



## Original Research Article

## Ecological specialization and population trends in European breeding birds

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## ABSTRACT

Successful conservation strategies depend on the correct identification of animal species and populations at a higher risk of extinction. But not all species are equally sensitive to environmental changes. Specialist species are often considered more prone to extinction than generalist species. However, even considering the importance of the link between specialization and population trends of species (a potential proxy for extinction risk), only a few studies have provided evidence supporting this relationship.

Here, we tested whether the population trend of breeding birds in Europe is linked to a specific category of species' specialization, using continuous measures of avian specialization based on a trait-approach. We focused on five different indices of avian specialization: diet, foraging behavior, foraging substrate, habitat selection, and nesting site selection. We calculated the mean value and the standard deviation of the population trend for 139 bird species. Then, we tested for the presence of a phylogenetic signal in bird population trends, in order to investigate if the tendency for related species to resemble each other, often demonstrated regarding phenotypes, is present also for the species' trends in Europe.

We found evidence that bird species with negative trends were characterized by higher ecological specialization than species with positive trends. Specifically, population trends were negatively associated with nesting site specialization. We highlight that the species' degree of specialization can be used as a proxy for that species' ability to adapt and persist to environmental changes. Finally, the lack of a phylogenetic signal in either the mean value or standard deviation of the bird population trend suggests that the current status of a species is not strongly associated with the degree of phylogenetic relatedness.

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## 1. Introduction

Habitat degradation and fragmentation are significant drivers of biodiversity decline, compromising ecosystem functioning (Turner et al., 2007). Successful conservation strategies – especially in the midst of increasing biodiversity declines – strongly depend on the correct identification of species and populations at a higher risk of extinction (Colles et al., 2009). Importantly, not all species are equally sensitive to environmental changes: there are “winners” and “losers” (McGill et al., 2015). Species and populations have differential levels of extinction risk and differentiating between the winners and losers at both a species- and population-level is a fundamental question in ecology and conservation.

Generalist species – with their wide niche breadths – are able to exploit a range of available resources and for this reason, could be considered less exposed to conservation risks than specialist species (Callaghan et al., 2019; Devictor et al., 2008; Richmond et al., 2005). Conversely, specialist species – with their narrow niche breadth occupying a constrained range of resources in a given habitat – are likely more prone to extinction than generalist species (Clavel et al., 2011; Colles et al., 2009; McKinney, 1997). In fact, specialist species appear to be the species suffering the most significant declines under recent environmental changes, a pattern also suggested by paleoecological studies focusing on longer-term data (Colles et al., 2009). But phylogenetic studies, focusing on entire histories of lineages over millennial time-scales, demonstrate that a species' niche breadth can modulate a species' response to environmental changes (Benito et al., 2019; Colles et al., 2009).

If a species is a generalist, then that species' wide niche breadth likely provides the capacity to be adaptable against a disturbance phenomenon (Hammond et al., 2018; Vázquez and Simberloff, 2002). Conversely, a strong dependence on few specific resources, typical of specialist species (Begon et al., 2006), makes a species more susceptible when facing potential changes in resource availability (Balisi et al., 2018). Such changes in resource availability in the landscape are directly linked with environmental changes, including climate change (Hamududu and Ngoma, 2019), habitat fragmentation (Hagen et al., 2012), and urbanization (Rees and Wackernagel, 2008; Wackernagel et al., 2006). Thus, if species-specific levels of specialization can be fully understood, then these continuous levels of specialization can be used as a proxy of a species' ability to cope with environmental changes (Breiner et al., 2017; Morelli et al., 2019). But few studies have quantified whether the level of specialization of a given species is effectively correlated to the decline of their populations. Studies which have tested this relationship have been restricted to specific habitats (e.g., farmlands – Donald et al., 2001; Reif and Vermouzek, 2018; Siriwardena et al., 1998), have restricted their analysis to just one dimension of ecological specialization (e.g., overall habitat selection or diet type), or have only categorically investigated the difference between specialist and generalist species (Gregory et al., 2005).

Birds, compared with other taxa, have been the target of the longest and most comprehensive monitoring schemes throughout Europe (Butler et al., 2012; Donald et al., 2001; Reif et al., 2014). In recent decades there have been widespread declines in both ranges and abundances of several bird species across Europe (Gregory et al., 2007; Inger et al., 2015; Siriwardena et al., 1998). Many drivers – all some form of anthropogenic environmental changes – have been identified as leading to these population declines, including: (1) density of houses and human settlements (Tratalos et al., 2007), (2) decline of insects for insectivorous birds (Bowler et al., 2019), (3) direct or indirect effects of farming practices in agro-ecosystems, as for example agricultural intensification or use of pesticides (Donald et al., 2002, 2001; Sanderson et al., 2013; Vickery et al., 2004), or (4) habitat fragmentation and reduction of suitable environments for bird species (Andrén, 1994; Carrete et al., 2009; Reino et al., 2013). Because we have detailed knowledge on the threats to birds, the population declines of birds (Stephens et al., 2016), and detailed understanding of ecological life history requirements for many species (Morelli et al., 2019), birds represent an excellent taxon to test the empirical relationship between species' specialization and extinction risk.

To test this empirical relationship, we integrated recently published data on population trends (categorized as increasing, stable, or declining) of breeding bird species in Europe (Stephens et al., 2016), with a traits-based approach used to classify avian species along five dimensions of ecological specialization: diet, foraging behavior, foraging substrate, habitat selection, and nesting site selection (Morelli et al., 2019). First, we tested whether the mean population trend of avian species in Europe was linked with a specific dimension of a species' ecological specialization. Second, we tested if the population trend of breeding bird species is characterized by a phylogenetic signal (e.g., if strongly related species are subject to similar trends).

## 2. Methods

### 2.1. Population trends of European breeding bird species

Population trends for common breeding bird species across Europe were taken from Stephens et al. (2016). They estimated population trends by using data from the Pan-European Common Bird Monitoring Scheme (<http://www.ebcc.info/pecbm.html>) for 139 species for which reliable European species' indices were available up to 2010. For each species, the indices of abundance were available for a variable number of countries, depending on data availability (Stephens et al., 2016). In all cases, for the estimation of abundance trends, authors used existing compilations of annual abundance data based on surveys conducted annually using repeatable methods. For each bird species in each country, the population or abundance trend was estimated as “the slope of the regression of the natural logarithm of the abundance index on the calendar year across the time period encompassed by 1980 and 2010” (Stephens et al., 2016). We used only species that presented time series began in 2000 as maximum and finished in 2010, in order to guarantee at least 10 years of monitoring. The period of monitoring was

relatively homogeneous for all bird species used in this study. We used the data from 19 European countries, provided in [Stephens et al. \(2016\)](#) (Supplementary material, [Table S1](#)). Using the population trend values for 139 species in different countries, we estimated (1) the mean population trend and (2) the standard deviation (SD) of the mean population trend, for each species throughout the whole of Europe.

We treated the mean population trend as a measure or proxy that reflects the overall trend of a species throughout Europe, disregarding any potential bias related to heterogeneity in the data sources for the species in different countries. But to investigate the differential responses of a species among countries, we investigated the SD of the mean population trend. Here, we hypothesize that SD provides information about bird species that respond differently across Europe (higher SD) and species that respond homogeneously (lower SD). This information needs to be combined with the value of mean population trends to fully understand a species-specific response throughout Europe.

## 2.2. Ecological specialization of European bird species

We followed a definition of ecological specialization of bird species based on a set of multi-dimensional functional traits, relatively well described for European birds ([Pearman et al., 2014](#)). We used five indices of avian specialization: diet, foraging behavior, foraging substrate, habitat, and nesting site. The specialization indices are based on the application of the Gini index of inequality ([Colwell, 2011](#)), on a set of different traits. Therefore, the specialization indices for each bird species can assume values between 0 and 1, representing low to high specialization respectively. The multiple specialization indices were available for all 139 breeding bird species ([Morelli et al., 2019](#)). Additionally, we calculated an overall specialization index estimated for each breeding bird species which was the mean value of the five single specialization indices mentioned above, subsequently standardized between 0 (generalist species) to 1 (specialist species) ([Morelli et al., 2019](#)).

## 2.3. Phylogenetic signal of bird populations trend

Considering that the characteristics of bird species are evolutionarily related, they cannot necessarily be treated as independent sampling units in comparative analyses ([Harvey and Purvis, 1991](#)). The phylogenetic signal indicates the tendency for related species to resemble each other more than they resemble species drawn at random from a phylogenetic tree ([Blomberg et al., 2003](#)). A significant phylogenetic signal indicates species' traits that are more similar in close relatives than distant relatives, while no statistically significant phylogenetic signal indicates that species' traits are more similar in distant than close relatives or randomly distributed across the phylogeny ([Kamilar and Cooper, 2013](#)). However, the phylogenetic signal simply describes a tendency or pattern for species to resemble each other, referring to their degree of phylogenetic relatedness, with no implication as to the mechanisms behind such resemblance ([Blomberg et al., 2003](#)).

Here, we tested whether the trends of populations of breeding bird species in Europe are related to their degree of phylogenetic relatedness. We modelled the inter-specific variation in bird population trends across the phylogeny, obtaining the phylogenetic relationships from '[www.birdtree.org](http://www.birdtree.org)'. We downloaded 1000 phylogenetic trees from the backbone tree based on [Ericson et al. \(2006\)](#) for the 139 bird species that were the focus of this study. The consensus tree was obtained applying the 50% majority rule (i.e., the proportion of a split to be present in all trees). We used the following R packages: 'ape' ([Paradis et al., 2004](#)), 'phangorn' ([Schliep, 2011](#)) and 'Rphylop' ([Revell and Chamberlain, 2014](#)) to work with the phylogenetic trees.

## 2.4. Statistical analyses

To test the phylogenetic signal ([Blomberg and Garland, 2003](#)) of bird population trends (mean and SD) for 139 European bird species, we used Blomberg's K and K\* statistics ([Blomberg et al., 2003](#)). When K approaches 1, trait evolution follows a mode of evolution that is consistent with Brownian motion, and if  $K > 1$  closely related species are more similar than expected under Brownian motion, while if  $K < 1$  closely related species are less similar than expected ([Blomberg et al., 2003](#)). Finally, if K values are closer to zero the trait has no detectable phylogenetic signal ([Blomberg et al., 2003](#)). Blomberg's K and K\* statistics were estimated using the R package 'phylosignal' ([Keck et al., 2016](#)).

To test a potential correlation between SD of mean population trend and the number of countries where population trends were monitored, we ran a linear model. We ran generalized linear models to test whether population trends of breeding birds were associated with a species-specific level of specialization. To test for potential multicollinearity issues among predictor variables, we used the test of variance inflation factors (VIF) on the candidate full model, using the package 'fmsb' for R ([Nakazawa, 2017](#)). Only variables with  $VIF < 2$  were added in the model. First, we modelled mean bird population trend as the response variable with the five specialization indices (diet, foraging behavior, foraging substrate, habitat, and nesting site) as predictor variables. Second, we modelled SD of mean population trend log-transformed as the response variable, with the five specialization indices as predictor variables. In both cases, a model averaging approach was applied, based on an information-theoretic approach that examined several competing hypotheses simultaneously to identify the most parsimonious set of variables via the Akaike's information criterion (AIC) ([Burnham and Anderson, 2002](#)). To calculate model estimates, we used a model-averaging approach, 'dredging' all possible subsets of the full model, with the 'dredge' function in the 'MuMIn' package for R ([Bartoń, 2013](#)). Model-averaged parameter estimates were calculated from the subsequent top models, with  $\Delta AIC < 4$ .

With this procedure, the relative importance of each specialization index was quantified by summing the Akaike weights across all possible models containing such variables as predictors.

All statistical tests were performed with R statistical programming environment version 3.6.0 (R Development Core Team, 2019) and significance was concluded at  $\alpha \leq 0.05$ .

### 3. Results

Of 139 bird species used in this study (Supplementary material, Tables S2) 62 species showed a negative trend, while 77 species showed a positive overall trend throughout Europe (Table 1). Overall, bird species with negative trends in Europe were characterized by higher values in the five specialization indices than species with positive trends (Table 1). The four bird species characterized by the most negative trend overall in Europe were *Calandrella brachydactyla*, *Emberiza rustica*, *Galerida cristata* and *Lanius minor*. From these species, two (*Emberiza rustica* and *Lanius minor*) showed negative trends in all countries where species were monitored (Supplementary material, Table S2). *Calandrella brachydactyla* was classified as habitat specialist, while *Galerida cristata* and *Lanius minor* were classified as foraging substrate and diet specialist, respectively. *Emberiza rustica* was not a specialist in any of the five specialization categories focused. The four bird species characterized by the most positive trend overall in Europe were *Bombycilla garrulus*, *Burhinus oedicephalus*, *Ficedula albicollis* and *Sylvia hortensis*. All these species showed positive trends in all countries where species were monitored (Supplementary material, Table S2). *Bombycilla garrulus* and *Ficedula albicollis* were classified as habitat specialist species, while *Burhinus oedicephalus* was classified as foraging substrate specialist and *Sylvia hortensis* was not categorized as a specialist in any specialization category.

The phylogenetic signal of mean values and standard deviations of population trends of European bird species was not statistically significant (Table 2). Negative population trends in species occur in different tips of the avian phylogeny of the 139 species in this study (Fig. 1).

There was a negative relationship between the mean value of the species' population trends and the overall specialization index: species with higher levels of specialization had more negative population declines (Fig. 2A). Conversely, there was a positive relationship between the SD of a species' population trend and the overall specialization index (Fig. 2B). The SD of population trends was not correlated with the number of countries where population trends were monitored (Supplementary material, Table S3, Fig. 2C). To account for potential uncertainty in the underlying population trends, we additionally classified the mean bird population trend across Europe into two categories for each species – “positive” or “negative” – and found that the mean values of ecological specialization were always higher for species classified as negative (Fig. 3A–E).

When investigating the relationship between the five different dimensions of ecological specialization, we found statistical evidence that the mean population trend of European breeding birds is negatively associated with nesting site specialization of species, but no evidence for a statistically significant relationship between the other specialization indices (Table 3, Fig. 3). The nesting site specialization was also the variable with high relative importance accounting for variations in population trends of avian species (Table 3). Table S4 in Supplementary material is showing the model selection outputs based on our model averaging approach, from all possible subsets of the full model and AIC values.

We also found evidence that the SD of mean population trends is positively associated with foraging substrate specialization of bird species, while it is not significantly associated with the other specialization indices (Table 3). Additionally, foraging substrate specialization was also the variable with high relative importance accounting for variations in SD of mean population trends of avian species (Table 3). Table S5 in Supplementary material is showing the model selection outputs based on our model averaging approach, from all possible subsets of the full model and AIC values.

### 4. Discussion

We found a significant relationship between a species' degree of specialization and average population trend (a potential proxy for risk of extinction of a species) throughout Europe. We also found no evidence of a phylogenetic signal in either the population trend or standard deviation of the population trend, suggesting that the current status of a species (declining, stable, or increasing) is not strongly associated with the degree of phylogenetic relatedness. Our results highlight that trends of populations seem to be unrelated to their degree of phylogenetic relatedness, suggesting that conservation concerns (in regards to population trends) are not strongly clustered in specific branches of avian phylogeny in Europe. A species' population trend is not necessarily linked to family-specific traits, probably because there are a plurality of causes driving bird population declines (Bowler et al., 2019; Fuller et al., 1995; Herrando et al., 2016; Morelli, 2012) that differentially affect species-specific niches. Because there is a distinct phylogenetic signal of ecological specialization, but not population trends (Morelli et al., 2019), it is likely that ecological specialization plays a significant role in the probability of a species' population

**Table 1**

Mean values of five specialization indices (diet, foraging behavior, foraging substrate, habitat and nesting site) for 139 European bird species included in this study, depending on the mean population trend of species in Europe.

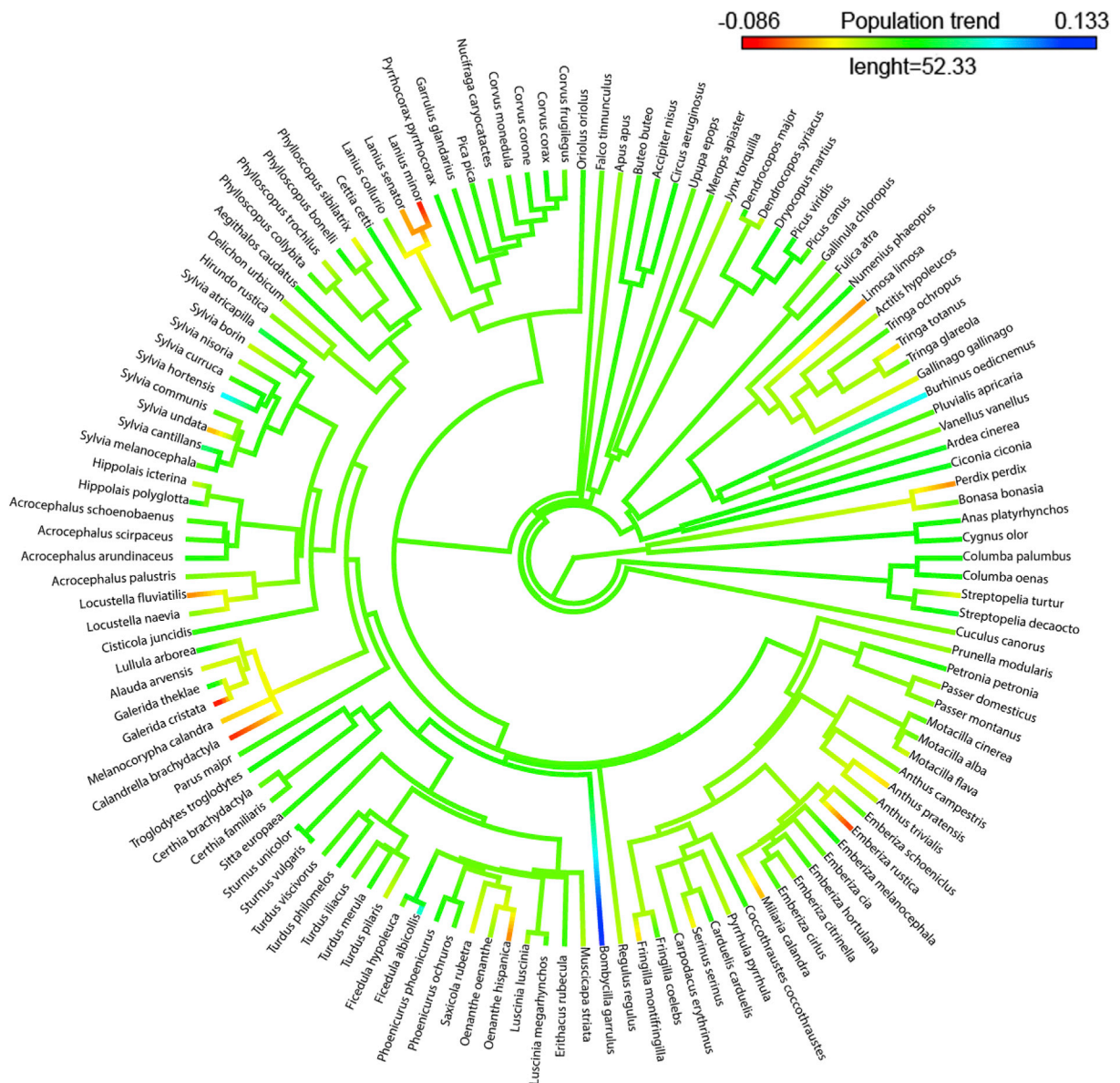
| Mean population trend     | Diet  | Foraging behavior | Foraging substrate | Habitat | Nesting site |
|---------------------------|-------|-------------------|--------------------|---------|--------------|
| Negative (n = 62 species) | 0.482 | 0.626             | 0.370              | 0.434   | 0.199        |
| Positive (n = 77 species) | 0.450 | 0.542             | 0.310              | 0.423   | 0.162        |



**Table 2**

Phylogenetic signal of mean values and standard deviation (SD) of the population trend for 139 European bird species included in this study. The table shows K statistic, K\* statistic and associated p values for each value.

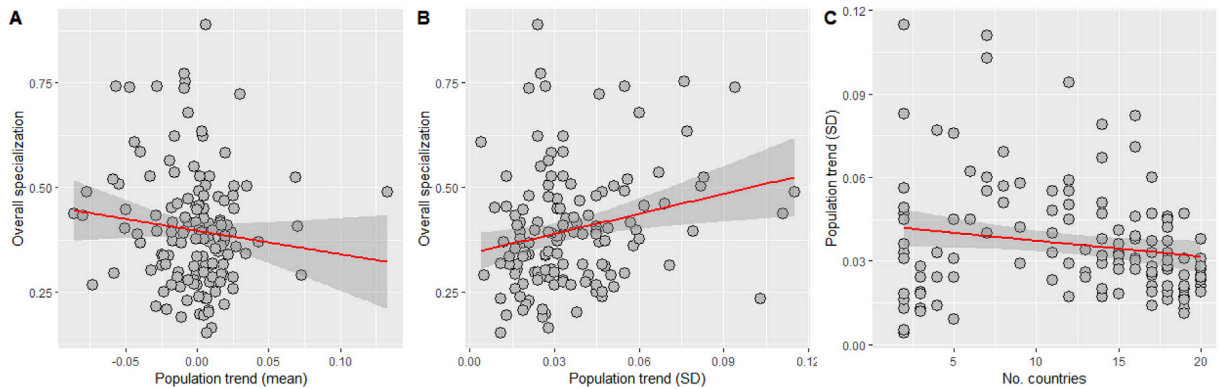
| Specialism index      | K statistic | P value (K) | K* statistic | P value (K*) |
|-----------------------|-------------|-------------|--------------|--------------|
| Mean population trend | 0.128       | 0.645       | 0.166        | 0.605        |
| SD population trend   | 0.140       | 0.483       | 0.180        | 0.505        |



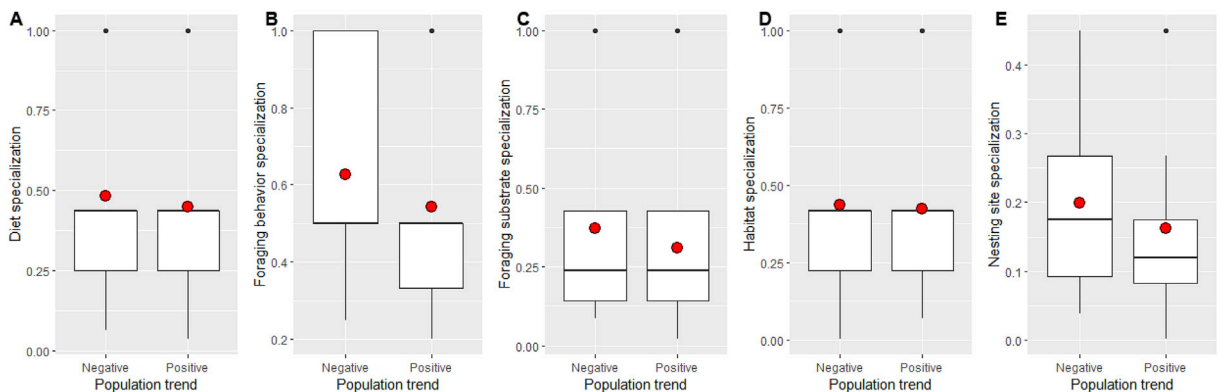
**Fig. 1.** Fan dendrogram representing the mean population trend for 139 European bird species included in this study, in a coloured gradient from positive trend (dark blue, species increasing population numbers) to negative trend (red, species declining population numbers). Tips represent the avian phylogeny of the 139 breeding species included in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

increasing or decreasing. Ultimately, our results – based on continental-scale data including >100 species – provide robust evidence that specialist species are those most in decline throughout Europe.

We found strong associations between the overall specialization of a species and population trends. But the degree of specialization of a species is complex and multi-faceted (Luck et al., 2013), and the degree of specialization in just one



**Fig. 2.** Associations between overall specialization index and mean population trend (A), the standard deviation of mean population trend (B) and the association between the standard deviation of mean population trend and the number of countries where population trends were monitored (C), for 139 European bird species included in this study.



**Fig. 3.** Association between diet specialization (A), foraging behavior specialization (B), foraging substrate specialization (C), habitat specialization (D) and nesting site specialization (E) with mean bird population trends classified into two categories as positive or negative. The box plots show medians, mean values (red circle), quartiles, 5- and 95-percentiles and extreme values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 3**

Results of generalized linear models, accounting for variation in mean population trend (Model 1) and standard deviation of population trend (Model 2) for 139 European breeding bird species included in this study, in relation to avian specialization measured in five ecological dimensions: diet, foraging behavior, foraging substrate, general habitat and nesting site. Outputs show the results after model averaging. Significant variables are highlighted in bold. 'SE' is the standard error. 'Rel. imp.' is the relative importance of each variable. See Table S4 and Table S5 for the results based on our model averaging approach.

| Variables                                     | Estimate      | SE           | t             | P            | Rel. imp.   |
|---|---------------|--------------|---------------|--------------|-------------|
| <i>Model 1: Mean pop. trend</i>               |               |              |               |              |             |
| Intercept                                     | 0.006         | 0.007        | 1.152         | 0.251        |             |
| Diet specialization                           | −0.002        | 0.008        | −0.229        | 0.819        | 0.27        |
| Foraging behav. specialization                | −0.009        | 0.008        | −0.986        | 0.326        | 0.37        |
| Foraging subst. specialization                | −0.001        | 0.009        | 0.149         | 0.882        | 0.27        |
| Habitat specialization                        | 0.007         | 0.008        | 0.823         | 0.412        | 0.31        |
| <b>Nesting site specialization</b>            | <b>−0.042</b> | <b>0.023</b> | <b>−1.988</b> | <b>0.048</b> | <b>0.74</b> |
| <i>Model 2: Standard deviation pop. trend</i> |               |              |               |              |             |
| Intercept                                     | −3.653        | 0.157        | −23.44        | <0.001       |             |
| Diet specialization                           | 0.153         | 0.163        | 0.870         | 0.386        | 0.35        |
| Foraging behav. specialization                | −0.251        | 0.187        | −1.411        | 0.161        | 0.45        |
| <b>Foraging subst. specialization</b>         | <b>0.384</b>  | <b>0.187</b> | <b>2.037</b>  | <b>0.044</b> | <b>0.74</b> |
| Habitat specialization                        | 0.164         | 0.169        | 0.827         | 0.409        | 0.37        |
| Nesting site specialization                   | 0.794         | 0.463        | 1.262         | 0.209        | 0.62        |

ecological dimension (e.g., diet specialization) may be enough to determine the level of extinction risk for a given species. For this reason, we retain that the most appropriate strategy is to focus separately on each dimension of avian specialization, using a multi-dimensional index of specialization. We highlight the importance of investigating multiple dimensions of

ecological specialization, as we found that not all dimensions of ecological specialization are equally important in explaining the population trends of species (Table 3). We found that the degree of specialization in nesting site selection was negatively associated with population trends, with the highly specialized bird species in their nesting sites showing significant declines in their populations throughout Europe. Repeating the statistical approach, but running a single univariate model using only nesting site specialization as predictor, we confirmed the previous results of our model incorporating all five specialization indices: population trends of breeding birds were negatively associated with the level of nesting site specialization of species (Supplementary material, Table S6).

Species that need more specific characteristics for nesting site selection, highly dependent on a specific range of resources for nesting (Begon et al., 2006), are more exposed to suffer the variability in resources available as a result of environmental changes (Balisi et al., 2018). Thus, such species should receive higher priority for conservation assessments.

Following our results, the bird species with the most negative population trends in Europe were the Crested Lark *Galerida cristata* and the Lesser Grey Shrike *Lanius minor*. Both species have relatively large population sizes (175,000,000–249,999,999) and are categorized as Least Concern (BirdLife International, 2019). However, these species' population trends are decreasing globally. Both species are specialized in at least one life history dimension. For example, Crested Larks builds its nest on the ground, sometimes in proximity to human settlements (Lesiński, 2009), and breeds and forage mainly in open habitat with a high proportion of scattered trees and shrubs, reflected in a high foraging substrate specialization score. The Lesser Grey Shrike, on the other side, has a high level of diet specialization, based on large insects (Lefranc and Worfolk, 1997). This relatively high specialization in at least one ecological dimension can highlight these species' extinction risk and how this fact is not well reflected in their overall specialization index. Another example is the case of the European turtle dove *Streptopelia turtur*; a species is declining in almost all European countries and is characterized by a high level of specialization, especially regarding habitat, foraging behavior, and foraging substrate. The European turtle dove is currently categorized as Vulnerable (BirdLife International, 2019).

Conversely, the bird species with the most positive population trend in our study was the Bohemian Waxwing *Bombycilla garrulus*, a species characterized by a population size estimated to be between 14,000,000–29,999,999 mature individuals, with a globally increasing population trend, and a conservation threat level classified as Least Concern (BirdLife International, 2019). This bird is considered a habitat specialized species, breeding mainly in coniferous forests throughout the most northern parts of Europe, Asia and western North America (Cramp and Perrins, 1994). The bird species with the second most positive population trend in Europe was the Western Orphean Warbler *Sylvia hortensis*, which is a perfect example of a generalist species (a generalist in all five categories of specialization used in this study) with a large population size, increasing population trend and consequently classified as Least Concern (BirdLife International, 2019).

In this study, we used two different measures related to the avian population trend in different countries: (1) the mean population trend, reflecting the overall trend of a species throughout Europe, and (2) the standard deviation of the mean values, reflecting the variability in population trends among populations of a given species in different countries. The standard deviation of the mean values was used in this study to deal with the potential differences in regional trends for some species. A species declining or increasing across all countries probably has a homogeneous response across the continent, represented by a relatively lower SD. Of course, this association is not mathematically dependant, since a species with only positive trends but very different values across countries could show a larger SD than a species with positive and negative trends, both near zero. Additionally, the SD values could be positively correlated with the number of countries where a species' trend has been quantified. Our results were aimed at identifying a broad correlation between population trends and species-specialization across the continent of Europe. But importantly, species can show differential population trends in space (reflected by high SD values in our analysis) and potentially different specialization techniques throughout a species' range (i.e., local-level adaptations) (Ravigné et al., 2009). Dissimilar population trends of the same species in different countries, however, could be due to intrinsic characteristics of the regions (or countries), perhaps subject to different conservation policies. Some groups of species (e.g., farmland or forest birds) are facing different scenarios in different European countries (Gregory et al., 2007; Reif and Vermouzek, 2018; Tryjanowski et al., 2011). One emblematic example from the farmland birds could be the case of the Ortolan bunting *Emberiza hortulana*. This species presents a negative trend in Finland, Poland and Sweden, while the population trend is positive in Germany, Latvia and Spain (Stephens et al., 2016). In Italy, the species is mainly recorded as declining, but with some local areas where the species seems to be increasing (Morelli et al., 2012). Future work should test the spatial scale of our results, specifically testing whether the broad patterns identified here correspond with local-level patterns and relationships, with an aim to better understand the relationship between ecological specialization and the variability of population trends throughout different regions.

Our analysis was restricted to birds in Europe, but global datasets in population changes (e.g. Dornelas et al., 2018) and trait data are becoming increasingly available for many taxa in many different parts of the world (e.g. Moretti et al., 2017; Schneider et al., 2019). Hence, our approach here should be tested for other taxa and in different regions of the world, providing generalizable results necessary for conservation efforts. We recommend future work should aim to develop multi-taxa ecological specialization measures and test these measures across latitudinal and longitudinal gradients which have been correlated with species richness patterns (Mimet et al., 2019).

Identifying the winners and losers is important to appropriately manage limited resources for conservation (McKinney and Lockwood, 1999; Newbold et al., 2018; Regos et al., 2016). As biodiversity is consistently being diminished as a result of anthropogenic environmental changes (Ceballos et al., 2017), an ability to predict species most at-risk of extinction is critical to mitigating these threats. Using long-term population trends as a proxy for extinction risk in birds, we confirm

previous studies that extinction risk tends to be higher for species with a narrow ecological niche (Clavel et al., 2011; Colles et al., 2009; McKinney, 1997). Our approach of measuring species' ecological specialization relies on a suite of natural history information, fundamental to better understand a species' adaptability to future environmental changes (Bury, 2006; Callaghan et al., 2018). We highlight that a species' degree of specialization can be used as a proxy for that species' ability to adapt and persist in the Anthropocene.

## Data availability statement

The datasets generated during and/or analysed during the current study are available in the [Appendix A: Supplementary data](#).

## Declaration of competing interest

Authors of the manuscript "Ecological specialization and population trends in European breeding birds", Federico Morelli, Yanina Benedetti, Corey T. Callaghan" declare that they have no conflict of interest.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e00996>.

## References

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355. <https://doi.org/10.2307/3545823>.
- Balisi, M., Casey, C., Van Valkenburgh, B., 2018. Dietary specialization is linked to reduced species durations in North American fossil canids. *R. Soc. Open Sci.* 5, 171861. <https://doi.org/10.1098/rsos.171861>.
- Bartoń, K., 2013. *MuMIn: Multi-Model Inference*, R Package.
- Begon, M.E., Townsend, C.R., Harper, J.L., 2006. *Ecology: from Individuals to Ecosystems*, fourth ed. John Wiley & Sons, Ltd, Oxford.
- Benito, B.M., Gil-Romera, G., Birks, H.J.B., 2019. Ecological memory at millennial time-scales: the importance of data constraints, species longevity and niche features. *Ecography (Cop.)*. <https://doi.org/10.1111/ecog.04772>, 04772.
- BirdLife International, 2019. IUCN red list for birds [WWW Document]. URL: <http://www.birdlife.org>.
- Blomberg, S.P., Garland, T., 2003. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.* 15, 899–910.
- Blomberg, S.P., Garland, T.J., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution (N. Y.)* 57, 717–745. <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>.
- Bowler, D.E., Heldbjerg, H., Fox, A.D., de Jong, M., Böhning-Gaese, K., 2019. Long-term declines of European insectivorous bird populations and potential causes. *Conserv. Biol.* 1–11. <https://doi.org/10.1111/cobi.13307>, 0.
- Breiner, F.T., Guisan, A., Nobis, M.P., Bergamini, A., 2017. Including environmental niche information to improve IUCN Red List assessments. *Divers. Distrib.* 23, 484–495. <https://doi.org/10.1111/ddi.12545>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer, Verlag, New York, NY, USA.
- Bury, R.B., 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. *Herpetol. Conserv. Biol.* 1, 56–61.
- Butler, S.J., Freckleton, R.P., Renwick, A.R., Norris, K., 2012. An objective, niche-based approach to indicator species selection. *Methods Ecol. Evol.* 3, 317–326. <https://doi.org/10.1111/j.2041-210X.2011.00173.x>.
- Callaghan, C.T., Major, R.E., Wilshire, J.H., Martin, J.M., Kingsford, R.T., Cornwell, W.K., 2019. Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos* 1–14. <https://doi.org/10.1111/oik.06158>.
- Callaghan, C.T., Martin, J.M., Kingsford, R.T., Brooks, D.M., 2018. Unnatural history: is a paradigm shift of natural history in 21st century ornithology needed? *Ibis (Lond. 1859)* 160, 475–480. <https://doi.org/10.1111/ibi.12555>.
- Carrete, M., Tella, J.L., Blanco, G., Bertellotti, M., 2009. Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes. *Biol. Conserv.* 142, 2002–2011. <https://doi.org/10.1016/j.biocon.2009.02.012>.
- Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.S.A.* 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>.
- Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* 9, 222–228. <https://doi.org/10.1890/080216>.
- Colles, A., Liow, L.H., Prinzing, A., 2009. Are specialists at risk under environmental change? Neoeological, paleoecological and phylogenetic approaches. *Ecol. Lett.* 12, 849–863. <https://doi.org/10.1111/j.1461-0248.2009.01336.x>.
- Colwell, F.A., 2011. *Measuring Inequality*. Oxford University Press, Oxford, UK.
- Cramp, S., Perrins, C., 1994. *The Birds of the Western Palearctic*. Oxford University Press, Oxford, UK.
- Devictor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117, 507–514. <https://doi.org/10.1111/j.0030-1299.2008.16215.x>.
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 25–29. <https://doi.org/10.1098/rspb.2000.1325>.
- Donald, P.F., Pisano, G., Rayment, M.D., Pain, D.J., 2002. The Common Agricultural Policy, EU enlargement and the conservation of Europe's farmland birds. *Agric. Ecosyst. Environ.* 89, 167–182. [https://doi.org/10.1016/S0167-8809\(01\)00244-4](https://doi.org/10.1016/S0167-8809(01)00244-4).
- Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D., Akhmetzhanova, A.A., Appeltans, W., Arcos, J.M., Arnold, H., Ayyappan, N., Badihi, G., Baird, A.H., Barbosa, M., Barreto, T.E., Bässler, C., Bellgrove, A., Belmaker, J., Benedetti-Cecchi, L., Bett, B.J., Bjorkman, A.D., Błażewicz, M., Blowes, S.A., Bloch, C.P., Bonebrake, T.C., Boyd, S., Bradford, M., Brooks, A.J., Brown, J.H., Bruehlheide, H., Budy, P., Carvalho, F., Castañeda-Moya, E., Chen, C.A., Chumblee, J.F., Chase, T.J., Siegfried Collier, L., Collinge, S.K., Condit, R., Cooper, E.J., Cornelissen, J.H.C., Cotano, U., Kyle Crow, S., Damasceno, G., Davies, C. H., Davis, R.A., Day, F.P., Degraer, S., Doherty, T.S., Dunn, T.E., Durigan, G., Duffy, J.E., Edelist, D., Edgar, G.J., Elahi, R., Elmendorf, S.C., Enemar, A., Ernest, S.K. M., Escribano, R., Estiarte, M., Evans, B.S., Fan, T.-Y., Turini Farah, F., Loureiro Fernandes, L., Farneda, F.Z., Fidelis, A., Fitt, R., Fosaa, A.M., Daher Correa Franco, G.A., Frank, G.E., Fraser, W.R., García, H., Cazzolla Gatti, R., Givan, O., Gorgone-Barbosa, E., Gould, W.A., Gries, C., Grossman, G.D., Gutiérrez, J.R., Hale, S., Harmon, M.E., Harte, J., Haskins, G., Henshaw, D.L., Hermanutz, L., Hidalgo, P., Higuchi, P., Hoey, A., Van Hoey, G., Hofgaard, A., Holeck, K., Hollister, R.D., Holmes, R., Hoogenboom, M., Hsieh, C., Hubbell, S.P., Huettmann, F., Hufard, C.L., Hurlbert, A.H., Macedo Ivanauskas, N., Janík, D., Jandt, U.,



- Jazdzewska, A., Johannessen, T., Johnstone, J., Jones, J., Jones, F.A.M., Kang, J., Kartawijaya, T., Keeley, E.C., Kelt, D.A., Kinnear, R., Klanderud, K., Knutsen, H., Koenig, C.C., Kortz, A.R., Král, K., Kuhn, L.A., Kuo, C.-Y., Kushner, D.J., Laguionie-Marchais, C., Lancaster, L.T., Min Lee, C., Lefcheck, J.S., Lévesque, E., Lightfoot, D., Lloret, F., Lloyd, J.D., López-Baucells, A., Louzao, M., Madin, J.S., Magnússon, B., Malamud, S., Matthews, I., McFarland, K.P., McGill, B., McKnight, D., McFarney, W.O., Meador, J., Meserve, P.L., Metcalfe, D.J., Meyer, C.F.J., Michelsen, A., Milchakova, N., Moens, T., Moland, E., Moore, J., Mathias Moreira, C., Müller, J., Murphy, G., Myers-Smith, I.H., Myster, R.W., Naumov, A., Neat, F., Nelson, J.A., Paul Nelson, M., Newton, S.F., Norden, N., Oliver, J.C., Olsen, E.M., Onipchenko, V.G., Pabis, K., Pabst, R.J., Paquette, A., Pardede, S., Paterson, D.M., Pélissier, R., Peñuelas, J., Pérez-Matus, A., Pizarro, O., Pomati, F., Post, E., Prins, H.H.T., Priscu, J.C., Provoost, P., Prudic, K.L., Pulliainen, E., Ramesh, B.R., Mendivil Ramos, O., Rassweiler, A., Rebelo, J. E., Reed, D.C., Reich, P.B., Remillard, S.M., Richardson, A.J., Richardson, J.P., van Rijn, I., Rocha, R., Rivera-Monroy, V.H., Rixen, C., Robinson, K.P., Ribeiro Rodrigues, R., de Cerqueira Rossa-Feres, D., Rudstam, L., Ruhl, H., Ruz, C.S., Sampaio, E.M., Rybicki, N., Rypel, A., Sal, S., Salgado, B., Santos, F.A.M., Savassi-Coutinho, A.P., Scanga, S., Schmidt, J., Schooley, R., Setiawan, F., Shao, K.-T., Shaver, G.R., Sherman, S., Sherry, T.W., Siciński, J., Sievers, C., da Silva, A.C., Rodrigues da Silva, F., Silveira, F.L., Slingsby, J., Smart, T., Snell, S.J., Soudzilovskaia, N.A., Souza, G.B.G., Maluf Souza, F., Castro Souza, V., Stallings, C.D., Stanforth, R., Stanley, E.H., Mauro Sterza, J., Stevens, M., Stuart-Smith, R., Rondon Suarez, Y., Supp, S., Yoshio Tamashiro, J., Tarigan, S., Thiede, G.P., Thorn, S., Tolvanen, A., Teresa Zugliani Toniato, M., Totland, Ø., Twilley, R.R., Vaitkus, G., Valdivia, N., Vallejo, M.I., Valone, T.J., Van Colen, C., Vanaverbeke, J., Venturoli, F., Verhey, H.M., Vianna, M., Vieira, R.P., Vrška, T., Quang Vu, C., Van Vu, L., Waide, R.B., Waldock, C., Watts, D., Webb, S., Wesolowski, T., White, E.P., Widdicombe, C.E., Wilgers, D., Williams, R., Williams, S.B., Williamson, S., Willis, M.R., Willis, T.J., Wipf, S., Woods, K.D., Woehler, E.J., Zawada, K., Zettler, M.L., 2018. BioTIME: a database of biodiversity time series for the Anthropocene. *Global Ecol. Biogeogr.* 27, 760–786. <https://doi.org/10.1111/geb.12729>.
- Ericson, P.G.P., Anderson, C.L., Britton, T., Elzanowski, A., Johannsson, U.S., Källersjö, M., Ohlson, J.L., Parsons, T.J., Zuccon, D., Mayr, G., 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. *Biol. Lett.* 2, 543–547.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* <https://doi.org/10.2307/2387188>.
- Gregory, R.D., van Strien, A., Voríšek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B., Gibbons, D.W., 2005. Developing indicators for European birds. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 360, 269–288. <https://doi.org/10.1098/rstb.2004.1602>.
- Gregory, R.D., Voríšek, P., van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., Burfiel, I.J., 2007. Population trends of widespread woodland birds in Europe. *Ibis (Lond. 1859)* 149, 78–97. <https://doi.org/10.1111/j.1474-919X.2007.00698.x>.
- Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E., Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimarães, P.R., Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E., Maia, K.P., Marquitti, F.M.D., McLaughlin, O., Morellato, L.P.C., O'Gorman, E.J., Trøjelsgaard, K., Tylanakis, J.M., Vidal, M.M., Woodward, G., Olesen, J.M., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. In: *Advances in Ecological Research*. Academic Press Inc., pp. 89–210. <https://doi.org/10.1016/B978-0-12-396992-7.00002-2>.
- Hammond, T.T., Palme, R., Lacey, E.A., 2018. Ecological specialization, variability in activity patterns and response to environmental change. *Biol. Lett.* 14, 20180115. <https://doi.org/10.1098/rsbl.2018.0115>.
- Hamududu, B.H., Ngoma, H., 2019. Impacts of climate change on water resources availability in Zambia: implications for irrigation development. *Environ. Dev. Sustain.* 1–22. <https://doi.org/10.1007/s10668-019-00320-9>.
- Harvey, P.H., Purvis, A., 1991. Comparative methods for explaining adaptations. *Nature* 351, 619–624.
- Herrando, S., Brotons, L., Anton, M., Páramo, F., Villero, D., Titeux, N., Quesada, J., Stefanescu, C., 2016. Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. *Environ. Conserv.* 43, 69–78. <https://doi.org/10.1017/S0376892915000260>.
- Inger, R., Gregory, R., Duffy, J.P., Stott, I., Vo R I Sek, P., Gaston, K.J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* 18, 28–36. <https://doi.org/10.1111/ele.12387>.
- Kamilar, J.M., Cooper, N., 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philos. Trans. R. Soc. B* 368, 20120341.
- Keck, F., Rimet, F., Bouchez, A., Franc, A., 2016. PhyloSignal: an R package to measure, test, and explore the phylogenetic signal. *Ecol. Evol.* 6, 2774–2780. <https://doi.org/10.1002/ece3.2051>.
- Lefranc, N., Worfolk, T., 1997. *Shrikes. A Guide to the Shrikes of the World*.
- Lesiński, G., 2009. Breeding ecology and population decline of the crested lark *Galerida cristata* in Warsaw, Poland. *Ornis Hung.* 17–18, 1–11.
- Luck, G.W., Carter, A., Smallbone, L., 2013. Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. *PLoS One* 8, e63671. <https://doi.org/10.1371/journal.pone.0063671>.
- McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in the anthropocene. *Trends Ecol. Evol.* 30, 104–113. <https://doi.org/10.1016/j.tree.2014.11.006>.
- McKinney, M., 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Systemat.* 28, 495–516. <https://doi.org/10.1146/annurev.ecolsys.28.1.495>.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453.
- Mimet, A., Buitenwerf, R., Sandel, B., Svenning, J., Normand, S., 2019. Recent global changes have decoupled species richness from specialization patterns in North American birds. *Global Ecol. Biogeogr.* 28, 1621–1635. <https://doi.org/10.1111/geb.12978>.
- Morelli, F., 2012. Plasticity of habitat selection by red-backed shrikes (*Lanius collurio*) breeding in different landscapes. *Wilson J. Ornithol.* 124, 51–56. <https://doi.org/10.1676/11-103.1>.
- Morelli, F., Benedetti, Y., Möller, A.P., Fuller, R.A., 2019. Measuring avian specialization. *Ecol. Evol.* 9, 8378–8386. <https://doi.org/10.1002/ece3.5419>.
- Morelli, F., Prusini, F., Furlani, M., 2012. Declining in Europe but increasing in Italy? Preliminary indications of a possible increase of Ortolan bunting *Emberiza hortulana* in central Italy. *Alula XIX* 87–96.
- Moretti, M., Dias, A.T.C., Bello, F. de, Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Eilers, J., Berg, M.P., 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Funct. Ecol.* 31, 558–567. <https://doi.org/10.1111/1365-2435.12776> [https://doi.org/10.1111/\(ISSN\)1365-2435.SICB.2018](https://doi.org/10.1111/(ISSN)1365-2435.SICB.2018).
- Nakazawa, M., 2017. “fmsb” Functions for Medical Statistics Book with Some Demographic Data - R Package.
- Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W., Purvis, A., 2018. Widespread winners and narrow-ranged losers: land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biol.* 16, e2006841. <https://doi.org/10.1371/journal.pbio.2006841>.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Pearman, P.B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N.E., Thuiller, W., 2014. Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Global Ecol. Biogeogr.* 23, 414–424. <https://doi.org/10.1111/geb.12127>.
- R Development Core Team, 2019. *R: A Language and Environment for Statistical Computing*.
- Ravigné, V., Dieckmann, U., Olivieri, I., 2009. Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* 174, E141–E169. <https://doi.org/10.1086/605369>.
- Rees, W., Wackernagel, M., 2008. Urban ecological footprints: why cities cannot be sustainable—and why they are a key to sustainability. In: *Urban Ecology*. Springer US, Boston, MA, pp. 537–555. [https://doi.org/10.1007/978-0-387-73412-5\\_35](https://doi.org/10.1007/978-0-387-73412-5_35).
- Regos, A., Domínguez, J., Gil-Tena, A., Brotons, L., Ninyerola, M., Pons, X., 2016. Rural abandoned landscapes and bird assemblages: winners and losers in the rewilding of a marginal mountain area (NW Spain). *Reg. Environ. Change* 16, 199–211. <https://doi.org/10.1007/s10113-014-0740-7>.
- Reif, J. b., Škorpilová, J., Vermouzek, Z., Stastný, K., 2014. Population changes of common breeding birds in the Czech Republic from 1982 to 2013: an analysis using multispecies indicators. *Sylvia* 50, 41–65.

- Reif, J., Vermouzek, Z., 2018. Collapse of farmland bird populations in an Eastern European country following its EU accession. *Conserv. Lett.*, e12585 <https://doi.org/10.1111/cons.12585>.
- Reino, L., Beja, P., Araújo, M.B., Dray, S., Segurado, P., 2013. Does local habitat fragmentation affect large-scale distributions? The case of a specialist grassland bird. *Divers. Distrib.* 19, 423–432. <https://doi.org/10.1111/ddi.12019>.
- Revell, L.J., Chamberlain, S.A., 2014. Rphylip: an R Interface for PHYLIP R Package.
- Richmond, C.E., Breitburg, D.L., Rose, K.A., 2005. The role of environmental generalist species in ecosystem function. *Ecol. Model.* 188, 279–295. <https://doi.org/10.1016/j.ecolmodel.2005.03.002>.
- Sanderson, F.J., Kucharz, M., Jobda, M., Donald, P.F., 2013. Impacts of agricultural intensification and abandonment on farmland birds in Poland following EU accession. *Agric. Ecosyst. Environ.* 168, 16–24. <https://doi.org/10.1016/j.agee.2013.01.015>.
- Schliep, K.P., 2011. phangorn: phylogenetic analysis in R. *Bioinformatics* 27, 592–593.
- Schneider, F.D., Fichtmueller, D., Gossner, M.M., Güntsch, A., Jochum, M., König-Ries, B., Le Provost, G., Manning, P., Ostrowski, A., Penone, C., Simons, N.K., 2019. Towards an ecological trait-data standard. *Methods Ecol. Evol.* <https://doi.org/10.1111/2041-210x.13288>.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., Wilson, J.D., 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *J. Appl. Ecol.* 35, 24–43. <https://doi.org/10.1046/j.1365-2664.1998.00275.x>.
- Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotens, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehtikoinen, A., Lindström, A., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P., Willis, S.G., 2016. Consistent response of bird populations to climate change on two continents. *Science* 352, 84–87. <https://doi.org/10.1126/science.aac4858>.
- Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D., Gaston, K.J., 2007. Bird densities are associated with household densities. *Global Change Biol.* 13, 1685–1695. <https://doi.org/10.1111/j.1365-2486.2007.01390.x>.
- Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Toboła, M., Herzon, I., Goławski, A., Konvička, M., Hromada, M., Jerzak, L., Kujawa, K., Lenda, M., Orłowski, G., Panek, M., Skórka, P., Sparks, T.H., Tworek, S., Wuczyński, A., Żmihorski, M., 2011. Conservation of farmland birds faces different challenges in western and central-eastern Europe. *Acta Ornithol.* 46, 1–12. <https://doi.org/10.3161/000164511X589857>.
- Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., da Fonseca, G.A.B., Portela, R., 2007. Global conservation of biodiversity and ecosystem services. *Bioscience* 57, 868–873. <https://doi.org/10.1641/B571009>.
- Vázquez, D.P., Simberloff, D., 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am. Nat.* 159, 606–623. <https://doi.org/10.1086/339991>.
- Vickery, J., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biol. Conserv.* 119, 19–39. <https://doi.org/10.1016/j.biocon.2003.06.004>.
- Wackernagel, M., Kitzes, J., Moran, D., Goldfinger, S., Thomas, M., 2006. The Ecological Footprint of cities and regions: comparing resource availability with resource demand. *Environ. Urbanization* 18, 103–112. <https://doi.org/10.1177/09562478060603978>.