

Ecological traits predict population trends of urban birds in Europe

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ABSTRACT

The population dynamics of urban animals has been so far remarkably understudied. At the same time, urban species' population trends can provide important information on the consequences of environmental changes in cities. We modelled long-term population trends of 93 bird species breeding in urban areas in 16 European countries as a function of species' traits, characterising variability in their urbanization and ecology. We found that: (i) earlier colonisers have more negative population trends than recent colonisers; (ii) more urbanized open habitat species had more positive population trends than less urbanized open habitat species; (iii) highly urbanized birds breeding above the ground had more negative trends than highly urbanized ground breeders. These patterns can be explained by several processes occurring in cities as well as outside city borders. Namely, (i) pre-industrial colonisers might struggle to persist in rapidly changing urban areas, limiting their foraging and breeding opportunities of the birds. (ii) Open habitats are under pressure of intensive agricultural exploitation in rural areas, which may negatively affect populations of less urbanized birds. In contrast, urban areas do not experience such pressure keeping the trends of urbanized open habitat species more positive. (iii) Differences in population trends between highly urbanized ground and above-ground breeders suggest that the latter may lose their breeding opportunities in modern buildings that do not provide suitable breeding sites. Our results indicate

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that even once successful, city dwellers may not keep pace with changes in urban areas, but these areas may also provide suitable habitats for biodiversity.

1. Introduction

The Earth's surface has been undergoing rapid urbanization in the last century, resulting in a growing proportion of the human population living in cities, which recently exceeded 50 % and might grow up to 68 % by 2050 (United Nations, 2018). The biodiversity is largely negatively affected by urban area expansion linked with, for example, native habitat loss (McKinney, 2002) and the introduction of non-native organisms (Trentanovi et al., 2013). At the same time, some species can survive in urban areas because they hold specific combinations of ecological characteristics, being advantageous for life near humans (Ruas et al., 2022; Saito & Koike, 2015; Sol et al., 2017). The resulting urban communities are often similar to each other, contributing to the phenomenon known as "biotic homogenisation" (Clergeau et al., 2006; Markacci et al., 2021; McKinney & Lockwood, 1999).

Species show considerable variability in their association with urban areas with consequences for their performance within the city borders (Lizée et al., 2011; Vallet et al., 2010). This association can be expressed by two measures highlighting its different aspects: time since urbanization (*TSU*) and relative urbanness (*RU*). *TSU* is based on the observation that cities were colonized by different species in different time periods (Bea et al., 2011; Evans et al., 2010; Rutz, 2008). The longer the colonisation occurred in the past, the higher the *TSU*. This might be an important characteristic for urban species adaptation and population dynamics. Still, this variable was only rarely considered in urban ecology research (but see Møller, 2010a). There is evidence that the urbanized species tolerate more human proximity (Møller, 2010b; Symonds et al., 2016) and have higher population densities (Møller et al., 2012) with increasing time since urbanization. *RU* is a recently derived measure based on species distribution modelling and remote sensing data. It is determined as the species' relative occurrence in the areas of night lights (VIIRS), which is a versatile measure of human presence (Callaghan et al., 2020). The closer the association is, the more urbanized the species (Callaghan et al., 2019).

Most studies on urban ecology of animals so far focused on the identification of the traits that govern the establishment and survival of populations in cities (Castaneda et al., 2019; Evans et al., 2011; Gallo et al., 2017; Jokimäki et al., 2016; Sol et al., 2014), while studies focusing on population trends of urban animal species are very rare. At the same time, urban areas change quickly (Richards & Belcher, 2020); as a consequence, changes in the population abundance of urban species are also likely to occur. In order to study such changes, we obtained national population trends of 93 bird species that frequently breed in urban areas from Pan-European Common Bird Monitoring Scheme (PECBMS), one of the most comprehensive datasets on animal population trajectories worldwide (Brlík et al., 2021). We assessed the influence of factors possibly underlying the observed urban bird population trends in different European countries. Specifically, we suggest that three factors can shape urban bird population trends. We study these relationships by linking the trends to species' traits that mirror the influence of a given factor, i.e., the species' position along the gradient from woodland to open habitats, the species' association with wetlands, and the site of species' nest.

Firstly, one of the conspicuous environmental changes that cities experience in Europe is expanding green areas (Richards & Belcher, 2020). This process is often deliberately managed by humans to facilitate physical and social benefits provided by the green vegetation (Velasco et al., 2016), but the expansion can also be driven unconsciously by other factors such as spontaneous vegetation succession (Richards & Belcher, 2020). This phenomenon benefits not only humans but also the biodiversity of urban areas (Carrus et al., 2015; Lepczyk

et al., 2017). In Europe, green areas expansion is manifested by increasing urban tree cover (UTC; Nowak & Greenfield, 2020). The increase in UTC may therefore result in growing populations of urbanized woodland birds within cities, where they may find more suitable breeding and foraging sites (Vélová et al., 2023).

Secondly, urban areas hold a rich array of freshwater habitats like streams, rivers, fishponds and artificial ponds in city parks. Although some of these freshwater habitats in cities may be under pressure because of pollution (Mancini et al., 2005; Villalobos-Jiménez et al., 2016), invasive species (Hassall, 2014; Oertli & Parris, 2019) and disturbances (e.g., removal of littoral vegetation; Oertli & Parris, 2019), these habitats may hold wide array of bird diversity (Andrade et al., 2018). This might be due to the absence of some native predators (Fischer et al., 2012; Roshnath et al., 2019), the absence of human hunters (Møller, 2008) and low-intensity use (e.g., for recreational fishery) by the public and authorities (Oertli & Parris, 2019). Cities maintain a warmer climate compared to the surrounding landscape (Bornstein, 1968; Sachanowicz et al., 2019), which might benefit some waterbird species, especially in winter, when there are more non-freezing waterbodies, and frequent provisional feeding by people. In some cases, this might subsequently lead to establishing breeding populations (Møller et al., 2014).

Third, ground breeding is a disadvantage for urban birds (Jokimäki et al., 2016), since some ground-dwelling predators (e.g., beech marten (*Martes foina*), red fox (*Vulpes vulpes*), feral cats) are abundant in cities (Duduš et al., 2014; Kauhala et al., 2015). Also, disturbance by pedestrians or unleashed dogs (Fernández-Juricic, 2002) and the limited area of suitable, persistent breeding habitats (e.g., brownfields) due to building development might play a role. In contrast, the species breeding higher above the ground on buildings or in the tree canopy or cavities are less affected by these risks (Tomasevic & Marzluff, 2017). Therefore, the nest site is also an important trait potentially influencing the population trend of urban birds.

We suggest that the influence of the three above-mentioned factors on national population trends of bird species that frequently breed in urban areas will interact with the strength of birds' association with urban areas expressed as *TSU* and *RU*, respectively. In general, birds urbanized for a longer time (i.e., those having higher *TSU*) should be more susceptible to the adverse changes that occur in urban areas, but they should also better exploit the benefits the urban areas provide (Atwell et al., 2012). In the case of *RU*, the more urbanized species (i.e., those with higher *RU* values) should be more affected (either negatively or positively) by factors acting in the urban environment than the less urbanized species. To explore these expectations, we set an interaction model of each trait with *TSU* and *RU*, respectively. Our study aims to investigate these interactions.

2. Methods

2.1. Bird population trends

We obtained the data for the calculation of population trends from the Pan European Common Bird Monitoring Scheme (PECBMS; <https://pecbms.info/>), a continent-wide programme that aims to monitor the populations of common bird species and produces relevant data on 170 species of European breeding birds. The project involves member states of the European Union (except Malta), Norway, the United Kingdom, and Switzerland. The field data are collected by experienced volunteer fieldworkers using standardised monitoring techniques of point counts, linear counts and territory or spot mapping (Bibby et al., 2000; Brlík et al., 2021; Sutherland, 2006). The species must meet the following two

criteria to be included in PECBMS data set; (i) the population size is > 50 000 pairs in the area covered by PECBMS (with a few exceptions of species for which PECBMS covers most of their breeding ranges), (ii) the species must be detectable using the sampling methods defined as a standard for monitoring of diurnal territorial bird populations (owls and some waterbirds are excluded). To improve the representation of various habitat types within the scheme, specific methods of site selection are employed in respective countries, including random selection, systematic random selection, systematic selection, and free choice by fieldworkers. However, certain habitats may still be over- or underrepresented. Therefore, post-hoc stratification and weighting procedures are implemented during data processing (Brlík et al., 2021). A more detailed PECBMS methods description is available in Brlík et al. (2021).

The field data collected by volunteers are collated each year by the national coordinators, who calculate the national annual population index for every species in each country. The index is estimated using a log-linear model in the TRIM software, taking potential overdispersion and serial correlation (i.e., the nonindependence of data from the same plot surveyed in consecutive years) into account (Bogaart et al., 2020; van Strien et al., 2001). The model runs on annual raw counts on all monitoring sites in a given country and quantifies the relative population change of a given species in a given year (in percentage) in relation to a base year (usually the first year of the time series). For the purposes of this study, these annual national population indices for every species were obtained from national coordinators and used to compute the population trends of respective species in each country.

For each species, the country-level population trend was expressed as a slope of a linear regression fitted through the logarithm of the annual national population indices. We computed these population trends for the period 2000–2016, which represents a compromise between the number of countries with data available and the length of the time series (longer time series would result in fewer countries and vice versa). As a result, we used data from 16 countries for further analysis (Belgium, Czechia, Denmark, Estonia, Finland, France, Germany, Italy, Ireland, Latvia, Netherlands, Norway, Poland, Spain, Sweden, Switzerland). For historical reasons, two of these countries (Germany and Belgium) were divided into two different regions (East and West Germany, Belgium Wallonia and Brussels, respectively) by their national coordinators, and population indices were calculated separately for these regions. We thus considered these regions as additional “countries”, and hereafter we refer to 18 countries for simplification.

2.2. Birds' association with urban areas

Birds' association with urban areas was expressed using two different measures, *TSU* and *RU*. *TSU* was estimated for the species separately in every country based on the information from national ornithological literature scanned by national coordinators. It is defined as the period when the species had established a vital and thriving urban population in a given country. The pioneer settlement was not considered for *TSU* because of a high chance that it would go unnoticed, especially before the increase in the numbers of ornithologists and birdwatchers, and therefore could potentially introduce bias into the data. We were unable to express *TSU* as a continuous measure due to imprecise information in the literature sources. Instead, we expressed *TSU* as an ordinal variable with four values corresponding to four periods: 1 – after 1990; 2 – 1950–1990; 3 – first half of the 20th century; 4 – before the beginning of the 20th century. These periods broadly correspond to important historical changes in the development of urban areas: 1 – post-industrial economy and deep socioeconomic changes in the former Soviet bloc, 2 – economic conjuncture after World War II, 3 – fast urban development and two major armed conflicts in Europe, 4 – industrial revolution linked with massive migration of people into urban areas. *RU* was extracted from Callaghan et al. (2020). It is a quantitative measure of species' relative occurrence in urban areas that are characterised as areas of night lights (VIIRS). This measure is currently the only

continuous urban score proxy available on a continental scale for all species in this study (Callaghan et al., 2021) and it has been validated in recent literature, demonstrating its suitability for ecological research (Callaghan et al., 2019, 2020, 2021). It is a log-transformed species-specific urban score subtracted by the range-specific urbanness value. So, the higher the *RU*, the more the species occurs in urban areas and vice versa (Callaghan et al., 2019, 2020). *RU* is expressed at the species level, so it did not vary across countries.

Data on *TSU* and *RU* were only available for a subset of all 170 bird species included in PECBMS because *TSU* is only defined for urban birds, and *RU* was not expressed for several species. So, we limited our study to 93 species for which both *TSU* and *RU* were available. This resulted in 551 country-species combinations used for further analysis (see Supplementary table S1) because not all species occurred in all countries as urban breeders.

2.3. Other ecological traits

We considered the following traits that are known to shape bird population trends (Cuervo & Møller, 2020; Hanzelka et al., 2019; Laaksonen & Lehtikoinen, 2013; Massa & La Mantia, 2010; Reif et al., 2023; Reif & Hanzelka, 2020). *Cavity nesting* separated the species nesting in cavities or artificial nest boxes, both in trees and on buildings, from the other species. Species categorization was performed using the information from Billerman et al. (2020). *Nest site* (Koleček et al., 2014) sorted the species that place their nests directly on (value = 1) or close to the ground in shrubs and other low vegetation (2) and high above the ground (3). The information was obtained from Billerman et al. (2020). *Habitat niche position* and *breadth* for each species were extracted from Hanzelka et al. (2019). It is based on the classification of the species according to their preferences along the gradient from forest interior (1) to open treeless landscape (7). Each species was assigned by Hanzelka et al. (2019) to three habitat types along this gradient, and the mean of their values was the *habitat niche position*, while the range was the *habitat niche breadth*. *Wetness* was extracted from Hanzelka et al. (2019) and classified the species according to their association with increasingly wet habitats. It discriminated the species associated with dry habitats (1) from wetland birds (2) and water birds (3). *Climate niche position* and *breadth* were extracted from Hanzelka et al. (2019), who calculated the mean temperature (position) and the range of temperatures (breadth) in the European breeding range of each species during its breeding season. *Diet niche position* was excerpted for each species from Hanzelka et al. (2019) and classified the species according to the proportion of plant and animal tissues in their diet from obligatory herbivores (1) to obligatory carnivores (5). *Dietary dependence on insects* gave more emphasis on invertebrates in the diet because the former trait merged carnivory and insectivory. For this purpose, the species were sorted from those fully independent (0) to those fully dependent (2) on insects in their diet. The values were extracted from Reif & Hanzelka (2020).

We also computed principal component analysis (PCA) using the Vegan package (Oksanen et al., 2007) to characterise the species' *life history strategy*. For this purpose, we used species-specific mean values of *body mass*, *egg mass*, *clutch size* and *number of broods per year* obtained in Storchová & Hořák (2018). The most important component revealed by this PCA explained 51.00 % of the variability and classified the species from those with slow strategies ('K-selected' species with large egg mass and body mass, smaller clutches and longer incubation) to those with fast strategies ('r-selected' species; Begon et al., 1986), see Supplementary Fig. 1.

2.4. Statistical analysis

Prior to model composition, we performed pairwise correlation tests of all traits, see Supplementary table S8. To avoid multicollinearity issues due to predictors' correlations, we decided to exclude the traits with a correlation coefficient higher than 0.6 from further analysis

(Dormann et al., 2013). We found two pairs of highly correlated traits: *climate niche range* and *climate niche position* ($r = 0.62$), *diet niche position* and *dietary dependence on insects* ($r = 0.65$). We decided to keep *climate niche position* and *dietary dependence on insects* since these two traits seem to be more important for bird population trends according to previous research (Jiguet et al., 2010; Reif & Hanzelka, 2020).

In the next step, we composed six models to test the influence of factors that might be responsible for the variability in the country-specific long-term population trends (period 2000–2016) of European urban bird species obtained from PECBMS (see section 2.1). Each model contained the explanatory variables describing species' association with urban areas (*TSU* and *RU*) and the other bird species' traits as the main effects and one two-way interaction. All interactions included *TSU* or *RU* and one of the following traits: *nest site*, *habitat niche position*, and *wetness*. We also composed more complex models containing multiple interactions in the pilot analyses, but these models had problems with convergence, so we stayed with testing each interaction in a single model. We also compared the full and simpler models using the Akaike Information Criterion (as computed by the MuMIn package; Bartoń, 2022) to find the best subset of the species' traits; however, the full model, i.e., the model containing all traits, was always the most competitive one (the models differed from the best model with $\Delta AIC > 2$). Therefore, we kept all trait variables included.

The models were generalised linear mixed models (GLMM) with Gaussian error structure and identity link function fitted using the glmmTMB package (Magnusson et al., 2021). Besides the fixed effects described above, each GLMM contained the crossed random effects of country and species following Gamero et al. (2017). We checked model diagnostics using DHARMA (Hartig & Hartig, 2017) and performance (Lüdecke et al., 2021) packages.

All analyses were performed in R software, version 4.2.2. (R Core Team, 2020). We concluded statistical significance at level $p < 0.05$.

3. Results

The six models relating population trends of European urban bird species to variables describing their association with urban areas (expressed as *TSU* and *RU*) and to the interactions of these variables with several other traits showed relatively moderate performance explaining 11.3–13.2 % (marginal R^2) variability in bird trends (Table 1). *TSU* was significant as a main effect in five models, *RU* in two models (Table 1). The interaction effects of *TSU* were not significant in any model, whereas the two out of three tested interactions with *RU* were significant (Table 1).

The relationships of species population trends with *TSU* were consistently negative (Supplementary Tables S2-S7): the earlier

Table 1

Summary of models relating population trends of European urban bird species to variables describing their association with urban areas (time since urbanization – *TSU*, relative urbanness – *RU*), other species' traits and interactions between *TSU* or *RU* and the selected traits. Statistically significant effects are in bold. See Supplementary Tables S2-S7 for the full results of each model. Conditional (R^2_c) and marginal (R^2_m) coefficients of determination are presented.

ID	Main effects	Interaction effects	R^2_c	R^2_m
Model 1	<i>TSU</i> , <i>RU</i> , other species' traits	<i>TSU</i> x <i>wetness</i>	41.4 %	11.7 %
Model 2	<i>TSU</i> , <i>RU</i> , other species' traits	<i>TSU</i> x habitat niche position	41.1 %	11.5 %
Model 3	<i>TSU</i> , <i>RU</i> , other species' traits	<i>TSU</i> x <i>nest site</i>	42.0 %	11.4 %
Model 4	<i>TSU</i> , <i>RU</i> , other species' traits	<i>RU</i> x <i>wetness</i>	42.1 %	11.3 %
Model 5	<i>TSU</i> , <i>RU</i> , other species' traits	<i>RU</i> x habitat niche position	41.4 %	11.6 %
Model 6	<i>TSU</i> , <i>RU</i> , other species' traits	<i>RU</i> x nest site	41.8 %	13.2 %

urbanized birds had more negative trends than the more recently urbanized species (Fig. 1). The main effect *RU* was once positive (Supplementary Table S7), indicating that more urbanized species had more positive trends and once negative (Supplementary Table S6) indicating the opposite. However, these main effects were only present in the models that contained a significant interaction of *RU* with one of the other species' traits, so they must be interpreted in the light of these interactions. Specifically, the interaction of *RU* and *Nest site* showed that the more urbanized ground-breeding birds had more positive population trends than less urbanized ground-breeding birds (Fig. 2). The pattern became weaker, but the direction remained the same in species breeding in shrubs or low vegetation, and the pattern reversed in species breeding in trees (Fig. 2). The interaction between *RU* and *Habitat niche position* showed a marked difference in trends between woodland birds and open landscape birds in the least urbanized species (Fig. 3). In this case, woodland birds had more positive population trends than open habitat birds (Fig. 3). However, the difference disappeared with progressing urbanization, and the pattern was even slightly reversed in the most urbanized species (Fig. 3).

The other species' traits not included in the interactions with *TSU* and *RU* were considered to account for possible effects of other factors potentially shaping the population trends. Three of these traits showed significant effects (Supplementary Tables S2-S7). *Life history strategy* was negatively associated with the bird's population trends (Supplementary Tables S1-S4, S6), meaning that K-selected species had more positive population trends than birds belonging to r-selected species. *Cavity nesting* was positively associated with the population trends (Supplementary Tables S1-S5) and showed that cavity-nesting species had more positive trends than those not nesting in cavities. *Habitat niche position* was significantly negatively related to the bird population trends in addition to the models where it was included in the interaction with *TSU* or *RU* (Supplementary Tables S5), showing that birds breeding in open areas have more negative trends than birds breeding in woodland areas.

The *nest site* was not significant in any model apart from where it was included in the interaction with *RU* (Supplementary Table S7). *Climate niche position*, *Dietary dependence on insects*, *Wetness* and *Habitat niche breadth*, were not significant in any of the fitted models (Supplementary Tables S2-S7).

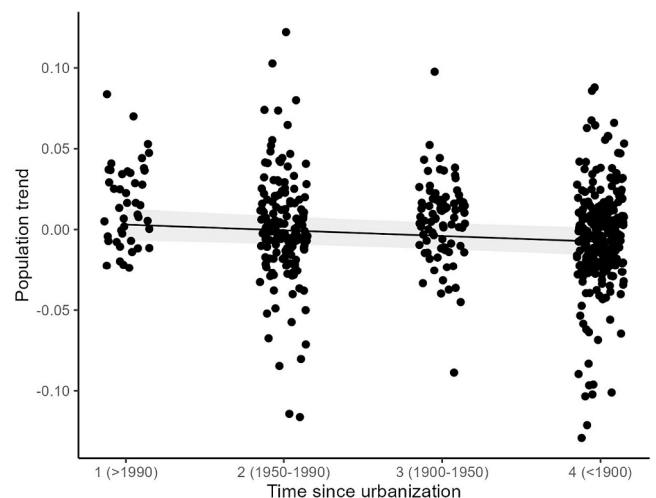


Figure 1. The relationship between population trends of European bird species breeding in urban areas and time since their urbanization. The higher the value, the longer time since urbanization. The results are estimated by a generalised linear mixed model (see Supplementary Table S7 for full model results). The 95% confidence interval is shown.

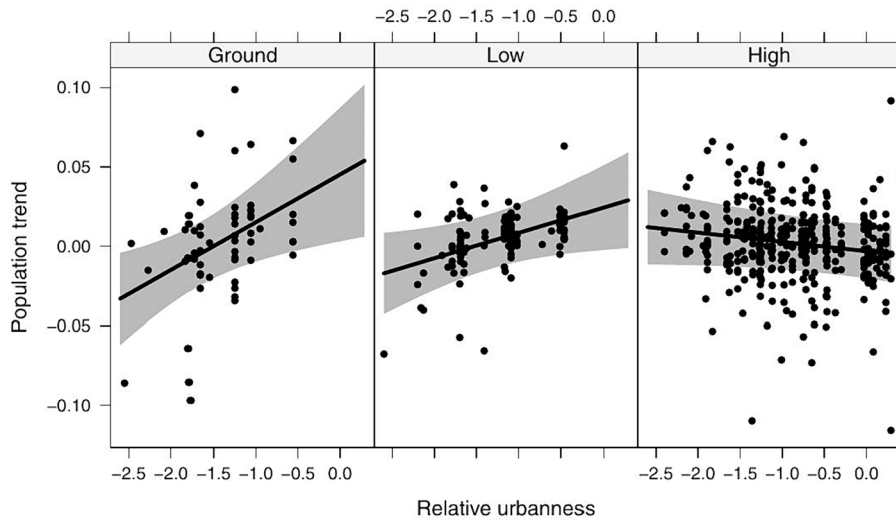


Figure 2. The relationship between population trends of European bird species breeding in urban areas and their relative urbanness in the interaction with species’ nest site. Relative urbannes expresses species’ association with urban areas, the higher the value, the more urbanized species. Figure is divided into three parts according to the nest site selection: breeding on the ground – left, breeding close to the ground in shrubs and low vegetation – centre, breeding high above ground on trees or buildings – right. The results are estimated by a generalised linear mixed model (see [Supplementary Table S7](#) for full model results). The 95% confidence intervals are shown.

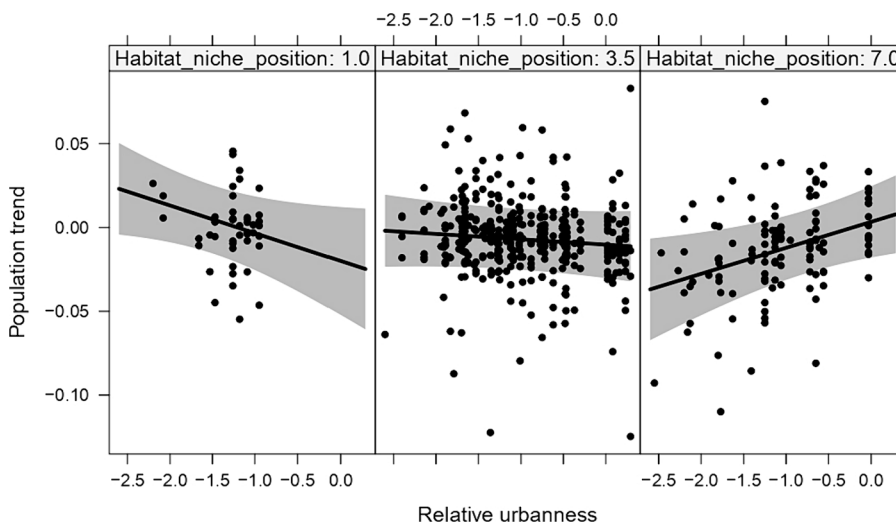


Figure 3. The relationship between population trends of European bird species breeding in urban areas and their relative urbanness in the interaction with species’ habitat niche position. Relative urbannes expresses species’ association with urban areas, the higher the value, the more urbanized species. Habitat niche position is the gradient from forested landscape (lower values) to the fully open landscape (higher values). The results were estimated by a generalised linear mixed model (see [Supplementary Table S7](#) for full model results). The 95% confidence intervals are shown.

4. Discussion

National population trends of bird species breeding in urban areas of 18 European countries were analysed in relation to two different measures of species’ urbanization – time since urbanization (*TSU*) and relative urbanness (*RU*). These measures quantify for how long a given species has bred in urban areas of a given country (*TSU*) and how strongly it is associated with urban areas in Europe (*RU*). By relating the population trends to these measures and the other species’ traits, we found the following three main patterns. (i) The more recently urbanized species had significantly more positive population trends than pre-industrial urban dwellers. (ii) Highly urbanized species of open habitats had more positive population trends than highly urbanized birds of woodland habitats, while the reverse was true for less urbanized species. (iii) Within highly urbanized species, birds breeding on the ground had more positive trends than above-ground breeders.

Species that colonized urban areas in the pre-industrial era (e.g., house sparrow (*Passer domesticus*), house martin (*Delichon urbicum*)) had more negative population trends than the recent colonisers. This pattern can be driven by the rapid environmental change in cities, especially in vegetation and buildings, that affects the availability of breeding and foraging opportunities (Møller, 2010b; Tryjanowski et al., 2017). By that means, the earlier urbanized birds are losing the habitat present in urban areas in the time when they colonised the cities, and therefore their urban populations are declining. One of the groups of disappearing urban birds might be species breeding on buildings. Ongoing modernisation of cities leads to fewer breeding opportunities for these species (fewer cavities, new surfaces inhibiting the possibility of placing the nest), and therefore these might suffer population declines (Rosin et al., 2021). Another possible mechanism for disappearing of pre-industrial urban birds could be the removal of the organic waste from the public space, which served as a food source for many species with generalist

diets, such as house sparrow (Bernat-Ponce et al., 2018). Finally, species that colonized cities a long time ago may decline steeply after some of their predators become urbanized (Tomialojc, 2021). We didn't find any support for interactions of *TSU* and other species traits. It is possible that the environmental changes the early urban colonizers face are diverse and not confined to a single or a few habitats.

RU showed an interaction with habitat niche position when more urbanized open habitat species had more positive trends than more urbanized woodland habitat species, while open habitat species had more negative trends than woodland habitat birds within less urbanized species. This interaction remained significant ($P = 0.039$) even after excluding waterbird species that typically breed in open habitats and have recently increased their populations in European cities (Keller et al., 2020). These results do not support our initial expectation that expansion of urban tree cover (Nowak & Greenfield, 2020) will provide opportunities for population increases of urbanized species breeding in woody vegetation. It is possible that the recent greening of European cities does not provide habitat of sufficient quality for breeding birds. The habitat quality may be compromised by, for example, use of non-native tree species for these purposes (Pyšek, 1998) that often host impoverished ecological communities (Hejda et al., 2017).

Another possible mechanism that may contribute to the absence of the initially expected pattern is that the urban parks and gardens are actually a mid-range habitat type that is more suitable for woodland edge and generalist species. As a result, the data do not reveal a linear relationship between habitat niche position, *RU*, and long-term population trend. Additionally, the increase in less urbanized woodland birds could be attributed to the maturing of urban forests and parks, leading to the presence of different bird communities in less developed vegetation areas (Fernández-Juricic, 2000; Zawadzka et al., 2018). Finally, improvement of population trends of woodland birds among less urbanized species likely mirrors general increases of woodland bird populations in various European countries (Bowler et al., 2021; Ram et al., 2017; Storch et al., 2023) that are linked to the amounts of forests or to forest management (Reif et al., 2022; Schulze et al., 2019) and not to factors acting in urban areas.

The difference in population trends between more and less urbanized open habitat species is interesting and rather unexpected. We suggest that this pattern is driven by agricultural intensification. Many studies provide evidence for ongoing agricultural intensification in rural areas across Europe negatively influencing biodiversity (Donald et al., 2006; Reif & Hanzelka, 2020; Stoate et al., 2009), whereas urban areas do not provide conditions for intensive agricultural use. At the same time, urban areas offer suitable habitats for various open habitat species due to the presence of brownfields and extensive sites under construction. Consequently, European cities might harbour some species of open landscape birds, which are often in decline in the European range due to intensive agriculture (Donald et al., 2001; Reif & Vermouzek, 2019). In our dataset, such conditions may be reflected by less negative trends in more urbanized open habitat species (e.g., marsh warbler (*Acrocephalus palustris*), greater whitethroat (*Curruca communis*)) than in less urbanized open habitat species (e.g., skylark (*Alauda arvensis*), yellow wagtail (*Motacilla flava*)). Therefore, human settlements might act as refugia for some open landscape birds (Fuller et al., 2009; Šálek et al., 2018). In addition, as the abundant population in rural areas is one of the prerequisites of successful colonisation of cities (Evans et al., 2010), we suggest that the negative national population trends of open habitat birds widely reported in the last decades (Burns et al., 2021; Flohre et al., 2011; Gregory et al., 2019) may effectively hamper the progress of their urbanization.

Most studies focusing on the use of different nest sites by urban birds conclude that the ground breeding species are at a disadvantage compared to birds breeding above the ground (Lakatos et al., 2022; McMahon et al., 2020). This may happen due to frequent disturbance by humans and their pets, as well as due to a higher risk of nest predation from the side of predators associated with human settlements, such as

beech marten or feral domestic cats (Duduš et al., 2014; Krauze-Gryz et al., 2019). Surprisingly, we did not find support for this pattern. Instead, the highly urbanized birds breeding on the ground had more positive population trends than highly urbanized birds breeding in bush or trees and buildings (Fig. 2). We offer several explanations for this unexpected pattern. First, highly urbanized species should be able to cope with the high human or predator pressure in cities which likely persists for decades (e.g., mallard (*Anas platyrhynchos*)). From this perspective, the absence of the negative population trends in ground breeders is not that surprising because the species being vulnerable to this kind of risk would simply not survive in urban areas, and such species are most likely not urbanized at all. In contrast, species breeding on buildings may greatly suffer from recent changes in building technologies – studies indicate that species such as barn swallow (*Hirundo rustica*) or house martin cannot find suitable nest sites in cities (Balaji, 2014; Teglhøj, 2017). This adverse impact is likely to be particularly strong in the highly urbanized species that do not have habitat alternatives. Also, the trees in urban parks and streets are carefully managed, and the old branches and trees (often ones offering cavities) are removed. This might lead to a reduced number of breeding opportunities available and subsequently to higher inter-specific competition of native and non-native bird species (Dodaro & Battisti, 2014). Second, another mechanism underlying the observed pattern in trends might be the same that we propose for the interaction between species' position along the woodland-open habitat gradient and relative urbanness, i.e., agricultural intensification, when urban areas may act as refuges for the open-habitat species (Černý et al., 2020; Šálek et al., 2004). As ground breeding is often associated with a preference for open habitats (Minias & Janiszewski, 2023; Storchová & Hořák, 2018), ground breeders may thrive in cities to avoid the impacts of agricultural intensification. Third, the positive trends of highly urbanized ground breeders might also be linked to positive trends in wetland birds that have exploited urban areas successfully in the last decades (e.g., moorhen (*Gallinula chloropus*), mute swan (*Cygnus olor*)), because breeding in wetlands typically occurs on the ground (Storchová & Hořák, 2018).

Our results highlight the importance of novel variables describing species' urbanization, namely its timing (*TSU*) and objectively measured affinity to urban areas (*RU*). Despite their importance, previous studies only rarely took them into account (Guetté et al., 2017; Møller et al., 2012). Their limited use by researchers was probably caused by problems in acquiring suitable data. For instance, in the case of *TSU*, the historical ornithological literature containing information on the timing of urbanization is difficult to access, often written in national languages. In the case of *RU*, birds' affinity to urban areas was traditionally described by categorical variables (Blair, 1996; Kark et al., 2007; Palacio, 2020) and the continuous measure of urbanization became only recently available, even though it is expressed at the continental scale only (Callaghan et al., 2019, 2020; Guetté et al., 2017). For future studies, we recommend further use and elaboration of these urbanization variables by, for example, obtaining more detailed information on the timing of urbanization in the case of *TSU* and by regional-specific expression of *RU*. As *RU* is based on artificial light at night, future use of this measure may be compromised by recent efforts to reduce light pollution in European cities (Ministry of the Environment of the Czech Republic, 2022).

Even though the results of this study could be well explained by factors acting within cities as well as outside city borders, they have to be treated with caution. This is because using national population trends, which are based on data not necessarily restricted to urban areas, may inevitably be influenced by other mechanisms that act outside urban areas and could not be included in our models. National trends are frequently used for inferences about forest and farmland birds (see Gregory et al., 2019) and we followed this approach here for urban birds. However, in this case, the results should be interpreted with caution because the species had shorter evolutionary time to adapt to this environment, resulting in more generalist species occupying cities

compared to the other habitats (Callaghan et al., 2019). This may weaken the influence of urban environment on the national population trend, particularly concerning less urbanized species whose populations in some European countries include rural areas.

To our knowledge, our study is the first one that investigates drivers of population trends for birds breeding in urban areas at large spatial and temporal scales. For the future research, a more detailed approach to establishing species' population trends for specific environments, in this case for the urban areas or even their specific types, would be highly valued. Such studies may specifically focus on comparison of trends between urban and rural areas of the same country or on spatial patterns in trends across countries.

4.1. Conservation implications

Based on our results, we can formulate the following recommendations for conservation practice:

1. Although urban areas are considered a threat to biodiversity due to their expansion, also the processes altering the habitats within city boundaries can be important, as the decreasing trends of early urban colonizers indicate. It seems that such species can no longer efficiently exploit the opportunities provided by urban environments and may become at risk because they do not have many alternative habitats. Therefore, a thorough risk assessment for such species is needed.
2. Population trends of highly urbanized woodland birds indicate that the expansion of urban tree areas is not providing benefits for biodiversity until now. If this applies to other taxa too, recent initiatives for the greening of the cities might become a lost opportunity. Therefore, a deeper investigation of the suitability of woody plant species for support of biodiversity is needed, and, at the very least, native trees should be preferred.
3. Population trends of highly urbanized open habitat species are encouraging, suggesting that urban areas may act as refuges for such species. This underscores the importance of unbuilt open habitats within city borders. They not only serve for the recreation of human inhabitants and visitors, but also as habitats for biodiversity. Therefore, the existence of such areas should be considered in urban planning.
4. The effect of nest location on population trends of birds breeding in urban areas indicates that species breeding higher above the ground may suffer from the lack of breeding opportunities. It may be due to the use of building materials that do not provide nest sites for birds. Although it is unlikely to change it, conservation practice can mitigate the negative impacts by providing alternative nest sites such as nest boxes.

5. Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly typing assistant to improve language and readability of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Jan Grünwald: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Ainārs Auniņš:** Writing – review & editing, Investigation. **Mattia Brambilla:** Writing – review & editing, Investigation. **Virginia Escandell:** Writing – review & editing, Investigation. **Daniel Palm Eskildsen:** Writing – review & editing, Investigation. **Tomasz Chodkiewicz:** Writing – review & editing, Investigation. **Benoît Fontaine:** Writing – review & editing, Investigation. **Frédéric Jiguet:** Writing – review & editing,

Investigation. **John Atle Kålås:** Writing – review & editing, Investigation. **Johannes Kamp:** Writing – review & editing, Investigation. **Alena Klvaňová:** Writing – review & editing, Project administration, Data curation. **Lechosław Kuczyński:** Writing – review & editing, Investigation. **Aleksi Lehikoinen:** Writing – review & editing, Investigation. **Åke Lindström:** Writing – review & editing, Investigation. **Renno Nellis:** Writing – review & editing, Investigation. **Ingar Jostein Øien:** Writing – review & editing, Investigation. **Eva Šilarová:** Writing – review & editing, Project administration, Data curation. **Nicolas Strebel:** Writing – review & editing, Investigation. **Thomas Vikstrøm:** Writing – review & editing, Investigation. **Petr Voříšek:** Writing – review & editing, Project administration, Data curation. **Jiří Reif:** Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are shared in Supplementary Online Materials (Supplementary Table S1), the code will be available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.111926>.

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