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Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe

Michal Ferenc¹, Ondřej Sedláček^{1*}, Roman Fuchs^{2,3}, Marco Dinetti⁴,
Maurizio Fraissinet⁵ and David Storch^{1,6}

¹Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 12844 Praha 2, Czech Republic, ²Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 12844 Praha 2, Czech Republic, ³Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic, ⁴Ecologia Urbana, Viale Petrarca 103, 57124 Livorno, Italy, ⁵Associazione Studi Ornitologici Italia Meridionale, ASOIM – Via Luca Giordano 12, 80046 San Giorgio a Cremano, Italy, ⁶Center for Theoretical Study, Charles University in Prague and Academy of Sciences of the Czech Republic, Jilská 1, 11000 Praha 1, Czech Republic

ABSTRACT

Aim To compare macroecological patterns between bird communities of European cities and regional species assemblages in the surrounding landscape, and to reveal geographical trends in the urbanization of native avifauna.

Location Forty-one towns and cities in continental Europe.

Methods We compiled data on the species richness and community composition of urban avifauna from 41 European city breeding bird atlases, and of species assemblages comprising nine grid cells (each about 50 km × 50 km) from the EBCC Atlas of European Breeding Birds (hereafter regional assemblages). Species–area relationships (SARs), latitudinal trends in diversity and the distance decay of community similarity were compared using regression models (generalized linear models). Observed urban communities were compared with randomly assembled ones to reveal systematic effects of the urban environment on native bird communities across Europe. We employed variance partitioning to quantify the relative effect of environmental parameters and the spatial position of cities on species richness.

Results The species–area relationships did not differ significantly between cities and regional assemblages. Species richness of both types of communities increased towards higher latitudes, although the relationship was unimodal for regional assemblages, in contrast to cities. The increase in beta diversity with distance was on average less pronounced in cities than in regional assemblages, and was lower between individual cities than between communities of the same size randomly drawn from regional species assemblages. Moreover, average beta diversity was lower in northern cities, which are characterized by a relatively higher proportion of species from regional species pools.

Main conclusions The species–area relationship and latitudinal trends are largely congruent between cities and the regional assemblages. However, city avifaunas tend to be relatively more uniform across space, revealing biotic homogenization. Urban communities in northern cities are more uniform as a higher proportion of bird species breeds in cities.

Keywords

Beta diversity, birds, distance decay of similarity, European cities, homogenization, latitudinal gradient of species richness, species–area relationship, urbanization, variance partitioning.

*Correspondence: Ondřej Sedláček, Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 12844 Praha 2, Czech Republic.
E-mail: zbrd@email.cz

INTRODUCTION

Urbanization is increasing across the globe and urban areas are one of the fastest growing land-use types (McDonald, 2008). Today, more than the half of the world's population lives in urban areas. In Europe, about 70% of the population lives in towns and cities and this number is predicted to increase to 85% by 2050 (Kabisch & Haase, 2011). Understanding ecological phenomena and processes in cities is important from both a scientific (McDonnell & Pickett, 1990; Chiari *et al.*, 2010) and conservation point of view (Turner *et al.*, 2004; Evans *et al.*, 2009; Fuller *et al.*, 2009). The negative ecological consequences of conversion of a habitat to an urban area include a reduction and fragmentation of natural habitats, intensive disturbance regimes, anthropogenic light and noise pollution (Gilbert, 1989; Marzluff *et al.*, 2008) and changes in the species composition of animal and plant communities (Chace & Walsh, 2006; McKinney, 2006). These processes have been studied along urbanization gradients in various taxonomic groups (Pautasso *et al.*, 2011; Price *et al.*, 2011; Buczkowski & Richmond, 2012; Lososová *et al.*, 2012; Ramalho & Hobbs, 2012; Ricotta *et al.*, 2012). Highly urbanized areas, characterized by their relatively high density of built up areas and high proportion of impervious surfaces, generally support only a few abundant species (Møller *et al.*, 2012) that are often the same among different urban locations. This leads to biotic homogenization (McKinney, 2006), characterized by a similarity of urban communities across large spatial scales.

Birds are a taxonomic group that is significantly affected by urbanization, and their species richness and community structure have been thoroughly studied in this respect (Evans *et al.*, 2009; Garaffa *et al.*, 2009; Stagoll *et al.*, 2010). To date, the majority of studies have explored bird–habitat relationships at the intra-city level, and have focused on comparisons of avian communities along urbanization gradients (e.g. Blair, 1996; Fernández-Juricic, 2001; Melles *et al.*, 2003; Gagné & Fahrig, 2011) or in urban and neighbouring rural areas (Crooks *et al.*, 2004; Fuller *et al.*, 2009; Garaffa *et al.*, 2009). Only a few studies have compared the avian communities of cities at a continental scale (Jokimäki *et al.*, 1996, 2002; Clergeau *et al.*, 1998, 2001; Jokimäki & Kuisanlahti-Jokimäki, 2003). Additionally, most studies implicitly or explicitly assume that human settlements are relatively well defined and discernible landscape units (Clergeau *et al.*, 2001; Garaffa *et al.*, 2009; MacGregor-Fors, 2010; MacGregor-Fors *et al.*, 2011). However, there are few studies that focus on the actual ecological differences between cities and adjacent semi-natural landscapes. Recently, Pautasso *et al.* (2011) compared the macroecological patterns of bird assemblages in urbanized and semi-natural ecosystems systematically sampled world-wide, and showed that macroecological patterns do not vary significantly between cities and the surrounding landscape. In contrast, MacGregor-Fors *et al.* (2011) showed that human settlements have steeper species–area relationships than adjacent landscapes. Although these studies focused on comparing diversity patterns in urban and rural habitats over larger geographical regions, the areas which were

sampled for estimating avian assemblage structure were relatively small and homogeneous (Pautasso *et al.*, 2011) or were limited to comparisons between cities within a restricted geographical region (MacGregor-Fors *et al.*, 2011). Comprehensive studies of whole cities on a continental scale that investigate the general impact of urbanization on biological communities are still lacking.

We compare macroecological patterns between cities and semi-natural landscape by using datasets on the bird communities of European cities and of broader regional species assemblages. The objective of this study is to test if and how avian species richness and community structure vary with city size, geographical position and habitat composition, and how these patterns differ from patterns in species assemblages in the surrounding landscape. Toward this objective, the following hypotheses were tested:

1. The species–area relationship is steeper for cities than for samples taken within the surrounding landscape (MacGregor-Fors *et al.*, 2011; Pautasso *et al.*, 2011). This hypothesis assumes that cities represent islands of habitat that is qualitatively different from the surrounding semi-natural landscape, and since island species–area relationships (SARs) have steeper slopes than contiguous mainland SARs (Rosenzweig, 1995), this should apply for cities as well.
2. Cities are relatively similar to each other in terms of their species composition, and beta diversity between cities does not increase with distance as rapidly as in the case of the semi-natural surrounding landscape (Luck & Smallbone, 2011). This hypothesis assumes that cities are occupied by a relatively uniform set of species which tolerate the particular conditions of a built-up environment (McKinney, 2002, 2006; Clergeau *et al.*, 2006).
3. Spatial diversity patterns of cities are consistent with those of the surrounding landscape. Although cities may differ from the surrounding landscape in many respects, as previously stated, the bird fauna present in cities reflects the fauna present in the surrounding landscape, so that diversity patterns in cities (e.g. latitudinal trends in species richness) are directly dependent on the overall diversity patterns of the region.
4. There are latitudinal trends in the proportion of species which are able to live in cities. There are several latitudinal trends in species life histories (Cardillo, 2002; Jetz *et al.*, 2008), abundances and other properties (Newton & Dale, 1996), and it is thus reasonable to assume that these trends are also revealed in geographical trends in terms of the degree of adaptability of different birds to the urban environment. This hypothesis also predicts that the level of community similarity between cities will vary across Europe.

MATERIALS AND METHODS

Bird and habitat data

For the purposes of this study we analysed data on native bird species richness and community composition extracted from published breeding bird atlases of European cities and towns

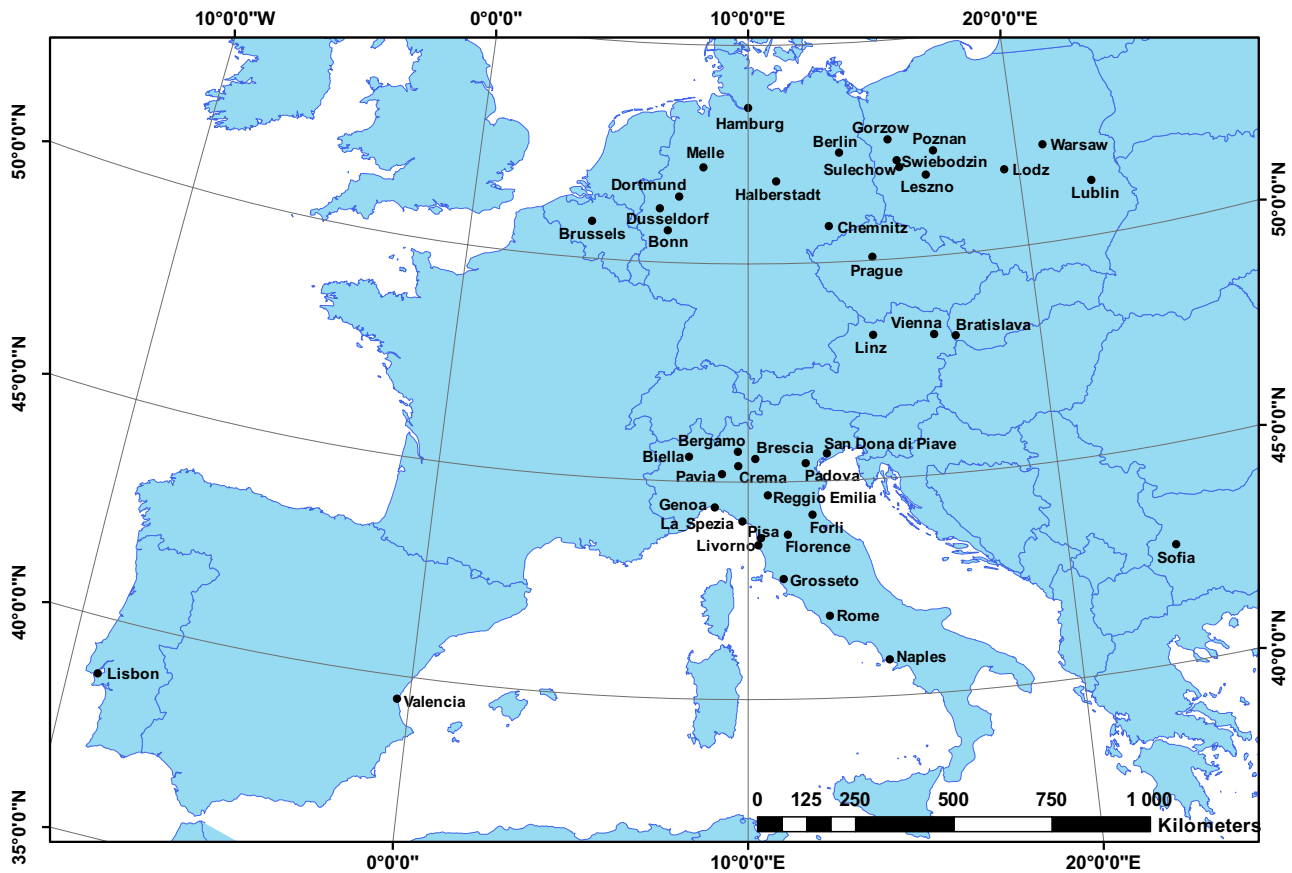


Figure 1 Geographical distribution of the European cities analysed.

(Fig. 1 and Appendix S1 in Supporting Information). City borders were demarcated as defined by the authors of individual atlases, which mostly followed the administrative borders of the cities. Exotic (introduced) bird species were excluded from our dataset because of the non-natural processes of city colonization and maintenance of urban populations (Francis & Chadwick, 2012). Older atlases that covered the period before 1980 (London), those which mapped only a restricted part of the city (Paris) or which did not use standard methods of data collection (several Italian cities) were excluded from this study. Data on regional species assemblages were obtained from 50 km × 50 km grid cells of the EBCC Atlas of European Breeding Birds (Hagemeijer & Blair, 1997). The regional species assemblages were defined as sets of bird species breeding in nine grid cells around each city. The central square included the whole city or most of the city area if it overlapped the borders of the grid cell. The remaining eight squares defined the area that surrounded the central square. To verify that our results were not sensitive to the specification of regional assemblages, we conducted additional analyses based on only four grid cells surrounding each city. The obtained results were very similar and did not change our conclusions (Appendix S2 in Supporting Information). We ran separate analyses for all birds and for passerines only (order Passeriformes) to verify if the patterns concerning all birds also hold for a phylogenetically and morphologically homogeneous

group. Passerines form a substantial part of urban avifauna (Chamberlain *et al.*, 2009) and the diversity patterns they exhibit should be less sensitive to variation introduced by taxonomical differences in the ability to utilize urban areas.

The impacts of the following variables on city species richness were evaluated for this study: city area, geographical position (latitude, longitude), length of the survey period, habitat composition of the city. City area was calculated as a multiple of the number of atlas grid cells and the area of a single grid cell within the city. Data on habitat composition were extracted using the geographical information system ArcGIS 9.3 (ESRI Institute, 2008) from maps retrieved from CORINE databases run by the European Environment Agency (EEA, 2010; <http://www.eea.europa.eu>). Habitat types were grouped into the following categories (see Appendix S3 for the grouping of original CORINE variables): artificial surfaces, managed urban greenery, agricultural landscape, natural biotopes, inland waters and marine waters. Proportions of these habitat categories were used to describe the habitat composition of cities (CITY dataset; see Appendix S4).

Analyses

In analysing the SAR using multiple linear regression, we attempted to control for the possible confounding effect of the

length of the atlas survey period. A multiple regression analysis using city area and length of the survey period as a covariate was used to assess the effect of latitude on the richness of urban bird species. A quadratic term of latitude was also used to evaluate changes in the performance of the model. In order to evaluate the role of spatial autocorrelation we fitted simultaneous autoregressive (spatial error) models following Kissling & Carl (2008) and inspected their potential qualitative differences. The effect of latitude on proportional species richness, while controlling for the effects of city area and the length of the survey period, was evaluated using a generalized linear model (GLM) with quasibinomial distribution of errors and the logit-link function.

Additional data were generated using simulations according to the following methods.

1. Random resampling of different numbers of atlas grid cells of the EBCC Atlas of European Breeding Birds (Hagemeijer & Blair, 1997) made it possible to construct SARs for regional species assemblages ($n = 100$ samples). For each run of the model, a number ranging from one grid cell to nine grid cells representing a regional assemblage, were randomly chosen from each region (3×3 grid cells around each city). Subsequently, the area (as a multiple of the number of chosen cells and a single EBCC atlas grid cell area) and species richness of each such sample was calculated. We constructed 100 resampling-based SARs and compared 95% confidence intervals (CIs) of slopes of the resampling-based and data-derived SARs.

2. Random resampling ($n = 1000$ simulations) of a set of species from regional assemblages was also conducted to create a simulated 'city' in which the number of bird species corresponded to the species richness of a real city. This approach provided a comparison of beta diversity of cities with the beta diversity of random species assemblages containing the same number of species.

Beta diversity was calculated using the Simpson (β_{sim}) index (Simpson, 1943; Lennon *et al.*, 2001), which only takes into account dissimilarity due to spatial turnover in species composition but not due to differences in species richness (Baselga, 2010). The pairwise comparison of beta diversity between cities versus beta diversity between simulated communities was conducted by the Mann–Whitney U -test. Since multiple tests ($n = 1000$) were conducted, the significance level of each test was adjusted using Bonferroni correction and set to $\alpha = 0.05 \times 10^{-3}$.

The distance decay of similarity was evaluated both between cities and between their respective regional assemblages by regressing β_{sim} on a spatial distance of the compared units (Nekola & White, 1999; Soininen *et al.*, 2007). A bootstrapping procedure was used to assess 95% CIs for regression coefficients of these relationships. Spatial variability in beta diversity was examined by regressing the mean β_{sim} of individual cities and of regional species assemblages on latitude.

In order to separate the effects of environmental, geographical (latitude, longitude) and spatial (distances of cities) variables on bird species richness in European cities, the variance partitioning method was used. The significance of individual partitions was tested by means of multiple regression (Borcard *et al.*,

2011). Four groups of explanatory variables were compiled. The first group included city area and habitat composition variables describing the cities (CITY dataset). The second group of variables comprised the longitude and latitude of each particular city representing the main geographical gradients. To account for the confounding effect of spatial autocorrelation between European cities, Moran eigenvector maps (MEM) were computed (Dray *et al.*, 2006) and positive eigenvectors representing positive spatial autocorrelation (Peres-Neto & Legendre, 2010) were used as the third explanatory dataset. The fourth explanatory dataset represented the number of species in regional species pools of cities (regional assemblages).

There was no need to transform the species richness data (except for the SAR, which was plotted along logarithmic axes for both area and species number). Geographical distances and β_{sim} were square-root transformed, whereas area was log-transformed. All the statistical analyses were conducted using the R software (R Development Core Team, 2011). The 'vegan' package (Oksanen *et al.*, 2011) was used to compute dissimilarity indices, variation partitioning and to perform redundancy analysis. The 'spacemakeR' package (Dray, 2010) and associated packages were used to construct connectivity matrices and MEMs. Package 'proj4' (Urbanek, 2011) was used to project geographical coordinates (coordinate system WGS 1984) to a projected coordinate system (Lambert azimuthal equal area) and the 'fields' package (Furrer *et al.*, 2012) to compute geographical distances.

RESULTS

Species richness of cities

Bird species richness was strongly correlated with city area (log–log scale, slope = 0.21; $P < 0.001$; adjusted $R^2 = 0.62$; Fig. 2) even after accounting for the length of the survey period (slope = 0.21; $P < 0.001$; adjusted $R^2 = 0.61$). The SAR for resampled regional assemblages had a slope of 0.18. However, the 95% CIs of the slope of SAR for cities [confidence interval (CI): 0.16–0.26] and for regional assemblages (CI: 0.11–0.28) overlapped (Fig. 2). The SAR for passerines showed a similar pattern (slope = 0.16; CI: 0.09–0.22; $P < 0.001$; adjusted $R^2 = 0.38$) and remained significant after accounting for the confounding effect of atlas survey period length (slope = 0.18; $P < 0.001$; adjusted $R^2 = 0.39$). The SAR of resampled passerine regional assemblages was not statistically different (slope = 0.11; CI: 0.06–0.18) from the passerine SAR of the cities. The proportional species richness increased with increasing city area, with 70–80% of all species from the regional species pool (respective regional assemblage) present in the largest cities, reaching almost 100% when considering only passerines.

Bird species richness of European cities, contrary to the prediction, increased with increasing latitude (all species: adjusted $R^2 = 0.41$; $P < 0.001$; Fig. 3a; passerines: adjusted $R^2 = 0.52$; $P < 0.001$; Fig. 3b). The relationships were linear and a quadratic term did not improve the performance of the models. Both relationships remained significant after accounting for the effects of city area and atlas survey period length (all species:

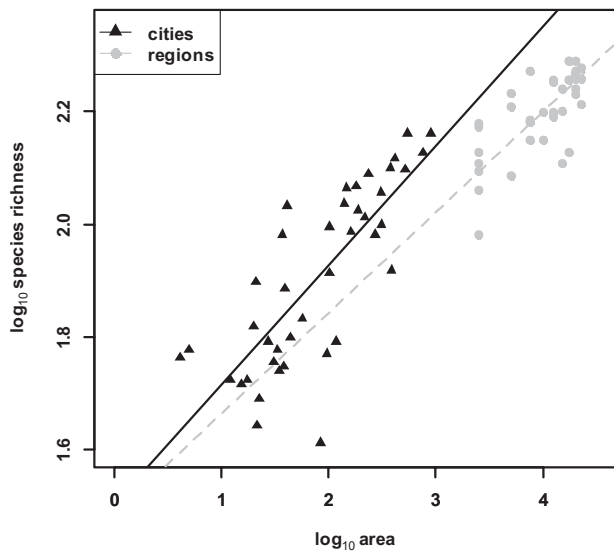


Figure 2 Species–area relationship (SAR) of cities (triangles; solid line, slope = 0.21; 95% CI: 0.16–0.26) and the SAR of resampled regional species assemblages (circles represent the output of just a single sample and are intended as an illustration of the range of possible values; dashed line, slope = 0.18; 95% CI: 0.11–0.28).

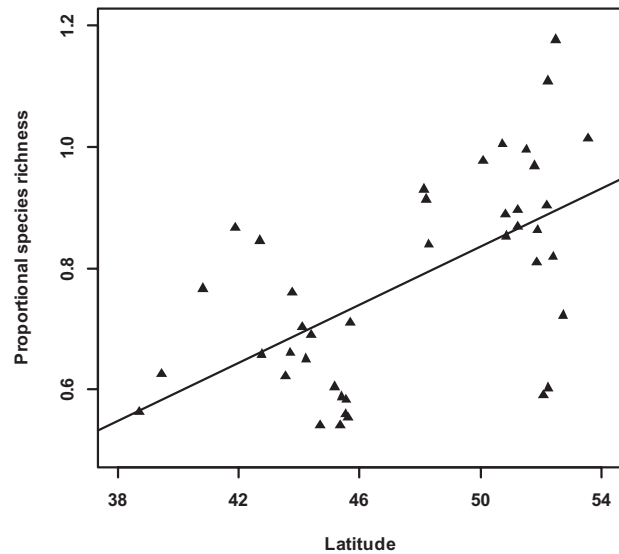


Figure 4 The latitudinal trend in proportional bird species richness (proportion of species richness of cities relative to species richness of regional species assemblages) of European cities (y -axis is arcsine transformed; adjusted $R^2 = 0.34$; $P < 0.001$).

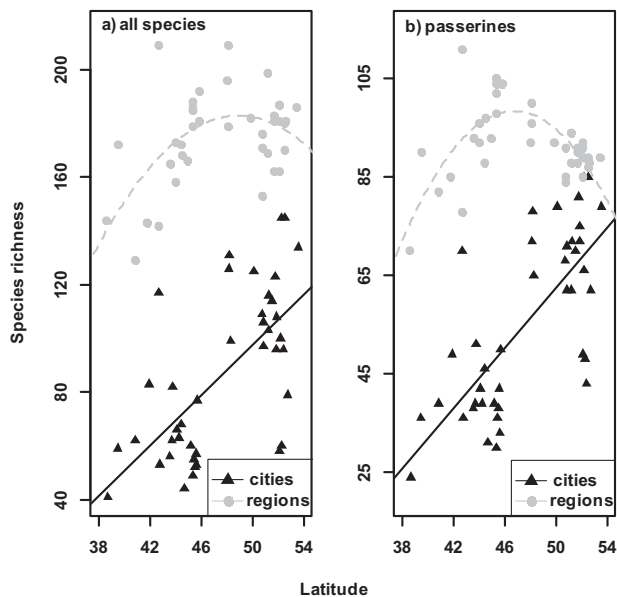


Figure 3 The latitudinal trend in bird species richness of European cities (triangles) and their regional species assemblages (circles). (a) All bird species (cities: adjusted $R^2 = 0.41$; $P < 0.001$; regional assemblages: adjusted $R^2 = 0.24$; $P < 0.01$). (b) Passerines (cities: adjusted $R^2 = 0.52$; $P < 0.001$; regional assemblages: adjusted $R^2 = 0.43$; $P < 0.001$).

adjusted $R^2 = 0.85$; $P < 0.001$; passerines: adjusted $R^2 = 0.68$; $P < 0.001$). In contrast, the species richness of regional assemblages was highest in the middle latitudes of the study area in Europe and slightly decreased towards northernmost locations.

Hence, a quadratic term significantly improved the model (ANOVA: $P < 0.05$) in both instances (all species: adjusted $R^2 = 0.24$; $P < 0.01$; Fig. 3a; passerines: adjusted $R^2 = 0.43$; $P < 0.001$; Fig. 3b). No qualitative changes were detected while utilizing simultaneous autoregressive error models. The GLM model revealed that the proportional species richness of entire urban bird communities (see Fig. 4), as well as the proportional species richness of passerines, significantly increased with latitude ($P < 0.001$ in both cases), and this continued to be the case when controlling for the effect of city area and length of the atlas survey period.

Figure 5 shows the partitioning of variance in species richness of cities that might be assigned to city area and habitat composition, geographical position, regional assemblage richness and spatial autocorrelation. These variables altogether explained 89.3% of the variance in bird species richness of European cities. City area together with habitat composition explained a significant proportion of the variation ($a = 13.6\%$; $P < 0.05$). Other simple variables such as latitude and longitude, regional assemblage richness and spatial predictors alone (MEMs) did not explain a significant proportion of the variance in bird species richness among European cities (Fig. 5). However, from the diagram it is clear that the habitat composition and area of the studied European cities exhibit a relatively strong autocorrelation, and in combination with MEMs they thus explain 32.5% of the variance in bird species richness. Some spatial predictors describe similar patterns to the latitude and longitude, and these two sets of variables taken together further explain 14.8% of the species richness. The rest of the variance (22.1%) can be attributed to the joint influence of MEMs, geographical trends (latitudinal and longitudinal) and habitat

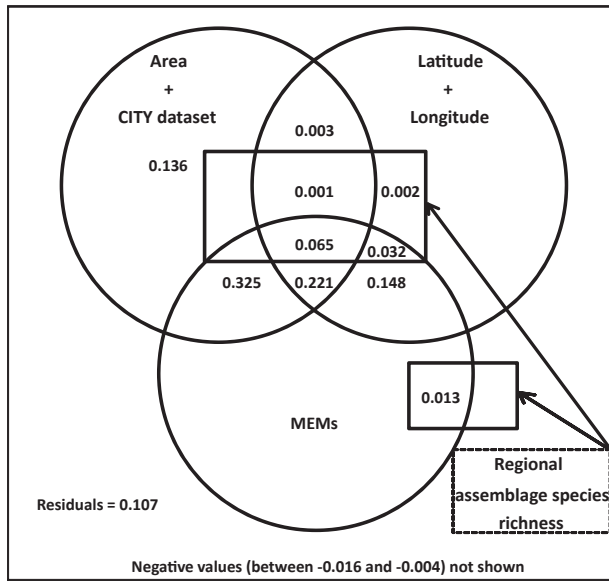


Figure 5 The partitioning of variance in bird species richness of European cities explained by (1) environmental variables, i.e. proportional habitat composition of city (CITY dataset) + city area ($P < 0.05$); (2) longitude + latitude ($P > 0.05$); (3) spatial filters (MEM, Moran eigenvector maps, $P > 0.05$); and (4) regional species assemblage richness ($P > 0.05$); and the shared influence of combinations of explanatory variables. Numbers represent proportion of explained variance.

descriptors of the studied cities. The influence of species richness of the regional assemblages was negligible (Fig. 5).

Beta diversity between cities

First, we compared the beta diversity (β_{sim}) between real bird communities of European cities with beta diversity between simulated communities. All of the 1000 simulated communities (both for all birds and passerines separately) had significantly higher β_{sim} (all 1000 Mann-Whitney U-tests significant at the Bonferroni corrected significance level $\alpha = 0.05 \times 10^{-3}$), indicating that there is a higher uniformity of real bird communities in cities.

The analysis of the distance decay of similarity showed that beta diversity both between cities (slope = 0.007; $t = 15.65$; $P < 0.001$; bootstrapped 95% CI: 0.0063–0.0081) and between their regional assemblages (slope = 0.0111; $t = 32.43$; $P < 0.001$; bootstrapped 95% CI: 0.0104–0.0117) increased with increasing distance (Fig. 6). The beta diversity of regional assemblages changed more rapidly with distance than beta diversity between cities, and the 95% CIs of the two slopes did not overlap (1000 replicates; see the CI limits and Fig. 6). The same was true for passerines, since the β_{sim} of passerine communities in cities increased with distance at a lower rate (slope = 0.008; $t = 16.66$; $P < 0.001$; bootstrapped 95% CI: 0.0072–0.0093) than it did in the case of regional passerine assemblages (slope = 0.0126; $t = 34.78$; $P < 0.001$; bootstrapped 95% CI: 0.0119–0.0133).

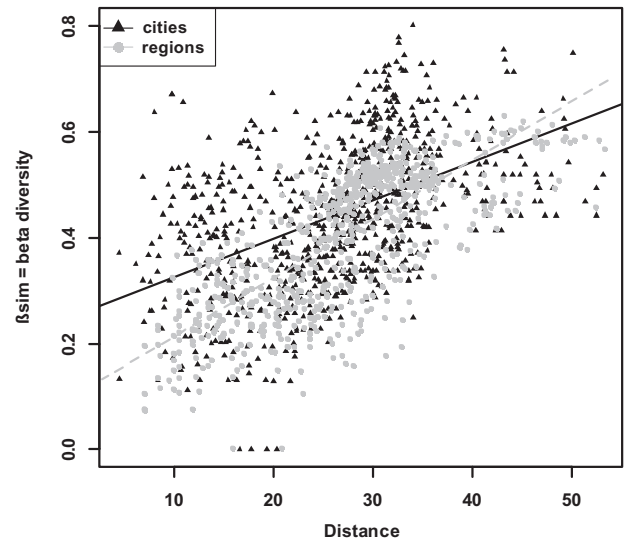


Figure 6 Beta diversity of bird communities (β_{sim} , square-root transformed) between cities (triangles) (slope = 0.007; $t = 15.65$; $P < 0.001$) and between the regional species assemblages (circles) (slope = 0.0111; $t = 32.43$; $P < 0.001$), respectively, plotted against the geographical distances (square-root transformed) between them.

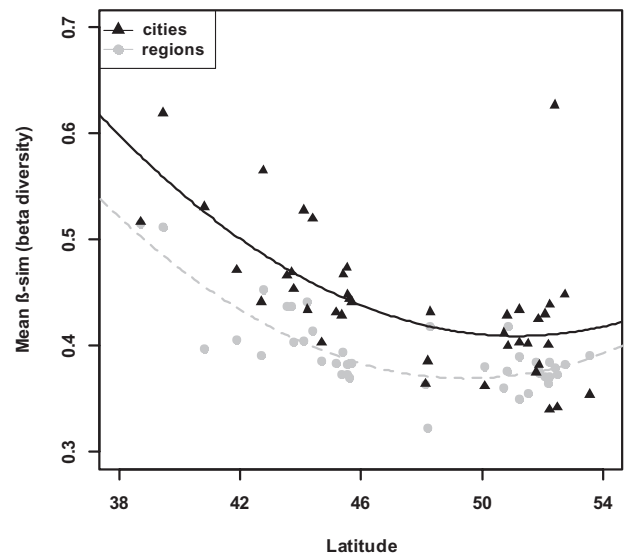


Figure 7 Latitudinal trend in mean beta diversity (β_{sim}) of European cities (triangles) (adjusted $R^2 = 0.38$; $P < 0.001$) and in mean beta diversity (β_{sim}) of respective regional species assemblages (circles) (adjusted $R^2 = 0.62$; $P < 0.001$).

The mean beta diversity (β_{sim}) between cities showed a significant decline with latitude (all species: curvilinear pattern, adjusted $R^2 = 0.38$; $P < 0.001$; Fig. 7; passerines: linear pattern, adjusted $R^2 = 0.23$; $P < 0.001$), meaning that cities in the southern part of our study area are distinct from the other cities studied and that the dissimilarity of bird communities declines with cities located at latitudes further north. A similar decline of

the mean beta diversity with a curvilinear pattern was found for the regional bird assemblages (all species: adjusted $R^2 = 0.62$; $P < 0.001$; Fig. 7; passerines: adjusted $R^2 = 0.70$; $P < 0.001$).

DISCUSSION

The general aim of this study was to investigate macroecological patterns of bird communities in cities relative to their surrounding landscapes. As predicted, we found a strong SAR for urban bird communities. Although the SAR has been widely studied in urban habitat patches of different sizes (Fernández-Juricic & Jokimäki, 2001; Mörtberg, 2001; Garaffa *et al.*, 2009; Oliver *et al.*, 2011; Pautasso *et al.*, 2011), such a relationship for the avifauna of entire human settlements has only recently been described by MacGregor-Fors *et al.* (2011) for towns in west-central Mexico. Interestingly, although the sizes of the human settlements sampled in Mexico were smaller than those compared in the present study, the slope of the SAR on the log–log scale was very similar (0.21 in Europe, 0.19 in Mexico). This suggests that species richness rises relatively uniformly with increasing city size, irrespective of the geographical region.

The resampling procedure producing SARs of regional species assemblages revealed that the slope of the SAR of cities was steeper, but the difference was not significant. Similar results have been recently shown by Pautasso *et al.* (2011), who found no significant difference in SAR between urbanized and non-urbanized environments. High spatial heterogeneity of habitats in human settlements (Cadenasso *et al.*, 2007; Pecher *et al.*, 2010; Pickett *et al.*, 2011) could buffer the lower species richness attributable to biotic homogenization in the highly urbanized areas of city centres (Chace & Walsh, 2006; McKinney, 2006). This may also explain why species richness is reported to increase faster with sampling area within human settlements than in narrowly defined, and therefore more homogeneous, natural habitats (e.g. semi-natural grasslands) (MacGregor-Fors *et al.*, 2011; Pautasso *et al.*, 2011).

The lack of difference in SAR slope between cities and regional species assemblages has to be interpreted with caution, as the area pertaining to the simulated assemblages is larger than the cities themselves. The possibility that the SAR for cities would have a different slope from the SAR of rural areas of smaller size also cannot be ruled out. However, this would require a nonlinear SAR in the logarithmic space and consequently different slopes of the SARs for different ranges of areas, which is not supported by our data. In analysing the data in this study, we cannot reject the hypothesis that the SARs for both cities and resampled assemblages are effectively identical.

According to the generally reported latitudinal gradient in species diversity (Hillebrand, 2004; and citations therein), a decline of bird species richness with increasing latitude was expected for both regional species assemblages and cities throughout Europe. However, bird species richness of regional species assemblages showed a curvilinear relationship, with the highest number of species living in the middle latitudes of our study area. This pattern could potentially be caused by the non-random sample of European bird communities used in this

study. However, there is no clear latitudinal trend in species richness detectable on a Europe-wide continental scale, as the peak of bird diversity lies in east-central Europe (Huntley *et al.*, 2007; Assunção-Albuquerque *et al.*, 2012); this is congruent with our results.

The number of bird species breeding in cities of continental Europe showed a similar pattern, but the relationship was linear, forming a clearly reversed latitudinal trend. This holds true for both all birds and passerines only, and the relationships remained highly significant even after accounting for city size. Moreover, variance partitioning showed that the species richness of cities was relatively independent of the overall number of species breeding around the cities (species richness of regional assemblages). Therefore, phenomena different from the SAR and the size of the species pool contribute to the latitudinal increase of urban bird species richness across Europe. We propose two possible explanations for this. First, environments with higher climatic variability may promote generalist species that have larger range sizes, population sizes and wider ecological niches (Pielou, 1979; Thuiller *et al.*, 2005; Julliard *et al.*, 2006), i.e. species which are hypothesized to be better able to cope with the particular conditions of the urban environment (Devictor *et al.*, 2008a; Møller, 2009). Indeed, our data show a latitudinal increase in the proportion of species that are able to breed in human settlements, relative to the regional species pools. We suggest that the environmental filter of urban habitats varies geographically, with more species being able to successfully invade urban habitats at higher latitudes. However, a more detailed analysis of colonization by birds of cities across different geographical regions is needed to confirm this (Møller *et al.*, 2012). Alternatively, the character of cities may systematically change with latitude due to differences in the history of urbanization or urban planning (Antrop, 2004). However, only a small portion of the variation in our data could be attributed to the joint effects of latitude and habitat composition. Thus, we suggest that latitudinal changes in the character of urbanization contribute little to the observed latitudinal trend in species richness.

Investigation of the spatial patterns of avian community composition showed that beta diversity of both the cities and their respective regional assemblages increased with distance (Keil *et al.*, 2012). However, the distance decay of similarity was much steeper for regional species assemblages. Also, beta diversity between real cities was consistently lower than between simulated urban communities. Urban bird communities are thus more similar to each other across Europe compared with regional communities of adjacent landscapes, indicating a homogenization of bird communities caused by urbanization across a continental scale. The homogenizing effects of urban areas have also been inferred from studies conducted along urbanization gradients (Clergeau *et al.*, 2001; Jokimäki & Kainanlahti-Jokimäki, 2003; Crooks *et al.*, 2004; McKinney, 2006; Devictor *et al.*, 2008b), with bird species richness decreasing with urbanization, resulting in the dominance of only a few very abundant species in city centres (e.g. Clergeau *et al.*, 2006; Garaffa *et al.*, 2009). This phenomenon at the level of entire

cities was explored just recently by Luck & Smallbone (2011), who showed a weaker decline in taxonomic similarity with distance between towns compared with regional species pools in south-eastern Australia. They also pointed out the significant contribution of exotic species to community similarity, but since we excluded exotic species from our analyses, we suggest that the higher similarity between European cities compared with regional assemblages is the result of non-random filtering of regional bird communities by the urban environment (Croci *et al.*, 2008; Møller, 2009).

Perhaps the most interesting finding of this study is that the susceptibility of regional communities to the homogenizing effects of urbanization varies geographically. The beta diversity of urban avifaunas showed a clear latitudinal pattern across Europe, revealing that cities in northern areas are more uniform in bird species composition than those located in southern Europe. However, we also identified a similar latitudinal trend for regional species assemblages. This could be due to the higher beta diversity of Mediterranean fauna and flora (Underwood *et al.*, 2009; Rueda *et al.*, 2010), which is strengthened by the peninsular effect (Fraissinet & Fulgione, 2008). On the other hand, cities in southern Europe harbour a lower proportion of the regional bird community relative to more northern European cities, so this biogeographical setting may not be the sole effect generating the higher beta diversity in southern cities. The cities of the middle and northern latitudes of our study area in Europe share on average a larger proportion of their avifauna with the other cities studied. Birds occurring at these latitudes appear to be more widespread (Orme *et al.*, 2006) and could be more adaptable to the particular conditions of the urban environment, which can ultimately lead to less distinct urban bird communities at higher latitudes. Although our study has some limitations due to the differing sampling periods and the partial temporal mismatch between sampling of cities and their respective regional assemblages, the general patterns appear to be quite robust. These findings have important implications for further studies that focus on variation in the susceptibility of bird communities to urban environmental filters across large geographical regions.

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Additional references to the data sources and software packages used in this study are listed in Appendix S5.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Breeding bird atlases of European cities and towns used in this study.

Appendix S2 Supplementary analyses, where regional bird assemblages = communities of four grid cells.

Appendix S3 Grouping of original CORINE habitat types into categories analysed in this study.

Appendix S4 Habitat composition of European cities analysed.

Appendix S5 References to data sources and software packages used in the study.

BIOSKETCH

Michal Ferenc is a PhD student of ecology at Charles University, Prague. His research interests are in the fields of macroecology, urban ecology, conservation biology and avian ecology.

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