



Geographic trends in range sizes explain patterns in bird responses to urbanization in Europe

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ABSTRACT

The probability of occurrence of bird species in towns/cities increases with their range sizes, and Rapoport's rule states that range sizes increase with latitude. To test the hypothesis that the increasing number of bird species persisting in cities at higher latitudes of Europe is linked to their larger range sizes, we compiled data on bird communities of: a) 41 urban bird atlases; b) 37 city core zones from published sources; c) regions of nine grid cells of the EBCC Atlas of European Breeding Birds around each city. We tested whether the proportion of species from particular regional bird assemblages entering cities (i.e., proportional richness) was related to the geographical position, mean range size of regional avifaunas, proportion of vegetated areas and city habitat heterogeneity. The mean range sizes of the observed and randomly selected urban avifaunas were contrasted. The proportional richness of urban avifaunas was positively related to the geographic position and mean range size of birds in regional assemblages. The evidence favoured range sizes if considering the European range sizes or latitudinal extents, but was limited for global range sizes. Randomizations tended to show larger range sizes for the real avifaunas than in the randomly selected ones. For urban core zones, the results were less clear-cut with some evidence only in favour of the European range sizes. No role of vegetation or habitat heterogeneity was found. In conclusion, while vegetation availability or heterogeneity did not show any effects, spatial position and range sizes of birds in regional assemblages seemed to influence the proportional richness of cities and their core zones. Factors correlated with spatial position (e.g., climate) might increase the attractiveness of particular cities to birds. However, the effects of range sizes indicated that urbanization possibly has more negative impacts on the avifauna in the regions occupied by less widespread species.

KEYWORDS

Towns and cities; environmental filtering; homogenization; latitudinal gradient; Rapoport's rule; rarity

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INTRODUCTION

Urbanization is a process substantially transforming the original environment and its impacts are perceivable at all spatial scales (Seto et al., 2012; Grimm et al., 2015). Urbanized areas act as systematic environmental filters leading to the most significant ecological impact of urbanization, documented especially on avian communities, called biotic homogenization (Jokimäki & Kuislahti-Jokimäki, 2003; Clergeau et al., 2006; McKinney, 2006; Luck & Smallbone, 2011; Ferenc et al., 2014a; Sol et al., 2014; Morelli et al., 2016; Leveau et al., 2017). It is exemplified by higher avifaunal similarity among corresponding parts of the urbanization gradient of different cities than among different parts of the urbanization gradient within particular cities (Clergeau et al., 2001, 2006), or by higher similarity among cities than among their species pools (Luck & Smallbone, 2011; Ferenc et al., 2014a). The latter example represents a large scale homogenizing effect and is apparently stronger at higher latitudes of Europe. However, this pattern is paradoxically a

consequence of proportionally more species from particular regional assemblages entering European cities at higher latitudes (Ferenc et al., 2014a). The question therefore is: i) what makes these cities of higher latitudes more attractive to birds, or ii) what makes birds of higher latitudes more predisposed to persist in cities in comparison to south European species?

External factors might include differences in climate along the latitudinal gradient. Positive effects of urbanization due to greater food availability and predictability throughout the year (Jokimäki & Suhonen, 1993) might be more pronounced at higher latitudes, thereby making urban areas more attractive to birds in this region. Alternatively, differences in history of urbanization at different latitudes of Europe (Jokimäki et al., 2016b) might be reflected in the degree of original habitat alteration in urban areas, and thus, in their suitability and attractiveness to birds (Evans et al., 2009).

On the other hand, particular bird traits also show latitudinal patterns (Cardillo, 2002) and many studies pointed

to ecological, behavioural or life-history traits that enable or prevent them to persist in cities (e.g., Bonier et al., 2007; Kark et al., 2007; Croci et al., 2008; Hu & Cardoso, 2009; Conole & Kirkpatrick, 2011; Evans et al., 2011; Díaz et al., 2013; Sol, 2013; Leveau, 2013; Meffert & Dzioczek, 2013; Cardoso, 2014; Sol et al., 2014; Jokimäki et al., 2016a). Recently, it has been shown that commonness (i.e., geographic range or total population size) is a strong predictor of affinity of European bird species to towns and cities (Ferenc et al., 2018). Birds' range sizes vary in space (Orme et al., 2006) and species of higher latitudes tend to have larger ranges (Rapoport, 1982; Stevens, 1989; Cardillo, 2002). This so called Rapoport's rule holds quite well at least at the northern hemisphere (Rohde, 1996; Gaston et al., 1998), and it might affect bird responses to urbanization across latitudes in Europe.

The aim of this study was to reveal whether external factors make European cities of higher latitudes more attractive to birds or whether the assumed latitudinal trend in range sizes drives the observed patterns in proportions of species of regional assemblages occurring in cities (proportional richness hereafter). In order to do so, using two datasets on the European breeding avifauna of entire cities and city core zones, we tested the following hypotheses: i) Geographical position (especially latitude) has an independent effect on the proportional richness of birds, which might indicate a role of various factors correlated with geographical gradients, such as climate or urbanization history. ii) Patterns of habitat availability and/or habitat heterogeneity within cities of Europe drive the spatially structured differences in proportional richness of their avifaunas. iii) The proportional richness of cities is linked to the

Rapoport's rule predicting a latitudinal increase in range sizes of species of particular regional bird assemblages.

1. MATERIALS AND METHODS

1.1. Data collection

Data on breeding bird communities in a) 41 European cities (Fig. 1) were extracted from the urban bird atlases (atlas dataset); and b) 37 European city core zones (core zone dataset) were obtained from a dataset published by Jokimäki et al. (2016a, 2016b). St. Petersburg was excluded from this dataset due to incomplete data on its regional bird assemblage (see definition below). All non-natives were removed from the atlas dataset. The core zone dataset contained two non-native species (*Psittacula krameri*, *Alopochen aegyptiaca*), but their inclusion is highly unlikely to substantially influence the results. The atlas dataset contained species with possible, probable and confirmed breeding status to minimize inconsistencies due to different assignment of species into these categories across particular atlases. On the other hand, the core zone dataset contained only species with probable or confirmed breeding status (Jokimäki et al., 2016a). The composition and richness of regional bird assemblages was retrieved from the EBCC Atlas of European Breeding Birds (Hagemeijer & Blair, 1997). The regional avifauna of each city was defined as the bird assemblage of nine – if available – atlas grid cells (cell size: 50 by 50 km) surrounding each city. The central square included the city or most of the city area and the remaining eight squares surrounded the central square. The proportion of species from

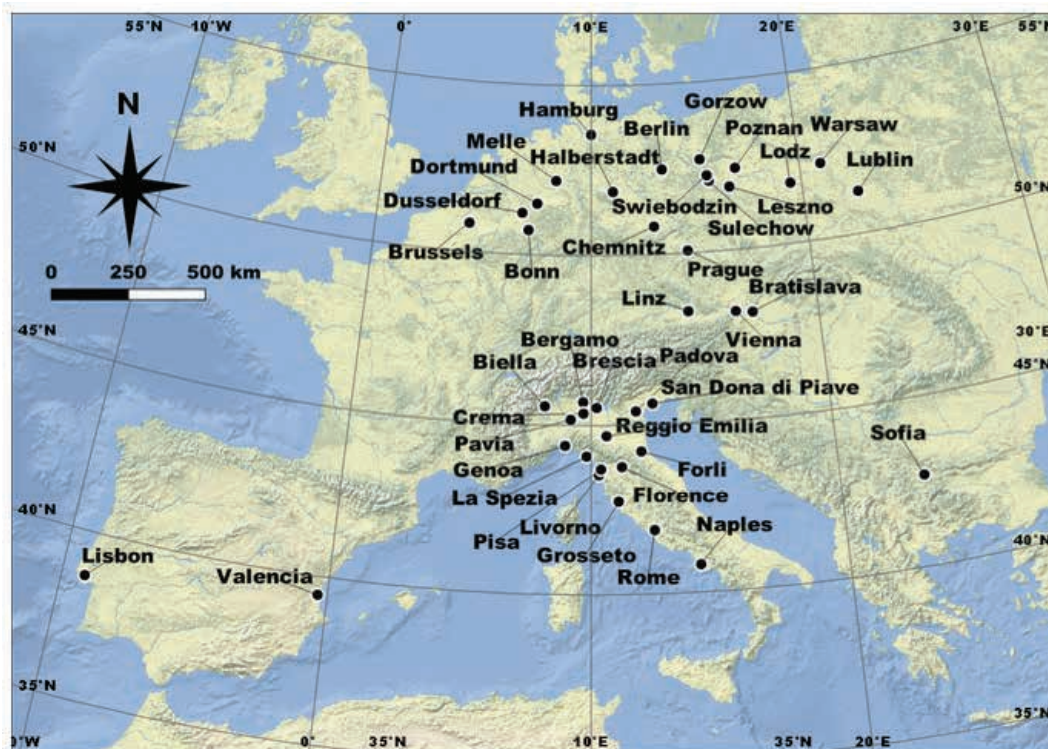


Figure 1. Geographical distribution of the European cities in the 'atlas dataset'

each regional assemblage occupying the corresponding city or city core zone was used as the response variable (see also Table S1 in Appendix S1 and Jokimäki et al., 2016a, 2016b).

In the atlas dataset, the city area was either directly extracted from a particular atlas or calculated as the product of the number of its grid cells and the size of a single cell. While relying on particular authors' expertise in city border definition, only atlases with comparable methodology were utilized (see, e.g., Dinetti et al., 1995). For example, the atlas of Paris was excluded as it covered only the inner-city and not the entire city area (Malher et al., 2010). In the core zone dataset, only the innermost historical city centres were included and their area recorded (Jokimäki et al., 2016a). Furthermore, the proportion of i) 'vegetated', ii) 'built-up' and iii) 'other' land cover was recorded for each city (Ferenc et al., 2014a; Jokimäki et al., 2016a) and the Shannon index (Shannon's H) reflecting their habitat heterogeneity was calculated thereof (Shannon, 1948). Finally, we recorded the European breeding range size (i.e., the number of occupied grid cells of the EBCC atlas); latitudinal range extent in Europe (i.e., the number grid cells between the northernmost and southernmost location of occurrence in the EBCC atlas); and the global range size (BirdLife International, 2018) for each bird species.

1.2. Data analysis

Subsequently, we constructed generalized linear models (with quasibinomial error distribution due to overdispersion and the logit-link function) to relate the proportional richness to the predictor set. In the case of the atlas dataset, both city area and time span of data collection of urban bird atlases influence the recorded species richness, and consequently, the proportional richness of each city. Therefore, these two variables were included in all models to account for their effects. Similarly, for the core zone dataset, all models contained the study plot area. These models were regarded as the baseline models.

A full model containing latitude, longitude, proportion of vegetated area, Shannon index of habitat heterogeneity and either mean European range size (MERS hereafter) or mean latitudinal extent in Europe or mean global range size of birds in particular regional assemblages was created. Thereaf-

ter, we constructed the minimal adequate models by backward elimination of predictors while retaining only those causing a significant increase in residual deviance when removed. Finally, we tested for the presence of residual autocorrelation in the resulting models using Moran's I.

To test whether bird species present in cities are non-randomly selected from regional assemblages according to their range sizes, we performed a randomization test for the atlas dataset. We randomly selected from each regional bird assemblage the same number of species as was actually present in the corresponding city. This procedure was repeated 10,000-times and we recorded the proportion of MERS, mean latitudinal extent and mean global range size of randomized communities that were smaller than those observed in cities.

All analyses were carried out in R (R Core Team, 2017) using the following packages: 'tidyverse' (Wickham, 2017) for data manipulation and plotting, 'fields' (Nychka et al., 2017) for geographical distance calculation and 'ape' (Paradis et al., 2004) for Moran's I calculation.

2. RESULTS

The first premise of this study was an increasing proportional richness of urban avifauna with increasing latitude: although such a latitudinal trend of proportional richness was detected in the case of the atlas dataset ($R^2_{\text{ADJ}} = 0.34$, $p < 0.001$; Fig. 2a) this relationship did not hold for the birds of city core zones ($R^2_{\text{ADJ}} = 0.00$, $p = 0.36$; Fig. 2b). The second premise of increasing geographical ranges or extent of species with latitude held in dependence on the utilized measure: the MERS of urban birds showed an increasing latitudinal trend in the case of the atlas dataset ($R^2_{\text{ADJ}} = 0.42$, $p < 0.001$; Fig. S3.1a in Appendix S3), while this pattern was reversed at higher European latitudes as the core-zone dataset revealed ($R^2_{\text{ADJ}} = 0.43$, $p < 0.001$; Fig. S3.1b in Appendix S3). The pattern was very similar for the mean latitudinal extent of species in regional assemblages (atlas dataset: $R^2_{\text{ADJ}} = 0.88$, $p < 0.001$; Fig. S3.2a in Appendix S3; core zone dataset: $R^2_{\text{ADJ}} = 0.83$, $p < 0.001$; Fig. S3.2b in Appendix S3). In contrast, the mean global range sizes of species

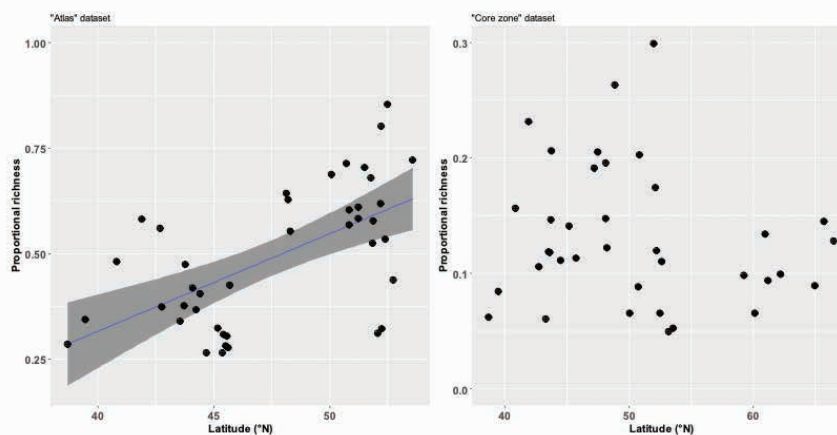


Figure 2. Relationship between the proportional richness of European urban avifaunas (a) atlas dataset ($R^2_{\text{ADJ}} = 0.34$, $p < 0.001$); b) core zone dataset ($R^2_{\text{ADJ}} = -0.004$, $p = 0.36$) plotted against latitude. The trend was fitted by OLS regression, shaded areas depict 95% confidence intervals.

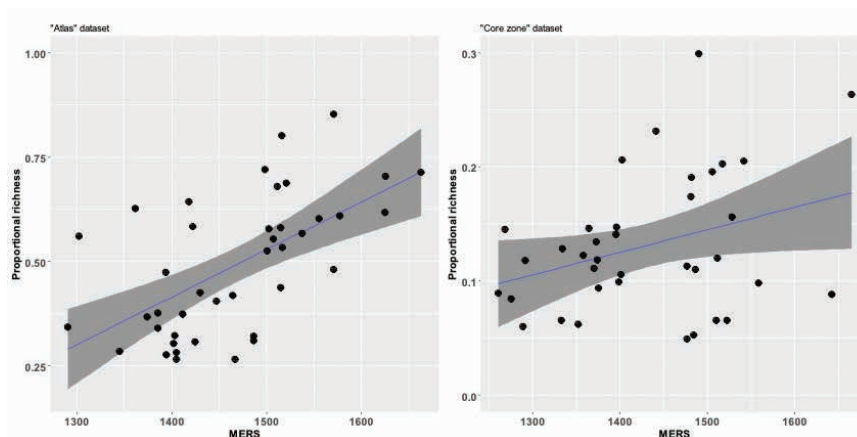


Figure 3. Relationship between the proportional richness of European urban avifaunas (a) atlas dataset ($R^2_{ADJ} = 0.34$, $p < 0.001$); b) core zone dataset ($R^2_{ADJ} = 0.08$, $p < 0.001$) plotted against the mean European range size (MERS; based on the number of occupied EBCC atlas grid cells) of species of particular regional assemblages. The trend was fitted by OLS regression, shaded areas depict 95% confidence intervals.

in regional assemblages increased with latitude consistently in both datasets (atlas dataset: $R^2_{ADJ} = 0.34$, $p < 0.001$; Fig. S3.3a in Appendix S3; core zone dataset: $R^2_{ADJ} = 0.81$, $p < 0.001$; Fig. S3.3b in Appendix S3).

Our results lend support to our central hypothesis: the model for all species in the atlas dataset revealed (Table 1; Table S2.1 in Appendix S2) that spatial position represented by latitude (0.033 ± 0.014 , $t = 2.32$, $p < 0.05$) and longitude (0.02 ± 0.008 , $t = 2.56$, $p < 0.05$) as well as MERS of species in the regional assemblages (0.0017 ± 0.0007 , $t = 2.48$, $p < 0.05$; Fig. 3a) had a significant positive effects on the proportional richness of birds in European cities. On the other hand, only MERS (0.0017 ± 0.0008 , $t = 2.04$, $p < 0.05$; Fig. 3b) had an influence on the proportional richness of birds in the core zones of the European cities. If the model included the mean latitudinal extent of species in regional assemblages, it was significant (0.18 ± 0.03 , $t = 5.87$, $p < 0.001$) along with longitude (0.02 ± 0.007 , $t = 2.43$, $p < 0.05$) in the case of the atlas dataset (Table 1; Table S2.1 in Appendix S2; Fig. S3.4a in Appendix S3;). However, no model could

be built upon our predictors in the case of the core zone dataset (Table 1; Table S2.1 in Appendix S2; Fig. S3.4b in Appendix S3;). Similarly, when including the mean global range sizes of birds in regional assemblages, only latitude had a significant positive effect (0.07 ± 0.01 , $t = 2.32$, $p < 0.001$) on the proportional richness of birds in the case of the atlas dataset (Table 1; Table S2.1 in Appendix S2; Fig. S3.4a in Appendix S3) and no model could be constructed for the core zone dataset (Table 1; Table S2.1 in Appendix S2; Fig. S3.4b in Appendix S3). None of the resulting models showed any residual autocorrelation at the 5% significance level.

Due to the strong correlation between latitude and mean global range size of birds in regional assemblages, we conducted additional post-hoc analyses. They showed that if the initial full model for the atlas dataset included either of the range size descriptors (MERS, mean latitudinal extent or mean global range size), but not latitude, the range size descriptor was always retained in the final model. The same was true for latitude, when leaving out the range size descriptors from the

Table 1: Simplified representation of models constructed by backward elimination showing significant predictors (at the 5% significance level) of proportional richness of urban avifaunas in European cities (atlas dataset) and city core zones (core zones dataset) and their effect ('+' indicates a positive effect). Shaded columns represent different measures of mean geographic range sizes of birds in particular regional assemblages (see Methods for definitions)

Dataset	mean European range size	latitude	longitude	Shannon's H	% vegetation cover
atlas	+	+	+		
core zones	+				
Dataset	mean latitudinal extent	latitude	longitude	Shannon's H	% vegetation cover
atlas	+		+		
core zones					
Dataset	mean global range size	latitude	longitude	Shannon's H	% vegetation cover
atlas		+			
core zones					

initial full model. On the other hand, no such effect was revealed in the case of the core zone dataset (results not shown).

The role of range sizes of birds in determining their proportional richness in cities was further emphasized by the randomization test using the atlas dataset, as the observed urban assemblages had significantly higher MERS than would be expected by chance at the 5% significance level. Similar results were obtained by analysing latitudinal extents of birds, although there were two cities where the avifauna had mean latitudinal extents as if they were randomly assembled from the regional assemblages. However, with using global range sizes, only seven out of 41 cities had avifaunas with higher mean global range sizes than would be expected by chance, while the rest of the cities had mean global range sizes as if the urban avifaunas were assembled randomly.

3. DISCUSSION

Urban avifaunas of European cities and city centres seem to be influenced by both their spatial position at the continent *per se* as well as by the range sizes of species representing the potential species pool in particular regions. Although we detected no influence of vegetation availability or habitat heterogeneity on the proportional richness of urban avifaunas, the effect of geographic location might indicate an influence of unmeasured external factors that are linked to spatial position, such as climatic conditions. On the other hand, features of bird species also influence the richness of urban avifaunas, with relatively more species entering cities in regions occupied by more widespread species.

Cities located towards the north-east of continental Europe (based on the atlas dataset excluding Nordic countries) with relatively continental climate tend to host higher proportions of birds from regional assemblages. Such patterns might be related to the climate moderating effects of urban areas due to the heat-island phenomenon (Erz, 1966; Arnfield, 2003) resulting in greater availability of food resources during the critical periods and their better predictability throughout the year (Jokimäki & Suhonen, 1993). Such effects might enhance the habituation and establishment of populations of particular species within cities (Møller et al., 2014; Tryjanowski et al., 2015). However, the pattern of increasing proportional richness of birds did not hold for the northernmost city core zones (based on the core zone dataset) with the harshest climate, which makes this interpretation dubious. Furthermore, urbanization at higher latitudes of Europe is a relatively recent phenomenon (Jokimäki et al., 2016b) and the responses of bird species might be delayed. That means that avifaunas of different regions have had unequal amount of time to respond to urbanization by adaptation or by going extinct (Essl et al., 2015). The city-age effect can go both ways: i) younger cities can have higher proportional richness as some species (e.g., forest specialists) will still go extinct in the future or ii) younger cities can have lower proportional richness due to less time for adaptation. Again, the fact that the Nordic cities are the youngest, but do not have the

highest proportional richness, disfavours the first explanation, but not the second one. Nevertheless, the discrepancy among the two datasets showing an increase in proportional richness with latitude in the case of entire cities, but no such pattern in the case of city core zones, could partly arise because of their different scales of observation. The possibly positive effects of urbanization observable at the scale of entire cities (such as the heat-island phenomenon [Erz, 1966; Arnfield, 2003]) might be overridden by its negative impacts in the most urbanized city core zones (Clergeau et al., 2006).

Surprisingly, neither the proportion of vegetation cover nor the habitat heterogeneity played any role in determining the proportional richness of urban avifaunas. This points to the fact that although such factors are of prominent importance in determining bird species richness of urban communities at smaller scales (Evans et al., 2009; Ferenc et al., 2014b, 2016), their importance is not necessarily detectable at large spatial scales (MacGregor-Fors et al., 2010). Instead, spatial patterns of species range sizes seem to be a substantial part of the explanation although our initial hypothesis of the link between Rapoport's rule (Rapoport, 1982; Stevens, 1989) and bird responses to urbanization does not hold. We found some evidence in favour of the influence of MERS and mean latitudinal extent, for which Rapoport's rule does not hold, but limited evidence in favour of global range sizes, for which the Rapoport's rule does hold. On the one hand, the link between MERS and proportional richness of cities persisted regardless of whether we focused on entire cities or on city core zones including Nordic cities. On the other hand, the latitudinal extent showed an influence only in the case of entire cities, while not in the case of city core zones. And finally, global range sizes showed no influence in either case. As shown by the randomization tests for MERS or mean latitudinal extent, the urban assemblages systematically filter widespread species, but the evidence is much weaker if considering mean global range sizes. However, even under this scenario, urban avifaunas never showed smaller mean range sizes than the randomly selected assemblages. The discrepant results for MERS or mean latitudinal extent versus mean global range sizes might have two very different reasons: i) the strong correlation between latitude and global range size might lead to a situation when these two variables mask each-others influence on proportional richness. Indeed, the post-hoc analyses revealed such an effect and the mean global range size was always present in the final model if latitude was omitted from the initial full model (and vice-versa), at least in the case of the atlas dataset. ii) The shape of ranges of many northern bird species might be elongated in the west-east direction across Eurasia, but they might be relatively narrow in the north-south direction. Such species might in some ways experience less variable environments than species having global ranges more elongated in the north-south direction, but this would require further testing, which is out of scope of this study.

Indeed, the ability of species to cope with variable environmental conditions and its link to their geographic range sizes might be behind the observed relationships (Stevens,

1989). Widespread birds might have high environmental tolerance possibly due to their ecological, behavioural or physiological flexibility, which can be beneficial under urban conditions (Bonier et al., 2007). Traits of widespread species thus might be directly beneficial for survival in cities or indirectly connected to urbanization by influencing the commonness of species (Ferenc et al., 2018). Less common birds might simply be extinction-prone in urban areas or less likely to colonize them (Sol et al., 2014). Alternatively, species with larger ranges tend to be more numerous locally (Brown, 1995, 2013; Gaston et al., 2000; Gaston & Blackburn, 2008), which can enhance their occurrence in cities due to mass effects (Shmida & Wilson, 1985), favourable metapopulation dynamics (Brown & Kodric-Brown, 1977; Hanski, 1995) or by lowering their local extinction risk (Purvis et al., 2000).

Evidence of the influence of species' commonness on their occurrence in towns and cities is accumulating (Dale et al., 2015; Jokimäki et al., 2016b; Ferenc et al., 2018). Our findings have some important implications for assessing the ecological impacts of urbanization on birds in different geographic locations. Geographical regions showing apparent compositional

uniformity of urban bird assemblages are not necessarily the ones most negatively impacted by urbanization (Ferenc et al., 2014a). Based on our results, we have to take into account geographic location, the geographically changing patterns of range sizes of birds and the enhanced potential of more widespread species to persist in towns and cities. In a similar vein, the urban filter is not necessarily more permeable in regions showing greater distinctness of urban avifaunas. The growth of cities thus poses a greater threat to the bird assemblages in regions composed of less widespread species having a weaker ability to respond to the challenges of urbanization.

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APPENDIX 1

Table S1: Data on 41 European cities and their breeding bird communities

City	Longitude	Latitude	Area (km ²)	Time span of city-atlas data collection (yrs)	% vegetation cover	Shannon index heterogeneity	Species richness - city	Species richness - region	Proportional species richness - city	Mean range size of birds in regional assemblages		
										Europe (# of EBCC squares)	Latitudinal extent (# of cells between southern- & northernmost EBCC squares)	Global (x 10 ⁶ km ²)
Bergamo	9,667	45,7	39	4	0,299	1,036	77	181	0,425	1430,2	28,6	16,188
Berlin	13,4	52,5	900	12	0,168	0,889	145	170	0,853	1571,1	30,8	16,194
Biella	8,067	45,567	30,7	1	0,412	0,955	57	188	0,303	1402	28,3	16,046
Bonn	7,100	50,734	141	12	0,2	1,039	109	153	0,712	1663,2	31,4	16,743
Bratislava	17,110	48,144	376	13	0,336	1,084	126	196	0,643	1418,3	29,3	16,095
Brescia	10,233	45,533	15,5	5	0,222	0,869	52	185	0,281	1404,7	28,3	16,224
Brussels	4,35	50,85	162,38	12	0,107	0,527	97	171	0,567	1537,4	30,7	16,375
Crema	9,683	45,367	22,75	2	0,079	0,881	49	185	0,265	1404,7	28,3	16,224
Dortmund	7,467	51,517	310	6	0,165	1,007	114	162	0,704	1625,4	31,2	16,847
Dusseldorf	6,783	51,233	217	6	0,176	0,952	103	169	0,609	1577,3	30,9	16,705
Florence	11,25	43,783	102,4	2	0,321	1,069	82	173	0,474	1393,9	28,0	15,937
Forlì	12,05	44,233	44,25	3	0,013	0,728	63	172	0,366	1374,3	27,8	16,291
Genoa	8,933	44,411	57	5	0,27	1,075	68	168	0,405	1447,4	27,9	16,902
Gorzow	15,25	52,733	21,1	1	0,236	0,787	79	181	0,436	1515,2	30,5	16,019
Grosseto	11,1	42,767	17,6	2	0,029	0,788	53	142	0,373	1411,5	27,0	16,511
Halberstadt	11,033	51,883	41	5	0,156	0,989	108	187	0,578	1502,2	30,7	16,027
Hamburg	10	53,567	763	4	0,245	1,007	134	186	0,72	1498,5	30,7	16,008
Chemnitz	12,917	50,833	188	4	0,169	1,03	106	176	0,602	1555,1	30,7	16,453
La Spezia	9,817	44,1	20	2	0,262	1,086	66	158	0,418	1464,4	28,3	15,192
Leszno	16,567	51,867	37	4	0,082	0,802	96	183	0,525	1500,9	30,2	15,750
Linz	14,283	48,3	102,75	2	0,267	1,044	99	179	0,553	1507,4	30,0	16,414
Lisbon	-9,135	38,707	84	15	0,073	0,899	41	144	0,285	1345	26,3	17,600
Livorno	10,317	43,55	38,1	2	0	0,695	56	165	0,339	1385,4	27,3	14,895
Lodz	19,467	51,783	236	9	0,225	1,038	123	181	0,68	1511,6	30,3	15,917
Lublin	22,570	51,248	147,55	10	0,176	1,024	116	199	0,583	1422,4	29,8	15,422

City	Longitude	Latitude	Area (km ²)	Time span of city-atlas data collection (yrs)	% vegetation cover	Shannon index habitat heterogeneity	Species richness - city	Species richness - region	Proportional species richness - city	Mean range size of birds in regional assemblages		
										Europe (# of EBCC squares)	Latitudinal extent (# of cells between southern- & northernmost EBCC squares)	Global (x 10 ⁶ km ²)
Melle	8,333	52,2	311	3	0,242	0,696	100	162	0,617	1624,8	31,3	16,682
Naples	14,25	40,833	117,2	5	0,148	1,008	62	129	0,481	1571	28,3	16,445
Padova	11,867	45,417	35	4	0	0,655	55	179	0,307	1424,8	28,9	16,004
Pavia	9,15	45,183	33,5	2	0,168	1,029	60	186	0,323	1403,2	28,3	16,408
Pisa	10,4	43,717	27,4	2	0,019	0,753	62	165	0,376	1385,4	27,3	14,895
Poznan	16,917	52,4	270	20	0,195	1,027	96	180	0,533	1516,6	30,4	16,051
Prague	14,417	50,083	519,4	5	0,171	1,032	125	182	0,687	1520,7	30,5	16,019
Reggio Emilia	10,633	44,7	21,5	2	0,004	0,536	44	166	0,265	1466,8	28,6	16,627
Rome	12,5	41,9	385	5	0,131	0,956	83	143	0,58	1514,7	28,4	16,123
San Dona di Piave	12,567	45,633	12,1	2	0	0,661	53	192	0,276	1394,1	28,6	15,575
Sofia	23,333	42,7	181	10	0,126	0,854	117	209	0,56	1302,3	27,4	15,806
Sulechow	15,617	52,083	4,16	2	0,01	0,583	58	187	0,31	1486,4	30,3	15,802
Swiebodzin	15,533	52,25	5	2	0,199	0,909	60	187	0,321	1486,4	30,3	15,802
Valencia	-0,367	39,467	96,53	16	0,05	0,844	59	172	0,343	1290,3	26,0	16,482
Vienna	16,373	48,208	414,89	10	0,207	0,947	131	209	0,627	1361,6	29,0	15,655
Warsaw	21,011	52,23	545,3	20	0,227	1,036	145	181	0,801	1516,2	30,2	15,612

APPENDIX 2

Table S2: Minimal adequate models constructed by backward elimination showing significant predictors (at the 5% significance level) of proportional richness of urban avifaunas in European cities (atlas dataset) and city core zones (core zones dataset); parameter values and the associated standard errors and test statistics are shown. Variables shaded in grey were included in all models to account for their effects (data collection time span was not considered for the core zones dataset).

Dataset	mean European range size (MERS)	latitude	longitude	Shannon's H	% vegetation cover	area	data collection time span
atlas	0.0017 ± 0.0007, t = 2.48, p < 0.05	0.033 ± 0.014, t = 2.32, p < 0.05	0.02 ± 0.008, t = 2.56, p < 0.05			0.82 ± 0.09, t = 9.35, p < 0.001	0.004 ± 0.01, t = 0.41, p = 0.61
core zones	0.0017 ± 0.0008, t = 2.04, p < 0.05					-0.001 ± 0.14, t = -0.09, p = 0.93	
Dataset	mean latitudinal extent	latitude	longitude	Shannon's H	% vegetation cover	area	data collection time span
atlas	0.18 ± 0.03, t = 5.87, p < 0.001		0.02 ± 0.007, t = 2.43, p < 0.05			0.82 ± 0.09, t = 9.34, p < 0.001	0.004 ± 0.01, t = 0.37, p = 0.71
core zones							
Dataset	mean global range size	latitude	longitude	Shannon's H	% vegetation cover	area	data collection time span
atlas		0.07 ± 0.01, t = 2.32, p < 0.001				0.90 ± 0.09, t = 9.98, p < 0.001	-0.06 ± 0.01, t = -0.33, p = 0.75
core zones							

APPENDIX 3

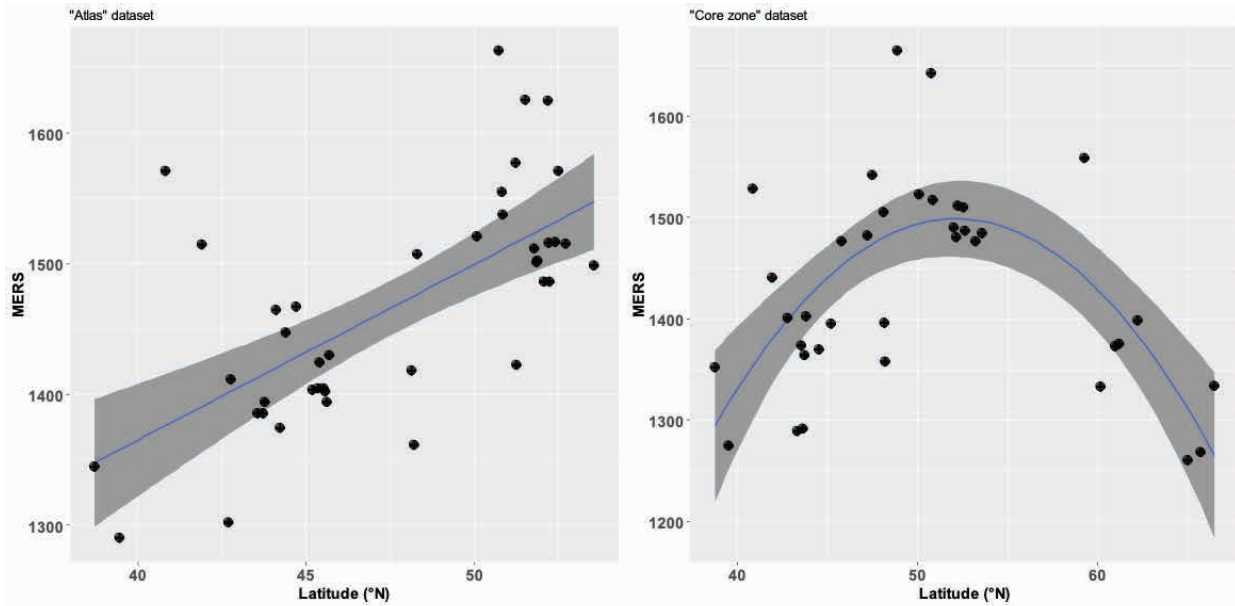


Fig. S3.1: Mean European range size (MERS) of birds in regional assemblages (defined as nine EBCC grid cells around each city) plotted against latitude **a)** atlas dataset ($R^2_{ADJ} = 0.42, p < 0.001$); **b)** core zone dataset ($R^2_{ADJ} = 0.43, p < 0.001$). Trends fitted by OLS regression, shaded area depicts 95% confidence intervals.

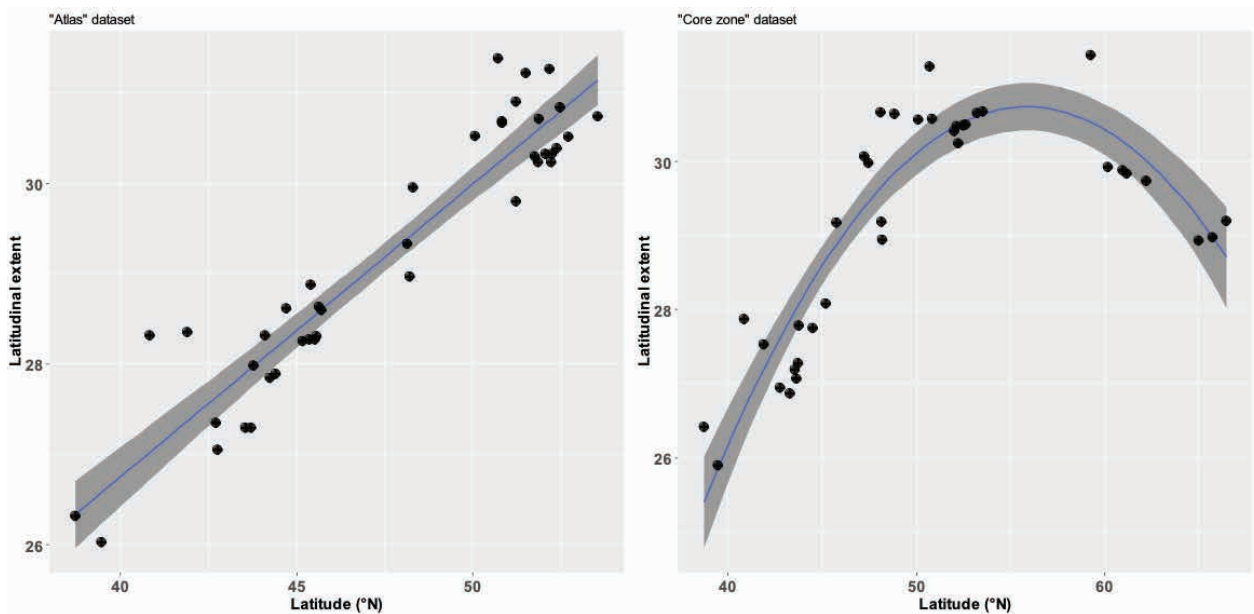


Fig. S3.2: Mean latitudinal extent (defined as the number of cells between the southernmost and northernmost occupied EBCC atlas grid cells) of birds in regional assemblages (defined as nine EBCC grid cells around each city) plotted against latitude: **a)** atlas dataset ($R^2_{ADJ} = 0.88, p < 0.001$); **b)** core zone dataset ($R^2_{ADJ} = 0.83, p < 0.001$). Trends fitted by OLS regression, shaded area depicts 95% confidence intervals.

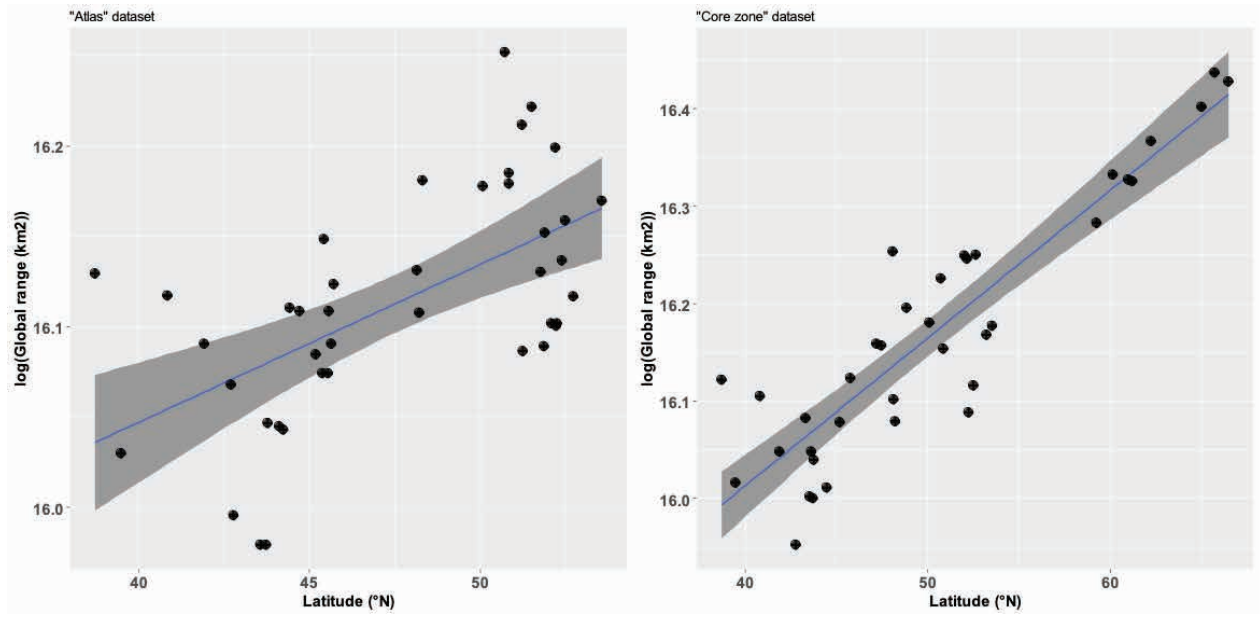


Fig. S3.3: Mean global range size of birds in regional assemblages (defined as nine EBCC grid cells around each city) plotted against latitude: **a)** atlas dataset ($R^2_{ADJ} = 0.34$, $p < 0.001$); **b)** core zone dataset ($R^2_{ADJ} = 0.81$, $p < 0.001$). Trends fitted by OLS regression, shaded area depicts 95% confidence intervals.

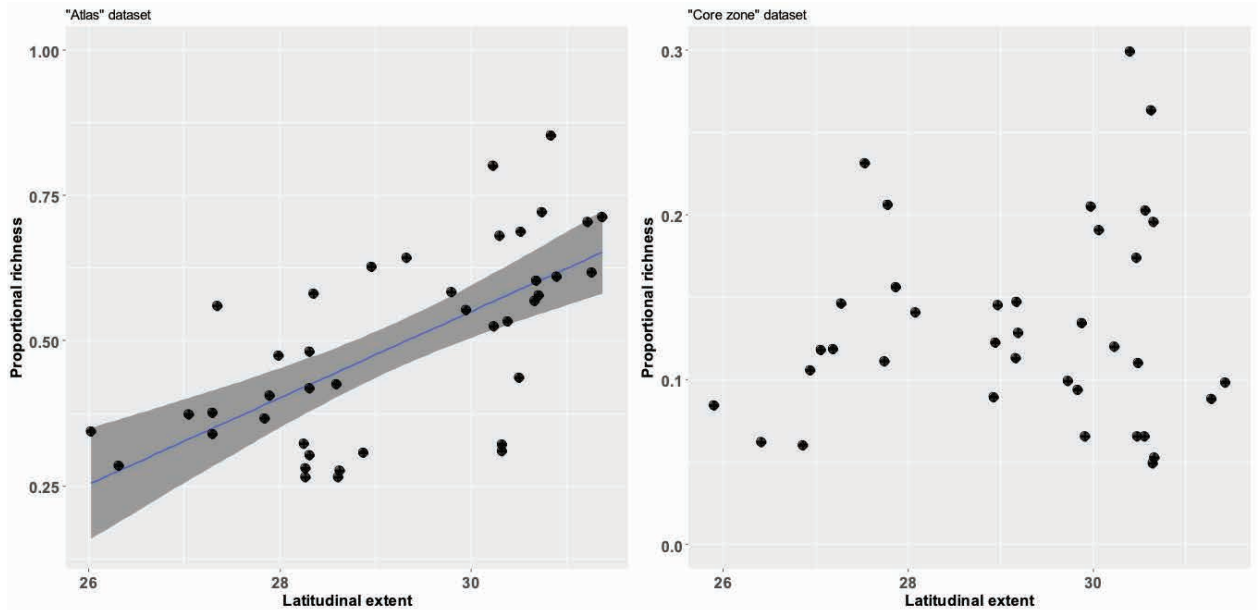


Fig. S3.4: Relationship between the proportional richness of European urban avifaunas (a) atlas dataset ($R^2_{ADJ} = 0.42$, $p < 0.001$); b) core zone dataset ($R^2_{ADJ} = -0.016$, $p = 0.51$) plotted against the mean latitudinal extent (defined as the number of cells between the southernmost and northernmost occupied EBCC atlas grid cells) of species of particular regional assemblages. The trend was fitted by OLS regression, shaded area depicts 95% confidence intervals.

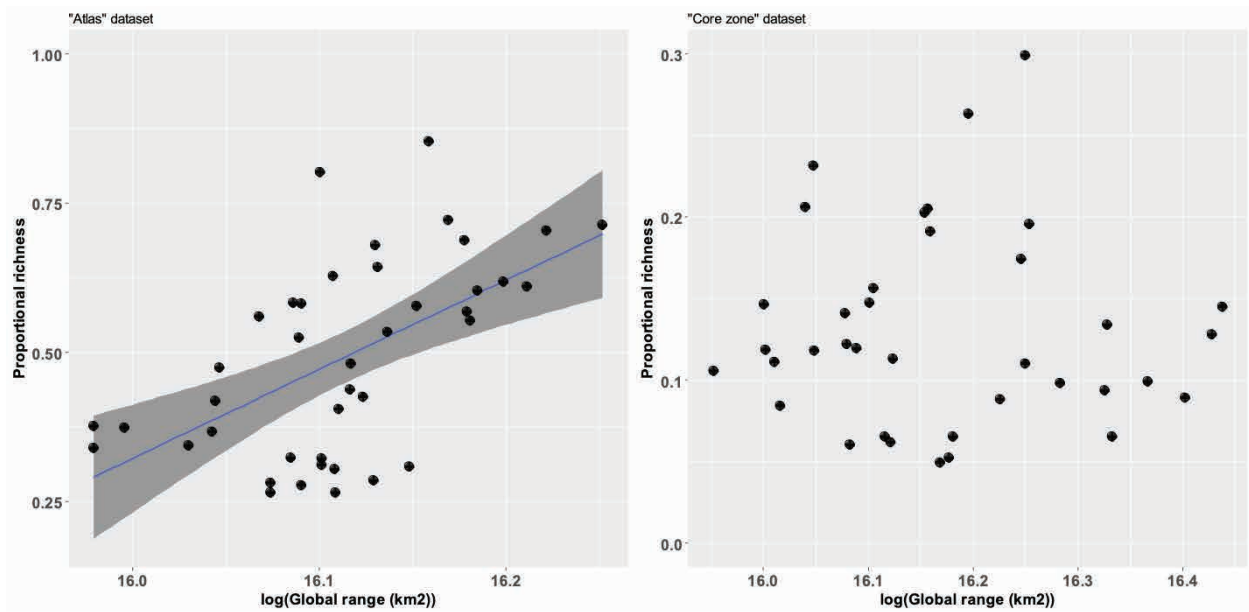


Fig. S3.5: Relationship between the proportional richness of European urban avifaunas (a) atlas dataset ($R^2_{ADI} = 0.30$, $p < 0.001$); b) core zone dataset ($R^2_{ADI} = -0.028$, $p = 0.86$) plotted against the mean global range size (ln-transformed) of species of particular regional assemblages. The trend was fitted by OLS regression, shaded area depicts 95% confidence intervals.