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Avian trait specialization is negatively associated with urban tolerance

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Generalist species – with their wide niche breadths – are often associated with urban environments, while specialist species are likely to be most at-risk of increasing urbanization processes. But studies which quantify the relationship between trait specialization (i.e. niche breadth) and urban tolerance are generally methodologically limited, with repeatable robust methods to easily quantify this relationship among different regions and time scales often lacking. Our objective was to use novel methods to quantify the relationship between trait specialization and urban tolerance over a broad spatial scale. We used ~ 2 million citizen science observations and spatially intersected these with remotely-sensed VIIRS night-time light values and a novel continuous measure of a species' trait specialization for 256 European bird species. We found a negative relationship between avian urban tolerance and an overall specialization index. Nesting site niche breadth was especially negatively associated with higher urban tolerance scores. Our results highlight that species with a high degree of trait specialization likely have a lower capacity to persist in urban ecosystems, and hence, could be most at-risk in novel urban ecosystems. We suggest that trait specialization can be used as a proxy for the degree of risk posed by urban environments to a given species.

Keywords: biodiversity, citizen science, spatial and temporal sampling, specialization, trait-based approach, urban tolerance

Introduction

Anthropogenic rapid environmental changes (e.g. habitat loss, exotic species, pollution) are increasingly leading to novel interactions of species with their constantly changing environments in the 21st century (Sih et al. 2011, Sih 2013). This is especially true in novel urban ecosystems: one of the most drastic examples of rapid environmental change is urbanization (Grimmond 2007, Du and Hang 2017). Urbanization, and its associated habitat loss and fragmentation, generally has adverse impacts on biodiversity (Marzluff 2001, McKinney 2002, 2006, Devictor et al. 2008, Sol et al. 2017).

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But some species can adapt, survive and even thrive in urban environments (Møller 2009, Evans et al. 2011b, McDonnell and Hahs 2015). Understanding the ecological characteristics of those species most likely to tolerate novel environments – and simultaneously those species least likely to tolerate novel environments – is a fundamental question for applied research and conservation of biodiversity within urban ecosystems (Moreno 1988, Clavero et al. 2011).

Niches – the role of each species within an ecosystem, including interactions with biotic and abiotic factors (Soberón and Nakamura 2009) – can change across diversity gradients (Pigot et al. 2016, Pellissier et al. 2018). And along a diversity gradient, species can have differing levels of specialization across multiple life history characteristics (e.g. habitat, diet, nesting substrate) reflecting differing species' requirements across a diversity gradient dependent on species-specific characteristics (Devictor et al. 2010). For example, in areas with higher productivity, species are predicted to have either a smaller niche breadth (i.e. specialists) than species in areas with lower productivity (i.e. generalists) or niche breadths with a greater percentage of overlap – allowing for greater species coexistence in the same niche space (MacArthur 1965, MacArthur and Levins 1967). But this pattern may differ among different habitat types (Doxa et al. 2010), highlighting the importance of context-specific interpretation of ecological specialization (Devictor et al. 2010). Urban land transformation can sometimes have a disproportionately negative impact on primary productivity (Imhoff et al. 2004), which may in part explain a general trend that reproductive success is lower in urban areas compared with non-urban areas (Chamberlain et al. 2008). Thus, urban environments – with their dynamic heterogeneous resources (Pickett et al. 2017) – are an example of such a diversity gradient, promoting the establishment of species with wider niche breadths and thus niche overlap (Pagani-Núñez et al. 2019). Species' responses to urbanization are then likely to separate based on a species' degree of specialization (i.e. how specialized or restricted a niche breadth that a species encompasses is): along an urbanization gradient, there is likely to be a gradient in species' specialization with generalist species more positively associated with increased urbanization. Indeed, increased niche breadth is associated with a species' presence in urban environments (Clergeau et al. 2006, Bonier et al. 2007, Kark et al. 2007, Sol et al. 2014, Palacio 2019). Because niche breadth is linked with a species' degree of specialization, a species' degree of specialization likely predicts a species' ability to persist in novel urban environments: species with a high degree of specialization are likely to be at a higher risk of extinction threat in urban environments (i.e. low urban tolerance; Clergeau et al. 2006, Bonier et al. 2007, Kark et al. 2007, Evans et al. 2011b, Sol et al. 2014, Palacio 2019). Highlighting such species with low urban tolerance provides a generalized understanding of a species' ability to tolerate novel urban environments (Lepczyk et al. 2017), fundamental for recommendations for urban biodiversity management (Soanes et al. 2019).

Most previous work investigating the relationship between species' specialization and urban tolerance, however, has historically been spatially or temporally constrained – likely due to logistical constraints – e.g. investigating patterns in a single city (Leveau 2013, Han et al. 2019, Han et al. 2019) or few cities (Croci et al. 2008, Maklakov et al. 2011, Luck et al. 2013) and sometimes using data over relatively few surveys. Broad-scale analyses investigating these relationships have been historically rare, but are increasingly common (Bonier et al. 2007, Møller 2009, Aronson et al. 2014, 2016, Guetté et al. 2017, Palacio 2019). Comparisons made among various studies are also limited, as there is little consensus on the measurement of species' specialization or urban tolerance in the literature; and many studies employ vastly different approaches for both of these. Species' specialization is often simply measured using binomial and categorical characteristics, often relying on a single dimension as a measure of niche breadth. For example, previous studies have looked at diet (Palacio 2019) or habitat (Moreira et al. 2001, Devictor et al. 2008) alone, and others have classified birds categorically as mountain generalists or specialists (Lehikoinen et al. 2019). Such approaches fail to account for the complicated measures of species' specialization (Morelli et al. 2019). Albeit, some studies do indeed use composite measures of niche position (Evans et al. 2011a). Analyses are also usually methodologically limited as they simply compare lists of species found in urban environments with lists of species found outside urban environments (Møller 2009) or by a priori grouping species – based on their expected response to urban environments – e.g. into avoiders, adapters and exploiters (McKinney 2002, Kark et al. 2007, McDonnell and Hahs 2015). This approach fails to account for species-specific differences in responses to urbanization (Evans et al. 2011a, Callaghan et al. 2019b).

The main limitation for previous studies, however, has largely been that of available data to make broad generalizations about the relationship between specialization and urban tolerance. Citizen science data (i.e. semi-structured and unstructured broad-scale programs) are drastically changing the spatial and temporal scale of ecological research questions, providing data about many species at large spatial scales, especially in urban environments (McCaffrey 2005, Cooper et al. 2007). Birds are also very popular with citizen scientists (Sullivan et al. 2014), and at the same time, the most complete taxa regarding basic life history information – a necessary component of understanding species' specialization. Thus, birds represent an excellent focal taxon to investigate how a species' degree of specialization influences urban tolerance.

We integrated two novel approaches to understand the relationship between species' specialization and urban tolerance: 1) one which measures species specialization based on a suite of traits (Morelli et al. 2019), providing a continuous measure of overall specialization for specific life-history characteristics; and 2) a method which leverages citizen science data to assign species-specific urban tolerance scores to bird species at macro-ecological scales (Callaghan et al. 2019b).

We begin by investigating the relationship between overall specialization and urban tolerance, but importantly, we move past this approach and provide a novel analysis which focuses this question along five unique axes of specialization: diet, foraging substrate, habitat, nesting site and foraging behaviour. These axes were chosen because they represent five dimensions likely to influence a species' ability to persist in urban environments (Chamberlain et al. 2008). Because each of these axes of avian specialization is related to a different set of traits, we expected different associations – in terms of direction and intensity – between each level of specialization and the urban tolerance of a species, with a general negative relationship between species specialization and urban tolerance. For example, diet specialization of birds is likely related to the level of urban tolerance because species with broad diet breadths are likely able to find many different food sources in urban habitats compared with specialist species (Coogan et al. 2018). Species that are highly specialized in their foraging substrate, habitat and nesting site life history would likely be at higher risk in urban areas, where the types of substrates/habitats/nesting sites are limited due to the exclusion of some natural habitats (Støstad et al. 2017). Lastly, we expected species with generalist foraging behaviour strategies would be correlated with urban tolerance because they would be especially adapted to finding food in unique and novel urban ecosystems. Together, understanding species' urban tolerance at macro-ecological scales as it relates to different life history axes will further our understanding of species at risk to increasing urbanization.

Methods

Avian specialization

In this study, we focused on five indices of avian specialization for European breeding birds, based on a trait-approach (Morelli et al. 2019). The species-trait approach is traditionally used to focus on the functional aspects of biodiversity (Violle et al. 2007, de Bello et al. 2010). The avian traits used in this study comprise 72 variables, which describe the ecological niche occupied by each species. The traits include range of food types or diet, foraging behaviour, foraging substrate, type of habitat used and nesting site. The data on ecological traits were obtained from published literature and all variables are from European breeding birds, developed for European bird species based on two databases of species traits (Pearman et al. 2014, Storchová and Hořák 2018). The diet is focused on diet all year, but this is strongly correlated to the diet of species during the breeding period (Morelli et al. 2019). We also used an overall specialization index, which is the mean value considering the five individual indices (Morelli et al. 2019). The indices of specialization are multidimensional and were calculated by applying the Gini coefficient, an index of inequality (i.e. a measure of statistical dispersion) on a scale between 0 and 1, reflecting a gradient from low to high specialization respectively

(Morelli et al. 2019). For further details on the creation of the ecological specialization metrics see Morelli et al. (2019).

Species-specific relative urban scores

eBird data were used to assign species-specific urban scores – a measure of species-specific urban tolerance. eBird (Sullivan et al. 2009, 2014, 2017) is a successful citizen science project relying on volunteer birdwatchers who submit their observations via a mobile phone app or online platform. It is semi-structured, and collects data in the form of checklists, allowing a user to submit a complete or incomplete list of birds seen and/or heard while birdwatching. Filters are set by regional volunteers (Gilfedder et al. 2019) which provide expected species and abundances of species based on associated spatiotemporal coordinates of a checklist, and when an observation exceeds these filters, it undergoes stringent review before being added to the eBird dataset. We downloaded the eBird basic dataset (version ebd_relMay-2019) and filtered these data between 1 January 2010 and 31 May 2019 to ensure the period of richest data, and to minimize the likelihood that drastic changes in our underlying measure of urbanization would influence our results. We additionally applied the following criteria for a checklist to be included in our analysis, minimizing the influence of abnormal checklists on our analyses (Callaghan et al. 2017): 1) only complete checklists were included in analyses; 2) only checklists which recorded birds for > 5 min and < 240 min were included in analyses; 3) only checklists which travelled < 1 km or covered an area of < 100 ha were included in analyses. We only used a species presence, and did not use abundance estimates from eBird checklists for further analyses. Lastly, we only used checklists from within the European breeding season – defined as May, June, July, August – to minimize the undue leverage that accounting for intra-annual differences in a species use of urban areas.

Each of these checklists were then assigned a measure of continuous urbanization using VIIRS night-time lights at a 15 arc-second resolution (Elvidge et al. 2017). VIIRS night-time lights is a proxy for a continuous measure of urbanization (Pandey et al. 2013, Zhang and Seto 2013, Stathakis et al. 2015) as measured from space, with potentially less biases than census-based data reliant on individuals to respond to surveys (e.g. human population density). Remote sensing research has highlighted that 1) night-time lights provides an efficient way to map urban areas in India (Pandey et al. 2013), 2) night-time lights can characterize change in urbanization levels (Zhang and Seto 2013) and 3) night-time lights can delineate both urban sprawl, urban morphology and urban extension (Elvidge et al. 2018). Yet, this remote sensing approach is likely currently limited to macro-ecological analyses given that it is best at mapping urbanization at global scales, and that the current resolution (15 arc-seconds) is larger than other remote sensing products. Previous work using VIIRS night-time lights with birds has demonstrated that the urban scores assigned to birds behave similarly when assigned using underlying VIIRS night-time

lights and human population density (Callaghan et al. 2019a, b, 2020a). Google Earth Engine (Gorelick et al. 2017) was used to assign each eBird checklist – and thereby associated bird observations – a measure of VIIRS night-time lights. We used a reduction technique to assign each eBird checklist an aggregated measure of VIIRS night-time lights. Monthly scenes of average radiance ($nW\,cm^{-2}\,sr^{-1}$) between 1 January 2014 and 1 January 2019 were used, and the temporal median radiance was calculated per pixel. The 500 m resolution radiance values were then reprojected to a pixel size of 1 km, using a composite stack of the 2014–2019 VIIRS night-time light layers. Others have previously demonstrated that changes in the mean value of night-time lights can represent spatial and temporal trends (Guetté et al. 2018). We only included observations that occurred throughout Europe, ensuring that every European species had the same possible values of VIIRS night-time lights throughout the continent. For example, we did not include all possible global observations of rock pigeon – only those from Europe – ensuring that the species' affinity to urban areas in other parts of the world (which may be different to its affinity to urban areas in Europe) would not impact its urban score relative to other European species.

Every bird species was accordingly left with a distributional response to urbanization, representing the density of observations as it relates to urbanization (Fig. 1). We defined the median of this distribution as a species-specific urban score (Callaghan et al. 2019a, b). We then calculated the range of urbanization each species could have experienced (i.e. encompassing both the possible range of urbanization throughout a species' range and the bias of sampling in regards to urbanization) by collating all eBird checklists within a minimum convex polygon for each species, regardless of whether the species was found on a checklist, and taking the median of the VIIRS night-time lights values. Each species was then assigned a relative urbanness score which was defined as the log-transformed species-specific urban score subtracted by the range-specific urbanness value. Thus, higher relative urban scores (i.e. positive values) indicate a relatively higher proportion of a species' observations in more urbanized areas (i.e. more urban-tolerant) and conversely, lower relative urban scores (i.e. negative values) indicate a lower relative proportion of a species' observations in urbanized areas (i.e. least urban-tolerant). These urban scores are relative to one another (i.e. a species with a relative urban score of 1 is more urban-tolerant than a species with a relative urban score of −1). Only species which had > 100 observations throughout Europe during the breeding season (May–August) were considered for further analysis (Callaghan et al. 2019a, b). We also eliminated shorebirds (i.e. Charadriiformes) and grebes (i.e. Podicipediformes) because they largely rely on waterbodies as a key part of their life history, and the presence of water can be independent of 'urbanization' in an area (i.e. many cities are coastal) thus influencing those species' urban scores. After combining eBird data with our criteria, we were left with a total of 256 bird species considered for analyses (Supplementary material Appendix 1 Table A1).

Phylogenetic signal of species-specific relative urban scores

Phylogenetic signal is defined as the tendency for related species to resemble each other, more than they resemble species drawn at random from a phylogenetic tree (Blomberg et al. 2003) – because all organisms descend from common ancestors (Futuyma and Agrawal 2009). The presence of phylogenetic signal, then, needs to be considered when modelling a particular response across species, because species cannot be treated as independent sampling units in comparative analyses (Harvey and Purvis 1991). We modelled interspecific variation of urban tolerance across a phylogeny, obtaining the phylogenetic relationships among species from <www.birdtree.org>. We downloaded 100 phylogenetic trees from the backbone tree based on Ericson et al. (2006) for 256 bird species (Supplementary material Appendix 1 Fig. A1). The consensus tree was obtained applying the 50% majority rule (i.e. the proportion of a split to be present in all trees). In order to manage phylogenetic trees, we used the following R packages: 'ape' (Paradis et al. 2004) for reading, writing and manipulating phylogenetic trees; 'phangorn' (Schliep 2010) for visualizing phylogenetic trees; and 'Rphylip' (Revell and Chamberlain 2014) for various phylogenetic methods. We tested for the presence of phylogenetic signal (Blomberg and Garland 2002) in the relative urban tolerance score for 256 European bird species, by calculating Blomberg's K and K*, using the 'phylosignal' package for R (Keck et al. 2016). Blomberg's K and K* are two statistics of phylogenetic signal introduced by Blomberg et al. (2003), which perform a permutation test where species identities are maintained in the phylogeny while the trait values of species are permuted. Both are reliable statistics, but K* is less dependent of permutations of trait values among the tips of the phylogeny used because it relies on the mean squared error of the trait values using the variance–covariance matrix from the phylogenetic tree (Blomberg et al. 2003).

Statistical analysis

After considering the potential phylogenetic relatedness of the species-specific relative urban score, and because we did not find any strong phylogenetic signal in that variable (Table 1, Supplementary material Appendix 1 Fig. A1), we ran two generalized linear models (GLMs), using a Gaussian distribution. First, the relative urbanness was modelled as the response variable, while overall specialization was modelled as the predictor variable. Second, we modelled the relative urbanness as the response variable and all five specialization indices as predictor variables: diet, foraging behavior, foraging substrate, overall habitat and nesting site. We explored multicollinearity among predictor variables and found minimal correlation among predictor variables (Supplementary material Appendix 1 Fig. A2). Further, a test of variance inflation factors (VIF) of the candidate full model was applied to check for multicollinearity issues among predictor variables, using the package 'fmsb' for R (Nakazawa 2014). All variables
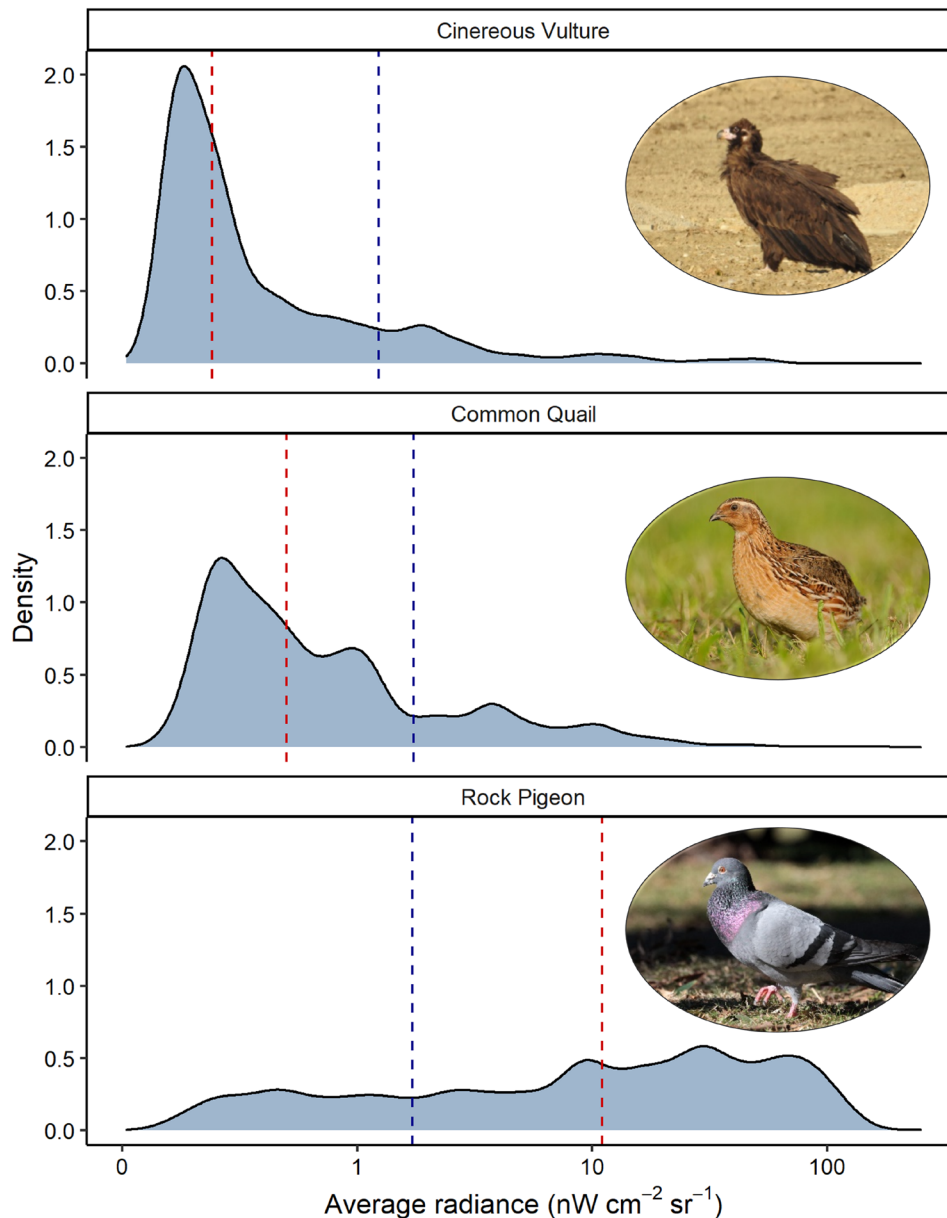
Figure 1. Three example species – cinereous vulture *Aegypius monachus*, common quail *Coturnix coturnix* and rock pigeon *Columba livia* – and their distributional response to VIIRS night-time lights on a logarithmic scale. The red line represents the median of their distributional response, which was taken as the species-specific urban score (i.e. urban tolerance measure) whereas the blue dashed line represents the range-wide urbanness of all eBird checklists within that species' minimum convex polygon. The relative urbanness was then defined as the difference between the log-transformed species-specific urban score and the range-wide urbanness of all eBird checklists. Only observations during the breeding season (May, June, July, August) were used. Photo credits: cinereous vulture – Yongchul Kim, common quail – Ján Svetlík, rock pigeon – Corey Callaghan.

Table 1. Phylogenetic signal of urbanization tolerance of bird species (relative urban score). The table shows the values of Blomberg's K and K* (Keck et al. 2016), and respective p-values, representing the lack of phylogenetic relatedness of the relative urban tolerance variable (Revell and Chamberlain 2014).

Variable	Blomberg's K	K*
Relative urban score	0.111	0.127
p-value	0.063	0.061

had VIF < 2 and thus were included in the model procedure. The Akaike's information criterion (AICc) was used to determine the model that 'best' explained variation in the data (Burnham and Anderson 2002). To corroborate our global model results and to calculate the best model estimates, we employed a model averaging approach, 'dredging' all possible subsets of the global model with the dredge function in the 'MuMIn' package (Bartoń 2009) and averaging over the models with Δ AICc < 4. All statistical tests were performed

with R software ver. 3.5.1 (<www.r-project.org>) and relied heavily on the tidyverse workflow in the R environment (Wickham 2017). Statistical significance was concluded at $\alpha \leq 0.05$.

Results

A total of 207 935 eBird checklists from 75 283 unique locations, representing 1 878 490 total observations were used to assign relative urban tolerance scores to the 256 species in the analysis (Supplementary material Appendix 1 Table A1). The bird species with the highest relative urban tolerance score was the pallid swift *Apus pallidus* (1.29), followed by rock pigeon *Columba livia* (1.22) while the species with the lowest relative urban tolerance score was the beared vulture *Gypaetus barbatus* (−2.88) followed by pin-tailed sandgrouse *Pterocles alchata* (−2.79). All but 9 species had a negative relative urbanness score, suggesting that the majority of species (96%) are found in relatively non-urban areas compared with the eBird sampling throughout that species' spatial range of observations (Supplementary material Appendix 1 Table A1). The mean relative urban tolerance score was -1.60 ± 0.72 with a median of −1.65 (Supplementary material Appendix 1 Fig. A3). We did not find statistically significant evidence of a phylogenetic signal in the relative urban tolerance scores among the 256 species (Table 1, Supplementary material Appendix 1 Fig. A1).

We found moderate evidence that as the relative urbanness of breeding birds decreases so does the overall specialization of species (Fig. 2A, Table 2). The results of the best generalized linear model introducing all specialization indices showed a negative and statistically significant association between the relative urbanness of breeding birds and nesting site specialization (Table 3, Fig. 2F, Supplementary material Appendix 1 Table A2). All the other associations were not statistically significant (Table 3, Fig. 2). These results were also supported by the model averaging approach as nesting site was in every top model and negatively associated with urban tolerance, and habitat specialization was also consistently in the top models with a negative relationship (Supplementary material Appendix 1 Table A2).

Discussion

We used almost 2 million observations of 256 species throughout continental Europe – integrated with a novel measure of avian trait specialization – to demonstrate a clear association between urban tolerance and overall specialization: specialist
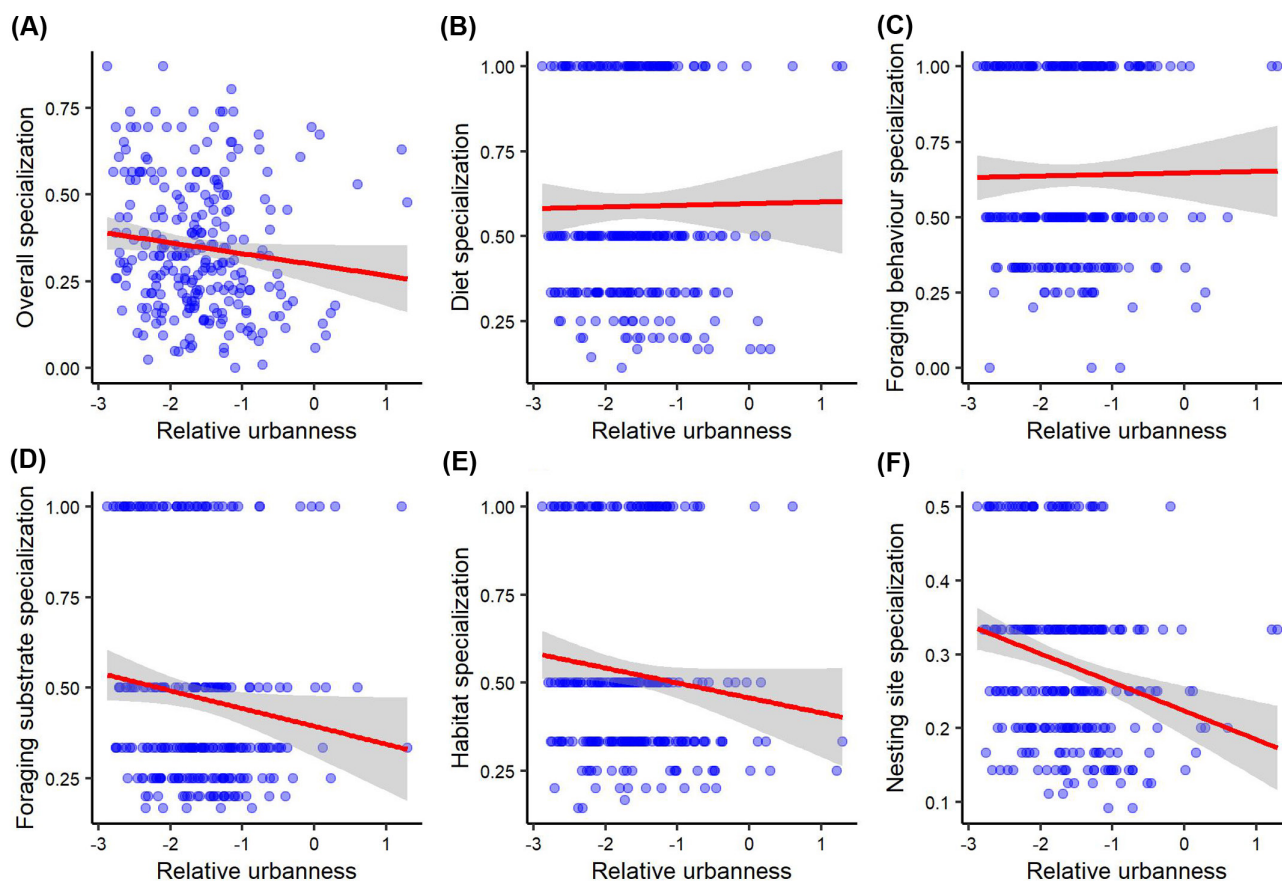

Figure 2. Association between species-specific relative urban scores and (A) overall specialization, (B) diet, (C) foraging behavior, (D) foraging substrate, (E) general habitat and (F) nesting site specialization measures, in European breeding birds (n = 256).

Table 2. Results of a GLM, accounting for variation in relative urbanness in relation to overall avian specialization in European breeding birds (n = 256). SE – standard error. Significant variables are highlighted in bold.

Variables	Estimate	SE	t-values	p-values
(Intercept)	−1.438	0.094	−15.299	<0.001
Overall specialization	−0.455	0.237	−1.922	0.0557

species are most at-risk of urbanization. Further, we extended previous research by using five different measures of trait specialization (e.g. diet, foraging behaviour, foraging substrate, habitat and nesting site), and found that nesting site had the strongest significantly negative response followed by habitat specialization, albeit with a non-significant response. Generalized understandings such as those presented here demonstrate the importance of understanding measures of trait specialization (i.e. niche breadth) as it relates to a species' ability to cope with novel urban ecosystems.

Two key mechanisms can lead to the relatively higher proportion of generalists in urban environments than specialists: colonization and adaptation. The former happens when species move into novel urban environments and successfully colonize empty niches (Evans et al. 2009, 2011b), while the latter happens slowly as urbanization processes encroach on natural habitat. In both instances, changes to the underlying habitat, such as exclusion of natural habitats (Støstad et al. 2017), and changes in the environmental conditions (e.g. heterogeneity of resources) likely explains the ability of generalist species to colonize urban environments (Guetté et al. 2017). Species with generalist life history strategies are thus more readily able to colonize and/or persist in the novel conditions in urban environments. By further segregating the overall specialization index into five components, we were able to highlight that nesting site specialization is the most important trait influencing a species' ability to subsist in urban environments, compared with non-significant associations between the other traits and urban tolerance (Fig. 2). This is probably best explained because nesting sites (and associated habitat types) are often limited in urban environments, due in part to the homogenization of habitat and likely ecological

Table 3. Results of a GLM, accounting for variation in relative urban tolerance in relation to avian specialization measured in five ecological dimensions: diet, foraging behavior, foraging substrate, general habitat and nesting site, in European breeding birds (n = 256). SE – standard error. Significant variables are highlighted in bold.

Variables	Estimate	SE	z-values	p-values
(Intercept)	−1.221	0.164	−7.428	<0.001
Diet	0.100	0.150	0.669	0.504
Foraging behaviour	0.177	0.158	1.121	0.263
Foraging substrate	−0.194	0.174	−1.117	0.265
Habitat	−0.126	0.170	−0.743	0.458
Nesting site	**−1.367**	**0.428**	**−3.193**	**0.002**

function (Groffman et al. 2014). Thus, species with highly specialized nesting sites (e.g. hollows) are likely unable to find the necessary requirements for viable reproduction in urban environments because these resources are generally scarce, compared with species with generalist nesting site strategies. Conversely, food available for foraging is likely less homogenized among urban areas, which is why it had a weaker signal in our analysis, and food may be made available by homeowners (Reynolds et al. 2017), potentially limiting the influence of diet specialization on urban tolerance. Our approach differed from other previous studies which have looked at the trait-urbanization relationship in a more fine-scaled manner, as we did not explicitly investigate different diets (Beissinger and Osborne 1982, Fuller et al. 2008, Evans et al. 2011a) or nesting sites (Kark et al. 2007, Croci et al. 2008, Conole and Kirkpatrick 2011), or feeding strategies (Guetté et al. 2017) for instance. Such studies can highlight important urban planning processes (e.g. that insectivores are at particular risk from urbanization; Chace and Walsh 2006) but they often fail to account for the complicated measures of niche specialization (Morelli et al. 2019). Indeed, future work should continue to elucidate specific life history traits which predict a species' risk to urban ecosystems (Kark et al. 2007, Fuller et al. 2008, Evans et al. 2011a, Guetté et al. 2017, Palacio 2019). Importantly, our analysis highlights a broad general ecological pattern: the degree of overall species' specialization is negatively correlated with urban tolerance.

We did not find a statistically significant phylogenetic signal of urban tolerance in our analysis (Table 1, Supplementary material Appendix 1 Fig. A1), contradicting other studies which have found a strong phylogenetic signal in urban tolerance of birds (Callaghan et al. 2019b). However, the previous study assessed 477 species in Australia, whereas our study was focused on European species. Our study did confirm other studies in Europe which have also found a lack of phylogenetic signal in urban tolerance (Evans et al. 2011a). Urban environments probably filter subsets of species environmentally (Webb et al. 2010) and phylogenetically (Morelli et al. 2016, Sol et al. 2017) leading to reduced phylogenetic diversity in urban environments (La Sorte et al. 2018). This discrepancy between a strong phylogenetic signal in Australia (Callaghan et al. 2019b) but a weak signal in Europe may be explained by the difference in time since urbanization in Europe, compared with Australia. Given Europe has been urbanized for a far-longer period, it is possible that urban environments have already selected particular subsets of phylogenetic clades (Morelli et al. 2016). This could explain the little relative difference among clades' urban tolerance (i.e. lack of phylogenetic signal) in our analysis as the most urban-tolerant species in each clade have already been selected. We do note that by removing Charadriiformes and Podicipediformes clades to prevent potential biases related to their urban tolerance scores, the resulting phylogenetic analysis is fragmentary. However, we are confident that this potential bias didn't affect the main findings of our study, being uniformly distributed across the sampling sites. Future work should continue to investigate the phylogenetic signal

of urban tolerance given the currently contradictory results in the literature (cf. this study and Callaghan et al. 2019b).

Our analysis provided a robust understanding given our sample size which was larger than many previous similar studies: 256 species in our study compared to 55 (Evans et al. 2011a), 110 (Croci et al. 2008), 119 (Guetté et al. 2017) and 40 (Kark et al. 2007). This generalized understanding of the relationship between traits and urban tolerance was made possible by capitalizing on opportunistic data collection by keen birdwatchers through eBird citizen science data (McCaffrey 2005). This type of broad-scale global data differs from smaller-scale standardized monitoring programs (e.g. Breeding Bird Surveys, International wetland bird counts) because eBird is a semi-structured citizen science project. As such, there are various biases that need to be considered in such analyses, such as a disproportionate sampling effort towards urban areas or the fact that some species may be sampled from relatively few 'well-known' sites. We acknowledge that this may influence our results, but highlight that this bias is likely a systematic bias (i.e. the same for all species), which means the relative ranking of urban tolerance of species would be robust. This is particularly true given that species in similar phylogenetic clades are sampled with similar detectabilities (e.g. large-bodied waterfowl are generally more detectable than small-bodied passerines) making relative comparisons among species with similar traits justified. Another potential bias is the influence of range size on a species' urban score calculation: species with small current ranges are likely to have less potential to experience urban habitats. We highlight that our analysis here accounts for these differences by standardizing a species' urbanness relative to the eBird sampling and potential urbanness levels within that species' convex polygon thus reflecting the urbanness of a species when accounting for the availability of urban area within a species' distribution. This impacted small-range species more-so than large-range species (Supplementary material Appendix 1 Table A1). Nevertheless, further research should expand on our methods to investigate the interaction between urban tolerance and range size.

Our analysis was focused on birds, with their rich history in citizen science and trait data, but the fundamental components of our analyses – 1) biodiversity observations and 2) trait-data – are increasingly available for many other taxa. For instance, citizen science biodiversity data are increasingly available for many taxa through projects such as iNaturalist (Chandler et al. 2017). At the same time, large global databases on traits are becoming increasingly available and standardized (Moretti et al. 2017, Schneider et al. 2019). Our methodological framework, reliant on a publicly-available global remote-sensing layer (Elvidge et al. 2017) and a generalized method to measure trait specialization (Morelli et al. 2019), ensures that our approach is likely applicable to many different taxa in different parts of the world, dependent on available data. We rely on VIIRS night-time lights, which have been previously been shown to be a good predictor of

urban environments and urban sprawl (Pandey et al. 2013, Zhang and Seto 2013), but we aggregate these data to relatively large spatial scales (1 km reduction) to match the broad continental scale of our analysis and account for noise in the eBird sampling. Future work should investigate how VIIRS night-time lights measures urban environments at smaller spatial scales (e.g. within an urban greenspace) and identify the utility of our approach at these scales. We also recommend future work should investigate these macroecological patterns among different taxa. We also did not test intra-annual or inter-annual changes in urban tolerance of birds, potentially likely in a migratory system, as our analysis was focused on overall urban tolerance across the breeding season. Future work, however, should investigate these patterns throughout the full annual cycle (Marra et al. 2015), as it is possible that our analysis did not fully capture intra-annual changes in urban tolerance and potential intra-annual changes in trait specialization (e.g. diet-switching throughout the year). And because VIIRS night-time lights provides a time series of urbanization, future work should also expand our methods to account for temporal trends in urbanization (Guetté et al. 2017, 2018).

We provide evidence supporting the theory that urbanization is generally excluding specialist species (Sorace and Gustin 2009, Concepción et al. 2015, Guetté et al. 2017). A species' environmental tolerance (i.e. niche breadth) is a fundamental component of its ability to persist in urban environments (Bonier et al. 2007). Contrary to previous studies, our approach focused on a more comprehensive understanding of trait specialization (i.e. measured broad categories of trait specialization). By fully understanding the general relationship between trait specialization and urban tolerance, we highlighted that overall trait specialization can be used as a proxy for a species' ability to cope with urban environments. Further, species that have highly specialized nesting site niche breadths are particularly susceptible to urbanization.

Data availability statement

All eBird data are freely available for download (), but the data for urban scores and specialization indices are available in Supplementary material Appendix 1 Table A1. Code and data are available in Zenodo digital repository. (Callaghan et al. 2020b).

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