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No place for ground-dwellers in cities: A meta-analysis on bird functional traits

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A B S T R A C T

Urbanization is one of the most severe forms of environmental alteration, in which increasing human settlement leads to an unprecedented loss of natural areas, thereby threatening global biodiversity and associated ecosystem functions. Consequently, the evidence base needs to be strengthened in order to understand how this man-made alteration affects urban biodiversity, and hence develop appropriate conservation measures. According to our expectations, urbanization processes influence the abundance of passerine birds through functional traits, what we studied within the framework of a systematic review using phylogenetically controlled meta-analyses. We tested four specific predictions: (i) Migration strategy will influence responses to urbanization, and tropical migrants will be the least numerous in urban areas; (ii) Birds nesting at ground level will be negatively affected by urbanization, while birds nesting at higher levels will suffer less; (iii) In terms of foraging technique, ground probers will be negatively; and (iv) birds with insectivorous diet will be the most disadvantaged in cities. Bird species (N = 53) were studied along urbanization gradients that ranged from highly urbanized areas to adjacent natural areas. Our findings revealed that the impact of urbanization on the abundance of bird species is modulated by certain functional traits. Partial or short distance migrants, ground nesters, ground gleaners and granivores were the group of species most negatively influenced by urbanization. Species sensitive to urbanization were those that are linked in some way to open grassland areas. This indicates that cities need more intact and extensively managed grasslands to sustain bird communities, which provide valuable ecosystem services.

1. Introduction

The loss of biodiversity associated with urbanisation is generally assumed to reflect the fact that only certain species have the capability to tolerate or adapt to such rapid human-induced environmental alterations (Sol et al., 2014). In urban ecosystems, multiple and hierarchical, human-driven filters affect community assembly. These filters include climatic and biogeographical factors, human

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facilitation, urban form and development history, socioeconomic and cultural factors and the interaction of species (Aronson et al., 2016). Species' traits determine how these filters modify the species pool and reveal, which traits make it possible to thrive in cities. Although previous research has shown that the total number of bird species declines significantly, once an area is undergoing urbanization, some bird species do seem to flourish in cities (Reis et al., 2012). Studies have reported repeatedly that urbanisation affects species diversity negatively, but has a positive effect on the abundance of certain bird species (Blair, 1996; Lepczyk et al., 2008). Furthermore, this phenomenon can be non-linear, which means that species do not decrease or increase in a linear manner along gradients of urbanization, rather there is a steady state from rural to suburban areas followed by a strong decrease toward urban areas. In addition to non-linearity, there can be also a quadratic relationship between the extent of urbanized areas and species richness, as revealed by Chiari et al. (2010). They showed that bird species richness changes in a quadratic manner with a higher proportion of urban areas and peaking in mid-urbanized areas compared to rural ones in Florence. However, a threshold effect induced by city size might also exist, when above the threshold, urbanization significantly also affects the community structures (Garaffa et al., 2009; Máthé and Batáry, 2015). City characteristics may thus play an important role in shaping urban bird occurrence (Batáry et al., 2018; White et al., 2005), but individual species preferences and biological characteristics can be crucial as well (Korányi et al., 2021).

In addition to evaluating commonly used biodiversity metrics such as, abundance and species richness data, another approach to evaluate ecosystem functions provided by biodiversity is to focus on functional diversity, which influences key ecosystem processes through functional traits (Sol et al., 2020). Studying functional traits has revealed that disturbed habitats, such as those affected by urbanization, lose functional diversity by diminishing species with distinct ecological traits. Bird functional traits can influence species' ability to cope with urbanization pressure because there are associations between traits and urban bird densities (Evans et al., 2011). Nevertheless, only certain species, which are characterized by specific traits, are more capable of tolerating environmental alterations that are caused by urbanization, knowing these exact traits is essential (Patankar et al., 2021). There is a decrease in species preferring shrub habitats and aquatic or open landscapes due to urbanization, but the number of forest preferring species can increase (Croci et al., 2008). The same study detected a decline of ground-nesting species while omnivorous species can have higher abundance in cities in contrast to granivorous species (Croci et al., 2008; Evans et al., 2011; Máthé and Batáry, 2015). Nevertheless, other studies did not find the same negative urbanization effect on granivores or even insectivores (Meffert and Dziock, 2013).

As there are several articles about trait responses to urbanization pressures, the results are sometimes contradictory. Urbanization also influences migratory behaviour. Resident birds prefer cities the most, while long-distance migrants often avoid them (Evans et al., 2011; Jokimäki et al., 2014), but in another studys there was no clear shift in migratory status along the urbanisation gradients (Meffert et al., 2013). Birds of many different European cities have great dispersal ability, whereas in Britain, no clear association between urbanization indices and dispersal ability has been found (Møller, 2009, Evans et al., 2011). In summary, the urban matrix changes the composition of bird populations, which is manifested by filtering of functional traits. Despite there is a growing number of studies on the response of bird traits to urbanization, there is no clear consensus on which exact species with which traits are most vulnerable to urbanization. Research that takes phylogenetic relatedness into account is also needed to build a more comprehensive insight about the complex consequences of urban sprawl. By analysing several articles with many different bird species in a meta-analysis, we can get a more robust picture of the traits that most determine the urban distribution of a species.

The main goal of our study was to clarify how bird functional traits are related to urbanization. Our main hypothesis was the general idea that urbanisation affects bird species with specialised traits most negatively and generalist birds less so (Evans et al., 2011). Based on this hypothesis and existing knowledge of bird responses to urbanization, we made the following predictions: (1) Species with long distance migratory strategies (species that migrate to tropical areas) will be more disadvantaged than resident or short term migrants (Kark et al., 2007; Evans et al., 2011); (2) human disturbance will be greatest at ground-level, hence ground nesting species will be negatively impacted by urbanization (Kark et al., 2007; Evans et al., 2011); (3) following the same argument, ground probers and ground gleaners will be the most negatively influenced species (Marzluff, 2001; Jokimäki and Huhta, 2000); (4) insectivorous species will decline the most due to urbanization (Kark et al., 2007; Evans et al., 2011); (5) concerning our selected traits, species with less specialized traits (e.g. residents, cavity nesters or species with mixed diet) will predominant in heavily urbanized areas (Conole and Kirkpatrick, 2011). To test these predictions, we performed a set of meta-analyses based on a comprehensive systematic literature review to synthesize the overall effect of urbanization on the functional diversity of European bird species. Our analyses take into account and quantitatively summarize previous findings, while considering also phylogenetic relatedness between study species, in order to understand the crucial consequences of urban growth on biodiversity and its associated ecosystem services.

2. Methods

2.1. Literature search and selection criteria

We conducted the systematic review using the Web of Science Core Collection database (until 7th April 2020) for topics including the following PICO (Population, Intervention, Comparator and Outcome) combination of search terms (Higgins and Green, 2008): (bird OR avian) AND (urban OR suburban OR rural). We refined the searches by excluding (editorial material OR review OR meeting abstract OR book chapter) document types in Web of Science Core Collection, and by restricting them to: document type (article) AND Web of Science categories: (ecology OR environmental sciences OR ornithology OR biodiversity conservation OR zoology OR urban studies OR environmental studies OR multidisciplinary sciences). The literature search resulted in a total of 3694 potential publications. We followed the PRISMA guidelines for the filtering process (Boutron et al., 2021), each step of the selection process can be observed on the PRISMA flow diagram in supplementary Fig. S1.

We stored and managed the downloaded article references in Mendeley reference manager software (Mendeley Desktop, Version

1.19.8 2008–2019). The filtering process consisted of three steps: first, we filtered the articles based on their title, then based on the abstracts, and finally we screened the remaining articles based on the full text, keeping only those that matched our strict selection criteria. We focused on studies based on urbanization gradients that contained bird species abundance data. After the title and abstract filtering, we acquired and screened the full text of each potentially relevant article to obtain the final list used for the analysis. To select the appropriate articles, we defined well specified inclusion criteria: (1) Articles that examined the abundance of passerine bird species along a long urbanisation gradient (urban vs. suburban vs. natural areas or urban-natural gradient); (2) Articles that contained research conducted only in European cities; (3) Articles that examined cities and included at least three spatial replicates per urbanisation gradient category (urban-suburban-natural); (4) We omitted articles considering rural areas as a reference level, because we wanted to compare the degree of urbanisation with natural areas; (5) Articles that reported mean, standard deviation, standard errors of mean and sample size for urbanisation gradient categories, or studies that reported different statistical scores (Spearman's rank correlation coefficient, F, t or Chi-square values and related sample size) of urbanization effects on bird populations for effect size calculations. Articles investigating birds at a community level without referring to individual species or representing only functional guilds, or articles with only species richness data, were excluded from the analysis. Altogether, we found 371 relevant research papers after screening and 8 of these met the selection criteria comprising 93 observations for bird abundance data (Table 1). The majority of bird urbanization studies were focused at a community level (Batáry et al., 2018), which rarely report species population level data or analyses. Nevertheless, the included studies provided plenty of data, which gave a solid basis for a set of meta-analyses testing the effect of urbanization on passerine birds' functional traits.

2.2. Data extraction and functional traits

Based on Batáry et al. (2018), we standardised categorical classes based on the descriptions given in the articles to get a more homogenous and more comparable classification. Our re-categorised urban land use typology was the following: "Natural" – natural or semi-natural areas with or without human presence; "Suburban" – residential areas of cities with family houses and associated lawns and private gardens which provide relatively high vegetation cover; "Urban" – the most sealed city zone, dominated by commercial/industrial buildings and blocks of flats; usually this class contains the least vegetation cover.

To examine how urbanization alters the functional traits of birds, we took four functional traits into consideration, which were later linked to the species data from the screened articles: migration status, nest location, foraging technique and diet (Table S2). The migration status consisted of resident, temperate/short-term migrants and tropical/long-term migrants. The nest location followed a gradient of substrate height, ranging from the ground to tree level (open on ground, open in shrub, open in tree and cavity nester). The foraging technique also followed an analogous substrate height gradient, and consisted of: ground prober, ground gleaner, understory gleaner, bark forager and canopy foliage gleaner/hawker. The dietary trait had three levels: granivore, mixed diet and insectivore. All functional traits were collected from Cramp et al. (1994).

2.3. Effect size calculation

Test statistics that described the relationship between measures of abundance of individual passerine birds and urbanization gradients were converted to Pearson's correlation coefficient (r) using standard conversion formulas (Lajeunesse, 2013). For each observation, calculating effect size was performed as follows: (1) From two-level categorical data (urban vs. natural classes), Hedges' *g* (i.e. the unbiased standardised mean difference) was calculated based on the mean, standard deviation and sample size (number of study sites) of species abundance (population level) of urban and natural areas. After we obtained these values, we transformed them to Pearson's ***r***. (2) From three-level categorical data (urban-suburban-natural), Hedges' *g* was calculated for each level separately, then transformed to Pearson's ***r***. Combined effect sizes from urban-suburban and suburban-natural contrasts were computed separately considering multiple comparisons within a study (Borenstein et al., 2021). (3) From continuous urbanisation gradients, Pearsons's ***r*** was calculated from *t*, $\chi 2$ or Spearman's ρ statistics. Effect sizes were negative when abundance decreased with increasing urbanization, or positive when species abundance increased with increasing urbanization. As our analysis covered species abundance, some species were present at higher occurrence rates than others, in particular urban-tolerant species were more abundant than specialist species in more urbanized areas, such as *Corvus corone* or *Parus major*. Therefore, we calculated composite effect sizes for each

Table 1
List of 8 published articles included in meta-analysis of urbanisation effects on bird functional traits. N: number of sampling points. Number of species: species number included in meta-analysis. Only species which were present at every sampling site were included.

Source	Country	N	Number of species	Comment
Antonov and Atanasova (2003)	Bulgaria	396	1	effect size transformed from chi-square
Hedblom & Söderström (2010)	Sweden	474	13	effect size transformed from chi-square
Huhtalo & Järvinen (1977)	Finland	30	6	
Kontsiotis et al. (2019)	Greece	63	19	
	England	14	18	effect size transformed from Spearman's rank correlation coefficient
Máthé & Batáry (2015)	Romania	61	9	
Palomino & Carrascal (2006)	Spain	194	21	
Sorace and Gustin (2008)	Italy	26	16	
Sorace and Gustin (2010)	Italy	27	17	

individual species from all studies using random effect meta-analyses, where we had data for a given species. The final dataset consisted of 53 observations. This enabled us to analyse a non-biased dataset with no species and no trait strongly over or underrepresented.

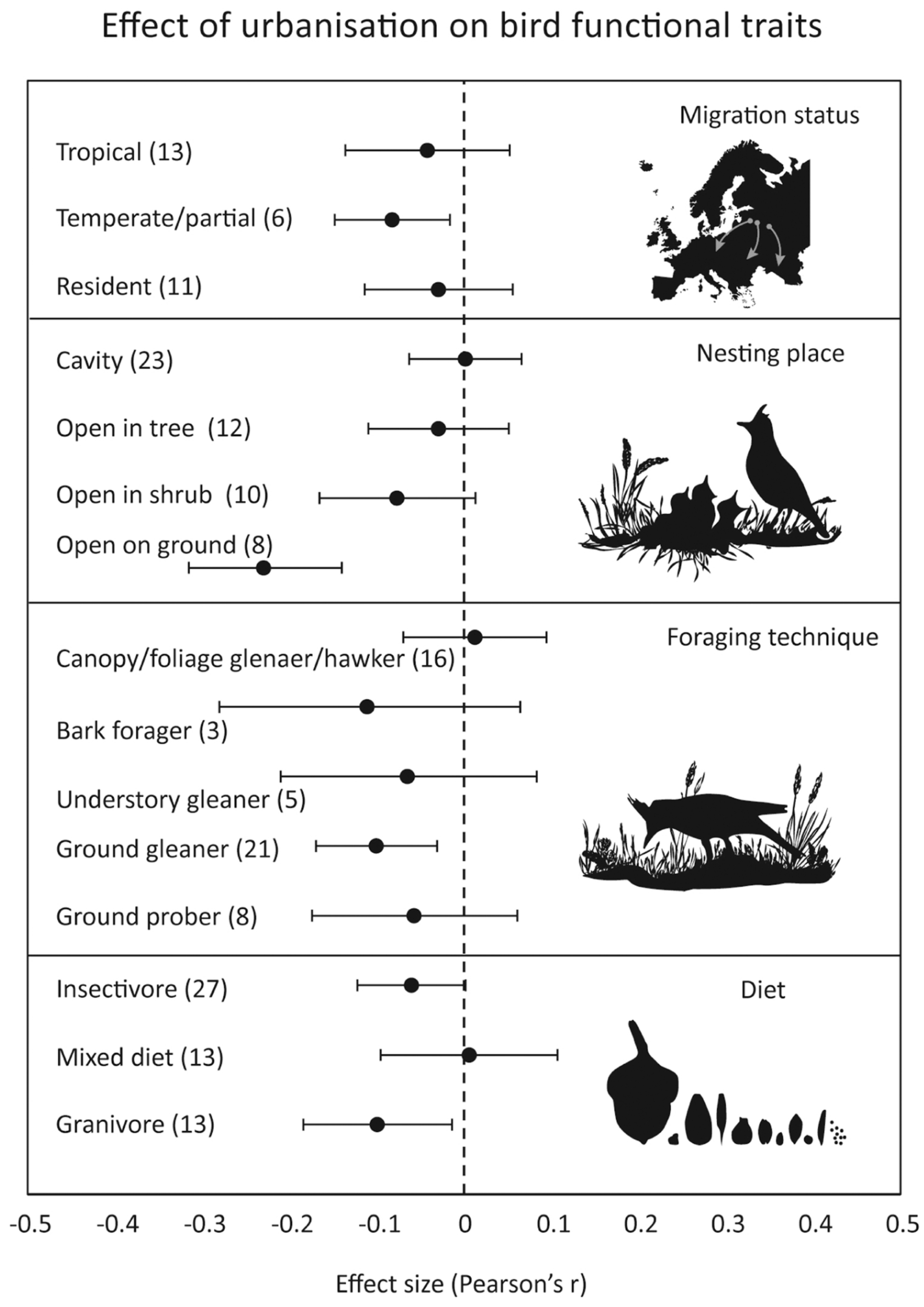

Fig. 1. Forest plot representing the effect of urbanization on bird functional traits, expressed as standardized mean Pearson's r with 95 % confidence intervals. If the individual trait level confidence intervals do not overlap zero, it indicates a significant effect. Graphical interpretation of the studied functional traits (on the right side of the plot) indicates the significant effect sizes. Sample sizes are given in parentheses, which shows the number of observations for every trait separately (number of bird species belonging to the listed trait categories).

2.4. Meta-analysis

After we calculated the standardized values of Pearson's *r*, we started the analytical process. For statistical modelling, Pearson's *r* values were transformed into Fisher's *z*, and for graphical visualization of data, back-transformed data were used. We performed hierarchical meta-analysis for species abundance which allowed the specification of nesting factors. Afterwards, we performed separate fixed effect models for each chosen trait (Harrison, 2011).

2.5. Controlling for phylogenetic relatedness

An obvious weakness of conventional meta-analyses at the species level is that the lack of independence across research articles cannot be taken into account (Chamberlain et al., 2012), because the shared evolutionary history of different species generates non-independence (Schino, 2007). Therefore, meta-analyses with or without phylogenetic information can lead to differing biological conclusions with respect to the interpretation of the underlying processes responsible for the observed patterns. Phylogenetic meta-analysis approaches can provide a statistical template for a general meta-analysis that can account for other attributes that generate non-independence (Adams, 2008). We conducted the phylogenetic control by using a phylogenetically-informed meta--analysis (Adams, 2008; Lajeunesse, 2009; Hadfield and Nakagawa, 2010), in which phylogenetic effects are treated through the appropriate random-effect structure defining the phylogenetic component. The phylogenetic effect is modelled via the phylogenetic variance and correlation matrix of distances between species as extracted from a phylogenetic tree. The phylogenetic variance is estimated, while the phylogenetic tree (and the corresponding correlation matrix among species) should be provided. We obtained this information on phylogenetic relatedness in a tree format (Fig. S3) that is pruned for species included in this study from the BirdTree database (Jetz et al., 2012, http://birdtree.org). Our final results derive from the models containing the phylogenetic relatedness control.

2.6. Publication bias

Articles with stronger and significant effects are more likely to be published than articles with weak or no significant findings. This distinction may result in biased outcomes of meta-analyses. To explore the possibility of publication bias, we used graphical (funnel plots) and statistical (rank correlation test; Rothstein et al., 2005) methods. The Kendall's rank correlation test for funnel plot asymmetry investigates the relationship between the standardised effect size and sample size across the analysed articles. If the test results in a significant *P* value, publication bias might occur. The Kendall's rank correlation tests did not show significant relationships between effect size and the standard errors in the case of the models containing trait category values (Kendall's tau $= 0.12$, $p = 0.21$). Therefore, there was no evidence of publication bias (see also funnel plot in Fig. S2). We carried out all analyses with the metafor package (Viechtbauer, 2010) in R (R Development Core Team 2019).

3. Results

The effect sizes calculated from the meta-analysis models indicated an overall negative effect of urbanization on passerine bird species traits (Fig. 1). All estimates were negative, with the exception of the cavity nesting bird species, birds with foraging technique related to canopy/foliage gleaning/hawking and the group of species with the mixed diet trait. Those effects that were significant (i.e.

Table 2
Summary table of meta-analyses showing between-group and within-group heterogeneities (Q) explained by the moderators and residuals. The significant functional traits are explained in the results section. Even though the migration trait only approached significance, the effect of urbanization was detectable.

Between-group heterogeneity			
Functional traits	**d.f.**	***Q***	***P***
migration	3	7.16	0.066
residual	50	158.56	< 0.0001
nesting place	4	27.72	< 0.0001
residual	49	96.66	< 0.0001
foraging technique	5	11.24	0.046
residual	48	128.10	< 0.0001
diet	3	8.79	0.032
residual	50	153.82	< 0.0001
Within-group heterogeneity			
migration	2	1.07	0.582
residual	50	158.56	< 0.0001
nesting place	3	17.61	0.0005
residual	49	96.66	< 0.0001
foraging technique	4	4.63	0.327
residual	48	128.10	< 0.0001
diet	2	2.43	0.296
residual	50	152.82	< 0.0001

confidence intervals not overlapping zero in Fig. 1) were all negative. Our results revealed that birds that migrate only short distances, or spend the winter in the temperate, southern parts of Europe (mostly Mediterranean regions) were the most sensitive to urbanization. Regarding the nesting trait, bird species nesting on open ground surfaces were the most negatively affected by urbanization. Furthermore, nesting trait was the only one where there was significant between-group heterogeneity (Table 2), showing that ground nesting species were more negatively affected by urbanization than all other nesting trait levels. Regarding the foraging technique trait, we found that ground gleaner species were most negatively and significantly affected in cities. Finally, in the case of diet, granivorous birds were significantly negatively affected by urbanization.

4. Discussion

Our meta-analysis showed that urbanization shaped, and had an overall negative effect on, the abundance of bird species whose functional traits modulated this effect of urbanization. Our results highlighted that areas with different levels of urbanization contained birds with different functional trait categories. Two of our original predictions were upheld: ground nesting birds and ground probers were negatively affected by urbanization. However, there was no evidence either that long-distance migrants or insectivores were the most impacted groups for, respectively, the migration and diet traits. Instead, we found that short-distance/partial migrants and granivores were the most negatively impacted groups.

In the case of migration, bird species living in urban areas have various migration patterns. Partial migration is really widespread among bird species and a significant number of passerines belongs to this group (Chan, 2001). Human activities largely determine climatic conditions and resource availability in cities, thus anthropogenic activities have a major role in shaping bird migration behaviour (Greig el al, 2017). The highly altered urban habitats, the heat island effect and year-round resource availability together may increase the propensity of birds to remain in cities rather than migrate (Bonnet-Lebrun et al., 2020). However, this beneficial effect may only persist up to certain level of urbanisation (Tratalos et al., 2007), because above a certain level of urbanization, city size and housing density exerts threshold effect, which causes significant disruption to bird communities (Garaffa et al., 2009). Our initial prediction that long-distance migrants would be most affected by urbanization was not supported by the results – rather, partial or short distance migrants were the mostly negatively influenced. It is still unclear why this results may arise, but it might be influenced by a range of other factors such as the size of cities or filtering effects, which have not been specifically examined. One possible explanation could be that larger cities may facilitate partial migrant species to spend the winter in urban areas, because the resources are sufficient. Nevertheless, our results suggest the opposite, possibly because in our analysis, smaller cities and towns were in the majority. In these settlements, the resources that are more common in large cities may be scarce, thus partial migrant birds probably try to avoid highly urbanized areas, because migrating to nearby areas is much more efficient. Another explanation could be that migrant species are disadvantaged when competing for resources, because they arrive after resident species have already established territories (Evans et al., 2011).

Birds have a wide variety of nesting behaviours, nevertheless nesting in cities can be more difficult than in natural habitats. Ground nesters, such as skylark *Alauda arvensis*, waders (e.g., *Actitis hypoleucos*), waterfowl (e.g., *Aythya fuligula*) and coniferous forest species (e.g., *Lophophanes cristatus* and *Phoenicurus phoenicurus*) in particular suffer the most from a lack of suitable habitats (Jokimäki et al., 2018). Nest predation pressure caused by corvids, red squirrels *Sciurus vulgaris*, domestic cats and dogs is increased in highly urbanized areas (Jokimäki and Huhta, 2000), therefore ground-nesting birds are especially vulnerable. Our findings confirmed our initial prediction that among the examined nesting site classes, the most disadvantaged were the ground nesting species, as Croci et al. (2008) has also shown in French cities. Not only the presence of nest predators, but most probably the lack of undisturbed, large expanses of grassland areas, threatens the survival of native species nesting in cities (Tomasevic & Marzluff, 2017). With increasing urbanization processes, potential nest sites are rapidly disappearing, and only few species can benefit from cavities provided by buildings or other potential man-made structures which are not generally at ground level (Reynolds et al., 2019).

Studying foraging techniques can give us a perspective on the relationship between bird assemblages and environmental conditions (Nally, 1994), and between urbanization pressure and foraging behaviour, thus it can be an indicator of the urbanization effect. Our findings revealed that in highly urbanized areas, the most disadvantaged foraging behaviour is ground gleaning, which confirms our predictions. This foraging technique encompasses catching prey, like arthropods, by plucking them from the ground. This behaviour is strongly related to the presence of undisturbed, species-rich open grasslands with extensive management that provides food for ground gleaner species. Without these conditions, urban areas may prevent the survival of species belonging to this foraging technique guild.

Interestingly, our analysis showed that urbanization mainly affects granivorous species negatively, which contradicts our prediction and previous findings (Kark et al., 2007; Evans et al., 2011). One possible explanation may be that these bird species are less common in the cities we studied, potentially due to the lack of grasslands, which maintain important seeding plant species like weeds and grasses, or even agricultural cereals. Even though many cities have large semi-natural parks, often including in their central highly urbanized areas, which may act as biodiversity hotspots, these are mainly intensively managed and their frequent mowing prevents seed production. Previous studies may have found positive effects of urbanization on granivores because they were carried out in regions where providing food for birds (especially nuts and seeds) is widespread. For example, Evans et al. (2011) analysed data from the UK where bird feeding is extremely common (Plummer et al., 2019). Many studies considered here were from places where such provision of food is likely less common (Table 1), and hence results are probably more relevant to resources in the wider urban environment. More broadly, we have to add that classifying bird species according to foraging or dietary guilds is not always straightforward and can potentially be misleading. We classified each bird species into a single foraging guild, but the actual niches are usually wider and can vary seasonally (Mortimer, 2016). Therefore, our results from the dietary trait have to be interpreted with caution.

In our study, we focused on the effect of urbanization on different passerine birds and their functional traits, considering species abundances, but other notable aspects could be applied to further studies. One limiting factor was that we only analysed European passerine species, but cities and other human dominated settlements harbour other avian orders as well. Although our European-level study can also reveal important results, in a continent where urbanization has a long history and legacy, a global scale analysis may also be necessary to get a more comprehensive insight into the issue. Taking into account other moderators for the analyses, such as more accurate urbanization gradients and classes supplemented by the characteristics of the cities, latitudinal position of the cities, climatic variables and other functional bird traits would further help to understand the impact of increasingly rapid urbanization on ecosystems. Extension of the search criteria and involving more scientific repositories, with other type of information resources beyond peer-reviewed articles, could complement data for analysis.

Our studied functional traits indicated that the most obvious effect of urbanization is a disadvantage to ground-dwelling bird species with feeding and nesting behaviour closely related to open ground surfaces and granivorous feeding habits. These findings partially reconcile with the idea that urbanization negatively affects ground nesters and ground gleaner species. In the case of migration and dietary traits, we found different results than expected, which may require further research to clarify. A possible continuation of our research could be a more global meta-analysis at the community level, considering more cities, seasonal, national and continental-level effects, which could give a more accurate perspective on how urban sprawl shapes bird functional traits. Considering other avian orders that are also present in urban habitats could be important. Nevertheless, we also underline that publishing and archiving species level data is highly important to maximise the value of later meta-analyses and synthesis studies (Stewart, 2010). Finally, detecting the exact traits that enable or prevent species from thriving in urban environments is crucial to understand the larger context of urbanization, as the filtering effect of urban areas alters functional diversity and deteriorates ecosystem services.

5. Conclusion

We studied passerine bird functional traits along urbanization gradients in Europe with meta-analysis. Bird species with different traits showed variable responses to urbanization. The most obvious negative effect was on species that utilize open ground surfaces for surviving in altered urban habitats. Our research showed that bird species nesting and feeding at ground level significantly decreased in number with increasing urbanization, which indicates the lack of open, undisturbed grasslands in highly urbanized areas in European cities. Urbanization processes fundamentally alter ecological functioning and thus result in lower quality ecosystem service provision, which is essential for the well-being of human societies. Bird species that play an important role in maintaining urban ecosystem functions could be selected or maintained by their functional traits. By knowing which traits allow the survival of a range of bird species, and not just urban tolerant birds, the design of more wildlife friendly cities could be facilitated. To achieve this goal, identifying traits that contribute to a bird species' ability to survive in the urban environment is essential.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02217.

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Further reading

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