Insurance for the future? Potential avian community resilience in cities across Europe

Federico Morelli, et al. *[full author details at the end of the article]*

Received: 18 December 2018 / Accepted: 22 October 2019 / Published online: 17 January 2020
© Springer Nature B.V. 2020

Abstract

Urbanization is affecting avian biodiversity across the planet and potentially increasing species vulnerability to climate change. Identifying the resilience of urban bird communities to climate change is critical for making conservation decisions. This study explores the pattern in bird communities across nine European cities and examines the projected impact of climate change in order to detect communities facing a higher risk of functional change in the future. First, generalized linear mixed models were used to explore the potential resilience of urban bird communities in nine European cities and the effects of land cover, latitude, abundance of potential predators (dogs and cats), and bird species richness in each trophic guild. Bird community resilience was represented by an index of functional evenness, because it indicates relatively uniform functional space within the species assemblages. Second, bird community resilience in each city was compared with projected changes in temperature and precipitation for the year 2070 to explore potential future threats to conservation. The results showed that community resilience was not significantly associated with land use or abundance of predator. The number of granivorous and granivorous-insectivorous species increases the potential resilience of the community, while the numbers of insectivores, carnivores, and omnivores was negatively correlated with resilience. Of the nine cities, Madrid and Toledo (Spain) are projected to experience the largest change in temperature and precipitation, although their bird communities are characterized by relative high resilience. In contrast, Rovaniemi, at the Arctic Circle (Finland) is projected to experience the second highest increase in temperature among the focused cities, and their bird communities are characterized by low resilience. These findings indicate the importance of future research on the combined effect of functional diversity of species assemblages and climate change on urban biodiversity.

Keywords Biotic homogenization · Bird diversity · Community resilience · Conservation · Functional evenness · Urbanization

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10584-019-02583-7>) contains supplementary material, which is available to authorized users.

1 Introduction

1.1 Global urbanization and ecosystem transformation

We are living in a new self-induced era, called “the Anthropocene,” characterized by the increasing pressure of urban development on ecosystem dynamics across the entire planet (Crutzen and Stoermer 2000; Lewis and Maslin 2015). The change in land use produced by the urbanization process is one of the major drivers of environmental modification, with strong and deep impacts on both climate and global biodiversity (Foley et al. 2005; Grimm et al. 2008; Aronson et al. 2014). Expanded urbanization leads to habitat fragmentation and degradation (Spellerberg 1998; Schmiegelow and Mönkkönen 2002; Sklenicka 2016), a process which negatively impacts biodiversity at different levels of organization (Crooks et al. 2004; Wilson et al. 2016). Thus, the mitigation of the loss of biodiversity is partially dependent on our understanding of how urbanization structures biological communities and the subsequent development of wildlife management strategies that incorporate urban ecosystems (Miller and Hobbs 2002).

The effects of urbanization on biodiversity are complex and mainly negative (McKinney 2002; Grimm et al. 2008; Secretariat of the Convention on Biological Diversity 2012; Aronson et al. 2014; Ibáñez-Álamo et al. 2016; Morelli et al. 2016). Especially when trying to assess the effects of urbanization on overall biodiversity, emphasizing that approaches focusing only on species richness are limited by their failure to take the ecological role of species on communities into account (Safi et al. 2013). In fact, estimates of functional diversity often measure variation in ecosystem functioning better than taxonomic diversity measures (Petchey et al. 2004). Among the most recognized effects of urbanization on species assemblage composition stands the “biotic homogenization” of global communities (Clergeau et al. 2006; McKinney 2006). Biotic homogenization consists of the range expansion of cosmopolitan or generalist species and simultaneously the range contraction of regional and endemic species, a process which is particularly intense in dense urban settlements (Garcillán et al. 2014). Biotic homogenization was confirmed in several taxa (McKinney and Lockwood 1999; La Sorte et al. 2007; Knop 2016) but has so far mostly been studied in urban bird communities (Crooks et al. 2004; Devictor et al. 2007; Godet et al. 2015; Ibáñez-Álamo et al. 2016; Vázquez-Reyes et al. 2017). Urbanized areas (farmlands, villages, and cities) can provide additional habitat or food sources, attracting specific bird species (Evans et al. 2009a, b; Tryjanowski et al. 2015; Reynolds et al. 2017). However, urban bird communities are more homogeneous and often characterized by the absence of specialists when compared with communities from natural habitats (Jokimäki and Kaisanlahti-Jokimäki 2003; Shochat et al. 2010; Ferenc et al. 2014). These differences lead to a gradual decline in the overall functional diversity of species assemblages (Pauw and Louw 2012; Kang et al. 2015; Schütz and Schulze 2015), potentially also reducing the capacity of such communities to resist drastic changes in land use or weather. In fact, it has already been demonstrated that urban development patterns and green areas within cities affect ecosystem dynamics, modifying their abilities to cope with disturbance and modifying their ecological resilience (Alberti and Marzluff 2004).

1.2 Functional surrogates of potential community resilience

Ecological resilience is associated with the capacity of ecological systems to resist invasions, climate or land use changes (Haegeman et al. 2016). This term was introduced in ecology in

the 1970s by Holling (1973) and has been more recently defined as “the capacity of a given system to change in order to maintain the same identity” (Folke et al. 2010). Thus, resilience is associated with a sort of “elasticity” of the system. This property is associated with a relative functional redundancy of components of that system (Haegeman et al. 2016). Redundant or pseudo-redundant species can be described as species sharing many functional traits, belonging to the same guild or having a similar role in the ecosystem (Gitay et al. 1996). Theoretically, the loss or gain of such species should not strongly affect the overall ecosystem functions (Loreau 2004).

Some studies have suggested that indices of functional diversity such as functional evenness may be useful surrogates for the resilience of communities (Mason et al. 2005; Villéger et al. 2008; Lee and Martin 2017), even if in recent years some potential drawbacks were raised (Ricotta et al. 2014; Legras and Gaertner 2018; Kosman et al. 2019). These indices could be used to assess the level of utilization of available resources in a given space, by the species inhabiting it (Mason et al. 2005; Mouchet et al. 2010). In communities with high functional evenness, the resources would be more efficiently used due to a more uniform distribution of the abundance of species throughout functional space defined by the species traits (Lee and Martin 2017) (see a schematic exemplification in the Fig. S1, ESM). In contrast, in communities with low functional evenness available resources could be underexploited, making the community more susceptible to alterations, as for instance biological invasions (Elton 1958; Shea and Chesson 2002). More resilient ecological systems should be able to absorb larger shocks, alleviating the effects and reducing the significant modifications, offering a sort of insurance for the future, facing climate change scenarios (Folke et al. 2002). In this context, the characteristics of the species composing each community, as for example the type of diet, acquires significant importance to determine the overall resilience capacities of such a community. We can expect that communities composed of many species which are similar in terms of feeding traits (e.g., communities composed of several species characterized by a broad diet as omnivorous species), could be better prepared to face eventual change in land use or climate, because such communities are able to respond better by adapting to fluctuations in food resources. On the other hand, communities composed of several species characterized by a narrow diet (e.g., exclusively frugivorous) could be associated with a higher extinction risk (Terborgh and Winter 1980).

1.3 Climate change scenarios and the challenge for conservation of biodiversity

The effects of climate change could be an additional pressure on ecosystems, interacting with land use change and fragmentation (Eglington and Pearce-Higgins 2012), for example, by promoting biological invasions (Opdam and Wascher 2004; Bellard et al. 2013). Projections suggest that in the next decades human-induced climate change is expected to continue, and probably accelerate significantly in association with the global emissions of heat-trapping gases (some sources for projections: for America, <https://nca2014.globalchange.gov/>; for worldwide, <https://gisclimatechange.ucar.edu/>) (Hulme et al. 1999; NCAR Community 2012; Brown and Caldeira 2017).

There exists a vast amount of scientific literature focusing on the main effects of climate in bird populations, mainly produced by temperature and precipitation (Huntley et al. 2008; Askeyev et al. 2018; Trautmann 2018). The main effects of climate change on birds could be associated not only with changes in distribution range of avian species, phenology, and breeding success but also genetics and overall population sizes (Trautmann 2018). Briefly, the main effects of temperature can be associated with variation in the body mass (Andrew

et al. 2018), avian timing of reproduction (Visser et al. 2009), and reproductive performance of avian species (Conrey et al. 2016). Some studies have shown that extreme temperatures (e.g., heat waves or drastic fall on temperatures) during the early breeding season can negatively affect nesting success of grassland birds (Conrey et al. 2016; Zuckerberg et al. 2018). On the other hand, the main effects of precipitation on birds are associated with the direct survival of adults and nesting and hatching success. For example, it was demonstrated that large amounts of precipitations during the year preceding a breeding season, can increase the nesting success of some birds (Zuckerberg et al. 2018). However, excessive precipitations during the breeding season can reduce the nesting success (Zuckerberg et al. 2018). Additionally, intense rain events are expected to reduce food availability (e.g., insect resources) or directly foraging efficiency of birds (Siikamäki 1996). Furthermore, many of the effects of weather variables on birds are combined and associated with different ecological levels (species, populations, communities) (Møller et al. 2010; Skagen and Adams 2012; Stephens et al. 2016; Trautmann 2018).

The use of simulated scenarios to forecast the environmental implications of potential climate or land use changes is a recognized tool for the development of ecological policies (Princé et al. 2013). Climate change causes different ecological fingerprints (Parmesan 2006): bird populations will be affected in many ways, causing ecological adaptations in response to such changes (Butler and Taylor 2005; Barbet-Massin and Jetz 2015; Howard et al. 2015). Among the ecological responses, a potential geographic shift and spatial re-distribution of species assemblages is a critical focus for ecosystem functioning, with deep implications for conservation (Barbet-Massin and Jetz 2015; Princé and Zuckerberg 2015). Induced changes could also be species specific, altering the composition of bird communities, with potential effects on overall resilience. Additionally, global climate change is expected to strongly affect even the local climate of cities worldwide (Lauwaet et al. 2015), which constitutes important core areas for conservation of many bird species (Ives et al. 2016; Jokimäki et al. 2018). In fact, recent studies have highlighted the important role of cities for global or regional biodiversity conservation, by providing opportunities for settlement of species (Zerbe et al. 2003; Aronson et al. 2014; Møller and Díaz 2017). Cities can be characterized by a mix between global warming and the urban heat island effect (Oke 1973; Kim 1992). Early identification of specific conservation targets where climate can accelerate the already negative impact of urbanization should be a priority in an increasingly urbanizing planet.

The aims of this study were (a) to explore the patterns and geographic variation in resilience of urban bird communities in European cities, (b) to identify urban bird communities more likely to be threatened by climate change according to future projections in temperature and rainfall, and (c) to explore the characteristics of such bird assemblages in terms of species traits (e.g., diet), in order to increase our understanding of potential conservation concerns, and, therefore, attempts to mitigate the negative effects of such changes.

2 Methods

2.1 Study area, environment, and collection of bird data

Fieldwork was performed in nine cities, located along a large latitudinal gradient, in six European countries (Fig. 1). This approach, involving different urbanized areas, is particularly suitable for investigating general patterns (Ibáñez-Álamo et al. 2016). In this study were

Fig. 1 Mean, minimum, and maximum values of bird community resilience (FEve) in nine European cities. The resilience clocks indicate the values of community resilience: black clock hands indicate the mean values obtained considering all sampling sites, while white clock hands indicate minimum and maximum values

included only urban areas, with multi-story buildings, single family houses, roads, and parks. Our classification of environments as urban (percentage of built-up area > 50, building density > 10/ha, and residential human density > 10/ha) followed the description made by Marzluff et al. (2001). It has been used in many other studies focusing on urban avian ecology (Clergeau et al. 2006; Loss et al. 2009; Møller et al. 2015; Morelli et al. 2016). We collected data on vegetation cover and land use composition within a distance of 50 m from each survey point (Díaz et al. 2013). Land use/cover categories were classified in six types: building (which includes residential building, built with infrastructure and processing areas and roads), trees (isolated trees, tree lines, and patches), bushes (which includes plants from gardens), grass, bare soil, and water.

Data on bird species were collected during the 2016 breeding season. The surveys were locally adjusted to the start of the breeding season (e.g., early April in southern Spain or late May in northern Finland). Data on bird species were collected by expert ornithologists, following the standardized methodology of point counts randomly selected (Bibby et al. 1992; Voříšek et al. 2010) within each city (ESM, Table S1). All survey points were visited between 06:00 and 10:00 only during favorable weather conditions (i.e., no rain or strong wind). A total of 5 min in early spring and 5 min during a second visit in late spring allowed for inclusion of both early breeders and late migrants, minimizing issues related to differences in the detectability of bird species (Kéry et al. 2005). During the point counts, all individual

birds seen or heard within a 50-m distance from the observer were recorded, with the only exception being raptors and nocturnal species, because they are subject to a different strategy of survey. The location of each sampling point was recorded with a GPS to ensure that counts were made at the same points during the two surveys. For each sampling point, we also calculated the abundance of mammals as the mean number of dogs and cats seen within 50 m during the two 5-min point counts.

2.2 Surrogate of potential resilience of bird communities

The bird community in each sampling site was defined as the total number of bird species recorded during the two visits. Thus, species richness was expressed as the largest number of bird species of the combined data for the two surveys performed during the breeding season (Magurran 2004).

For each sampling site or bird community, we estimated two functional diversity indices which are traditionally associated with resilience of the community: functional evenness (FEve) (Villéger et al. 2008) and the measure FeveR for calculating the functional evenness of a species' assemblage (Ricotta et al. 2014). Both measures are based on a species-trait approach, which focuses on functional aspects of biodiversity (de Bello et al. 2010). Both indices used in this study as surrogate for bird community resilience were calculated using the feeding and breeding avian niche traits provided in Pearman et al. (2014). The bird traits consists of 73 variables describing the niche of each bird species, including (i) body mass, (ii) food type (14 variables), (iii) behavior used for food acquisition (9 variables), (iv) substrate from which food is taken (9 variables), (v) period of day during which a species are active (3 variables), and (vi) used habitats (38 variables) (Pearman et al. 2014). All variables, except for body mass, are binary variables (scored as either 0 or 1) (see a complete description of the used bird traits in the ESM, Table S2). The functional traits are associated with many different characteristics of birds including morphological, physiological, and phenological attributes of species, which are related to individual fitness via their effects on growth, reproduction, and survival (Violle et al. 2007).

The FEve indicates how regular is the degree to which the biomass of the species assemblage is distributed in niche space to allow effective utilization of the entire range of resources available (Villéger et al. 2008) and is calculated as follows:

$$\text{FEve} = \frac{\sum_{i=1}^{S-1} \min\left(\text{PEW}_i, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

where i is the species (or functional unit), S is the total species richness and PEW is the partial weighted evenness.

The FeveR index reflects the regularity in the distribution of abundances of species, together with the evenness in their pairwise functional dissimilarities (Ricotta et al. 2014), and is calculated as follows:

$$R_U = \frac{E_U^{-1} / N}{1^{-1} / N}$$

where E_U is the index of Bulla (1994) and N the number of species, calculated as follows:

$$E_U = \sum_i^N \min \left\{ \pi_i, \frac{1}{N} \right\}$$

where π_i is the relative contribution of species i to U (average community uniqueness U). The average community uniqueness U is the expected dissimilarity between one individual of species i chosen at random from a given community and all other j th species in the community, calculated as follows:

$$U = \sum_{j \neq i}^N p_i \times U_i = \sum_i^N p_i \sum_{j \neq i}^N \frac{p_j}{1-p_i} d_{ij}$$

where d_{ij} is the functional dissimilarity between species i and j (with $d_{ij} = d_{ji}$ and $d_{ii} = 0$), p_i and p_j are the relative abundance of species i and j , respectively, and U_i represents the expected dissimilarity between species i and all other species in the community (Ricotta et al. 2014).

The functional diversity indices used in this study were calculated using the “FD” package for FEve (Laliberté et al. 2015) and the function provided in Ricotta et al. (2014) for FeveR.

Additionally, we calculated species richness for each trophic guild: granivorous (diet containing primarily seeds and grain), insectivorous (diet containing primarily insects and other invertebrates), granivorous-insectivorous (diet containing primarily seeds, grain, insects, and other invertebrates), and carnivorous and omnivorous birds. The trophic guilds were defined by crossing information on bird species from published sources (Cramp and Perrins 1994; Storchová and Hořák 2018) and the 14 food types described in Pearman et al. (2014). With the species richness per each trophic guild, we estimated also the diet diversity in each community by applying the Shannon-diversity index (Shannon 1948).

3 Climate change projection data: differences in temperature and precipitation

Data on climate change projections were obtained from NCAR GIS Program, through Climate Change Scenarios, version 2.0, 2012. URL: <https://gisclimatechange.ucar.edu/>. Data access date: 25 May 2018 (NCAR community 2012). The climate change scenarios have been redesigned for the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report. The Community Climate System Model (CCSM) as a community-wide effort led by the National Center for Atmospheric Research (NCAR, URL: <https://ncar.ucar.edu/>), and it is a key component of the National Science Foundation program on Climate Modeling, Analysis and Prediction. We used the data provided by CCSM, because they are one of the world’s leading general circulation climate models, and a community wide effort led by NCAR. The data define the Representative Concentration Pathways (RCPs), which provide concentrations of atmospheric greenhouse gas (GHG) and the trajectory that is taken over time to reach those concentrations. The spatial resolution of CCSM-3 climate change projections is approximately $1.4 \times 1.4^\circ$ and represents a plausible alternative scenario for the future, not a prediction or forecast (Moss et al. 2008). We downloaded three projected scenarios for current and future climate change in the years comprised between 2017 and 2070: scenarios RCP 4.5, 6.0, and 8.5. In order to visualize the potential climate change expected in Europe, we used the differences in annual means (raw CCSM data) between 2017 and the simulated data for 2070 in (a) temperature ($^\circ\text{C}$) and (b) amount of precipitation (mm) in each cell provided in the CCSM data.

The three different scenarios were mapped for the European continent (ESM, Fig. S2) by using the ArcGIS 10.1 (ESRI 2012) tool “inverse distance weighted” (IDW). The IDW is a technique that interpolates a raster surface from several point values, taking into account the distances among points (Lu and Wong 2008). The distance among points is uniform across Europe and corresponds to the distance among the centroids of the cells provided in the CCSM data (ESM, Fig. S3). This technique (IDW) is adequate to visualize the areas more subject to potential changes in terms of both temperature and precipitation. We used the maps produced to overlap with the cities where bird community resilience was calculated, and then extracted the relative values of climate change expected for each city. For visualization of data, we set the IDW on six different classes from the minimum to the maximum values of delta temperature and precipitation, by using the natural breaks (Jenks) classification. This classification identifies the best group similar values and maximizes the differences between classes (De Smith et al. 2007).

Finally, in order to compare the congruence/mismatch between potential resilience of urban bird communities in nine European cities and climate change scenarios, we focused on the high pathway in which radiative forcing reaches 8.5 W m^{-2} by 2100 (Moss et al. 2008), because the worst scenario is the most suitable to better highlight potential areas of largest changes in temperature and precipitation in the continent. The main justification for this choice is supported by a recent study suggesting that the worst predictions of climate change are probably the most accurate (Brown and Caldeira 2017).

3.1 Statistical analyses

In order to investigate the strength and direction of the association between the two indices of functional diversity (FEve and FeveR), we used the Spearman correlation coefficient (Triola 2012). Because both indices were significantly positively correlated ($R^2 = 0.55$, $p = 4.6 \times 10^{-12}$), the subsequent analyses only focused on one of these indices. We chose FEve because this variable showed a largest range if compared with FeveR in each city, guarantying a better visualization of data. A linear regression was used to explore the potential association between the indices of functional diversity and bird diet diversity in avian communities.

To explore differences in avian niche traits among species of different trophic guilds, the analysis of dissimilarity was used. In this procedure, a dissimilarity matrix was constructed by the “Gower” dissimilarity measure among bird species, considering the 73 avian traits described above. We used the function “daisy” from the package “cluster” in R (Maechler et al. 2018). The average dissimilarity with all the 279 species in the pool was calculated for each bird species. The Kruskal-Wallis and post hoc Kruskal-Dunn were used to check for significant differences in species dissimilarities among the five trophic guilds. The post hoc contrasts were performed using the package “PMCMR” in R (Pohlert 2014).

We used Mantel tests to check for spatial autocorrelation of data (SAC) (Mantel 1967), based on Monte Carlo permutations with 9999 randomizations to test for significance (Oksanen et al. 2016). Sampling sites were treated as statistically dependent observations because the values of SAC between geographic distance (km) and FEve distance among sites was very low though statistically significant ($r_M = 0.048$, $n = 588$, $p = 0.001$) (Manly 2006). In order to alleviate SAC issues, the geographical coordinates of sampling sites were introduced as covariates to incorporate spatial variation during the modeling procedure (Legendre 1993; Dormann et al. 2007).

Generalized Linear Mixed Models (GLMMs) were used to study the patterns of bird community resilience (FEve) in relation to geographical coordinates of sampling sites, land use/cover composition around the point count, abundance of mammals (number of dogs and

cats), and bird species richness for each trophic guild (granivorous, granivorous-insectivorous, insectivorous, carnivorous, and omnivorous), modeled as fixed effects. In order to avoid any redundancy in the modeling procedure, we checked for the potential association between the index of FEve (which was estimated considering habitat, breeding and feeding traits) and the Shannon index estimated based on the species richness for each trophic guild by using a simple linear regression analysis. The association between these two variables was not statistically significant (ESM, Fig. S4; $F = 3.2$, $df = 1$, 586 , $p > 0.05$), justifying the use of both during the modeling procedure. The following predictor variables were too strongly correlated and thus were removed, in order to avoid multicollinearity issues (Graham 2003): building (negatively and significantly correlated with grass and tree), bare soil (negatively and significantly correlated to grass), and overall species richness (positively correlated to species richness for each trophic guild). City was included as a random effect to account for possible consistent differences among cities. Models were fitted by maximum likelihood, using the package “lme4” in R (Bates et al. 2014). The model selection was based on Akaike’s Information Criterion (AIC) (Burnham and Anderson 2002) with the package “AICcmodavg” in R (Mazerolle 2016).

All statistical tests were performed with R software version 3.2.4 (R Development Core Team 2019).

4 Results

4.1 Bird community resilience in nine European cities

A total of 107 bird species were recorded at 588 point counts distributed in nine European cities (Electronic supplementary material (ESM), Table S1). The complete list of species is provided in the ESM (Table S3). Species richness per point count ranged from a minimum mean of 7.52 species (min, 3; max, 12 species) in Munich to a maximum mean of 14.14 species (min, 3; max, 30 species) in Granada.

Overall, the two surrogates of bird community resilience varied between a minimum of 0.69 (FEve) and 0.80 (FeveR) and a maximum of 1.00 (FEve) and 0.99 (FeveR). The differences in FEve among cities were statistically significant (ANOVA: $F = 51.08$, $df = 8$, 579 , $P < 2e-16$). The lower mean value of bird community resilience (FEve) was found in Munich (mean, 0.87; min, 0.69; max, 0.95), while higher mean values were found in the Spanish cities of Madrid (mean, 0.95; min, 0.90; max, 1.00), Granada (mean, 0.94; min, 0.86; max, 0.99) and Toledo (mean, 0.94; min, 0.88; max, 0.98), as well as in the city of Prague (mean, 0.94; min, 0.85; max, 0.98) (Fig. 1).

The values of bird community resilience (FEve) in nine European cities were not significantly correlated with the environmental characteristics around the point counts (land use/cover composition) nor with the abundance of dogs or cats (Table 1). Additionally, we did not find evidence of latitudinal or longitudinal effects on resilience (Table 1, Fig. 1). Bird community resilience was higher in cities where the relative number of granivorous or granivorous-insectivorous species was higher, while it was negatively associated with the richness of insectivorous, carnivorous, and omnivorous-scavenger bird species (Table 1, Fig. 2).

Overall, avian trait dissimilarity was higher in carnivorous and omnivorous species than in granivorous, granivorous-insectivorous, and insectivorous birds. These differences were statistically significant (Kruskal-Wallis $\chi^2 = 43.98$, $df = 4$, $p = 2e-09$, ESM, Fig. S5).

Table 1 Results of GLMM, accounting for variation in bird community resilience (FEve) in relation to species richness for each trophic guild (granivorous, granivorous-insectivorous, insectivorous, carnivorous, and omnivorous), latitude, longitude, land use/cover composition around the point count, and abundance of mammals (dogs and cats)

Variables	Estimate	2.5%	97.5%	SE	<i>t</i>	<i>P</i>
Intercept	0.9325	0.8502	1.0148	0.0420	22.209	1.0e-16
<i>Diet (granivorous)</i>	0.0078	0.0046	0.0110	0.0016	4.828	1.4e-06
<i>Diet (insectivorous)</i>	− 0.0027	− 0.0046	− 0.0008	0.0010	− 2.745	0.0061
<i>Diet (granivorous-insectivorous)</i>	0.0026	0.0010	0.0043	0.0008	3.159	0.0016
<i>Diet (carnivorous)</i>	− 0.0145	− 0.0193	− 0.0097	0.0025	− 5.925	3.1e-09
<i>Diet (omnivorous)</i>	− 0.0090	− 0.0124	− 0.0057	0.0017	− 5.345	9.0e-08
Latitude	− 0.0002	− 0.0018	0.0014	0.0008	− 0.249	0.8032
Longitude	− 0.0011	− 0.0053	0.0031	0.0022	− 0.520	0.6034
Tree (coverage)	− 0.0001	− 0.0002	0.0001	0.0001	− 0.851	0.3949
Bush (coverage)	− 0.0001	− 0.0003	0.0001	0.0001	− 0.886	0.3758
Grass (coverage)	− 0.0001	− 0.0002	0.0001	0.0001	− 1.121	0.2624
Water (coverage)	− 0.0004	− 0.0008	0.0001	0.0002	− 1.604	0.1087
Dogs and cats (abundance)	0.0018	− 0.0005	0.0041	0.0012	1.499	0.1339

The full model is based on 588 sampling sites. Random effect included in the GLMM procedure: cities (groups = 9). Significant variables are set in italics

SE, standard error

Fig. 2 Pie charts showing the bird composition in nine European cities, in terms of species richness for each trophic guild: granivorous, granivorous-insectivorous, insectivorous, carnivorous, and omnivorous based on published sources (Cramp and Perrins 1994; Storchová and Hořák 2018)

4.2 Avian resilience and climate change scenarios

Considering the projection of climate change scenarios for Europe in the next 50 years, provided by the IPCC in the Fifth Assessment Report, the cities exposed to a larger change in temperatures (higher than 2.4 °C) are the Spanish cities of Madrid, Granada, and Toledo and the Finnish cities of Rovaniemi and Turku (Fig. 3). On the other hand, the European cities more exposed to changes in terms of average precipitation in mm are Madrid, Groningen, and Poznan (Fig. 3). Overall, the cities less exposed to a drastic variation in terms of temperature

Fig. 3 Graduated symbol maps of bird community resilience in nine European cities, represented by the size of the circles on a map of expected changes in **a** temperature (°C) and **b** precipitation (mm), under a high representative concentration pathway scenario in which radiative forcing reaches 8.5 W m⁻² (RCP8.5) by 2100 (Moss et al. 2008). The values of expected climate change in Europe were downloaded from the Climate Change Scenarios, version 2.0, 2012. URL: <https://gisclimatechange.ucar.edu/>. Data access date: 25 May 2018 (NCAR Community 2012). The maps represent the continuous patterns of the projections of climate change mapped by using the inverse distance weighted (IDW) technique

and precipitation under a high pathway climate change projection are cities from central Europe such as Prague and Munich (Fig. 3, ESM, Table S4).

Crossing the mean values of bird community resilience for the nine European cities with the values of expected delta temperature and precipitation, explored in a 3D plot, highlight some potential scenarios of urban bird conservation for the next 50 years: Even if Munich was the city with the lowest avian community resilience, it seems however that bird communities within that city are not affected by strong climate change events, but only by a relative moderate change in temperature, with temperature increases of 1.9–2.3 °C, but less strong changes in precipitation when compared with other European cities (ESM, Fig. S6). The Spanish cities with higher values of bird community resilience will face more notorious climate change events: Madrid (with the higher bird community resilience) could be affected by a relatively large change in the mean amount of monthly precipitation (110–170 mm) as well as increasing temperatures around 2.4–2.8 °C (ESM, Fig. S6). Granada and Toledo could face similar scenarios of increasing temperatures, but less strong changes in terms of mean amount of monthly precipitation (ESM, Fig. S6). The city of Prague was characterized by bird communities with relative high resilience, and simultaneously not exposed to so drastic climate change events in the next 50 years (ESM, Fig. S6). The Finnish city of Rovaniemi could suffer an important increase in average temperatures, while their bird species assemblages are characterized by lower resilience than other urban bird communities, suggesting a potential conservation problem.

5 Discussion

5.1 Climate change scenarios in cities and bird community resilience

In this study, we suggested potential future conservation concerns in urban bird communities, by crossing information on a surrogate of species assemblage resilience (FEve) (Mouchet et al. 2010) and the projection of scenarios facing climate change. Even if we examined three different scenarios, we used the high pathway climate change scenario because it could be the most plausible (Brown and Caldeira 2017).

Our findings provide important information about the cities that could face stronger climate change events, and the capacity of their bird communities to reduce any negative impact associated with them. Briefly, a high probability of climate change and simultaneously a low value of bird community resilience can be interpreted as the worst scenario, suggesting a potential conservation concern.

A higher pressure of climate change in terms of delta temperatures and delta precipitation should mainly affect cities from the Southern and Northern regions of Europe. The data derived from the projections made by NCAR Climate Change Scenarios (NCAR Community 2012) showed that cities like Granada, Madrid, and Toledo in Spain and Rovaniemi and Turku in Finland could suffer variation in temperatures larger than 2.6 °C before the year 2070 (ESM, Table S4). Additionally, Madrid and Toledo could also be exposed to a significant change in the amount of monthly precipitations. Finally, Madrid was also the biggest city surveyed in this study, with more than three million people (ESM, Table S1). This fact is important if we consider that the number of threatened bird species could be positively associated with human population size (Pautasso and Dinetti 2009). However, these two Spanish cities are characterized by species assemblages with higher resilience, a fact that

can offer insurance against the ability of communities to respond to challenges posed by climate change. On the other hand, from the two Finnish cities, Rovaniemi could constitute a potential problem for conservation in the future: this northern city could face an important increase in average temperatures, while their bird communities are mostly characterized by lower values of resilience within the cities used in our study. Especially in the case of Rovaniemi, most breeding species are (long)-distance migrants (Schaefer et al. 2008; Saino et al. 2011) and in most cases have a narrow type of diet, as insectivorous (Fig. 2).

Even if all cities could be exposed to potential climate change scenarios, the cities from the central part of the continent (Groningen, Munich, Poznan, and Prague) are less exposed to drastic changes in temperatures, when compared with the other cities studied (Fig. 3), suggesting a low conservation concern of urban bird communities. This is important when planning future conservation, regarding both urbanization and climate change. For example, Munich was the city with the lowest mean value of resilience of avian species assemblages, but considering that future scenarios suggest a relative small impact due to climate change, we consider that specific conservation actions attempting to promote resilience of urban bird assemblages in this city are not urgently needed. In contrast, other cities with low/medium levels of resilience, like Rovaniemi at the Arctic Circle, which will be exposed to important increases in temperature in the future, should be the focus of conservation practices or at least close monitoring schemes. The bird communities from Munich were characterized by a high proportion of insectivores and simultaneously a low proportion of granivorous species, when compared with the other European cities. When comparing Munich with the nearby city of Prague, Czech Republic, we can highlight how the risk of increase in the level of threat for bird communities in Prague could be lower, because the city presents species assemblages with high values of potential resilience, also being a city not subject to particular intensification of climate change.

Another important result to highlight from this study is the weak correlation between potential resilience of urban bird communities and land use/cover composition where the communities were assessed. This lack of association in our study may suggest that little variation in land use/cover composition or heterogeneity in urban green areas do not have a strong impact on the regularity of bird traits in functional space and how efficiently the resources are utilized. A study focused on anthropized environments (farmlands) showed how functional evenness of bird communities is only weakly correlated with the environmental characteristics of the area (green area size, canopy heterogeneity) (Lee and Martin 2017).

We found in the nine European cities that urban bird communities with high richness of granivorous or granivorous-insectivorous species were the communities with higher potential resilience. In contrast, urban bird communities with an overrated number of insectivorous, carnivorous, and omnivorous species were assemblages with lower potential resilience. The main reason why carnivorous and omnivorous species richness was negatively associated with potential community resilience could be explained by the fact that those bird species were characterized by higher trait dissimilarity, when compared with the entire pool of species (ESM, Fig. S5). The granivorous birds recorded in this study, on the other hand, were more similar in terms of breeding and feeding traits (ESM, Fig. S5). By increasing the number of species which are functionally closer, the functional redundancy will rise, achieving a higher functional evenness and potential bird community resilience.

Regarding the bird's foraging characteristics in relation to the potential resilience of species assemblages, however, we consider it relevant to highlight the limitations of simple traits describing the diet of a species. Further studies should also consider the fact that many species

are relatively plastic in terms of foraging ecology. Some species, as shrikes or sparrows, can exploit different types of diet depending on the geographical context and environmental conditions, being also scavengers at roadsides (Tryjanowski et al. 2003; Morelli et al. 2015). The diet plasticity of bird species, also in cities, can shift their main type of food between seasons; e.g., in the northern part of Europe, while most species need/use protein-rich arthropods during breeding season for their nestlings, they must change their diet for berries (e.g. Turdidae) or seeds (e.g. Paridae) during winter, because of a lack of insects. Geographic variation in trophic plasticity of bird species could play an important role in the overall potential resilience of the communities. Since specialist species are considered more prone to the processes that lead to extinction than generalist species (McKinney 1997; Colles et al. 2009), we can expect that a given community composed of many species characterized by high ecological plasticity in terms of foraging (but also behavior or breeding) should be better adapted to eventual environmental or climatic changes, because such species could respond better by adapting to different types of food or other resources. Further studies could also focus on the overall level of specialization of bird communities inhabiting cities (Morelli et al. 2019).

Finally, the fact that we did not find any evidence of latitudinal or longitudinal effects on avian potential resilience among the nine cities could be interpreted as a confirmation of the level of homogenization of urban settlements in Europe (Devictor et al. 2007).

5.2 Final considerations and some remarks on the use of a surrogate of community resilience

Recent studies have provided evidence of drawbacks for the use of this functional diversity index (e.g., Ricotta et al. 2014; Legras and Gaertner 2018), which is the evenness component of functional diversity. Briefly, the main concerns are related to the fact that an increase in FEve index values is not always synonymous with an increase in true functional evenness, mainly when comparing communities which differ in terms of abundance distribution (Legras and Gaertner 2018). However, in the present study, we estimated the FEve crossing a trait matrix with a matrix of solely presence/absence of species, therefore overcoming (or at least alleviating) this potential problem. Additionally, we explicitly compared the behavior of the index FEve with the new index proposed by Ricotta et al. (2014), which measures the regularity in the distribution and abundance of species in functional space, together with the evenness in their pairwise functional dissimilarities, to ensure that in our study both could be used similarly. Moreover, any index or metric used to quantify the hypothetical “resilience” of a species assemblage must be handled cautiously. An index is not a direct “measure,” especially because the resilience or capacity to respond to an alteration depends on many (and complex) factors: period of disturbance, intensity, relative plasticity of species, biotic interactions (explicit and hidden), and cascade effects (Spears et al. 2015; Morelli and Tryjanowski 2016). Ecological resilience was defined as a multifaceted concept (Cumming et al. 2005). Thus, we consider that any index should be more efficiently used when applied mainly to comparisons among sites or areas, but warmly suggest to test different indices.

Importantly, climate change effects can interact with the distribution of bird species, facilitating the expansion of invasive birds that could compete, displace, and/or prey on native species (Bellard et al. 2013). Therefore, this could potentially amplify the effects of changes in land use, precipitation, or temperature. Maintenance of the level of functional redundancy in bird communities can increase the overall tolerance of such species assemblages to potential scenarios of land use and climate change (Elmqvist et al. 2003). Thus, the capacity of species assemblages to face and recover from extreme events (such as climate or land use change) will determine their persistence.

In conclusion, our findings highlighted how an approach combining projections of climate change scenarios and potential resilience of species assemblages (using species trait-based methods) could be useful to identify in advance conservation concerns. We hypothesize that the approach used in this study could also be applied to other taxa such as insects and mammals. This may help establish adequate urban planning strategies for the promotion of a high diversity of communities in urban exploiter and tolerant species, increasing the level of protection of urban ecosystem functioning.

Acknowledgements We are grateful to all people who helped observers during the field work, as well as the reviewers and editors for their very constructive suggestions which helped us to improve the readability of our study

Funding information F.M. and Y.B. were financially supported by the Czech Science Foundation GAČR (project number 18-16738S).

References

- Alberti M, Marzluff JM (2004) Ecological resilience in urban ecosystems: linking urban patterns to human and ecological functions. *Urban Ecosyst* 7:241–265
- Andrew SC, Awasthy M, Griffith AD et al (2018) Clinal variation in avian body size is better explained by summer maximum temperatures during development than by cold winter temperatures. *Auk* 135:206–217. <https://doi.org/10.1642/auk-17-129.1>
- Aronson MFJ, La Sorte FA, Nilon CH et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc R Soc London B - Biol Sci* 281:20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Askeyev O, Askeyev A, Askeyev I (2018) Recent climate change has increased forest winter bird densities in East Europe. *Ecol Res* 33:445–456. <https://doi.org/10.1007/s11284-018-1566-4>
- Barbet-Massin M, Jetz W (2015) The effect of range changes on the functional turnover, structure and diversity of bird assemblages under future climate scenarios. *Glob Chang Biol* 21:2917–2928. <https://doi.org/10.1111/gcb.12905>
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4 - R Package
- Bellard C, Thuiller W, Leroy B et al (2013) Will climate change promote future invasions? *Glob Chang Biol* 19: 3740–3748. <https://doi.org/10.1111/gcb.12344>
- Bibby CJ, Burgess ND, Hill DA (1992) Bird census techniques (Google eBook). Academic Press
- Brown PT, Caldeira K (2017) Greater future global warming inferred from Earth's recent energy budget. *Nature* 552:45–50. <https://doi.org/10.1038/nature24672>
- Bulla L (1994) An index of evenness and its associated diversity measure. *Oikos* 70:167–171
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer Verlag, New York, NY
- Butler RW, Taylor W (2005) A review of climate change impacts on birds. *USDA For Serv Gen Tech Rep* 191: 1107–1109
- Clergeau P, Croci S, Jokimäki J et al (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biol Conserv* 127:336–344. <https://doi.org/10.1016/j.biocon.2005.06.035>
- Colles A, Liow LH, Prinzing A (2009) Are specialists at risk under environmental change? Neoeccological, paleoecological and phylogenetic approaches. *Ecol Lett* 12:849–863. <https://doi.org/10.1111/j.1461-0248.2009.01336.x>
- Conrey RY, Skagen SK, Yackel Adams AA et al (2016) Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines. *Ibis (Lond 1859)* 158:614–629. <https://doi.org/10.1111/ibi.12373>
- Cramp S, Perrins C (1994) The birds of the Western Palearctic. Oxford University Press, Oxford, UK
- Crooks KR, Suarez AV, Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol Conserv* 115:451–462. [https://doi.org/10.1016/S0006-3207\(03\)00162-9](https://doi.org/10.1016/S0006-3207(03)00162-9)
- Crutzen PJ, Stoermer EF (2000) The “Anthropocene.”. *Glob Chang Newsl* 41:17–18
- Cumming GS, Barnes G, Perz S et al (2005) An exploratory framework for the empirical measurement of resilience. *Ecosystems* 8:975–987. <https://doi.org/10.1007/s10021-005-0129-z>
- de Bello F, Lavorel S, Gerhold P et al (2010) A biodiversity monitoring framework for practical conservation of grasslands and shrublands. *Biol Conserv* 143:9–17. <https://doi.org/10.1016/j.biocon.2009.04.022>

- De Smith MJ, Goodchild MF, Longley PA (2007) Univariate classification schemes. In: geospatial analysis—a comprehensive guide to principles, techniques and software tools, 2nd edn. Troubador Publishing Ltd, p 516
- Devictor V, Julliard R, Couvet D et al (2007) Functional homogenization effect of urbanization on bird communities. *Conserv Biol* 21:741–751. <https://doi.org/10.1111/j.1523-1739.2007.00671.x>
- Díaz M, Møller AP, Flensted-Jensen E et al (2013) The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One* 8:e64634. <https://doi.org/10.1371/journal.pone.0064634>
- Dormann CF, McPherson JM, Araújo MB et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography (Cop)* 30:609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Eglington SM, Pearce-Higgins JW (2012) Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS One* 7:e30407. <https://doi.org/10.1371/journal.pone.0030407>
- Elmqvist T, Folke C, Nystrom M et al (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–494. <https://doi.org/10.2307/3868116>
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, UK
- ESRI (2012) ArcGIS desktop: release 10.1. Redlands, CA: Environmental Systems Research Institute
- Evans KL, Gaston KJ, Frantz AC et al (2009a) Independent colonization of multiple urban centres by a formerly forest specialist bird species. *Proc R Soc London B - Biol Sci* 276:2403–2410
- Evans KL, Newson SE, Gaston KJ (2009b) Habitat influences on urban avian assemblages. *Ibis (Lond 1859)* 151:19–39
- Ferenc M, Sedláček O, Fuchs R et al (2014) Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Glob Ecol Biogeogr* 23:479–489. <https://doi.org/10.1111/geb.12130>
- Foley JA, Defries R, Asner GP et al (2005) Global consequences of land use. *Science* 309:570–474. <https://doi.org/10.1126/science.1111772>
- Folke C, Carpenter S, Elmqvist T et al (2002) Resilience and sustainable development: building adaptive capacity in a world of transformations. *Ambio* 31:437–440
- Folke C, Carpenter SR, Walker B et al (2010) Resilience thinking: integrating resilience, adaptability and transformability. *Ecol Soc* 15:20
- Garcillán PP, Dana ED, Rebman JP, Peñas J (2014) Effects of alien species on homogenization of urban floras across continents : a tale of two mediterranean cities on two different continents. *Plant Ecol Evol* 147:3–9. <https://doi.org/10.5091/plecevo.2014.950>
- Gitay H, Wilson JB, Lee WG (1996) Species redundancy: a redundant concept? *J Ecol* 84:121–124
- Godet L, Gaüzère P, Jiguet F, Devictor V (2015) Dissociating several forms of commonness in birds sheds new light on biotic homogenization. *Glob Ecol Biogeogr* 24:416–426. <https://doi.org/10.1111/geb.12266>
- Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815. <https://doi.org/10.1890/02-3114>
- Grimm NB, Foster D, Groffman P et al (2008) The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Front Ecol Environ* 6:264–272. <https://doi.org/10.1890/070147>
- Haegeman B, Arnoldi J-F, Wang S, et al (2016) Resilience, invariability, and ecological stability across levels of organization. *bioRxiv* 1–15. <https://doi.org/10.1101/085852>
- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23. <https://doi.org/10.1146/annurev.es.04.110173.000245>
- Howard C, Stephens PA, Pearce-Higgins JW et al (2015) The drivers of avian abundance: patterns in the relative importance of climate and land use. *Glob Ecol Biogeogr* 24:1249–1260. <https://doi.org/10.1111/geb.12377>
- Hulme M, Mitchell J, Ingram W et al (1999) Climate change scenarios for global impacts studies. *Glob Environ Chang* 9:S3–S19. [https://doi.org/10.1016/S0959-3780\(99\)00015-1](https://doi.org/10.1016/S0959-3780(99)00015-1)
- Huntley B, Collingham YC, Willis SG, Green RE (2008) Potential impacts of climatic change on European breeding birds. *PLoS One* 3:e1439. <https://doi.org/10.1371/journal.pone.0001439>
- Ibáñez-Álamo JD, Rubio E, Benedetti Y, Morelli F (2016) Global loss of avian evolutionary uniqueness in urban areas. *Glob Chang Biol* 23:2990–2998. <https://doi.org/10.1111/geb.13567>
- Ives CD, Lentini PE, Threlfall CG et al (2016) Cities are hotspots for threatened species. *Glob Ecol Biogeogr* 25: 117–126. <https://doi.org/10.1111/geb.12404>
- Jokimäki J, Kaisanlahti-Jokimäki M-L (2003) Spatial similarity of urban bird communities: a multiscale approach. *J Biogeogr* 30:1183–1193
- Jokimäki J, Suhonen J, Kaisanlahti-Jokimäki M-L (2018) Landscape and urban planning urban core areas are important for species conservation: a European-level analysis of breeding bird species. *Landsc Urban Plan* 178:73–81. <https://doi.org/10.1016/j.landurbplan.2018.05.020>

- Kang W, Minor ES, Park C, Lee D (2015) Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. *Urban Ecosyst* 18:857–870. <https://doi.org/10.1007/s11252-014-0433-5>
- Kéry M, Royle JA, Schmid H (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecol Appl* 15:1450–1461. <https://doi.org/10.1890/04-1120>
- Kim HH (1992) Urban heat island. *Int J Remote Sens* 13:2319–2336. <https://doi.org/10.1080/01431169208904271>
- Knop E (2016) Biotic homogenization of three insect groups due to urbanization. *Glob Chang Biol* 22:228–236. <https://doi.org/10.1111/gcb.13091>
- Kosman E, Burgio KR, Presley SJ et al (2019). Conservation prioritization based on trait-based metrics illustrated with global parrot distributions. *Divers Distrib* 25:1156–1165. <https://doi.org/10.1111/ddi.12923>
- La Sorte FA, ML MK, Pyšek P (2007) Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. *Glob Chang Biol* 13:913–921. <https://doi.org/10.1111/j.1365-2486.2007.01329.x>
- Laliberté E, Legendre P, Shipley B (2015) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology: R package version 1.0-12
- Lauwaet D, Hooyberghs H, Maiheu B et al (2015) Detailed urban heat island projections for cities worldwide: dynamical downscaling CMIP5 global climate models. *Climate* 3:391–415. <https://doi.org/10.3390/cli3020391>
- Lee M-B, Martin JA (2017) Avian species and functional diversity in agricultural landscapes: does landscape heterogeneity matter? *PLoS One* 12:e0170540. <https://doi.org/10.1371/journal.pone.0170540>
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- Legras G, Gaertner J-C (2018) Assessing functional evenness with the FEve index: a word of warning. *Ecol Indic* 90:257–260. <https://doi.org/10.1016/J.ECOLIND.2018.03.020>
- Lewis SL, Maslin MA (2015) Defining the Anthropocene. *Nature* 519:171–180. <https://doi.org/10.1038/nature14258>
- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611. <https://doi.org/10.1111/j.0030-1299.2004.12685.x>
- Loss SR, Ruiz MO, Brawn JD (2009) Relationships between avian diversity, neighborhood age, income, and environmental characteristics of an urban landscape. *Biol Conserv* 142:2578–2585. <https://doi.org/10.1016/j.biocon.2009.06.004>
- Lu GY, Wong DW (2008) An adaptive inverse-distance weighting spatial interpolation technique. *Comput Geosci* 34:1044–1055. <https://doi.org/10.1016/j.cageo.2007.07.010>
- Maechler M, Rousseeuw P, Struyf A, et al (2018) Cluster: cluster analysis basics and extensions. R package version 2.0.7–1
- Magurran A (2004) Measuring biological diversity. Blackwell Science, Oxford, UK
- Manly BFJ (2006) Randomization, bootstrap and Monte Carlo methods in biology, third edn. Chapman and Hall/CRC, New York, NY
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220
- Marzluff JM, Bowman R, Donnelly R (2001) A historical perspective on urban bird research: trend, terms, and approaches. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian ecology and conservation in an urbanizing world*. Kluwer, New York, NY, pp 20–47
- Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary of functional components diversity. *Oikos* 111:112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Mazerolle MJ (2016) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package
- McKinney M (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu Rev Ecol Syst* 28:495–516. <https://doi.org/10.1146/annurev.ecolsys.28.1.495>
- McKinney ML (2002) Urbanization, biodiversity, and conservation. *Bioscience* 52:883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14:450–453
- Miller JR, Hobbs RJ (2002) Conservation where people live and work. *Conserv Biol* 16:330–337. <https://doi.org/10.1046/j.1523-1739.2002.00420.x>
- Møller AP, Diaz M (2017) Avian preference for close proximity to human habitation and its ecological consequences. *Curr Zool*:zox073. <https://doi.org/10.1093/cz/zox073>
- Møller AP, Berthold P, Fiedler W (2010) Effects of climate change on birds. Oxford University Press, Oxford, UK

- Møller AP, Díaz M, Flensted-Jensen E et al (2015) Urbanized birds have superior establishment success in novel environments. *Oecologia* 178:943–950. <https://doi.org/10.1007/s00442-015-3268-8>
- Morelli F, Tryjanowski P (2016) The dark side of the “redundancy hypothesis” and ecosystem assessment. *Ecol Complex* 28:222–229. <https://doi.org/10.1016/j.ecocom.2016.07.005>
- Morelli F, Bussire R, Goławski A et al (2015) Saving the best for last: differential usage of impaled prey by red-backed shrike (*Lanius collurio*) during the breeding season. *Behav Process* 119:6–13. <https://doi.org/10.1016/j.beproc.2015.07.006>
- Morelli F, Benedetti Y, Ibnz-lamo JD et al (2016) Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Glob Ecol Biogeogr* 25:1284–1293. <https://doi.org/10.1111/geb.12486>
- Morelli F, Benedetti Y, Mller AP, Fuller RA (2019) Measuring avian specialization. *Ecol Evol* 9:8378–8386. <https://doi.org/10.1002/ece3.5419>
- Moss RH, Nakicenovic N, O’Neill BC (2008) Towards new scenarios for analysis of emissions, climate change, impacts, and response strategies. IPCC, Geneva, Switzerland
- Mouchet MA, Villger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- NCAR Community (2012) Climate change scenarios, version 2.0. In: Community Clim. Syst. Model. version 3.0. <http://www.cesm.ucar.edu/models/ccsm3.0/> NCAR/UCAR. <https://gisclimatechange.ucar.edu/>. Access Date: 25/05/2018
- Oke TR (1973) City size and the urban heat island. *Atmos Environ* 7:769–779. [https://doi.org/10.1016/0004-6981\(73\)90140-6](https://doi.org/10.1016/0004-6981(73)90140-6)
- Oksanen J, Guillaume Blanchet F, Kindt R, et al (2016) Vegan: community ecology package. R package version 2.3-4. 291
- Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol Conserv* 117:285–297. <https://doi.org/10.1016/j.biocon.2003.12.008>
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Pautasso M, Dinetti M (2009) Avian species richness, human population and protected areas across Italy’s regions. *Environ Conserv* 36:22–31. <https://doi.org/10.1017/S037689290900544X>
- Pauw A, Louw K (2012) Urbanization drives a reduction in functional diversity in a guild of nectar-feeding birds. *Ecol Soc* 17:27. <https://doi.org/10.5751/ES-04758-170227>
- Pearman PB, Lavergne S, Roquet C et al (2014) Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Glob Ecol Biogeogr* 23:414–424. <https://doi.org/10.1111/geb.12127>
- Petchey OL, Hector A, Gaston KJ (2004) How do different measures of functional diversity perform? *Ecology* 85:847–857. <https://doi.org/10.1890/03-0226>
- Pohler T (2014) The pairwise multiple comparison of mean ranks package (PMCMR). R package version 4.3
- Princ K, Zuckenberg B (2015) Climate change in our backyards : the reshuffling of North America ’ s winter bird communities. *Glob Chang Biol* 21:572–585. <https://doi.org/10.1111/geb.12740>
- Princ K, Lorillre R, Barbet-Massin M, Jiguet F (2013) Predicting the fate of French bird communities under agriculture and climate change scenarios. *Environ Sci Pol* 33:120–132. <https://doi.org/10.1016/j.envsci.2013.04.009>
- R Development Core Team (2019) R: a language and environment for statistical computing
- Reynolds SJ, Galbraith JA, Smith JA, Jones DN (2017) Garden bird feeding: insights and prospects from a north-south comparison of this global urban phenomenon. *Front Ecol Evol* 5:24. <https://doi.org/10.3389/fevo.2017.00024>
- Ricotta C, Bacaro G, Moretti M (2014) A new measure of functional evenness and some of its properties. *PLoS One* 9:e104060. <https://doi.org/10.1371/journal.pone.0104060>
- Safi K, Armour-Marshall K, Baillie JEM, Isaac NJB (2013) Global patterns of evolutionary distinct and globally endangered amphibians and mammals. *PLoS One* 8:e63582. <https://doi.org/10.1371/journal.pone.0063582>
- Saino N, Ambrosini R, Rubolini D et al (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc R Soc B Biol Sci* 278:835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Schaefer HC, Jetz W, Bhning-Gaese K (2008) Impact of climate change on migratory birds: community reassembly versus adaptation. *Glob Ecol Biogeogr* 17:38–49. <https://doi.org/10.1111/j.1466-8238.2007.00341.x>
- Schmiegelow FKA, Mnkknen M (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecol Appl* 12:375–389
- Schtz C, Schulze CH (2015) Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover. *Ecol Evol* 5:5230–5239. <https://doi.org/10.1002/ece3.1778>
- Secretariat of the Convention on Biological Diversity (2012) Cities and biodiversity outlook: a global assessment of the links between urbanization, biodiversity, and ecosystem services. Montreal, Canada

- Shannon CE (1948) The mathematical theory of communication. *Bell Syst Tech J* 27:379–423
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Shochat E, Lerman S, Fernández-Juricic E (2010) Birds in urban ecosystems: population dynamics, community structure, biodiversity, and conservation. In: Aitkenhead-Peterson J, Volder A (eds) *Agronomy monograph 55. Urban ecosystem ecology*. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI, pp 75–86
- Siikamäki P (1996) Nestling growth and mortality of pied flycatchers (*Ficedula hypoleuca*) in relation to weather and breeding effort. *Ibis (Lond 1859)* 138:471–478
- Skagen SK, Adams AAY (2012) Weather effects on avian breeding performance and implications of climate change. *Ecol Appl* 22:1131–1145. <https://doi.org/10.1890/11-0291.1>
- Sklenicka P (2016) Classification of farmland ownership fragmentation as a cause of land degradation: a review on typology, consequences, and remedies. *Land Use Policy* 57:694–701
- Spears BM, Ives SC, Angeler DG et al (2015) Effective management of ecological resilience—are we there yet? *J Appl Ecol* 52:1311–1315. <https://doi.org/10.1111/1365-2664.12497>
- Spellerberg IF (1998) Ecological effects of roads and traffic: a literature review. *Glob Ecol Biogeogr Lett* 7:317–333
- Stephens PA, Mason LR, Green RE et al (2016) Consistent response of bird populations to climate change on two continents. *Science* 352:84–87. <https://doi.org/10.1126/science.aac4858>
- Storchová L, Hořák D (2018) Life-history characteristics of European birds. *Glob Ecol Biogeogr* 27:400–406. <https://doi.org/10.1111/geb.12709>
- Terborgh J, Winter B (1980) Some causes of extinction. In: Soule M, Wilcox B (eds) *Conservation biology: an evolutionary-ecological perspective*, 1st edn. Sinauer Associates Inc, New York, NY, pp 119–133
- Trautmann S (2018) Climate change impacts on bird species. In: Tietze DT (ed) *Bird species—how they arise, modify and vanish*, 1st edn. Springer, pp 217–234
- Triola MF (2012) *Elementary statistics*, 12th edn. Pearson International, London, UK
- Tryjanowski P, Karg M, Karg J (2003) Food of the red-backed shrike *Lanius collurio*: a comparison of three methods of diet analysis. *Acta Ornithol* 38:59–64
- Tryjanowski P, Skórka P, Sparks TH et al (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environ Sci Pollut Res* 22:15097–15103. <https://doi.org/10.1007/s11356-015-4723-0>
- Vázquez-Reyes LD, del Coro Arizmendi M, Godínez-Álvarez HO et al (2017) Directional effects of biotic homogenization of bird communities in Mexican seasonal forests. *Condor* 119:275–288. <https://doi.org/10.1650/CONDOR-16-116.1>
- Villéger S, Mason NWH, Moullot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301. <https://doi.org/10.1890/07-1206.1>
- Violle C, Navas M-LL, Vile D et al (2007) Let the concept of trait be functional! *Oikos* 116:882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Visser ME, Holleman LJM, Caro SP (2009) Temperature has a causal effect on avian timing of reproduction. *Proc R Soc B Biol Sci* 276:2323–2331. <https://doi.org/10.1098/rspb.2009.0213>
- Voříšek P, Křiváňová A, Wotton S, Gregory RD (2010) A best practice guide for wild bird monitoring schemes. Pan-European Common Bird Monitoring Scheme (PECMBS), Bruxelles, Belgium
- Wilson MC, Chen X-Y, Corlett RT et al (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landsc Ecol* 31:219–227. <https://doi.org/10.1007/s10980-015-0312-3>
- Zerbe S, Maurer U, Schmitz S, Sukopp H (2003) Biodiversity in Berlin and its potential for nature conservation. *Landsc Urban Plan* 62:139–148
- Zuckerberg B, Ribic CA, McCauley LA (2018) Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size. *Conserv Biol* 32:872–882. <https://doi.org/10.1111/cobi.13089>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Federico Morelli¹ • Yanina Benedetti¹ • Juan Diego Ibáñez-Álamo² • Piotr Tryjanowski³ • Jukka Jokimäki⁴ • Marja-Liisa Kaisanlahti-Jokimäki⁴ • Tomás Pérez-Contreras² • Philipp Sprau⁵ • Jukka Suhonen⁶ • Reuven Yosef^{7,8} • Mario Díaz⁹ • Anders Pape Møller¹⁰

✉ Federico Morelli
fmorellius@gmail.com

- ¹ Faculty of Environmental Sciences, Department of Applied Geoinformatics and Spatial Planning, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Prague 6, Czech Republic
- ² Department of Zoology, University of Granada, Granada, Spain
- ³ Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625 Poznań, Poland
- ⁴ Nature Inventory and EIA-services, Arctic Centre, University of Lapland, P.O. Box 122, FI-96101 Rovaniemi, Finland
- ⁵ Department of Biology, Ludwig-Maximilians-University Munich, Munich, Germany
- ⁶ Department of Biology, University of Turku, Turku, Finland
- ⁷ Ben Gurion University of the Negev, P.O. Box 272, 88000 Eilat, Israel
- ⁸ Rabin High School, Yotam Street, 88104 Eilat, Israel
- ⁹ Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), 28006 Madrid, Spain
- ¹⁰ Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, 91405 Orsay Cedex, France