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RESEARCH
PAPER

Evidence of evolutionary homogenization of bird communities in urban environments across Europe

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ABSTRACT

Aim The process of urbanization can lead to specialist species being replaced by generalist species in space and time, increasing similarity among bird communities. This phenomenon is termed biotic homogenization and is directly related to taxonomic and functional diversity. However, the effects of urbanization on phylogenetic diversity remain unclear. Our study addresses the effects of the process of urbanization on the evolutionary distinctiveness (a quantitative measure of the genetic or evolutionary uniqueness of species) of bird communities.

Location Europe.

Methods Mixed models were used to compare the effects of urbanization on the evolutionary distinctiveness of bird communities in rural and urban environments in six different European cities from different ecoregions.

Results Our study presents unique large-scale evidence of a negative impact of urban environments on the evolutionary uniqueness of birds. Compared with bird communities in rural environments, bird communities in urban environments have lower average evolutionary distinctiveness in all countries, independent of ecoregion, and these values are unrelated to the taxonomic diversity present in each country.

Main conclusions Our findings provide important information on the spectrum of effects on global biodiversity of changes in land use related to the process of urbanization. Therefore, urban environments are a factor of concern for maintaining diversity across the tree of life of birds, and we suggest that urbanization planning could help buffer against extreme loss of phylogenetic diversity caused by this process.

Keywords

Biotic homogenization, bird species richness, conservation, evolutionary distinctiveness, evolutionary homogenization, urbanization.

INTRODUCTION

Urbanization is increasing, and cities are one of the fastest growing land-use types across the globe (McDonald, 2008). Currently, more people live in urban than in rural areas. More than 50% of the global human population and almost 80% of the population in developed countries have lived in

cities since 2008 (United Nations, 2014). The change in land use as a product of the process of urbanization is considered one of the major drivers of environmental modification, with significant impacts on climate and biodiversity, across large areas of the globe (Foley *et al.*, 2005; Grimm *et al.*, 2008). Urbanization alters both biotic and abiotic ecosystem

properties (Grimm *et al.*, 2008), leading to a loss of biodiversity around the world.

Loss of biodiversity has emerged in the last decades as one of the most important concerns in the debate over worldwide conservation of natural resources (Thuiller *et al.*, 2011). Biodiversity is not restricted to species composition, but encompasses structure and ecosystem function. For this reason conservation involves more than simply preserving the existence of threatened species (Schwartz *et al.*, 2000; Geiger *et al.*, 2010; Clark *et al.*, 2014; Sol *et al.*, 2014). Conservation planning and management strategies are fundamentally based on information on the spatial distribution of biodiversity (Margules & Pressey, 2000; Rodrigues & Brooks, 2007; Wiens *et al.*, 2008). However, there are different interpretations of what constitutes biodiversity (variability among living organisms), because biodiversity includes multiple components that can be measured in different ways (Carmona *et al.*, 2012). Species richness is the simplest measure of taxonomic diversity (Magurran, 2004). However, communities can also be studied in terms of phylogenetic diversity (a measure of species evolutionary distances and relationships) (Zupan *et al.*, 2014) and functional diversity, which recognizes the variety of roles that different organisms play in an ecosystem (Olden & Rooney, 2006; Petchey & Gaston, 2006).

Destruction of native land cover caused by the process of urbanization can affect existing biodiversity in many ways (Kühn & Klotz, 2006) and has both direct and indirect effects on wildlife. However, cities do not necessarily only have negative effects on taxonomic diversity. Some studies have demonstrated that cities can still provide opportunities for settlement of species, potentially contributing to conservation of regional and global biodiversity (Zerbe *et al.*, 2003; Aronson *et al.*, 2014). For instance, an intermediate level of urbanization, characterized by more heterogeneous environments, may have less impact on overall biodiversity than higher or lower levels of urbanization (e.g. Jokimäki *et al.*, 1996; Chace & Walsh, 2006). One of the most recognized effects of urbanization on wildlife is termed biotic homogenization (Clergeau *et al.*, 2006). The observed effects of urbanization are range expansion of cosmopolitan or generalist species and simultaneous range contraction of regional and endemic species. Consequently, biotic homogenization occurs as specialists are replaced by generalists, mixing the taxonomic composition of different biotas and increasing similarities across communities in space and time (McKinney & Lockwood, 1999; McKinney, 2006). This process can occur at different spatial scales, mainly in environments that have been strongly modified by humans, because deep and convergent anthropogenic transformation of such areas constitutes nodes of intense species replacement and, for that reason, hotspots of accelerated biotic homogenization (Garcillán *et al.*, 2014). The effects of urbanization on taxonomic diversity and biotic homogenization of bird communities have been studied (e.g. Devictor *et al.*, 2007, 2008; Godet *et al.*, 2015). However, the potential effects on other components of biodiversity, such as phylogenetic diversity, are less clear.

Phylogenetic diversity, the total evolutionary history or phylogenetic branch lengths of all species in a community (Faith, 2002), has been proposed as an important additional component in nature conservation (Vane-Wright *et al.*, 1991; Winter *et al.*, 2013). Moreover, ecological experiments in small plots indicate that communities with greater phylogenetic diversity are more stable (Cadotte *et al.*, 2012). Evolutionary distinctiveness (ED), a measure of how isolated a species is in a phylogenetic tree, is based on the phylogenetic diversity that quantifies the loss of evolutionary diversity due to the extinction of a species. It is one factor that can be considered in setting conservation priorities for threatened species because it represents uniquely divergent taxa (Faith, 2008; Jetz *et al.*, 2014). The ED can play an important role in the conservation of biodiversity. Evidence suggests that certain clades are more vulnerable to human pressures than others, causing that portion of the Earth's evolutionary history to be disproportionately altered (Thuiller *et al.*, 2011).

Rural and urban areas constitute two main land-use categories associated with human activities (Newbold *et al.*, 2015). However, both provide different opportunities for settlement by bird species that can exploit agricultural landscapes and landscapes with low human modification and by bird species that can exploit more built-up areas and those with greater human impact, driving a change in species composition between rural and urban areas (Clergeau *et al.*, 1998; Tryjanowski *et al.*, 2015). Indeed, human settlements differ in their structural and biotic components in rural and urban areas (Clergeau *et al.*, 1998; Tryjanowski *et al.*, 2015). Rural areas can prove additional habitat (e.g. food sources) for some species, and thus for their conservation, because they are more natural environments (Evans *et al.*, 2009b), whereas urban areas usually have fewer natural food sources available (Tryjanowski *et al.*, 2015).

Understanding the causes and evolutionary consequences of biodiversity is critical for explaining variation in the urbanization process and modelling biotic responses to future human-induced changes. In fact, measuring how bird communities differ in species composition and diversity is one way to predict the consequences of habitat loss and environmental degradation (Devictor *et al.*, 2007). Bird species that have evolved more recently or have many common relatives, as is the case for generalists, have a weak ED (Jetz *et al.*, 2014). Considering that biotic homogenization contributes to the loss of specialist bird species, which theoretically have higher ED scores, we hypothesize that this process can also have a significant impact on the average ED of bird communities in urban environments. In the present study we analysed the effects of urbanization on the ED of bird communities, using the two extremes of rural and urban landscapes in six different European countries in different ecoregions.

METHODS

Study area, collection of bird data and type of environment

Fieldwork was performed in six cities, each paired with a nearby rural area, located along a large latitudinal gradient

Figure 1 Location of the six study sites in different countries used in the community evolutionary distinctiveness study in Europe. Different ecoregions are shown in a grey scale on the map. Black circles correspond to the centroid of the sampled sites monitored in each country. See Table 1 for coordinates and city names. Digital Map of European Ecological Regions from <http://www.eea.europa.eu/data-and-maps/data/digital-map-of-european-ecological-regions> (<http://www.eea.europa.eu/legal/copyright>).

across Europe (Fig. 1). The distance between urban and rural study sites was 1–20 km. The main benefit of this multiple paired approach is that both urban and rural sites share most environmental conditions including weather, soil type and species, amongst other factors (this argument is further developed in Díaz *et al.*, 2013). In fact, numerous studies of urbanization compare urban and rural habitats in a single city (e.g. Kark *et al.*, 2007), thus preventing generalization of their results. Our approach involves different urbanized areas, allowing for the investigation of general patterns but also facilitating urban–rural comparisons of bird assemblages by using paired sites that have similar local environmental conditions. All urban

study sites included areas with multistorey buildings, single family houses, roads and parks, while nearby rural areas had open farmland and woodland and did not contain continuous urban elements (i.e. multistorey buildings, family houses, roads and parks). Our classification of environments as urban (percentage of built-up area > 50%, building density > 10 ha⁻¹, residential human density > 10 ha⁻¹) or rural (percentage of built-up area 5–20%, building density < 2.5 ha⁻¹, residential human density 1–10 ha⁻¹) followed the description made in Marzluff *et al.* (2001), which has subsequently been used in several studies on urban avian ecology (Clergeau *et al.*, 2006; Loss *et al.*, 2009; Møller *et al.*, 2015). A three-fold difference in coverage by houses between urban and rural environments was evident (see Table S1 in the Supporting Information). The study areas were mapped on the Digital Map of European Ecological Regions (<http://www.eea.europa.eu/data-and-maps/figures/dmeer-digital-map-of-european-ecological-regions>).

Data on bird species were collected by expert ornithologists who used the point count method with unlimited distance (Bibby *et al.*, 1992); collection was carried out twice during the 2009 and 2010 breeding seasons (April–June) (Table 1) (see Díaz *et al.*, 2013). The present study is unique in its use of replicated pairs of data recorded in nearby urban and rural areas (Møller *et al.*, 2012, 2015). All survey points were visited once between 06:00 and 10:00, but only during favourable weather conditions. A total of 5 min in early spring and 5 min during a second visit in late spring allowed for the inclusion of late migrants, as well also covering the early breeders, thus minimizing issues related to differences in the detectability of bird species (Kéry *et al.*, 2005). The surveys were made in early April in southern Spain with a delay in the timing of point counts to ensure that counts were made in northern Finland by late May. The location of each point was recorded by GPS to ensure that counts were made at exactly the same points during the two surveys. The second series of point counts was made 3–4 weeks after the first series, by the same observer in each city and matched rural area to avoid interobserver variability between urban and rural study sites. The vegetation cover at three layers (trees, shrubs, herbs and grass) and cover with buildings and other anthropogenic structures, such as roads and parking lots, within a distance of 50 m of each survey point, were

Table 1 Summary of study areas (paired urban–rural sites) in six cities of different European countries, year of survey, number of sampled sites and ecoregions where sampled sites were visited.

Country	City	Year	Sampled sites	Ecoregion
Spain	Granada	2009	100	Iberian sclerophyllous and semi-deciduous forests
France	Orsay	2009	100	Southern Temperate Atlantic
Poland	Poznan	2010	100	Central European mixed forests
Estonia	Tallinn	2009	60	Sarmatic mixed forests
		2010	100	
Norway	Oslo	2010	98	Scandinavian and Russian taiga
Finland	Rovaniemi	2009	60	Scandinavian and Russian taiga

recorded (Díaz *et al.*, 2013). We obtained similar indices of abundance when controlling or not controlling for differences in coverage for the three vegetation layers and for anthropogenic structures (Møller *et al.*, 2012).

Point counts made during the main breeding season constitute an adequate method for obtaining information on the relative density of birds (Blondel *et al.*, 1970; Bibby *et al.*, 1992). During the point counts a trained observer recorded all individuals of all species of birds seen or heard at any distance from the survey point. The starting point (i.e. point 1) was chosen randomly. Each subsequent point was separated from others by a distance of 100 m to avoid counting the same individuals twice. This breeding bird survey method is used extensively for monitoring bird populations across Europe, as described by Voříšek *et al.* (2010).

Biodiversity and evolutionary distinctiveness

At each sample site, species richness was expressed as the largest number of species observed during surveys. Thus, results correspond to the number of bird species in the combined data for the four surveys performed over the 2 years. In order to explore differences in bird communities in terms of phylogenetic diversity we used the ED score (Frishkoff *et al.*, 2014). ED is based on the uniqueness of a species, measured as the ED score, using a phylogeny. The phylogenetic diversity was originally estimated using the sum of the branch lengths of the species present in the assemblage (Faith, 1992). The ED score for each species is based on phylogenetic diversity, which is the sum of all phylogenetic branch lengths connecting species (Cadotte *et al.*, 2008, 2012). The ED score is computed by applying a value to each branch equal to its length divided by the number of species subtending the branch (see Isaac *et al.*, 2007; EDGE of Existence, 2015). Using the ED score for each bird species present in a community, we estimated the community ED (CED) as the average ED considering all species that belong to the community.

Statistical analyses

In order to compare coverage by buildings between urban and rural sites, we used a Welch ANOVA for unequal variances. A first comparison of bird species richness between bird communities from rural and urban environments in all countries was performed using a paired *t*-test. We also tested whether species composition differed between rural and urban sites by means of an analysis of similarities (ANOSIM), a nonparametric technique useful for testing differences in species composition at different environments (Clarke, 1993). The ecological distance among sampled sites was based on the Jaccard similarity index. The ANOSIM statistic *R* is based on the difference of mean ranks between groups and within groups (Clarke, 1993). The statistical significance of *R* was calculated by means of 999 permutations. The ANOSIM was performed with the package 'vegan' in R (Oksanen, 2016).

We used Mantel tests to check for spatial autocorrelation (SAC) of data (Mantel, 1967). This test evaluates the similarity between two matrices – one measuring ecological distance (the difference in CED among sample sites; Legendre & Legendre, 2012) and one geographical distance among sample sites. We used Monte Carlo permutations with 999 randomizations to test for significance (Oksanen, 2016).

For modelling, the sample sites were treated as statistically dependent observations because the values of SAC between geographical distance and CED distance among sites was low but significant ($r_M = 0.098$, $n = 618$ sampled sites, $P = 0.001$) (Manly, 2006). In order to avoid issues with SAC, the geographical coordinates of sample sites were added as covariates to incorporate spatial variation in the modelling procedure (Legendre, 1993; Dormann *et al.*, 2007).

Mixed effects models can handle both fixed and random effects (Bolker *et al.*, 2009). In this study, we used generalized linear mixed models (GLMMs) to study the patterns of CED in relation to urban or rural environments, bird species richness and geographical coordinates of sample sites, modelled as fixed effects. Country was included as a random effect to account for possible consistent differences among countries (Fig. 2). Models were fitted by maximum likelihood, using the package 'lme4' in R (Bates *et al.*, 2015). In this study, the Akaike information criterion (AIC) was calculated to determine the models that 'best' explained variation in the data. (For an overview on the AIC see Burnham & Anderson (2002) and Boyce *et al.* (2002).) Model selection and multi-model inference were based on AIC in the package 'AICcmodavg' in R (Mazerolle, 2016). The best model was selected considering both the lowest AIC and the largest Akaike weights, because this model has the strongest support for the data (Mazerolle, 2016). We assessed the explanatory power of each predictor using model averaging over the most parsimonious models. All statistical tests were performed with R software (R Core Team, 2016).

Figure 2 Differences in community evolutionary distinctiveness (CED) in bird communities among European countries. The y-axis represents the estimated variable. The boxplots show the median (black bar in the middle of grey rectangles), mean (white rhombus), upper and lower quartiles and extreme values.

Figure 3 Comparison of bird species richness among the six European countries in rural and urban environments. The *y*-axis represents the estimated variable. The boxplots show the median (black bar in the middle of grey rectangles), upper and lower quartiles and extreme values.

RESULTS

A total of 4847 bird detections from 618 sample sites in different paired environments (urban–rural) were collected from the six European countries (Table 1). A list of the 116 bird species monitored in this study, with their ED score, is provided in Table S2.

Bird species richness per sample site ranged from an average minimum of 5.92 species (minimum 2, maximum 14 species) in Poland to an average maximum of 9.44 species (minimum 2, maximum 16 species) in France. Bird species richness was similar between rural and urban environments in all countries (Fig. 3), and the differences were not statistically significant (mean 8.16, SD 2.77 species for rural environments versus mean 7.48, SD 2.74 for urban environments; $t = 3.16$, d.f. = 307, $P > 0.05$). The species composition in bird communities differed between rural and urban environments ($R_{\text{ANOSIM}} = 0.28$, $P = 0.001$) and among countries for both types of environment, rural ($R_{\text{ANOSIM}} = 0.51$, $P = 0.001$) and urban ($R_{\text{ANOSIM}} = 0.43$, $P = 0.001$). However, large dissimilarities in bird communities were found within rural environments rather than within urban environments (see Fig. S1).

The results of GLMM procedures showed that CED was lower in urban than in rural environments in all countries (Table 2, Fig. 4). The estimate for the variable ‘environment: urban’ only ranged across negative values (confidence intervals; Table 2). The average ED was slightly positively corre-

lated with overall species richness and negatively correlated with the geographical latitude of sample sites, while the longitude of sample sites was not statistically significant (Table 2). A list of evaluated models, with the number of predictors considered, ΔAIC values and AIC weights for each model is provided in Table S3.

DISCUSSION

This study has provided evidence of the effects of the urbanization process on the ED of breeding birds, presenting large-scale evidence of a negative impact of urban environments on the average ED of bird communities. Our findings highlight how the urbanization process is having an impact not only on functional diversity of bird communities (by biotic homogenization), as already underlined in several studies (Devictor *et al.*, 2008; Reif *et al.*, 2013; Godet *et al.*, 2015), but also on phylogenetic diversity in terms of species uniqueness. The effects on the ED of bird communities have direct consequences for spatial concentration and thus potentially for global loss of evolutionary information.

Our results showed a slight, but positive, correlation between the average values of ED and the overall species richness in each bird community. This weak correlation could be due to the increase in the probability of finding unique species or species characterized by high ED scores in areas where overall richness is higher. However, bird species richness was not the most important driver of ED of bird

Table 2 Results of fixed-effect parameters in a GLMM, accounting for variation in community evolutionary distinctiveness (CED) in relation to bird species richness, urban or rural environment and latitude and longitude of sample sites.

Fixed effects	Estimate	CI (lower/higher)	SE	<i>t</i>	<i>P</i>
Intercept	9.865	(7.993, 11.738)	0.955	10.327	
Bird species richness	0.075	(0.040, 0.109)	0.017	4.286	1.82×10^{-5}
Environment: urban	-0.822	(-0.993, -0.652)	0.087	-9.455	2.2×10^{-16}
Latitude	-0.061	(-0.094, -0.029)	0.016	-3.741	0.00018

The full model is based on 618 sampled sites. Random effect included in the GLMM procedure: country (groups = 6). Only variables selected in the best model are shown in the table.

communities, as shown by the GLMM results. Despite the fact that the six countries belong to different ecoregions, the pattern found was the same for all of them. Bird species richness differed between urban and rural environments in each country in an inconsistent way. For example, in Finland and Norway species richness was higher in rural than in urban environments, but in France higher values were found in urban areas (Fig. 3). The average ED of bird communities showed a clear pattern, with higher values in rural environments in all countries. Considering that the distribution of ED is geographically clustered – with the highest values mainly associated with the landmasses of Australia, New Zealand, Madagascar, Africa and southern South America, while bird ED values among European countries are relatively uniform (Jetz *et al.*, 2014) – the pattern with higher values in

rural compared with urban areas found in this study is important, emphasizing the strong effect of urbanization on the composition of bird communities.

Finally, latitude was overall negatively correlated with the CED of birds. We hypothesize that this can be explained by a decrease in diversity from equatorial to polar regions (Mannion *et al.*, 2014). Our findings may mirror this pattern, at least partially, in terms of ED.

Our results are in line with those of other studies suggesting that human pressure constitutes a threat for evolutionarily distinct species (Frishkoff *et al.*, 2014). At the same time, the fact that in our study bird communities from urban environments always exhibited lower average values of ED indicates that species from recently diversified clades are most likely to profit from ongoing urbanization. However, it is

Figure 4 Comparison of community evolutionary distinctiveness (CED) among the six European countries in rural and urban environments. The *y*-axis represents the estimated variable. The boxplots show the median (black bar in the middle of grey rectangles), upper and lower quartiles and extreme values.

also possible, albeit less likely, that urbanization has produced many recent speciation events. For example, urbanization may contribute to an increase in genetic diversity. Genetic differentiation between urban birds and their rural ancestors may suggest such an evolutionary change (e.g. Partecke *et al.*, 2006; Baratti *et al.*, 2009; Evans *et al.*, 2009a; Björklund *et al.*, 2010; Delaney, 2014). Such differentiation is probably due to lack of dispersal and local adaptation in urban populations (Partecke *et al.*, 2004, 2006; Partecke & Gwinner, 2007; Cheptou *et al.*, 2008; Evans *et al.*, 2009a). We hypothesize that such an effect over time will result in microevolution and divergence between urban and rural populations. Theoretically, an increase in the phylogenetic diversity of a community should increase the evolutionary potential of that community, making it more adaptable to environmental changes (Sgrò *et al.*, 2011; Mouquet *et al.*, 2012). In fact, assuming a similar evolutionary potential for closely related species and larger differences among distantly related species, higher phylogenetic diversity within a community should therefore increase the probability of having some species with high evolutionary potential in the community, a sort of 'insurance effect' independent of species richness in the community (Winter *et al.*, 2013).

Our results support the hypothesis that modifying the functional diversity of a community results in functional homogenization, involving the replacement of ecological specialists by widespread generalists (Olden *et al.*, 2004). Just because the species that benefit from biotic homogenization are generalist species (McKinney & Lockwood, 1999), the large effect of this continuous replacement and the loss of specialization can also produce a strong impact on the phylogenetic diversity of bird communities from urban areas. However, we believe that several counter-measures could be adopted in order to mitigate the loss of biodiversity (in terms of functional and phylogenetic diversity) caused by urbanization. Urban green infrastructures, and especially urban forests, can play a crucial role in improving the conservation of biodiversity in areas characterized by urban land use (Haaland & van den Bosch, 2015). Urban forests represent key elements of green infrastructure in urban regions, capable of maintaining biodiversity (Capotorti *et al.*, 2015) by providing additional niches for several bird species, especially specialists (Alvey, 2006; Stagoll *et al.*, 2012).

Our study suggests that it may be possible to reduce artificial selective pressures in urban areas, shifting from considering just taxonomy to also include phylogeny. Similarly, recognition of the few species with higher values of ED in urban environments might inform prioritization of individual species, as well as the setting of conservation priorities. For example, the use of a set of bird species, and the use of species distribution models, can improve decision-making support for conservation purposes (Guisan *et al.*, 2013).

In conclusion, our findings underline how understanding the factors that drive the change in ED of bird communities and their interrelationships with urbanization can provide insights into the mechanisms that structure community com-

position in urban areas. We suggest that future studies should focus on conservation of biodiversity in urban areas, but also on aspects related to the dominant species and the amount of evolutionary uniqueness that each such species represents. Here, we argue that knowledge about the effects of urbanization on phylogenetic diversity can be useful for conservation planning. The conservation of biodiversity threatened by human impacts and, in particular, by the ongoing process of urbanization, will require a more complete vision of biodiversity, taking taxonomic and functional diversity into account, but also the ED represented by each species. This approach can help develop more efficient protocols for identifying areas to be protected in a rapidly changing world (Jetz *et al.*, 2014). Such a tool would be useful for measuring risk and the magnitude of the overall biodiversity loss caused by urbanization.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Table S1. Mean coverage and standard error in houses in rural and urban sites in six cities of different European countries.

Table S2. List of all bird species monitored in six European countries, common names and evolutionary distinctiveness scores as indicated in EDGE of Existence (2015).

Table S3. List of GLMM performed in this study, accounting for variation in community evolutionary distinctiveness (CED) in relation to bird species richness, urban or rural environment and latitude and longitude of sample sites.

Figure S1. ANOSIM results showing dissimilarity based on in bird community composition in sample sites using Jaccard index for compute the distance (dissimilarity) between rural and urban environments and among countries for rural and urban environments.

BIOSKETCH

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