017). The residuals from this best model were assigned to each urban hotspot. A linear model was selected to calculate the proportion of niches present for the given proportion of richness for each of the regional pools. We sought to explain the proportion of niches for the given proportion of richness following the same procedure as used for explaining the proportion of richness at a hotspot.

To model niche availability in cities, we ranked each species according to its *urban tolerance*, which we defined (as above) as the number of cities the species appears in divided by the number of regional pools. We measured niche availability in cities by first ordering all the species within a regional pool by their *urban tolerance* in ascending order. We then took the first 5% (61 species) of these species, representing the species most tolerant to the urban environment and thus we presume last to be removed, and recorded the niches to which these species belonged. We then repeated this process to give us the niches present at each 5% incremental increase in number of species, with increasing likelihood of being missing from cities. We explored niche availability by each attribute we used to build niches: foraging niche; trophic niche; nocturnality and morphology.

RESULTS

Of 221 cities with human population over two million, 141 contained qualifying hotspots, and 137 also had a qualifying eBird regional pool (Appendix S1). These 137 cities (covering 56 countries and a total human population of over 900 million) contained a total of 8443 urban hotspots with a mean of 61.6 ± 138.6 hotspots per city (max. = New York – 976; min. = single hotspots in Kampala, Prayagrej, Kanpur, Patna, Nanjing, Xi'an, Amman, Casablanca, Khartoum, Fuzhou, Salvador, Nagoya, Port-au-Prince and Recife). There were 20 cities (5862 hotspots) in the Nearctic realm, 40 (756 hotspots) in the Indomalayan, 39 (705) in the Palearctic, 24 (633) in the Neotropics, 3 (429) in the Australasia and 11 (58 hotspots) in the Afrotropics. In total, 5679 bird species (2613 (46%) at urban hotspots) were recorded in the regional pools from a total of 10824 global species representing 52% of global avian species richness (Clements et al., 2021). Specifically, around 24% of the world's bird species have been detected by citizen scientists in our sample of global cities.

Species richness within and between cities

The proportion of the regional species pool represented within urban hotspots was positively correlated with the proportion of land covered by closed forest, open forest, herbaceous vegetation, shrub, herbaceous wetland and agriculture, and was negatively correlated with elevation (Figure 1). Thus, hotspots with a higher proportion of

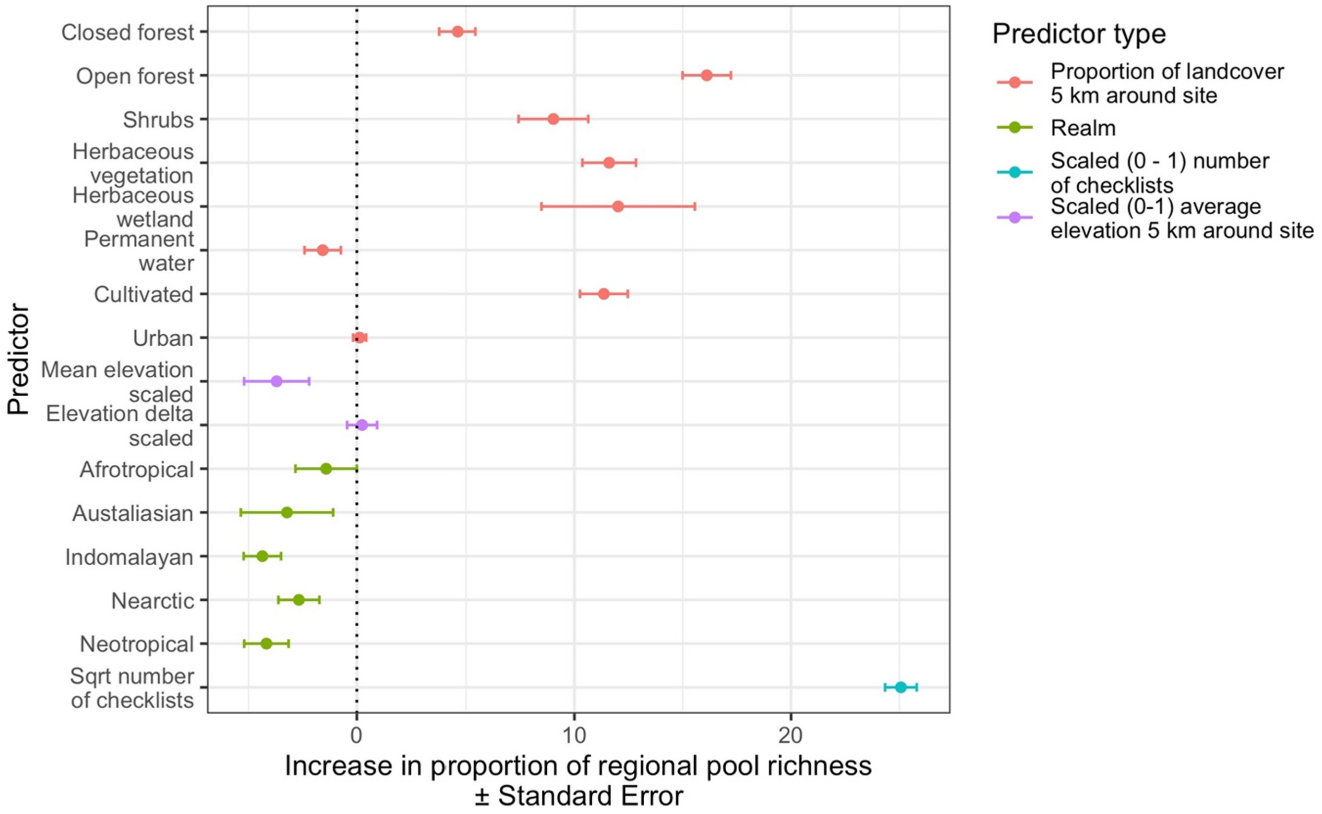

FIGURE 1 Model-averaged coefficients estimate ± standard error for the predictors explaining proportion of regional pool richness at urban hotspots. Predictors that had a significant effect on the proportion of regional pool richness at a hotspot have error bars that do not overlap zero. The effects of realms are estimated with the Palearctic as the reference level. All predictors that were explored in relation to percentage of regional richness are shown.

these landcovers in the surrounding 5 km landscape held a larger proportion of species from the city's regional pool. Proportion of richness was lower at hotspots within the Indomalayan and Neotropic realms than in other realms (Figures 1 and 2). The model without city as a random effect explained significantly less variation (10.7% vs. 33.1%; $p<0.001$).

Between cities the GLM variable reduction based on LOOCV mean test error reduced the two candidate variables to just one, average surface soil moisture (SSM) within a 50 km buffer around cities ($R^2=0.03$, $p=0.04$) (Figures 2 and 3). These predictors are provided in Appendix S4. SSM is the relative water content of the top few centimetres of soil, describing how wet or dry the soil is in its topmost layer, expressed in percent saturation. It is measured by satellite radar sensors and allows insights in local precipitation impacts and soil conditions (European Environment Agency, 2016). There was some evidence that cities at higher latitudes host a larger percentage of the regional species pool ($R^2=0.02$, $p=0.08$; Figure 3).

Phylogenetic signal for urban adaptability

In total, 89 families were included in the analysis from a possible 160 in our data set; 70 of the families removed contained fewer than 10 species. There was a significant phylogenetic signal for urban tolerance (lambda: 0.91, LR(lambda = 0): 7.02, $p=0.008$). This was driven by families with high *urban tolerance* such as Acanthizidae (Thornbills and allies), Tyrannidae (Tyrant flycatchers), Columbidae (Pigeons and Doves), Trochilidae (Hummingbirds) and Pycnonotidae (Bulbuls); and conversely families with low *urban tolerance* such as Otididae (Bustards), Pteroclidae (Sandgrouse), Turnicidae (Buttonquails), Trogonidae (Trogons) and Bucconidae (Puffbirds) (Figure 4).

Functional richness within urban hotspots

Niche representation (the proportion of niches for the given proportion of richness) within an urban hotspot was associated with herbaceous wetland cover and decreased with closed forest cover, shrub cover and urban cover—so areas surrounded by wetlands contained the most niches per species. The Australasian, Indomalayan, Nearctic and Neotropical realms had significantly more niche representation proportional to richness than other realms (Figure 5). The effects of landcover were robust to the number of niches we generated, that is the number of niches generated in the analysis did not change the significant effect of the

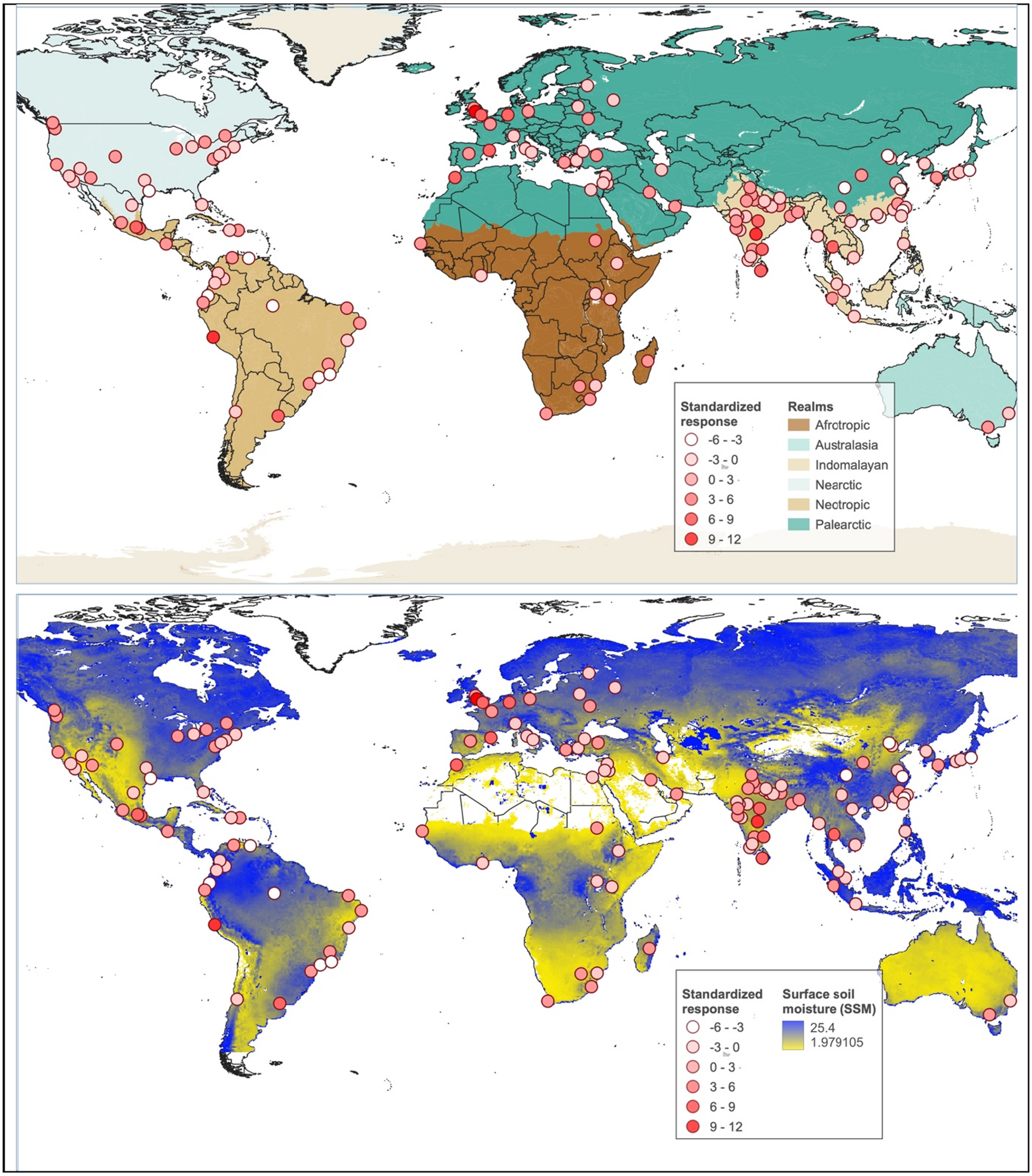

FIGURE 2 City random effect intercept from fitting the best-selected model for explaining the proportion of regional pool richness. Cities with a higher intercept have a larger proportion of regional pool richness compared to others.

landscape predictors, however, there was some variation in whether realms had a significant effect (SoM). The model without city as a random effect explained significantly less variation (10.2% vs. 34.3%; $p < 0.001$).

Out of 259 niches, 188 (72%) were represented in the urban environment. The loss of niches either started gradually and then increased dramatically with the final 10% of species (invertivore, omnivore, frugivore, granivore and nectarivore); or decreased continuously as more species were removed (aquatic predator, vertivore, aquatic herbivore, terrestrial herbivore and scavenger; Figure 6). Trophic niches poorly represented in

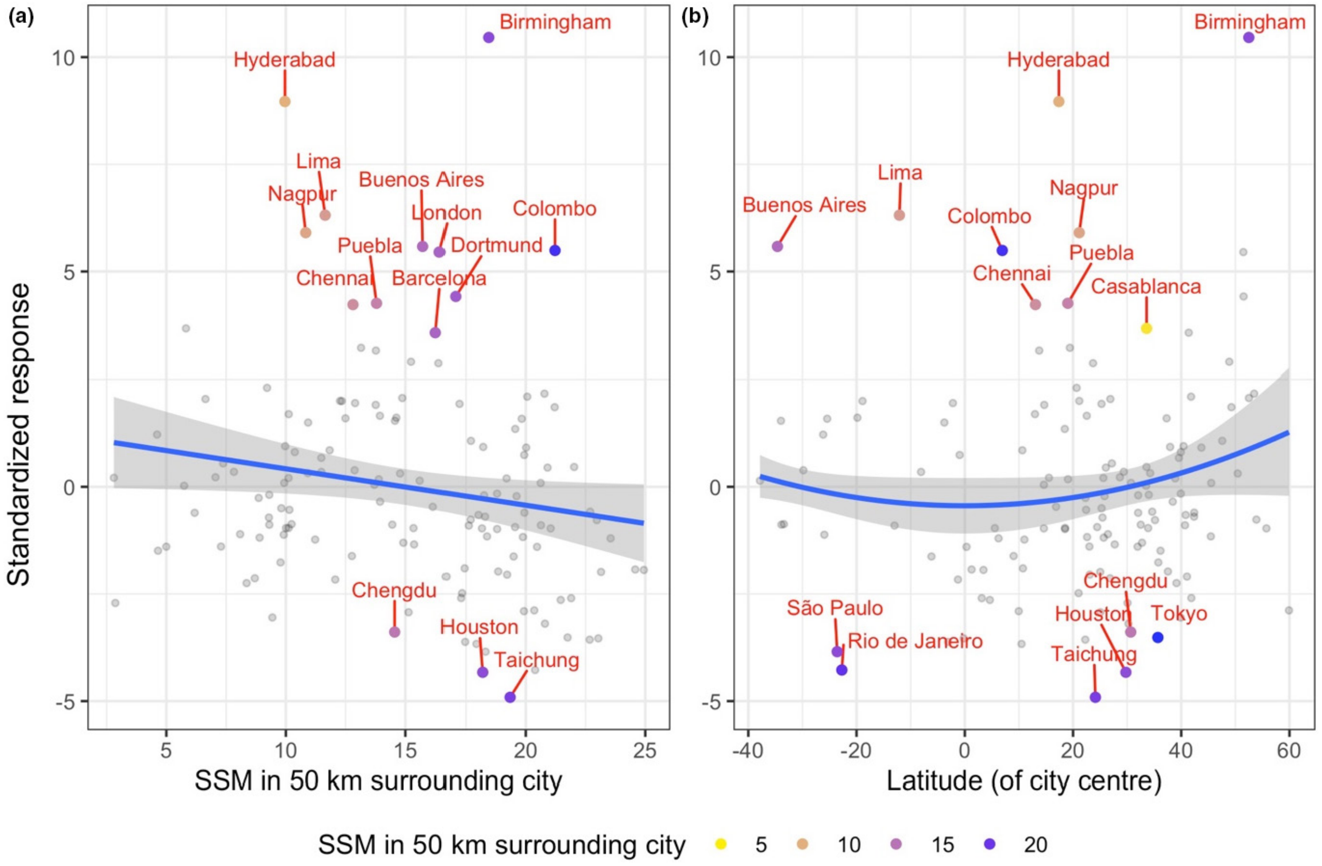

FIGURE 3 (a) Standardized response from fitting the best-selected model for explaining proportion of regional pool richness plotted against the average surface soil moisture (SSM) within a 50 km buffer around the city. This relationship is significant ($p = 0.04$, $R^2 = 0.03$). Cities are shown in red where their response is more than 15 times the standard error from predicting the response using the best-selected model. SSM increases as soil moisture increases. (b) Standardized response plotted against latitude with a quadratic model plotted ($p = 0.082$, $R^2 = 0.02$). Cities are shown where response is more than 15 times the standard error from predicting the response using the quadratic model, the SSM in the 50 km surrounding these cities is also shown. Generally, this shows that cities below the line and with a lower-than-expected response have higher SSM and are thus positioned in wetter areas of the globe. Both Colombo and Birmingham break this rule with higher-than-expected responses despite having high SSM.

the urban environment were those containing invertivores, frugivores and terrestrial herbivores (only 61%, 50%, 44% of their respective niches are ever-present in the urban communities). Invertivore niches missing in the urban environment contained families such as Pnoepygidae (Cupwings) and Grallariidae (Antpittas), while 'missing' frugivore niches contained species such as Bucerotidae (large Hornbills), Ramphastidae (Toucans) and Cracidae (Guans and Curassows). The three scavenger niches were the only set of niches for any trophic niche that were always represented in the urban environment, although aquatic herbivore and aquatic predator niches were usually filled (93% and 88%) in an urban environment.

DISCUSSION

We have shown that maintaining landcovers such as open forest, cultivation and herbaceous wetlands promotes avian biodiversity in cities across the world. Herbaceous wetlands were particularly important for avian functional diversity, likely because of the distinctive morphology of many wetland species (Van Tuinen et al., 2001). These results extend previous geographically constrained results on the importance of heterogeneric habitat to the global scale (Aronson et al., 2014; Ibáñez-Álamo et al., 2017). However, despite individual well-performing hotspots sharing landscape characteristics, considerable variation in site performance exists across cities, and over 99% of this variation remained unexplained. We have also shown that there is a phylogenetic signal for urban tolerance among species, although the strength of this should be treated with caution due to geographical biases in the data sets (Appendix S5).

We have shown that a range of habitats are positively associated with avian urban biodiversity rather than urban landcover being solely negatively associated (e.g. Escobar-Ibáñez et al., 2020; Sultana et al., 2022). Thus, the increase with in these habitats should promote urban avian diversity. Furthermore, these results hold and

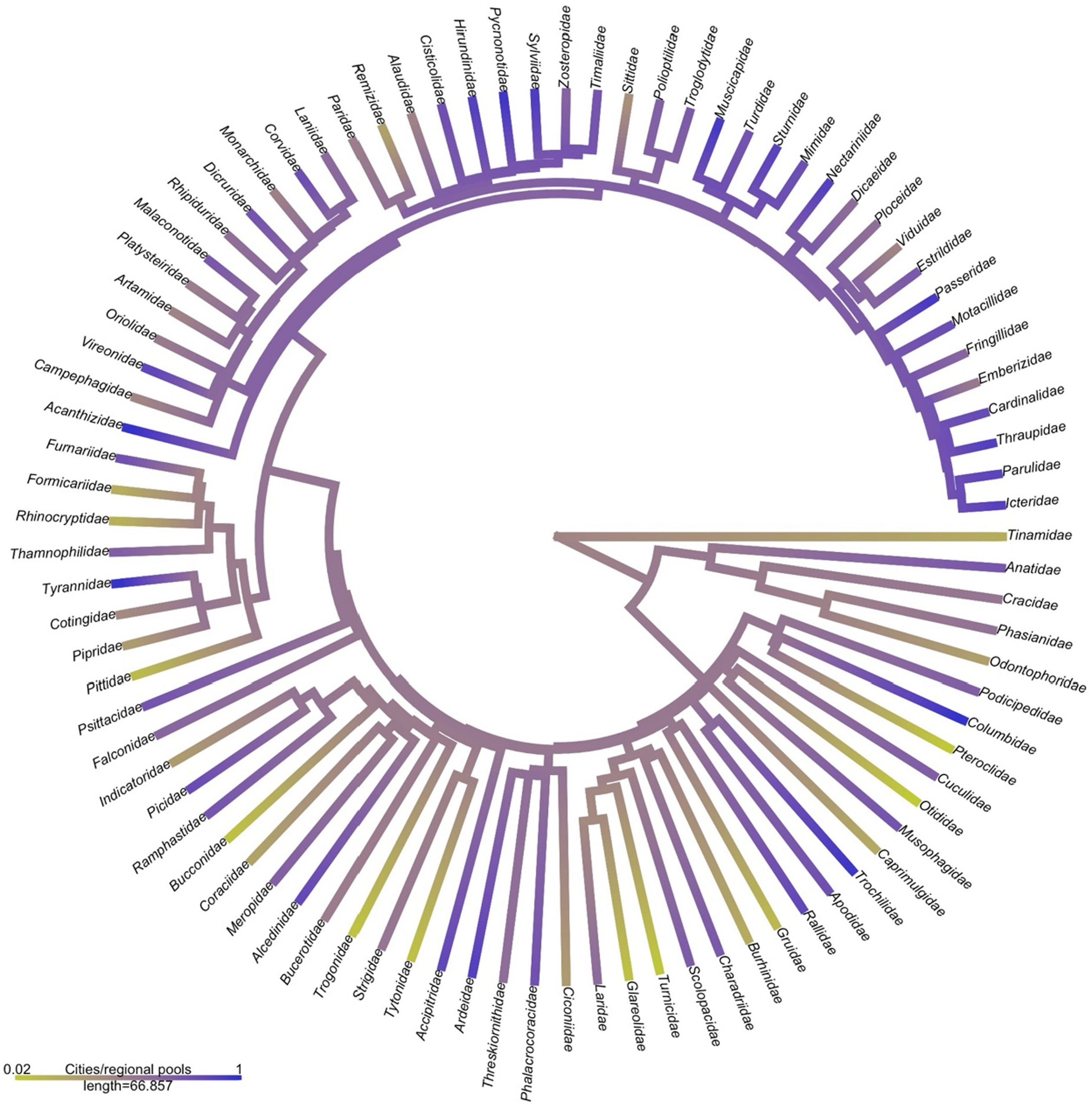

FIGURE 4 Phylogenetic response to *urban tolerance* (defined as the number of cities a species appears in divided by the number of regional pools a species appears in [where a species must be in the regional pool to appear in the city]). Values towards 1 show the most urban tolerant species that appear in most of the cities given they are in the corresponding regional pool, whereas values towards 0 show species with a lower *urban tolerance*. Only includes families that contain 10 or more species in our data set and that occur in more than two regional pools.

are consistent across 137 of the world's cities. What remains unclear is whether increasing the landcover of one of these habitats is better or worse than increasing the landcover of a mix of them, thus increasing habitat heterogeneity (often correlated with increased avian urban diversity (Uchida et al., 2020)).

Despite considering many predictors describing a city's local landscape, physical geography and governance, we found only one that explained avian richness, and this accounted for a tiny fraction of the variance. This was the surface soil moisture (SSM) within a 50 km buffer around cities, potentially indicating that cities in the wettest areas of the globe have a smaller proportion of the regional pool due to their aridification gradient from surrounding habitats (e.g. surrounding tropical moist forest with dense species packing (Cao et al., 2021)), compared to cities in arid areas that tend to be greener than the surrounding habitat (Filloy et al., 2019). Latitude explained slightly less variation than SSM with cities at higher latitudes having a slightly higher proportion of regional

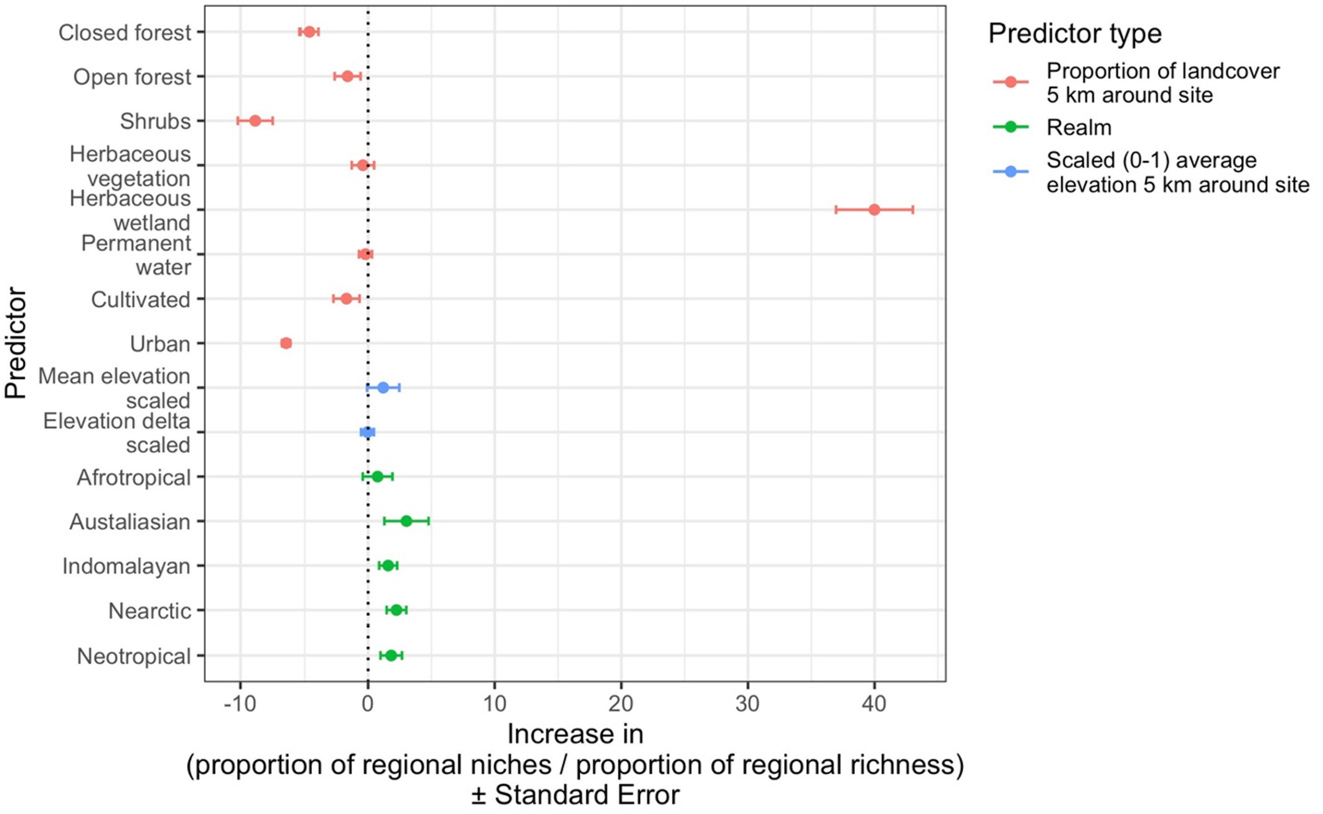

FIGURE 5 Model averaged coefficients (estimate±standard error) for predictors explaining proportion of regional pool niches for the given proportion of regional pool richness at urban hotspots. Predictors having a significant effect have error bars that do not overlap zero. The effects of realms are estimated with the Palearctic as the reference level. All predictors that were explored in relation to proportion of regional niches are shown.

species than those in the tropics. Although it might be expected that cities at higher latitudes would contain a significantly higher proportion of their regional species due to tropical niche packing, historical evolutionary adaptation to fragmentation and degradation at higher latitudes, and increased dispersal ability of avian species at higher latitudes (Betts et al., 2019; Bregman et al., 2016; Curtis et al., 2022; Møller, 2009; Sheard et al., 2020), these latitudinal effects will also filter the species present in the regional pool and so potentially weaken any effect in our species richness analysis. The diversity of structure, history, geography, politics, etc. across cities is huge and our predictors focused on city and regional landcover and geography (natural and social). We did not include predictors covering the history of how a city has been built (Johnson & Munshi-South, 2017), its colonial history (Whyte, 2018), socio-economic growth (Baldock et al., 2019) and social inequality (Lepczyk et al., 2017; Uchida et al., 2020). We are also missing historical data on the regional pool, such as whether a given small regional pool may be due to the region already having lost many of the most sensitive species due to land-use change, an example of shifting baseline syndrome (Soga & Gaston, 2018). Comparing cities to understand this variation is likely to remain very difficult, as there are many potential predictors describing the variation among cities, but a relatively constrained number of cities.

Herbaceous wetlands within cities can support the greatest number of different niches relative to species richness. The diversity of the vertivore and aquatic niches is lost simultaneously as species diversity is lost; however, the diversity of other niches reduces more slowly with species loss, and many niches persist even in species-poor sites. So not only are wetlands associated with increased numbers of niches per given richness but increasing richness in general also increases the number of aquatic niches present. This is likely related to the impressive morphological diversity among wetland birds (Van Tuinen et al., 2001); the difference between a pelican (Pelecanidae) and a crake (Rallidae) is dramatically greater than that between a chickadee (Paridae) and a warbler (Phylloscopidae). Natural wetlands continue to be lost in urban areas due to flood management and ongoing urban expansion (Cobbinah et al., 2021; Mao et al., 2018) which will reduce avian functional diversity. Furthermore, wetlands have an important role in connecting people with nature (Rutter et al., 2022) and, especially in deprived urban areas, may help to improve health and sense of community (White et al., 2021).

We developed a novel approach to measuring functional diversity within hotspots. This approach allows

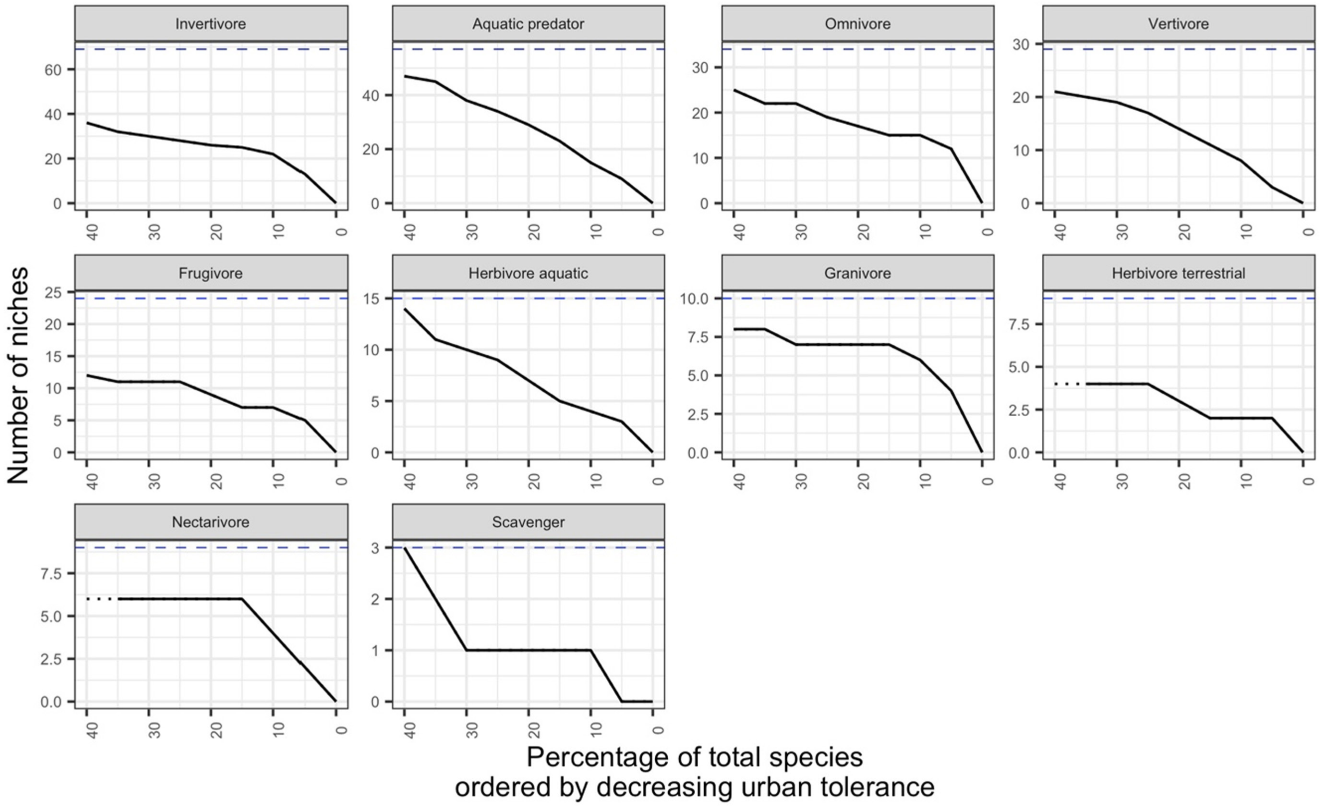

FIGURE 6 Niche loss by trophic niche shown as the number of niches present for each trophic niche taken at 5% increments with increasing species *urban tolerance* (defined as number of cities present/number of regional pools present). Only 40% of our species were ever present at a hotspot within cities (the remaining 60% were only in regional pools), thus we only show 5% increments from 40%. The dotted lines indicate the total number of niches for each trophic niche present in our data set. Solid lines that start at the dotted line indicate that all available niches start as present in the urban environment.

the functional diversity to be compared both within a local context and across the globe. While existing metrics such as functional divergence (*fdiv*) and functional richness (*fric*) (Mouchet et al., 2010) are useful for pairwise comparisons of hotspots, they do not provide a clear way to include the co-occurrence approach of regional pools (Fournier et al., 2020). Our approach of using a clustering algorithm to group species by morphology was shown to be largely insensitive to the number of clusters, a common problem when determining cluster number (Kodinariya & Makwana, 2013). We assumed that birds with a similar morphology and trophic niche play a similar role in ecosystems. This process created some large niches with several hundred species (and one of 1000) and some with just a single species. This approach has likely missed some of the subtleties in bill morphology for niche partitioning, especially in smaller species. However, we argue that we have made a reasonable approximation of real-life niches that allows niche richness from the regional pool to be validly measured. Nevertheless, we should be cautious of such an approach as it is likely to allow the morphologically unique species (in single species niches) to have a larger effect than those with more average morphologies (that are grouped into very large niches). Additionally, other non-morphological traits are likely to be important for surviving urbanization (Capilla-Lasheras et al., 2022) such as flight disturbance distance (Lin et al., 2012), nest site (Spotswood et al., 2021), resilience to noise (Planillo et al., 2020) and dominance (Martin & Bonier, 2018).

We have shown that a range of habitats are important for promoting avian diversity in cites. However, cities at higher latitudes and in drier habitats will have proportionately more of regional biodiversity than those in wetter or more tropical areas of the globe. Additionally, factors influencing bird richness in cities are likely to be as varied and complex as the cities themselves are—each city's history will translate into a unique set of impacts on their local environments (Ibáñez-Álamo et al., 2017; Morelli et al., 2016). We also demonstrated the importance of wetlands within cities for increasing avian functional and species diversity. For future research, current citizen science tools do not provide sufficient granularity across all world regions to model variation in city layouts. Stepping away from a hotspot approach and more directly quantifying where individual birds were recorded would allow more precise mapping of urban avifaunas. Additionally, we advocate moving beyond species and functional diversity to look at ecological networks. Understanding both resource availability via trophic cascades as well as interspecific competition should go some way towards explaining community composition of urban birds. This study should improve how cities are planned so that they are better places for nature, and thus improve humans' connection to nature that is so vital for our own well-being (Lepczyk et al., 2017).

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by James Richardson. The first draft of the manuscript was written James Richardson, and all authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in zenodo via https://doi.org/10.5281/zenodo.7799254 and https://doi.org/10.5281/zenodo.7798971. These data were derived from the following resources available in the public domain:https://ebird.org/http://datazone.birdlife.org/species/requestdishttps://www.birds.cornell.edu/clementschecklist/download/https://www.eea.europa.eu/data-and-maps/data/world-digital-elevation-model-etopo5http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v5_Dec20.ziphttp://www.bsceoc.org/avibase/https://doi.org/10.2905/42E8BE89-54FF-464E-BE7B-BF9E64DA5218https://doi.org/10.1093/biosci/bix014https://doi.org/10.5067/MODIS/MOD13Q1.006https://data.unhabitat.org/datasets/GUO-UN-Habitat::mean-population-exposure-to-pm2-5-by-country-2015-2019/https://data.unhabitat.org/documents/GUO-UN-Habitat::11-7-1-provision-and-access-to-open-spaces-in-cities-2020-2/https://data.unhabitat.org/documents/gdp-by-metropolitan-area-2017/https://nordpil.com/resources/world-database-of-large-cities/https://doi.org/10.5067/ZX7YX2Y2LHEBhttp://www.protectedplanet.net/

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SUPPORTING INFORMATION

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

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