CrossMark

Large-scale commonness is the best predictor of bird species presence in European cities

Michal Ferenc[1] · Ondřej Sedláček[1] · Roman Fuchs[2,3] · David Hořák[1] ·
Lenka Storchová[1] · Maurizio Fraissinet[4] · David Storch[1,5]

Abstract Urban bird communities are homogenized across
large spatial scales, suggesting that the urban environment acts
as an environmental filter. We hypothesize that large scale
commonness is a better predictor of urban affinity of birds
than any particular species trait. We estimated the relative
importance of taxonomy, reproductive, ecological and mor-
phological traits, and commonness of individual bird species.
We compiled data on i) breeding bird communities of 41
European cities from urban bird atlases, and ii) regional bird
assemblages defined by nine grid cells of the Atlas of
European Breeding Bird around each city, and quantified the
urban affinity of each species by comparing its incidence in
cities and in randomly drawn communities from respective
regional assemblages. Conditional inference tree-based ran-
dom forest analysis was utilized to assess the importance of
individual predictors. A sign test was used to detect differ-
ences between congeneric pairs of species with contrasting
affinity to cities. Birds associated with woody habitats and
those having altricial chicks had higher affinity for cities. Of
the other reproductive traits, only clutch size showed an asso-
ciation with urban affinity. Different bird orders differed sig-
nificantly in their urban affinity, exemplifying the homogeniz-
ing effect of cities. However, by far the most important factor
associated with bird tolerance to the urban environment was
species commonness, indicating that either the traits associat-
ed with commonness, or population effects driven by com-
monness, are responsible for their presence in cities.

Keywords European birds · urban affinity · traits · range size ·
population size

✉ Ondřej Sedláček
zbrd@email.cz

[1] Department of Ecology, Faculty of Science, Charles University,
Viničná 7, 128 44 Prague 2, Czech Republic

[2] Department of Zoology, Faculty of Science, Charles University,
Viničná 7, 128 44 Prague 2, Czech Republic

[3] Department of Zoology, Faculty of Science, University of South
Bohemia, Branišovská 31, 370 05 České
Budějovice, Czech Republic

[4] Università degli Studi di Napoli "Federico II", Dipartimento di
Agraria, ASOIM onlus, Via Università 100, 80055 Portici, NA, Italy

[5] Center for Theoretical Study, Charles University in Prague and
Academy of Sciences of the Czech Republic, Jilská 1, 11000 Praha
1, Czech Republic

Introduction

Urbanization is a transformation of the environment with far
reaching influences on biota, including loss of species and
functional diversity, and altered ecological processes
(McKinney 2006; Aronson et al. 2014). Considerable evi-
dence for the homogenizing effects of urbanization
(McKinney 2006; La Sorte et al. 2007; Ferenc et al. 2014;
Sol et al. 2014) suggests that urban areas act as environmental
filters and probably systematically favour some species based
on their traits, as shown, for example, by plants and inverte-
brates (Chocholoušková and Pyšek 2003; Bates et al. 2011;
Duncan et al. 2011). Identification of biological traits associ-
ated with persistence in cities has recently received consider-
able attention in birds, but the outcomes are ambiguous (e.g.
Bonier et al. 2007; Croci et al. 2008; Lepczyk et al. 2008; Hu
and Cardoso 2009; Evans et al. 2011; Sol et al. 2014).
Although many authors agree that off-ground nesting birds

🖄 Springer

have an advantage in urban areas due to reduced nest predation pressure (Croci et al. 2008; Conole and Kirkpatrick 2011; Evans et al. 2011; Leveau 2013; Cardoso 2014; Jokimäki et al. 2014; Dale et al. 2015), results regarding other traits are often inconsistent. For example, some claim that birds that tolerate urban environments tend to be larger (Croci et al. 2008), while others show that they are of intermediate size (Conole and Kirkpatrick 2011) or that body size is unimportant (Sol et al. 2014). Conflicting results have also been reported in regard to fecundity (Kark et al. 2007; Croci et al. 2008; Evans et al. 2011; Sol et al. 2014). Kark et al. (2007) were unable to find a difference in reproductive mode between urban avoiders and exploiters. Findings by Evans et al. (2011) and Sol et al. (2014) do not support other studies showing that omnivores or granivores are advantaged in comparison to insectivores (Croci et al. 2008; Conole and Kirkpatrick 2011; Leveau 2013), and that migratory species are disadvantaged under urban conditions (Kark et al. 2007; Croci et al. 2008; Leveau 2013). However, some traits, such as bill morphology that reflects the utilized food type (Schoener 1965; Lederer 1975) or tarsus length which is linked to habitat preference, have not been explored in this respect so far.

If some traits determine the urban tolerance of birds and if these traits are phylogenetically conserved, related species should respond to urbanization in a similar manner (Sol et al. 2014). However, contrasting patterns have been revealed at different spatial scales. Phylogenetic signal is recognizable on a global scale, as some bird families (e.g. Columbidae, Corvidae, Sturnidae) tend to have urban representatives in most parts of the world (Sol et al. 2014). In contrast, at a smaller scale Evans et al. (2011) and Cardoso (2014) found that closely related species often responded to urbanization in different ways, and that sensitivity to urbanization was rather randomly distributed across phylogeny. This indicates that various urban-adapted birds may not necessarily share any common features that affect their tolerance to urbanization. Different species may benefit from the urban environment for very different reasons, and unique sets of traits characterizing different species may have unique selective advantages in the urban environment. If this is the case, it is reasonable to look for factors other than particular morphological or life-history traits that are potentially responsible for the success of species in cities.

For these reasons, we hypothesize that generally widespread and common species are better able to colonize and persist in urban environments than less widespread and less common species. Our hypothesis thus accentuates the functional equivalence hypothesis emphasizing random community assembly where common species are advantaged, in contrast to the urbanisation tolerance hypothesis that assumes that specific traits determine urban success of individual species (Sol et al. 2014). The advantage of commonness may be due to, e.g., mass effects supporting colonization events

(Shmida and Wilson 1985) and/or functioning metapopulation dynamics that reduce the extinction probability (Hanski 1998), or just due to a greater ability to adapt to any environment, including the urban one. We have previously shown that bird communities of European cities are more homogeneous than their species pools (Ferenc et al. 2014), i.e. they are more similar to each other than communities of adjacent landscapes. Here we ask whether these homogenized urban bird communities are dominated by species with certain biological traits or, alternatively, by species that are generally widespread and common. Towards this aim we attempted to assess the role of: i) ecological and morphological traits, ii) reproductive traits, iii) taxonomy, and iv) large-scale commonness in determining bird species affinities to European cities.

Materials and methods

Study area and data

We collated data on the occurrence of breeding bird species in cities from 41 atlases of European cities (see Ferenc et al. 2014, and Supporting Information therein for details on the analysed cities). Since we were interested in the effects of urbanization on native European avifauna, non-native species were omitted from this study. Data on regional species assemblages were obtained from the 50 km × 50 km grid cells of the EBCC (European Bird Census Council) Atlas of European Breeding Birds (Hagemeijer and Blair 1997). Regional species assemblages for each city were defined as the set of bird species breeding in nine (if available) grid cells around each city, which has been previously shown to be a suitable definition of regional assemblages (Ferenc et al. 2014, and Supporting Information therein).

The European breeding range size of each species was calculated as the total number of occupied grid cells of the EBCC atlas. Data on European population sizes and global breeding range sizes were retrieved from BirdLife International (2013). To quantify species affinities to urban areas in Europe, we developed a ranking scheme relating the incidence (i.e. frequency of occurrence) of species in cities to their incidence in communities randomly composed from species of respective regional assemblages. It is not feasible to compute an exact average number of cities that would be occupied by a species if the communities were random subsets of the regional assemblages. Therefore we adopted a simulation approach: bird communities were simulated for each city by random resampling of regional assemblages, where the species richness of a real-city community and its simulated counterpart was held equal. After repeating this procedure 1000 times we calculated an approximate average number of cities which would be occupied by each species if the communities were randomly assembled. The ratio between the

incidence of each species in real cities and its average incidence across simulated city-assemblages gave the urban affinity score. This indicates if a species is present in cities more or less often than would be expected based on random sampling of species from the regional assemblages (score of 1.0 represents completely random occurrence in cities, i.e. a species occurs in cities with the same probability as anywhere else). Species ranks based on this scoring were further used as the response variable in subsequent analyses (see Online resource 1).

We also developed another ranking scheme: the urban affinity scores were multiplied by the frequency of species occurrences in regional assemblages across our study area, and species were ranked according to these new scores. The weighted ranking of urban affinity typically gives lower ranks to species occurring in, e.g., only one species pool and city, which thus have low sample size and the calculated urban affinity rank can be rather imprecise (see Online resource 1). However, because the analyses based on the weighted ranks gave similar results and brought no changes to the interpretations, we present these analyses only in Online resource 2.

We used two sets of traits to explain the affinity of species to urban areas: (i) Ecological and morphological traits: body mass, tarsus and bill length; habitat association (open, wetland, woodland); migratory strategy (sedentary + short distance migrants, long distance migrants); diet (carnivore, piscivore, granivore, herbivore, omnivore, feeding on insects or invertebrates); (ii) Reproductive traits: number of broods per year, clutch size, reproductive mode (altricial, semi-altricial, precocial), nest type (arboreal, ground, hole). The data on ecology, morphology and reproduction were extracted from the interactive version of the Birds of the Western Palearctic handbook (Cramp 2006). The taxonomy (classification to orders) of bird species was based on IOC World Bird List v2.11 (Gill and Donsker 2012). We ran separate analyses (except for the pairwise comparisons of congeneric species) for all birds and for passerines only (order Passeriformes) to verify if the results concerning all birds also hold for a phylogenetically and morphologically homogeneous group representing a substantial part of urban bird communities (Ferenc et al. 2014). The taxonomy and reproductive mode were not included as predictors in the case of passerines.

Analyses

To rank explanatory variables according to their importance in predicting urban affinity of birds, we applied a modified random forest analysis (Breiman 2001; Cutler et al. 2007) utilizing conditional inference trees as base learners (Hothorn et al. 2006). Binary recursive partitioning-based conditional inference trees (hereafter CIT) are suitable for the description of complex datasets (Hothorn et al. 2006; Strobl et al. 2009). The CIT approach is similar to traditional regression trees; both are

non-parametric methods insensitive to the frequency distribution of variables resulting in no need for their transformation (Jarošík 2011). Further common advantages are their ability to deal with nonlinear relationships and higher-order interactions, as well as their robustness to the collinearity of predictors (Breiman et al. 1984; De'ath and Fabricius 2000; Jarošík 2011). In the first step, the basic dataset was divided (if possible) into two groups which were as homogeneous as possible, based on a specific value (cut-off point) of a selected predictor (spliting criterion). Next, each new sub-group (node) was recursively split by a cut-off point of any splitting criterion, including the one(s) used in previous step(s). The lower nodes contained increasingly homogeneous groups of response variables, with terminal nodes being the most homogeneous in respect to the explanatory variables (Strobl et al. 2009). However, traditional regression trees tend to be biased in split criterion selection towards variables with a high number of potential cut-off points or many missing values (Hothorn et al. 2006; Strobl et al. 2007), and rely on cross-validation and pruning of overgrown trees while selecting the resulting tree (Breiman et al. 1984; Jarošík 2011). In contrast, CITs utilize permutation tests: i) to perform unbiased variable selection at each split and ii) to apply early stopping (instead of pruning) to prevent overfitting (Hothorn et al. 2006). The drawbacks of both methods are their strong dependence on the learning sample and thus their sensitivity to small changes in the data (Strobl et al. 2009).

To prevent potentially incorrect conclusions derived from a single tree we utilized the random forest approach (Breiman 2001; Cutler et al. 2007) based on CITs (hereafter CIT-RF). Individual CITs were fitted to 500 different subsamples (without replacement) of the original dataset instead of bootstrapped samples (Hothorn et al. 2006; Strobl et al. 2007). Data not appearing in the subsamples are called out-of-bag (OOB) data and were used for assessing the predictive ability of each tree (Breiman 2001; Cutler et al. 2007). The importance of predictors can be calculated by randomly permuting the values of a predictor for the OOB data and calculating the reduction in model accuracy in comparison to the original OOB data (Cutler et al. 2007; Strobl et al. 2007; Jarošík 2011). We calculated the importance of each variable under the conditional permutation scheme ensuring a lower preference for correlated predictors (Strobl et al. 2008). Finally, the raw predictor importance values were converted into percentages. This analysis was separately run for i) reproductive traits and ii) ecological and morphological traits. Although the commonness of species is a qualitatively different variable, analogical CIT-RF analyses were run with European range size included in the explanatory datasets to directly compare its importance with the importance of other traits. All analyses were conducted in R software (R Core Team 2013) using the `party´ package (Hothorn et al. 2013).
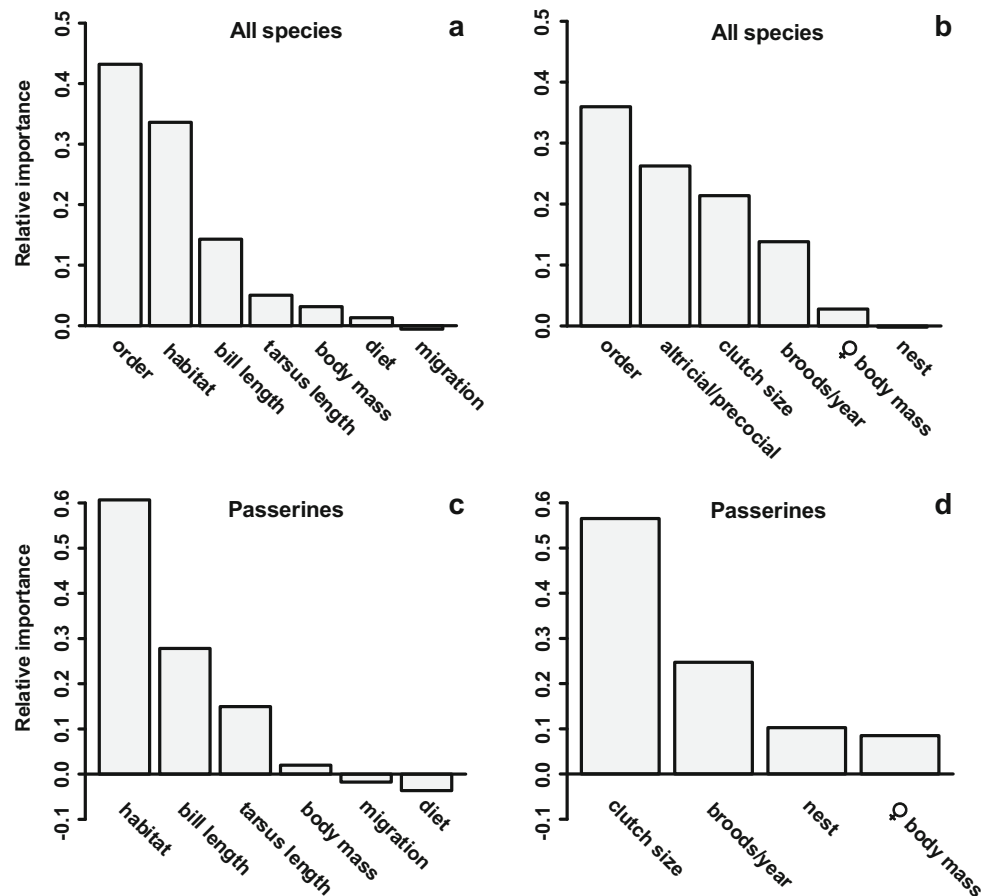
To test for the differences in continuous traits between bird species with high versus low urban affinity we conducted pairwise comparisons of closely related species (using absolute scores instead of ranks). Pairs of congeners were selected such that one of them had a higher and the second a lower score than the median urban affinity score. In some cases it was possible to select multiple pairs of congeners; therefore the contrasted pairs were repeatedly randomly chosen (100 randomizations) to ensure a non-arbitrary comparison of species pairs. Subsequently we tested the differences between congeners using the sign test in the R package 'BSDA' (Arnholt 2012), and the proportion of significant tests at the Bonferroni corrected significance level was recorded. The shortcoming of this analysis is that only a restricted number of pairs of bird species could be used (52 pairs), because some species could not be contrasted in respect to the median score (as all had either higher or lower scores than the median) or because some genera were represented by a single species only.

The non-parametric Kruskal-Wallis test of analysis of variance was used to test for the differences in ranks of urban affinity among groups of birds characterized by specific categorical variables. Correlations between continuous traits and the ranks of urban affinity of birds were evaluated using non-parametric Spearman's rank correlation coefficients. Correlations of global breeding range size, European breeding range size and European population size (all, except for European breeding range size, were ln-transformed) with the rank of urban affinity were analysed using parametric Pearson's correlation coefficients. In all tests, the significance threshold was set to 0.05.

Results

### Ecological and morphological traits

Of the ecological and morphological traits tested, the CIT-RF revealed taxonomic status (order identity) to be the most important predictor of bird urban affinity ranks (Fig. 1a). Relatively species-poor orders of Columbiformes, Apodiformes, Bucerotiformes and Caprimulgiformes had the highest ranks, followed by more numerous Piciformes and Passeriformes (Fig. 2). Orders with the lowest urban affinity included Otidiformes, Procellariiformes, Galliformes, Suliformes and birds of prey. The habitat association was the second most important predictor of bird urban affinity (Fig.
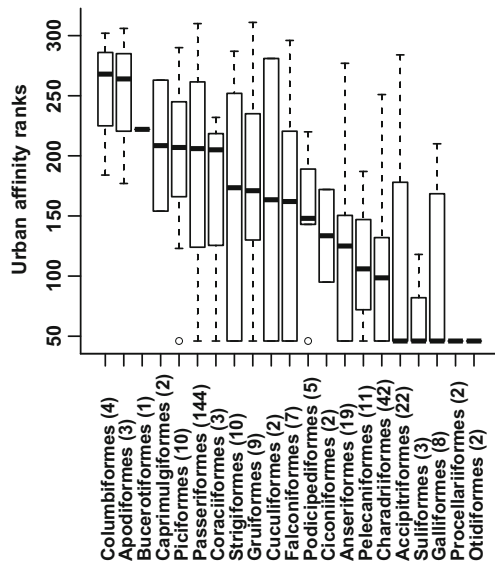
Fig. 2 Boxplots of urban affinity ranks of individual bird orders. Boxplots show the median, interquartile ranges, whiskers extending to 1.5 times the interquartile range, and outliers. Numbers in brackets indicate the number of species in each order

1a). Species associated with woodlands showed a higher affinity to cities than species of open habitats and wetlands (Kruskal-Wallis test: H = 38.18, p = 0.0000, Fig. 3). Simple correlations of morphological traits with urban affinity ranks showed that larger birds tend to avoid urban areas (Table 1). All the other predictors included in the CIT-RF analysis had relatively low importance.

The CIT-RF analysis based on passerines confirmed the importance of habitat associations in explaining bird urban affinities (Fig. 1c). Passerines associated with woodland habitats tended to have the highest urban affinity ranks (Kruskal-Wallis test: H = 10.66, p = 0.0049; see Online resource 3). Body size variables had a much smaller effect on urban affinity in passerines, although bill length showed some
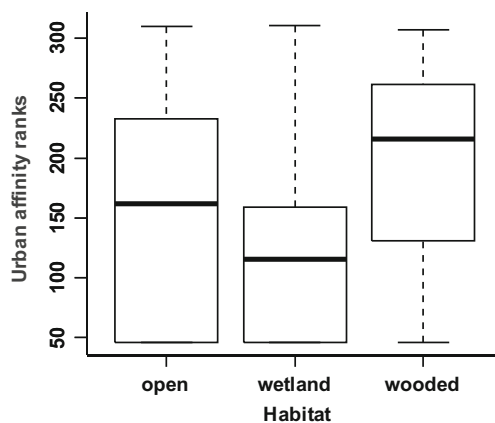
Fig. 3 The differences in urban affinity ranks between bird species associated with open, wetland, and woodland habitats. Boxplots show the median, interquartile ranges, and whiskers extending to 1.5 times the interquartile range

Table 1 Spearman's rank correlation coefficients between urban affinity ranks and continuous traits of bird species (all species and passerines only) considered in this study

Trait	Urban affinity ranks	
	all species	passerines
body mass	−0.38 *	−0.20 *
tarsus length	−0.37 *	−0.23 *
bill length	−0.36 *	−0.22 *
female body mass	−0.38 *	−0.19 *
clutch size	0.24 *	0.18 *
broods/year	0.29 *	0.09 (NS)

NS non-significant

*$p < 0.05$

importance (Fig. 1c). Simple correlations suggest that passerines with longer bills tend to avoid urban areas. The sign test showed no significant differences between congeners with different urban affinity scores.

Reproductive traits

The taxonomic status (order identity) and reproductive mode were among the most important predictors of urban affinity ranks for all bird species (Fig. 1b). Altricial species showed significantly higher affinity to cities compared with the other two strategies (Kruskal-Wallis test: H = 46.71, p = 0.0000; see Online resource 4). Simple correlations suggested that birds with larger clutch sizes and two or more broods per year have higher probability to occur in cities (Table 1).

For passerines, the clutch size and number of broods per year were also identified as relatively important predictors of urban affinity (Fig. 1d). A significant positive correlation was detected for clutch size, but not for the number of broods per year (Table 1). None of the reproductive traits was significantly different among congeneric species with different urban affinity scores.

Geographic distribution and population size

When European range size was included among the predictors in the CIT-RF analysis, all the other ecological and morphological or reproductive traits had a negligible relative importance (Fig. 4). We found a strong positive correlation between the urban affinity of birds and their European and global range sizes and population abundance. The European range size was the strongest predictor of urban affinity, followed by population size in Europe and global geographic range (Table 2; Fig. 5). Similar results hold for passerines

Table 2 Pearson's correlation coefficients between urban affinity ranks and the range size and population abundance of bird species (all species and passerines only)

Variable	Urban affinity ranks	
	all species	passerines
geographic range (World)	0.20 *	0.32 *
range size (Europe)	0.73 *	0.67 *
population size (Europe)	0.62 *	0.60 *

*p < 0.05

and woodland and non-woodland species separately (Table 2, Fig. 5, Online resource 5).

The analyses comparing congeners showed that species with higher affinity to urban areas have significantly larger European and global breeding range sizes, as well as European population sizes. All 100 out of 100 sign tests at the Bonferroni corrected significance level were significant, except for the global geographic range size with only 42 significant tests out of 100.
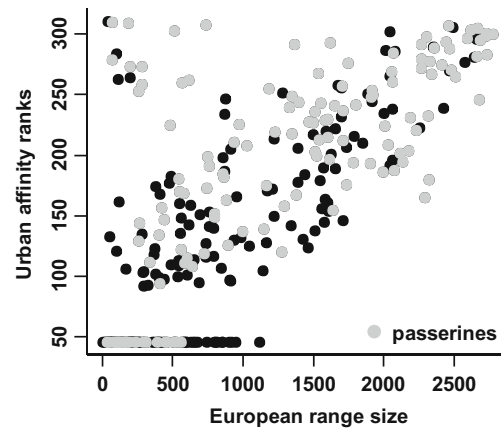
Fig. 5 The relationship between European range size and urban affinity ranks of all species ($r = 0.73$; $p = 0.0000$) with passerines shaded in grey

Discussion

Our hypothesis stating that commonness is the major factor determining bird presence in European cities has been largely supported. The worldwide and European range sizes of

Fig. 4 The relative importance of the European range size of species, ecological and morphological (a, c) and reproductive (b, d) traits in determining bird species urban affinity ranks based on CIT-RF analyses. Analyses were run for all species (a, b) and passerines (c, d) separately
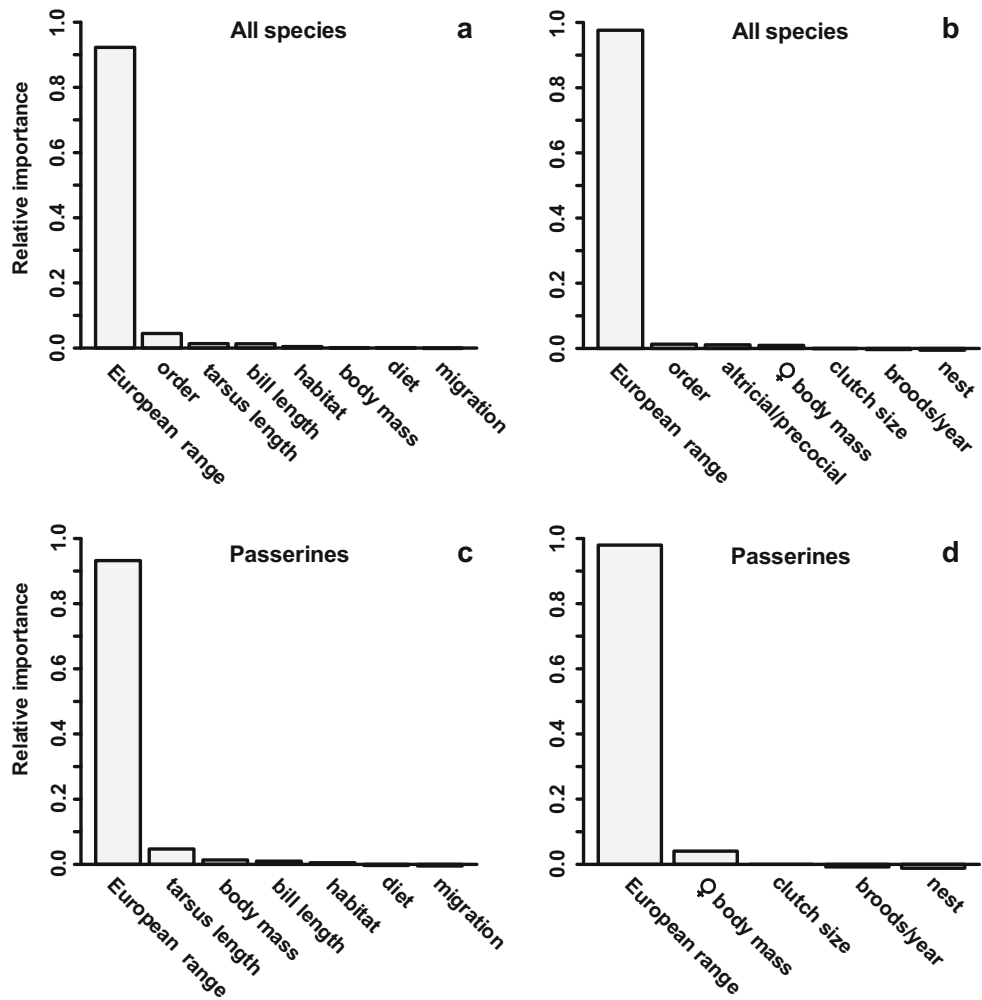
species and their European population sizes are by far the best predictors of their affinity to cities. Additionally, woodland birds seem to be advantaged in urban areas in contrast to birds of open or wetland habitats, and species with different urbanization tolerance have been shown to be non-randomly distributed among taxonomic groups (orders). Importantly, other ecological, morphological and reproductive traits received relatively weak support throughout our analyses. We therefore suggest that factors determining the overall bird rarity or commonness (either expressed in terms of their geographic distribution or population size) also determine their ability to pass the urban environmental filter and to persist under urban conditions (see also Dale et al. 2015; Aronson et al. 2016). This could be due to the fact species able to survive in large numbers in the human dominated landscape of Europe are pre-adapted for life in cities (Cardoso 2014). In other words, the traits responsible for widespread distribution and/or high abundances may simultaneously directly and positively influence bird survival in cities. An obvious example is wider environmental tolerance (Bonier et al. 2007; Croci et al. 2007). Alternatively, traits may act indirectly by enabling some species to be widespread and/or abundant, so that their potential for successful colonization of cities is higher (Symonds and Johnson 2006). We propose several non-exclusive mechanisms translating rarity/commonness into the urban affinity of birds: First, widespread species tend to be locally abundant (Gaston et al. 2000), so that common species are more resistant to local extinction due to their high local abundances (Purvis et al. 2000). A favourable metapopulation dynamics can further enhance their persistence in urban areas via the rescue effect (Brown and Kodric-Brown 1977; Hanski 1998). Rare species, on the other hand, may be absent from a city, because their abundances are too low in the surrounding habitats to enable invasion and establishment in the city. Second, the currently expanding urban environment represents an extreme form of environmental alteration, which requires new adaptive responses of species (Partecke and Gwinner 2007; Ibáñez-Álamo and Soler 2010). Initial urban populations of less common species might be too small for the emergence and fixation of beneficial mutations (Kimura 1983), resulting in their lower adaptability and persistence. Third, abundant species may have a higher probability of early colonization of cities. Birds inhabiting cities for longer periods of time become gradually adapted to this type of environment and attain higher within-city densities (Møller et al. 2012) resulting in higher urban population stability and persistence.

In our analyses, birds primarily associated with woodlands showed higher urban affinity in comparison to birds of open and aquatic habitats (*cf.* Dale et al. 2015). The absence of many non-woodland species from cities might be caused by the lower availability and/or inferior quality of non-woodland habitats in urbanized areas (Croci et al. 2008). Alternatively,

the dramatic decline in the population sizes of many farmland and wetland birds in Europe, due to intensifying agriculture and aquaculture (Voříšek et al. 2010; Wetlands International 2010), potentially contributes to the low incidence of these species in urbanized areas.

A clear taxonomical pattern in the urban affinity of birds was also revealed, consistently with Sol et al. (2014) who found a non-random phylogenetic pattern in bird sensitivity to urbanization. This indicates that specific combinations of traits represented by individual taxa determine the tolerance of species to urbanized areas (Kark et al. 2007; Croci et al. 2008; Leveau 2013). Our findings therefore explicitly demonstrate the non-random filtering of the assemblages entering cities (Bonier et al. 2007; Croci et al. 2008; Evans et al. 2011; Leveau 2013; Meffert and Dziock 2013), which may ultimately lead to the taxonomically and functionally homogenized avifauna of cities (McKinney 2006; Luck and Smallbone 2011; Ferenc et al. 2014; Sol et al. 2014). In contrast, no phylogenetic signal in urban tolerance was detected by Cardoso (2014) and Evans et al. (2011). However, the former study considered only passerines, and the latter disregarded species completely avoiding the urban environment.

Morphological traits as predictors of bird urban affinity received relatively weak support in our CIT-RF analyses, being surpassed by the influence of taxonomy or habitat choice. Moreover, the comparison of congeneric species did not reveal any morphological differences between species with high versus low affinity to cities. Similarly, reproductive traits did not appear to strongly affect the urban affinity of birds. Although our data suggest that birds with altricial nestlings are more frequently found in human settlements, it is not clear whether this strategy genuinely enhances their ability to persist in cities or if it is just a reflection of the taxonomic bias in urban tolerance. Clutch size was moderately correlated with urban affinity, and there was some indication of its importance in passerines, but the results are not clear-cut. Moreover, the lack of differences in reproductive traits between congeners indicated that closely related species with similar reproductive traits can have differing levels of urban tolerance. Higher potential reproductive output (i.e. larger clutches and/or the presence of replacement clutches) has been suggested to enable birds to be better urban exploiters (Chace and Walsh 2006; Croci et al. 2008), but this was not supported by other studies (Kark et al. 2007; Evans et al. 2011) and the role of reproductive traits remains ambiguous.

The strong support for large-scale commonness as a determinant of the response of an individual bird species to urbanization and the much weaker support for other traits (see also Lepczyk et al. 2008) might seem to contradict the conclusions of Sol et al. (2014). These authors suggest that mainly adaptive differences between species cause their differential responses to urbanization. However, our finding that closely related species with differing affinities to cities systematically

differed only in their large-scale commonness indicates that non-adaptive effects may be quite important. Unfortunately, it is not possible to tease apart the independent influence of adaptive vs. non-adaptive features based on our analyses. Some unmeasured traits responsible for the large-scale commonness of a species might be similar or identical to the traits providing an advantage in urbanized areas (e.g. wider environmental tolerance; Bonier et al. 2007; Croci et al. 2007) and thus the urbanization tolerance hypothesis (Sol et al. 2014) would still apply in such a case. Our results only show that species commonness is a much stronger predictor of urban affinity than any of the traits we explored.

Conclusions

Our key finding is that the large-scale homogenization of urban bird communities (Ferenc et al. 2014) is caused by an urban environmental filter preventing rarer birds to invade and/or persist in cities. Traits associated with the ability of bird species to colonize urban environments are thus indistinguishable from traits associated with their geographic distribution and abundance. The relevant traits might act either directly by influencing the urban adaptability and broader environmental tolerance of species, or indirectly by influencing bird population dynamics.

References

Arnholt AT (2012) BSDA: Basic Statistics and Data Analysis. R package version 1.01. http://CRAN.R-project.org/package=BSDA

Aronson MFJ et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B: Biological Sciences 281, https://doi.org/10.1098/rspb.2013.3330

Aronson MFJ, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, La Sorte FA, Williams NSG, Zipperer W (2016) Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963. https://doi.org/10.1002/ecy.1535

Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ (2011) Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. PLoS One 6:e23459. https://doi.org/10.1371/journal.pone.0023459

BirdLife International (2013) IUCN Red List for birds. Downloaded from http://www.birdlife.org. Accessed 25 Mar 2013

Bonier F, Martin PR, Wingfield JC (2007) Urban birds have broader environmental tolerance. Biol Lett 3:670–673. https://doi.org/10.1098/rsbl.2007.0349

Breiman L (2001) Random forests. Mach Learn 45:5–32. https://doi.org/10.1023/a:1010933404324

Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) Classification and regression trees. Wadsworth & Brooks, Monterey

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449. https://doi.org/10.2307/1935620

Cardoso GC (2014) Nesting and acoustic ecology, but not phylogeny, influence passerine urban tolerance. Glob Chang Biol 20:803–810. https://doi.org/10.1111/gcb.12410

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Chocholoušková Z, Pyšek P (2003) Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzen. Flora 198:366–376. https://doi.org/10.1078/0367-2530-00109

Conole LE, Kirkpatrick JB (2011) Functional and spatial differentiation of urban bird assemblages at the landscape scale. Landsc Urban Plan 100:11–23. https://doi.org/10.1016/j.landurbplan.2010.11.007

Cramp S (2006) The Birds of the Western Palearctic interactive. Oxford University Press and BirdGuides, Oxford

Croci S, Le Quilliec P, Clergeau P (2007) Geographical range as predictor of spatial expansion of invading birds. Biodivers Conserv 16:511–524. https://doi.org/10.1007/s10531-006-6732-2

Croci S, Butet A, Clergeau P (2008) Does urbanization filter birds on the basis of their biological traits? Condor 110:223–240. https://doi.org/10.1525/cond.2008.8409

Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT (2007) Random forests for classification in ecology. Ecology 88:2783–2792. https://doi.org/10.1890/07-0539.1

Dale S, Lifjeld JT, Rowe M (2015) Commonness and ecology, but not bigger brains, predict urban living in birds. BMC Ecol 15:12. https://doi.org/10.1186/s12898-015-0044-x

De'ath G, Fabricius KE (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:cartap]2.0.co;2

Duncan RP et al (2011) Plant traits and extinction in urban areas: a meta-analysis of 11 cities. Glob Ecol Biogeogr 20:509–519. https://doi.org/10.1111/j.1466-8238.2010.00633.x

Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? Glob Chang Biol 17:32–44. https://doi.org/10.1111/j.1365-2486.2010.02247.x

Ferenc M, Sedláček O, Fuchs R, Dinetti M, Fraissinet M, Storch D (2014) Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. Glob Ecol Biogeogr 23:479–489. https://doi.org/10.1111/geb.12130

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance-occupancy relationships. J Appl Ecol 37:39–59. https://doi.org/10.1046/j.1365-2664.2000.00485.x

Gill F, Donsker D (eds) (2012) IOC world bird list (version 2.11). http://www.worldbirdnames.org/. Accessed 18 May 2012

Hagemeijer W, Blair M (1997) The EBCC Atlas of European Birds. Poyser, London

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49. https://doi.org/10.1038/23876

Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: A conditional inference framework. J Comput Graph Stat 15:651–674. https://doi.org/10.1198/106186006x133933

Hothorn T, Hornik K, Zeileis A (2013) party: A Laboratory for Recursive Partytioning. R package version: 1.0–9

Hu Y, Cardoso GC (2009) Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? Behav Ecol 20:1268–1273. https://doi.org/10.1093/beheco/arp131

Ibáñez-Álamo JD, Soler M (2010) Does urbanization affect selective pressures and life-history strategies in the common blackbird (Turdus merula L.)? Biol J Linn Soc 101:759–766. https://doi.org/10.1111/j.1095-8312.2010.01543.x

Jarošík V (2011) CART and related methods. In: Simberloff D, Rejmánek M (eds) Encyclopedia of biological invasions. University of California Press, Berkeley and Los Angeles, pp 104–108

Jokimäki J, Suhonen J, Jokimäki-Kaisanlahti ML, Carbó-Ramírez P (2016) Effects of urbanization on breeding birds in European towns: Impacts of species traits. Urban Ecosyst 19:1565–1577. https://doi.org/10.1007/s11252-014-0423-7

Kark S, Iwaniuk A, Schalimtzek A, Banker E (2007) Living in the city: can anyone become an 'urban exploiter'? J Biogeogr 34:638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Kimura M (1983) The Neutral Theory of Molecular Evolution. Cambridge University Press, Cambridge

La Sorte FA, McKinney ML, Pyšek P (2007) Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. Glob Chang Biol 13:913–921. https://doi.org/10.1111/j.1365-2486.2007.01329.x

Lederer RJ (1975) Bill size, food size, and jaw forces of insectivorous birds. Auk 92:385–387. https://doi.org/10.2307/4084573

Lepczyk CA, Flather CH, Radeloff VC, Pidgeon AM, Hammer RB, Liu J (2008) Human impacts on regional avian diversity and abundance. Conserv Biol 22:405–416. https://doi.org/10.1111/j.1523-1739.2008.00881.x

Leveau LM (2013) Bird traits in urban-rural gradients: how many functional groups are there? J Ornithol 154:655–662. https://doi.org/10.1007/s10336-012-0928-x

Luck GW, Smallbone LT (2011) The impact of urbanization on taxonomic and functional similarity among bird communities. J Biogeogr 38:894–906. https://doi.org/10.1111/j.1365-2699.2010.02449.x

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Meffert PJ, Dziock F (2013) The influence of urbanisation on diversity and trait composition of birds. Landsc Ecol 28:943–957. https://doi.org/10.1007/s10980-013-9867-z

Møller AP et al (2012) High urban population density of birds reflects their timing of urbanization. Oecologia 170:867–875. https://doi.org/10.1007/s00442-012-2355-3

Partecke J, Gwinner E (2007) Increased sedentariness in European Blackbirds following urbanization: A consequence of local adaptation? Ecology 88:882–890. https://doi.org/10.1890/06-1105

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proc R Soc B Biol Sci 267:1947–1952. https://doi.org/10.1098/rspb.2000.1234

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, URL: http://www.R-project.org/

Schoener TW (1965) The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19:189–213. https://doi.org/10.2307/2406374

Shmida A, Wilson MV (1985) Biological determinants of species-diversity. J Biogeogr 12:1–20. https://doi.org/10.2307/2845026

Sol D, González-Lagos C, Moreira D, Maspons J, Lapiedra O (2014) Urbanisation tolerance and the loss of avian diversity. Ecol Lett 17:942–950. https://doi.org/10.1111/ele.12297

Strobl C, Boulesteix AL, Zeileis A, Hothorn T (2007) Bias in random forest variable importance measures: Illustrations, sources and a solution. BMC Bioinf 8. https://doi.org/10.1186/1471-2105-8-25

Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for random forests. BMC Bioinf 9. https://doi.org/10.1186/1471-2105-9-307

Strobl C, Malley J, Tutz G (2009) An Introduction to Recursive Partitioning: Rationale, Application, and Characteristics of Classification and Regression Trees, Bagging, and Random Forests. Psychol Methods 14:323–348. https://doi.org/10.1037/a0016973

Symonds MRE, Johnson CN (2006) Range size-abundance relationships in Australian passerines. Glob Ecol Biogeogr 15:143–152. https://doi.org/10.1111/j.1466-822x.2005.00198.x

Voříšek P, Jiguet F, van Strien A, Škropilová J, Klvaňová A, Gregory RD (2010) Trends in Abundance and Biomass of Widespread European Farmland Birds: How Much Have We Lost? BOU Proceedings: Lowland Farmland Birds III. www.bou.org.uk

Wetlands International (2010) State of the World's Waterbirds, 2010. Wetlands International, Ede