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Population trends of ground-nesting birds indicate increasing environmental impacts from Eastern to Western Europe: different patterns for open-habitat and woodland species

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Introduction: Bird populations reflect the influence of major environmental changes, and the analysis of their long-term population trends concerning species-specific ecological traits can provide insight into biologically relevant impacts of such changes. In this respect, nest site is a particularly informative trait because ground-nesting bird species are more prone, in contrast to species nesting above the ground, to the impacts of nest predation which can be linked to various environmental drivers including the intensification of agriculture or woodland management. Here we hypothesize that a) ground-nesting species present negative trends due to environmental pressures mentioned above, b) such declining trends should be more pronounced in Western than in Eastern Europe because, in Western countries, the environmental threats are likely greater, and c) the interaction between nest site and habitat association will point at the habitat types where the presumed drivers most likely operate.

Methods: We used population trends from 1980 to 2016 of 332 bird species in 16 European countries to test this hypothesis.

Results: We found that the long-term population trends of ground-nesting birds are more negative than the trends of species nesting above the ground indicating the effect of nest predation, and this difference increased from Eastern to Western European countries, probably due to steeply increasing populations of nest predators in the West. However, the effect of longitude interacted with the habitat association being strong in woodland species and weak in open-habitat species.

Discussion: This pattern suggests that the increased nest predation pressure in the West is linked to woodlands, probably due to higher abundances of mammalian herbivores that destroy forest ground and shrub layer, and thus leave the nests exposed to predators. In contrast, only a weak longitudinal pattern in open-habitat species indicates that the negative impacts of agricultural intensification are no longer confined to the Western part of the continent. Although nature conservation activities are generally successful in Europe, as indicated by benefits provided by the Natura 2000 network, our results uncovered substantial gaps in delivering such benefits.

KEYWORDS

birds, environmental indicators, nest predation, agricultural intensification, geographic gradients, Europe, forest management

Introduction

Bird populations reflect the influence of major environmental changes (Morelli et al., 2021), which makes birds widely used landscape-scale biodiversity indicators (Fraixedas et al., 2020). They integrate factors acting over large areas (Jørgensen et al., 2016), and their position at the top of food chains makes them suitable for informing about ecosystem functioning (Galetti et al., 2012). Therefore, investigating long-term trends in bird populations may provide important insights into the most important conservation issues (Gregory and Van Strien, 2010). In this respect, comparing the trends among bird species differing in their ecological traits is particularly informative (Reif et al., 2010; Estrada et al., 2016) because they can reflect the impacts of different pressures (Webb et al., 2010).

Agricultural intensification is one of the most important and persistent pressures on bird populations (Lees et al., 2022). Its impacts are reflected by decreasing population trends of open-habitat species (Chamberlain et al., 2000; Stoate et al., 2009; Stanton et al., 2018). Due to lower agricultural intensity in Eastern compared to Western Europe (Tryjanowski et al., 2011; Sutcliffe et al., 2015), a clear longitudinal gradient showing increasingly negative trends toward the West has been repeatedly reported (Donald et al., 2001; Reif and Hanzelka, 2020).

However, environmental pressures act in woodland habitats, too. While populations of forest bird species increase in Central and Eastern Europe (Bowler et al., 2021; Reif and Hanzelka, 2020) and recent studies uncovered the links to suitable forest management performed in this region (Machar et al., 2019; Schulze et al., 2019), trends of woodland birds are negative in Western Europe (Gregory et al., 2007; Reif, 2013). The driver may be unsuitable forest management with short rotation period and large clearcuts (Fraixedas et al., 2015; Ram et al., 2017), but also the pressure from the side of large mammalian herbivores (Newson et al., 2012). They destroy plant vegetation on the ground and in the shrub layer and leave bird nests expose to nest predators (Martin and Maron, 2012).

The impact of nest predation should be particularly strong in ground nesting species. Whereas the species nesting high above the ground in the tree canopy or cavities of tree trunks are relatively safe during their breeding period (Cockle et al., 2011; van der Hoek et al., 2017), the species nesting on or near the ground are much more prone to nest predation (e.g., Weidinger, 2004; Roos et al., 2018). In addition, they may suffer from human disturbance when human presence near a bird nest may cause its desertion (Bocz et al., 2017). In addition, nests on the ground are more likely to be destroyed by agricultural operations (Sheldon et al., 2007). Due to such exposure, European breeding populations of ground-nesting birds exhibit long-term declines (Fuller et al., 2002; Massa and La Mantia, 2010; Guerrero et al., 2012). Recently, McMahon et al. (2020) found that the ground nesters had more negative population trends than other birds and that this difference in trends was larger in Britain and Ireland than in mainland Europe. These authors speculate that increasing predation pressure may produce such a pattern.

We hypothesize that due to possible impacts of the above-mentioned drivers, bird species nesting on the ground should have particularly negative population trends. Moreover, as these pressures are supposed to increase from Eastern towards Western Europe, we predict that population trends of ground-nesting birds should follow this longitudinal gradient. We suggest that the interaction of nest site (ground vs. above ground) with species' habitat association (open vs. woodland habitats) will uncover the habitat types where the presumed drivers most likely operate.

We test our hypotheses using country-level data on European bird population trends (Burns et al., 2021). Specifically, we explore spatial variability in the country-level trends along the longitudinal gradient concerning the interaction between species' habitat association and nest site controlling for the influence of the other ecological traits known to affect bird populations (Hanzelka et al., 2019).

Materials and methods

We extracted data on long-term trends in breeding bird population sizes from Burns et al. (2021). This dataset contains trends of 332 bird species in 16 European countries from 1980 to 2018, covering the largest number of species in Europe over a considerably long time period representing 1887 species-country combinations (Supplementary Table S1). The dataset is based on the information provided by the EU member states in a report on the state of their bird populations to the European Commission in 2019 (Eionet, 2020). In this report, the trend data were constructed either from complete surveys over the focal period in respective countries or from extrapolation of limited national surveys. In a small number of species, expert opinion was applied to estimate the national trend (Burns et al., 2021).

Following Keller et al. (2020), the original population trend estimates provided in percent, that are highly imbalanced concerning the magnitude of decreases (cannot be larger than 100%) and increases (maximum is not limited and reaches tens of thousands in some cases) which hamper interspecific comparisons, were transformed to a unitless measure from −2 (largest possible increase) to + 2 (largest possible decrease). This transformation thus unifies the scale of population changes and makes population increases and decreases comparable (Keller et al., 2020).

From published sources (Storchová and Hořák, 2018; Hanzelka et al., 2019), we obtained data on species' ecological traits (Table 1; Supplementary Table S1). *Nest site* was a categorical variable discriminating ground nesters from the other species. Species' *habitat association* expressed position of each species along a gradient discriminating closed forest (1), open forest (2), forest edge (3), savannah, orchard or garden (4), scrubland (5), open country with solitary trees or shrubs (6), and open treeless landscape (7). Each species was assigned to 1–3 of these habitat types and the position was calculated as a mean across values of those types. *Habitat breadth* was the range of values of the habitat types used by the species along the same gradient. For instance, a species breeding both in closed forest (1) and at forest edges (3) had the habitat breadth value calculated as

TABLE 1 List and definitions of species ecological traits used in the analysis of long-term population trends.

Trait	Definition
Nest site	Location of the nest in respect to the ground: ground nesters vs. other species
Habitat association	Position along the gradient from closed forest (1) to open landscape (7)
Habitat breadth	Range of values between occupied habitats along the same gradient from closed forest (1) to open landscape (7)
Habitat wetness	Position along the gradient from dry habitats (1) to water bodies (3)
Association with urban areas	Tolerance to breeding in urban: urban avoiders (0) vs. urban tolerating or preferring species (1)
Diet	Increasing proportion of animal contents in diet from obligate herbivores (1) to obligate animovores (5)
Climatic niche position	Mean of spring temperature in species' breeding ranges in Europe
Climatic niche breadth	Range of spring temperatures in species' breeding ranges in Europe
Migration distance	Distance between centroids of species' breeding and non-breeding ranges
Life history strategy	Position along the gradient from 'slow' to "fast" strategies defined by six life history traits
Listing under Annex I	Listing under the Annex I of the European Union's Birds Directive: unlisted (0) vs. listed species (1)

3–1 = 2, whereas a species breeding solely in closed forest had the habitat breadth value calculated as 1–1 = 0. *Habitat wetness* reflected water balance of species' breeding habitat recognizing dry habitat types (1), wet habitats such as swamps or wet grasslands (2), and water bodies (3). *Association with urban areas* expressed species' relations to human settlements classifying the species as those avoiding these areas (0) and those tolerating or preferring these areas (1). *Diet* expressed species' position along the gradient of increasing animal content recognizing species feeding strictly on plants (1), species feeding mainly on plants (2), species feeding on both plants and animals in roughly the same proportions (3), species feeding mainly on animals (4), and species feeding strictly on animals (5).

Following three traits are based on the analysis of maps of species' breeding and non-breeding geographic ranges provided by BirdLife International and Nature Serve. (2018) and performed by Hanzelka et al. (2019). They overlaid European breeding range of every species with map of mean temperatures (in °C) in April-June for the period 1961–1990 (Haylock et al., 2008) and calculated the mean temperature and the range of temperatures in the breeding range of each species. The mean temperature can be considered as species' *climatic niche position*, while the range of temperatures can be considered as its *climatic niche breadth*. *Migration distance* was the distance (in km) connecting the centroid of species' breeding range in Europe and the centroid of its non-breeding range. Data on six life-history traits (namely body mass, egg mass, clutch size, number of breeding attempts, incubation time, and fledging time) were used to express species' *life-history strategy* as a position of every species along a gradient from slow ("K-selected" species) to fast ("r-selected" species) strategies represented by the first axis from the principal component analysis on those traits.

Finally, *listing under Annex I* recognized each species as listed (1) or unlisted (0) under the Annex I of the European Union's Birds Directive. Listed species are those of EU-wide conservation concern and enjoy delimitation of Special Protected Areas for improvement of their population status (Koschová et al., 2018).

For further analysis of the longitudinal patterns in population trends, we determined centroid of every country as its geographic center of gravity and expressed its *longitude* in decimal degrees. The longitudinal gradient covered by the focal countries spanned almost 11° (ca 2,500 km) from Ireland and the United Kingdom in the West to Finland, Hungary or Greece in the East. To take the unequal area of respective countries into account, we also considered *country's area*.

We related long-term population trends to nest site and other species' traits using linear mixed-effects models in R 3.4.1 (R Core Team, 2017), the package "nlme" (Pinheiro, 2021). In these models, population trend was the response variable, and the species' ecological traits together with countries' longitude and area were the fixed effects explanatory variables. Following the approach applied in similar studies (e.g., Hanzelka et al., 2019), the random effects contained hierarchical taxonomic levels of species/family/order as a random intercept to account for potentially similar trends of more closely related species (Jiguet et al., 2010; Gamero et al., 2017) and to account for the occurrence of the same species in different countries. To explore the predicted longitudinal gradient in population trends of ground-nesting birds associated with different habitat types, we tested a three-way interaction between habitat association, nest site, and countries' longitude. The other traits were included as the main effects. For inference, we used the full model containing the focal interaction and accounting for the effects of all other species traits.

This model was formulated as follows:

$$\begin{aligned}&\text{population trend} \sim \text{scale}(\text{habitat breadth}) + \text{scale}(\text{habitat wetness})\\&+ \text{scale}(\text{association with urban areas}) + \text{scale}(\text{diet})\\&+ \text{scale}(\text{climatic niche position}) + \text{scale}(\text{climatic niche breadth})\\&+ \text{scale}(\text{migration distance}) + \text{scale}(\text{life} - \text{history strategy})\\&+ \text{scale}(\text{listing under Annex I}) + \text{scale}(\text{countries}'\ \text{area})\\&+ \text{scale}(\text{countries}'\ \text{longitude}) * \text{scale}(\text{habitat association}) * \text{nest site, random}\\&= \sim 1|\text{order}/\text{family}/\text{genus}/\text{species, method} = "\text{ML}"\end{aligned}$$

Numerical predictors were standardized to zero mean and unit variance using the "scale" function in the analysis. Model residuals did not indicate any violation of model assumptions. As pairwise correlations between predictors showed $|r|<0.45$, indicating that multicollinearity was not an issue in our data.

TABLE 2 Relationships between bird population trends and predictor variables (species' traits and countries' longitude and area) estimated by a linear mixed model across 16 European countries. Numeric predictors were scaled to zero mean and unit variance. Significant relationships are in bold.

Predictor variable	Coefficient	SE	df	t	P
Intercept	−0.022	0.068	1,551	−0.327	0.743
Nest site (other)	**0.232**	**0.086**	**128**	**2.707**	**0.008**
Habitat association	−0.113	0.072	128	−1.573	0.118
Habitat niche breadth	0.017	0.035	128	0.48	0.632
Habitat wetness	**0.182**	**0.042**	**128**	**4.371**	**<0.001**
Association with urban areas	−0.003	0.038	128	−0.091	0.928
Diet	0.014	0.035	128	0.389	0.698
Climatic niche position	**0.092**	**0.027**	**128**	**3.464**	**0.001**
Climatic niche breadth	−0.01	0.029	128	−0.343	0.732
Migration distance	−0.011	0.035	1,551	−0.292	0.77
Life history strategy	**−0.187**	**0.034**	**128**	**−5.507**	**<0.001**
Listing under Annex I	0.044	0.035	128	1.258	0.211
country's longitude	**0.186**	**0.037**	**1,551**	**4.973**	**<0.001**
Country's area	−0.011	0.018	1,551	−0.638	0.523
Nest site (other) × habitat association	0.011	0.08	128	0.141	0.888
Nest site (other) × longitude	**−0.193**	**0.046**	**1,551**	**−4.233**	**<0.001**
Habitat association × longitude	**−0.114**	**0.037**	**1,551**	**−3.058**	**0.002**
Nest site (other) × habitat association × longitude	**0.124**	**0.046**	**1,551**	**2.724**	**0.007**

Results

Overall, positive population changes dominated the dataset since 952 species-country combinations showed positive population trends, 783 showed negative trends and 152 no change (Supplementary Table S1). Ground nesting species dominated among birds with the most negative population trends signifying their extinctions in respective countries (17 out of 24 such events concerned ground nesters) such as Hazel Grouse (*Bonasia bonasa*) in Belgium or Eurasian Dotterel (*Charadrius morinellus*) in Czechia (Supplementary Table S1). On the other hand, rapid population growth, that species typically show during colonization of new countries, was characteristic of the other species than the ground nesters (42 out of 59 events concerned species nesting above the ground), such as Common Firecrest (*Regulus ignicapilla*) spreading to Sweden or Middle Spotted Woodpecker (*Leiopicus medius*) to the Netherlands (Supplementary Table S1).

The three-way interaction between habitat association, nest site, and longitude was highly significant (Table 2). Specifically, population trends of woodland-habitat ground-nesting species changed from negative to positive with increasing longitude, whereas no longitudinal change was observed for woodland-habitat species nesting above the ground (Figure 1). These results show that population trends of woodland-habitat ground-nesting birds decrease in Western Europe. At the same time, the contrary is true in Eastern Europe (Figure 1). The contrasting patterns of change in population trends along the longitudinal gradient observed between ground and above-ground nesters were much less pronounced in species breeding in open habitat types (Figure 1). However, even in these habitat types, birds breeding on the ground had slightly more negative trends in Western longitudes than in the East (Figure 1). In general, ground nesting was less risky in Eastern than in Western Europe as shown by a significant two-way interaction between nest site and longitude (Table 2). Moreover, ground nesting was linked to negative trends across the habitat associations as indicated by a significant main effect of nest site and a non-significant interaction of nest site with habitat association (Table 2).

In addition to the nest site and its interaction with habitat association and longitude, long-term population trends were related to a climatic niche position, habitat wetness, and life-history strategy (Table 2). Specifically, population trends were more positive in species breeding in warmer than in colder areas of Europe, in species breeding in wetter than in drier sites, and in species with slower than faster life-history strategies (Table 2).

Discussion

Our analysis using bird population data across the European continent showed that the population of woodland-habitat ground-nesting species decreases sharply in direction of Western Europe. At

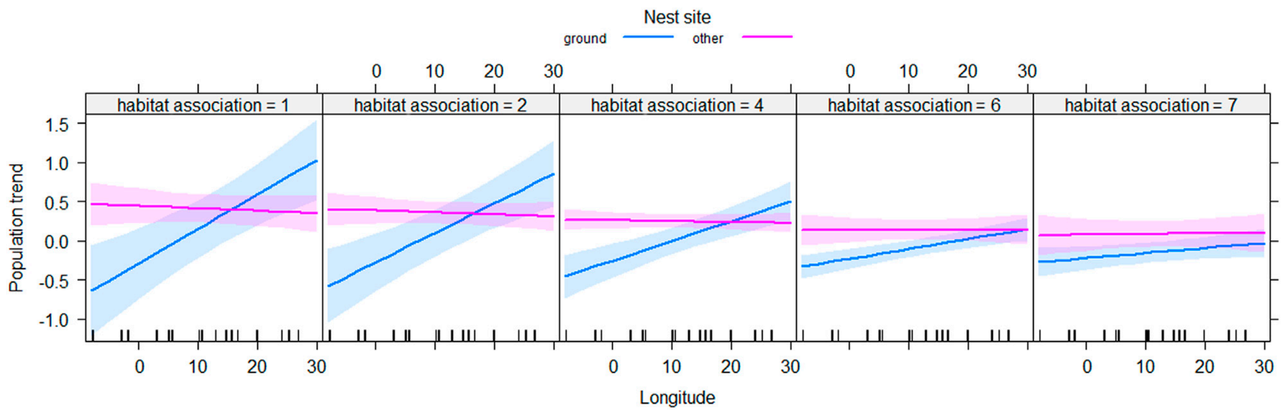

FIGURE 1
Relationship between bird population trends in 16 European countries and the three-way interaction of species' nest site (discriminating ground nesters from the other species), habitat association [gradient from closed forest (1) to open treeless landscape (7)], and countries' longitude. See Table 2 for coefficients estimated by the model.

the same time, such populations increase towards Eastern Europe. Moreover, the species nesting above the ground had slightly more positive population trends than ground nesters, even in open habitats and at different longitudes. The observed switch from population increases to decreases of woodland-habitat ground-nesting species from the East to the West of Europe can be explained by impacts of nest predation pressure in the interaction with other environmental drivers as discussed below.

The key factor that likely underpinned the observed pattern in bird trends is nest predation. Ground-nesting species are considered highly susceptible to nest predation in contrast to the species breeding above the ground (Martin, 1995). Therefore, one reason for the observed gradient in ground nesters' population trends may be increasing nest predation pressure towards the West. McMahon et al. (2020) suggest that the increased predation pressure is caused by increasing populations of opportunistic nest predators, such as corvids or feral cats, whose populations are particularly increasing in Western European countries such as the United Kingdom (Roos et al., 2018). These predators may threaten birds' nests on the ground if they are placed close to perching posts such as trees or shrubs (Huhta et al., 1996; Suvorov and Šálek, 2013; Atuo and O'Connell, 2017).

However, the generally higher nest predation pressure in the West cannot explain why the longitudinal gradient in population trends of ground nesters is associated with woodland birds and not with birds breeding in open habitats. We suggest that Western European populations of ground nesting woodland birds suffer from the adverse impacts of abundant populations of mammalian herbivores. Their browsing pressure can effectively destroy vegetation in forest ground and shrub layer resulting in increased nest exposure to predators (Martin and Maron, 2012). Indeed, a study from the United Kingdom (Newson et al., 2012) showed that high and increasing populations of woodland deer species have large-scale detrimental impacts on numerous ground nesting birds associated with woodland habitat including Common Nightingale (*Luscinia megarhynchos*), Willow Warbler (*Phylloscopus trochilus*) and Chiffchaff (*Phylloscopus collybita*). This impact particularly concerns the non-native deer species that are common in Western countries (Ferretti and Lovari, 2014).

The negative population trends of ground nesting woodland birds can be also linked to negative impacts of forest management. While forest mature in Central and Eastern Europe (Reif and Vermouzek, 2019; Schulze et al., 2019), the reverse is true in Western Europe where forests are harvested more intensively (Kuemmerle et al., 2016). The intensive forest exploitation can be particularly problematic for bird species sensitive to human presence, i.e. those with long flight initiation distance (Møller, 2008)–when woodland is approached by workers performing timber harvesting, birds are probably chased from their nests leaving them available for nest predators. Since nest predation is more likely acting on the ground nests than on the nests placed higher above the ground (McMahon et al., 2020), the more intensive forest management can underpin population declines of ground nesting woodland birds in Western Europe.

Agricultural operations may be another factor driving population declines of ground nesting birds–specifically the species associated with open habitats such as Northern Lapwing (*Vanellus vanellus*) (Sheldon et al., 2007). They are impacted by tractors applying pesticides and fertilizers that destroy of nests placed on the ground or kill the flightless chicks (such as in Common Quail, *Coturnix coturnix*, Ponce et al., 2018). Moreover, frequent occurrence of vehicles on the fields may result in chasing the adult birds from the nest and leaving it exposed to predators (Šálek and Zámečník, 2014). These factors can explain why we observed generally more negative trends in open-habitat ground nesters compared to the open-habitat species nesting above the ground.

As previous studies described a clear gradient of increasing agricultural intensity from Eastern to Western Europe (Donald et al., 2001; Reif and Hanzelka, 2020), one would expect that the population trends of open-habitat ground nesting birds will became more negative along this gradient. Our data indicate that this is not the case, though. The explanation may be that the agricultural practices greatly intensified in recent years in the East which had led to population collapse of farmland birds in some of these countries (Reif and Vermouzek, 2019), but it was not yet reflected by the studies based on older data (with population trends calculated for 1990s or 2000s) in contrast to our study with data covering the period up to 2018.

Our analysis was based on country-level population trends which may be viewed as too coarse for detecting geographic gradients. This is particularly problematic in the case of large countries that likely average more detailed patterns possibly present across their extensive areas. For this purpose, population trends expressed on a sub-country level would be much more suitable and the results of their analysis were likely stronger. On the other hand, detection of a significant longitudinal trend even with such a coarse dataset makes our results conservative. Moreover, although countries may be perceived as artificial units not recognized by organisms in nature, these units are relevant from the applied perspective–environmental policies and management approaches are typically formulated at the level of individual countries (e.g., Donald et al., 2007), and it is thus important to ask whether or not these formulations are linked to biodiversity indicators, such as bird population trends.

Conclusion

The observed population decline of Western-European populations of woodland-habitat ground nesting birds is surprising given the improvement of environmental conditions in numerous European countries over the last decades (Brauer et al., 2012; Crippa et al., 2016). This improvement was particularly strong in Western countries as a result of stringent environmental legislation and its enforcement (Lubbe-Wolff, 2001), which is also reflected by various environmental indicators (Ferreira et al., 2013). One example of this successful environmental condition improvement is the sites protected within the Natura 2000 network. These sites provide measurable conservation benefits for both target (Gamero et al., 2017) and non-target organisms (Pellissier et al., 2020). They may even result in a population increase of these organisms at the whole European level (Koschová et al., 2018). However, our results indicate that despite the observed improvement in environmental conditions, some of the European biodiversity cannot enjoy these benefits. Specifically, decreasing trends of woodland-habitat ground-nesting birds in Western Europe point to possible gaps in conservation management in these countries. As the pressure from the side of nest predators in the interaction with the intensity of forest management are the most likely drivers, we suggest that steps toward their regulation are needed.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because we work with published data from bird counts, such a review and approval are not applicable.

Author contributions

JR conceived the idea. JR and JK designed the research. JK collected the data. JR and JK conducted the analysis. YB drew the figure. JR led writing with contributions from all co-authors. All authors gave final approval for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2023.1156360/full#supplementary-material

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