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Geographic variation in the population trends of common breeding birds across central Europe

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Abstract

Recent declines of many European bird species have been linked with various environmental changes, especially land-use change and climate change. Since the intensity of these environmental changes varies among different countries, we can expect geographic variation in bird population trends. Here, we compared the population trends of bird species among neighbouring countries within central Europe (Czech Republic, Denmark, Germany, Switzerland) between 1990 and 2016 and examined trait-associations with population trends at both national and international scales. We found that Denmark had the highest proportion of declining species while Switzerland had the lowest. Species associated with farmland had negative trends, but the effect size tended to differ among countries. A preference for higher temperature was positively associated with population trends and its effect size was similar among countries. Species that were increasing across all four countries were associated with forest; while species that were decreasing across all countries were long-distance migrants or farmland birds. Our results suggest that land-use change tends to be a more regionally variable driver of common bird population trends than climate change in central Europe. For species declining across all countries, international action plans could provide a framework for more efficient conservation. However, farmland birds likely need both, coordinated international action (e.g. through a green agricultural policy) to tackle their widespread declines as well as regionally different approaches to address varying national effect trajectories.

Keywords: Conservation; Monitoring; Population dynamics; Population trends; Species traits

Introduction

Bird populations across Europe have been undergoing large changes in abundance due to different anthropogenic environmental drivers. In particular, land-use change, primarily agricultural intensification, has been linked with strong population declines (Donald, Green & Heath 2001; Eglington & Pearce-Higgins 2012; Jørgensen, Boehning-Gaese, Thorup, Tottrup, Chylarecki et al. 2016). Climate change has been also linked with declines but also some increases (Jiguet, Gregory, Devictor, Green, Voříšek et al. 2010; Stephens, Mason, Green, Gregory, Sauer et al. 2016). Since the intensity of both land-use change and climate change varies geographically, the impact on bird populations can be expected to vary (Donald et al. 2001). There has been considerable examination of the large-scale generalities of bird population change, but the spatial variation in trends has not been fully examined (Hanzelka, Horká & Reif 2019; Heldbjerg, Fox, Lehikoinen, Sunde, Aunins et al. 2019; Massimino, Johnston, Noble & Pearce-Higgins 2015; Morrison, Robinson, Clark & Gill 2010).

Land-use and climate change have been shifting in similar directions over the past decades across Europe, but with spatial variability in pace and intensity (Donald et al. 2001; Gingrich, Niedertscheider, Kastner, Haberl, Cosor et al. 2015). In general, farmland area has decreased, but land-use intensity on farmland has increased (EEA 2017; Kuemmerle, Levers, Erb, Estel, Jepsen et al. 2016). At the same time, the urban area has increased, as well as forest cover due to farmland abandonment and afforestation. However, there are marked differences among geographic regions, especially along an east-west gradient, which can be explained by different national histories and socioeconomic developments (Kuemmerle et al. 2016; Reif, Böhning-Gaese, Flade, Schwarz & Schwager 2011). Land-use changed across eastern Europe after the end of the Cold War due to changing land-use policies after EU accession (Reif et al. 2019). Regional variation in topography and climate can also influence land-use changes and the impacts of climate change (Kovats, Valentini, Bouwer, Georgopoulou, Jacob et al. 2014; Kuemmerle et al. 2016).

Previous studies on bird population trends in Europe have examined associations between species' population trends and their traits, niche or more generally species-specific characteristic (hereafter referred collectively to as traits), such as habitat preferences, as an approach to compare the roles of different environmental changes (Gregory, Škorpilová, Voříšek & Butler 2019; Julliard, Jiguet & Couvet 2004; Reif, Vermouzek, Voříšek, Šťastný, Bejček et al. 2010). This approach is based on the assumption that species' traits reflect their sensitivity or exposure to drivers, such as climate change or land use change. Negative associations between species' farmland use and their population trends has signaled the impact of agricultural intensification on birds (Gregory et al. 2019; Lemoine, Bauer, Peintinger & Boehning-Gaese 2007). In contrast to farmland birds, forest bird populations have been mostly stable (Gregory et al. 2019). Associations between species' temperature preferences and population trends have been taken as an indicator of the impact of climate change (Jiguet et al. 2010), with evidence of both increases of warm-adapted species and decreases of cold-adapted species (Stephens et al. 2016). Also, declines of bird species that undergo seasonal long-distance migration, usually to sub-Saharan Africa, have been widely reported, and linked to environmental change on both the breeding and wintering grounds (Sanderson, Donald, Pain, Burfield & van Bommel 2006; Vickery, Ewing, Smith, Pain, Bairlein et al. 2014).

Consistent with geographic variation in land-use and climate change throughout Europe, there is variation in the strengths of the associations between species traits and bird population trends (Devictor, van Swaay, Brereton, Brotons, Chamberlain et al. 2012; Hanzelka, Telenský & Reif 2015; Reif et al. 2011). Greater community shifts towards warm-adapted species have been found in more northerly regions of Europe, where species may be closer to their thermal tolerance limits or exposed to stronger climate change (Hanzelka et al. 2019; Jørgensen et al. 2016). Stronger population declines of farmland birds between 1970 and 1990 occurred in countries with more intensive agriculture, mostly in Western Europe (Donald et al., 2001). Following EU-accession and an associated agricultural intensification, farmland bird population declines accelerated also in former Eastern Bloc countries (Reif & Vermouzek

2019). For population changes between 1990 and 2008, the declines of farmland birds that were also long-distance migrants were especially linked with agricultural intensification (Jørgensen et al. 2016). Further quantification of the regional variability in bird population trends could help understand which threats need to be tackled at an international scale and which threats require additional regionalized action.

In this study, we compiled country-level population trends for bird species for the period 1990–2016 from four neighbouring countries of central Europe: Czech Republic, Denmark, Germany and Switzerland. These countries are geographically close and largely overlap in their species pools of breeding birds yet vary with regard to recent climate and land-use change, making this region suitable to study variability in national bird population trends. For each country, we examined the relationship between species traits and population trends to infer the strength of different environmental drivers on bird population and community change (Williams, Shoo, Isaac, Hoffmann & Langham 2008). Changes in biodiversity are often scale-dependent, hence, the species declining at a national level may not necessarily be the same as those most declining at the international level. Moreover, whether a species is declining internationally, or only nationally in a given country, could have important implications for conservation planning. To investigate this, we also compared traits associated with international winner and loser species, defined as those increasing and decreasing across all four countries, as well as identify species with the most contrasting trends among the countries.

We predicted that bird population changes would be more similar among countries with similar patterns of environmental change since 1990. Specifically, we predicted that (1) a preference for farmland would be a more important predictor of bird population trends in countries with stronger agricultural intensification, and (2) species temperature preference would be a more important predictor of population trends in the continental countries (Switzerland, Czech Republic), with warmer summers and cooler winter, compared with the more oceanic country with a milder climate (Denmark). A common phenomenon observed across taxa and geographic regions is a community shift towards generalist species

(Clavel, Julliard & Devictor 2011). Hence, we also predicted that species' habitat breadth (wider habitat breath equates to stronger generalism) would be positively related to population trends across all countries (Davey, Chamberlain, Newson, Noble & Johnston 2012; Morelli, Benedetti & Callaghan 2020).

Materials and methods

Bird population data

Data on bird populations for the four countries were obtained from the Czech Society for Ornithology (Česká společnost ornitologická, CSO, https://www.birdlife.cz/), the Federation of German Avifaunists, (Dachverband Deutscher Avifaunisten e.V, DDA, https://www.dda-web.de), DOF- Birdlife Denmark (Dansk Ornitologisk Forening, http://www.dof.dk/) and the Swiss Ornithological Institute (Schweizerische Vogelwarte Sempach, https://www.vogelwarte.ch).

In all countries, the programs use skilled volunteers to collect data on bird populations during the breeding season of each year. Surveys were conducted as either point or line transect counts, or territory mapping, following a standardized protocol, with usually at least two surveys per site per year. The national coordinators produced annual and national population size indices for each species, which contribute to their own multi-species breeding bird indicators. These population size indices express abundance of a species in respective years of the time series in per cent relative to the first year set to 100%. We used the species-specific indices as the basis of our analysis since they represent comparable values across all species and countries. The programs varied in some details, especially in survey duration and total sample size (Table 1). For Switzerland, the number of species whose breeding bird index is calculated based on data from the common breeding bird monitoring scheme was lower (67 species) compared to the other countries. This is partly because the Swiss common breeding bird monitoring scheme comprises fewer sampling sites, but also because some more targeted surveys are running for several species or species groups. Therefore, for Switzerland, species with an index based on data from other monitoring schemes than the common breeding bird monitoring were additionally included, but only for the species that were included in the common bird monitoring schemes of the other countries. For detailed information on each program, we refer the readers to Reif et al. (2013) for the Czech Republic; Moshøj et al. (2017) for Denmark; Kamp et al. (2020a) for Germany, and www.vogelwarte.ch/en/projects/monitoring for Switzerland

Because the datasets varied with regard to the species included (e.g. some datasets included waterbirds and seabirds, while others not), we restricted each dataset to birds belonging to the subset of families reported by all datasets. This was to ensure each dataset had a similar target species community and to facilitate a fair comparison among the patterns found in each dataset. The total number of species was 109, comprising 99 in Czech Republic, 85 in Denmark, 88 in Germany and 94 in Switzerland (see Appendix A: Table 1 for list of included and excluded families). However, we also ran analyses using the subset of shared species among all datasets (n = 66 species for which there was data in each country).

Trait data sources

We focused on five key traits that were previously linked with bird population trends in Europe.

Habitat (preference for either farmland or forest, as well as habitat niche breadth): We focused on two main types of habitat preferences, specifically farmland and forest. Farmland and forest are the dominant land covers in our study region of central Europe, and species' habitat associations with either farmland or forest are frequent within the common bird species included in our analysis. Additionally, we selected these habitat preferences because they align with the farmland and forest bird population indicators that have been calculated for different countries in Europe. Farmland and forest birds were defined according to the Pan European Common Bird Monitoring Scheme (PECBMS) classification (https://pecbms.info/methods/pecbms-methods) for Europe, which defines which species contribute to the official farmland and forest bird indicators. PECMBS makes different habitat classifications: for whole of

Europe as well as split by different geographic regions. We used a common habitat classification for all countries by defining farmland and forest birds according to whether they were listed on the Western or Central/Eastern classifications; species were assigned these habitat preferences if they were found on the respective habitat classification list for either or both regions (see Appendix A: Table 2 for classification). We note that each country uses slightly different habitat classifications for their own national farmland bird indicators but we used the PECBMS scheme to have a common set of species for comparison. We also note that farmland birds are birds that predominantly use farmland but can also be found elsewhere. Similarly, forest birds do not use only forest, but also adjacent other habitats or settlements. Habitat niche breadth (referred to hereafter as habitat breadth) was assessed as the number of different habitat types that a species uses following a published database (Storchová & Hořák 2018; Storchová, Hořák & Hurlbert 2018). We used all the 15 habitat types available in this database, which included deciduous forest, coniferous forest, woodland, shrub, savanna, tundra, grassland, mountain meadows, reeds, swamps, desert, freshwater, marine, rocks, and human settlements.

Migratory behaviour: Species were classified as having a long-distance migratory strategy or not (i.e., wintering beyond the western Palearctic, usually sub-Saharan Africa) based on Storchová et al. (2018).

Temperature preference: Species' temperature preferences were calculated by overlaying species distribution data (BirdLifeInternational & NatureServe 2012) with average (1969–1990) daily mean temperature maps (from E-OBS, to reflect average spatial patterns) (Haylock, Hofstra, Tank, Klok, Jones et al. 2008) delimitated to Europe on a 25 x 25 km equal area grid (Eckert IV projection) following others (Jiguet et al. 2010). Because some species were migrants, we used only the breeding distribution and spring (March to May) temperature data. We calculated the mean temperatures of occupied grid cells for each species to create a variable that organized species on a gradient from cool to warm temperature preference.

Associations among species traits were examined using either the Pearson correlation coefficients, r, (between two continuous variables or between one continuous and one binary variable) or a chi-squared statistic (between binary variables). For comparability, the latter was subsequently translated into the Pearson correlation coefficient following an available formula (Rosenberg 2010). While some traits were significantly correlated with each other, none were strongly correlated (all $r < 0.4$, Appendix A: Table 3). In Appendix A: Table 4, all trait data are provided.

Environmental data

We retrieved national-level annual data on mean daily temperature and cereal yield from the FAOstat database (http://www.fao.org/faostat/en/#data) for each country. Temperature data were provided as annual anomalies compared to a reference mean temperature for the period 1951–1980. We used simple linear regressions to test the effect of year (i.e., annual change) on each environmental covariate and the interaction between year and country to test whether the environmental changes differed among countries.

Population trend analysis

We first examined the population trends for all species within each country for the period 1990 to 2016. Species population trends were calculated using generalized least squares linear models that accounted for temporal autocorrelation of the annual population indices. Specially, we tested the effect of year (as a continuous variable) on the log of annual population indices. We included the ratio of the standard error/annual index value as weights to account for variation in the precision of the annual population index estimates. The coefficient for the effect of year was used as an estimate of the population trend of each species over the time-period. To visualize time-series of mean population indices in each country, we followed the approach of Soldaat et al. (2017) to create a multi-species indicator (MSI). Specifically, we used Monte Carlo simulations (n=1000) to propagate the uncertainty of the species annual indices to the MSI by drawing random values for each species assuming indices are log-normally distributed (with standard deviation as the ratio of the standard errors/indices). Species' randomly-drawn time-series were then re-scaled to be relative to 100 in the first year and the median values of the indices across all species calculated for each year and simulation run. MSIs were then summarized across simulation runs for each year by their median and lower and upper quartiles (2.5%). Pearson correlation coefficient was also used to quantify the correlation of trends between each pair-wise country combination.

We used linear models with species' trend estimates as the response variable and species' traits as explanatory variables, to investigate factors explaining variation in trends among species. We ran analyses using the dataset restricted to shared families among all countries as well as the dataset restricted to shared species among all countries. To reduce the influence of some extreme trends, and improve normality of the data, we capped extreme trend values at the 99% quantile. To help interpretation of our results and link our findings to previous analyses, we first tested the effect of each trait on population trends in single regression models (i.e., one trait per model), but we then built a multiple regression model to test the effect of each trait, after accounting for the effects of all other traits, for each country. We also examined the correlation among traits and variance inflation factors of the models to assess multicollinearity.

We next examined the similarities in bird community change across all countries. To examine the similarity in trait-associations, we modelled all the trend estimates using a linear mixed effect model with species as a random intercept (since most species were present in multiple countries) along with the five trait variables, and country, as fixed effects. Hence, this model estimated the mean effects of the traits across all countries. We also identified species that had consistent trends across the countries within the pool of 66 species occurring in all countries. We defined species as international winners and losers when they had trends in the same direction (positive or negative) across all countries, with the trends being significant in at least two countries. Then we built a binomial glm to test whether or not being an international winner or loser could be explained by the five trait variables.

Finally, we examined the dissimilarities in bird community change across the countries. To determine the differences in trait-associations, we built a similar linear mixed effect model as above except we additionally included a trait×country interaction term, for each trait one by one to the main effects model. The interaction coefficients represented the differences in trait effects between countries. For each trait, we reset the reference level of the country factor so that we could extract the largest interaction coefficient, i.e., the difference between the largest trait effect and the smallest trait effect. For example, if country A showed the strongest effect of temperature preference and country D showed the smallest effect of temperature preference, we extracted the interaction coefficient comparing A relative to D. We also identified species that showed the most contrasting trends across countries, called "international diverger" species. These were defined as species with a significant positive trend in at least one country and a significant negative trend in at least one other country. Again, we built a binomial glm to test whether or not being an international diverger species could be explained by the five trait variables, within the pool of 66 species occurring in all countries.

We ran another set of models including taxonomic ranks (order, family and genus) as random terms to control for phylogenetic relatedness. However, since the effect sizes were little affected, we present the simpler models without these random effects. All analyses were conducted in R version 3.6.3 (2020). Covariates were standardized to units of standard deviation to enable comparison of their effect sizes. Effects were treated as significant when their 95% confidence intervals did not overlap with zero.

Results

Environmental changes

All countries have undergone substantial land-use and climate changes during the study period between 1990 and 2016 (Fig. 1). Temporal dynamics of mean daily temperatures were very similar among all the countries. On average, mean temperature anomalies increased by 0.036°C (SE = 0.007) per year. By contrast, changes in cereal yield significantly differed among the countries ($F_{3,101} = 8.63$, $P<0.01$), with the largest increase in the Czech Republic, followed by Germany and Denmark, and with Switzerland showing the smallest increase.

Country-level trends

The highest proportion of decreasing species was found in Denmark while the highest proportion of increasing species was found in Switzerland (Fig. 2A) In line with these species-level changes, the multispecies index of the shared species decreased most strongly in Denmark and tended to increase in Switzerland (Fig. 2B). Differences in the uncertainty reflect differences in sample size of the countries, which was smallest in the Czech Republic, leading to the greatest uncertainty in the mean population trends. Correlations between population trends varied among countries but Denmark and Germany were most correlated ($r = 0.46$) and Denmark and Switzerland the least correlated ($r = 0.27$) with each other. Appendix A: Table 5 shows all pair-wise correlations of population trends among countries.

According to simple regression models, farmland preference was negatively associated with population trends for all countries, indicating that farmland birds had more negative trends than non-farmland birds within each country (Fig. 3). By contrast, forest preference was positively associated with population trends across all countries, although only significantly so for Denmark and Germany. Habitat breadth tended to be positively related to trends but the effect sizes were small and insignificant. Temperature preference also tended to be positively related, though only significantly so for Germany. Long-distance migration was negatively associated with population trends for all countries, significantly so for the Czech Republic and Switzerland. Effects of traits were generally similar when traits were simultaneously tested in a multiple regression model; however, the effects of farmland preference were weaker after accounting for the effects of the other traits, and only remained significant for the Czech Republic (Appendix A: Fig. 4).

Similarities across countries

Combining the trends for all countries, we found a positive relationship between species' temperature preferences and their trends, suggesting species preferring warmer temperatures increased more (or decreased less) than species preferring colder temperatures (Fig. 4). Habitat breadth also tended to have an average positive effect, but this was only seen with the larger sample size of all species. Long-distance migration and farmland preference had mean negative effects across all countries. Forest preference did not have a significant mean effect at the national scale (Fig. 4).

Eighteen species of the 66 (27%) shared species had consistent trend directions across all four countries. International loser species (10 species) were associated with being a long-distance migrant and preferring cooler temperatures (Fig. 5; see Appendix A: Fig. 5 for regression coefficients and 95% confidence intervals), but other international losers were farmland birds. International losers were *Alauda arvensis*, *Anthus pratensis*, *Anthus trivialis*, *Hippolais icterina*, *Muscicapa striata*, *Perdix perdix*, *Phylloscopus sibilatrix*, *Phylloscopus trochilus*, *Sylvia borin* and *Vanellus vanellus*. Forest use was the only trait associated with being an international winner (Fig. 5 & Appendix A: Fig. 5). International winners (8 species) were *Columba oenas*, *Corvus corax*, *Corvus corone*, *Cyanistes caeruleus*, *Dendrocopos major*, *Dryocopus martius*, *Phylloscopus collybita* and *Sylvia atricapilla*.

Differences among countries

While population trends tended to be negatively associated with long-distance migration, the effect sizes differed among countries (Fig. 4). The largest effect of long-distance migration was found in Switzerland, driven by mean increases of non-migratory species and mean decreases of migratory species (Appendix A: Fig. 3). The effect size for farmland preference also tended to differ among countries, but only significantly so in the analysis of all species (Fig. 4). The largest effect of farmland preference was found in the Czech Republic, driven by mean increases of non-farmland species and mean decreases of farmland species (Appendix A: Fig. 3).

Nineteen of the 66 (29%) shared species were significantly increasing in at least one country but significantly decreasing in at least one other country (Appendix A: Table 6). More than half (58%) of these species were decreasing the strongest in Denmark (Appendix A: Fig. 6). Habitat specialists were especially likely to be among the group of species most decreasing in Denmark (Chi-sq = 5.59, P = 0.02, Appendix A: Fig. 6).

Discussion

European-level indicators such as the Farmland Bird Index highlight the large-scale change of bird communities within Europe. However, such indices can mask regional variation. Our analysis reveals considerable variation in common bird population trends even among neighbouring countries. Considering the set of species common to all countries in our analysis, we found the largest number of declining species in Denmark and Germany, the largest number of increasing species in Switzerland, and mostly stable trends in the Czech Republic. Furthermore, while some species showed consistent trends across countries, a similar number of species showed contrasting trends. We found mostly similar effects of temperature preference and forest preference but more dissimilar effects of farmland preference and long-distance migration. This heterogeneity in the trajectory of the bird communities likely reflects the different histories of environmental change in each country.

Our findings suggest that climate change is a widespread and consistent driver of population change since temperature preference had a similar importance across all countries. The positive association between trends and species' temperature preferences suggest relative increases of warm-adapted species over cold-adapted species, as has been reported in previous analyses (Kamp et al. 2020a; Prince & Zuckerberg 2015; Reif et al. 2011; Stephens et al. 2016). However, temperature preference was not associated with international winner species (i.e., positive trends in all countries), suggesting that the winners of climate change might differ among countries. Forest use was the only trait associated with being an international winner and forest preference seemed to affect some species similarly across all countries. Europe-wide analyses of forest species abundances suggest mostly stable populations (Gregory et al. 2019) but increases have been found in some regions and time-periods (Hanzelka et al. 2019; Kamp et al. 2020a). The success of these species in our study region may be a consequence of an increase in forest cover, due to farmland abandonment and reforestation, as well as forest maturation (Reif, Storch, Voříšek, Šťastný & Bejček 2008; Reif, Voříšek, Šťastný, Bejček & Petr 2007; Schulze, Craven, Durso, Reif, Guderle et al. 2019). In Switzerland, climate change seems to facilitate the range expansion of some forest species that have colonized the largely forested montane or subalpine elevation belt (Knaus, Antoniazza, Wechsler, Guélat, Kéry et al. 2018). Urbanization may also play a role in the success of these international winners since some are rather generalist forest species, such as the great spotted woodpecker, which exploit habitats close to or within human settlements. However, other international winners, such as the black woodpecker, are typical of mature forest. Further analysis might tease apart preferences for different forest types of successional stages. For instance, recent atlas maps in Denmark show that 21 species associated with deciduous forests have increased their distribution since the 1970s, consistent with the general increase in deciduous forest cover, while 14 species associated with coniferous forest have shown a contraction in their distribution since the1990s (Vikstrøm & Moshøj 2020). Other forest or woodland international winners, such as the chiffchaff and blackcap, might have benefited from climate change, with shortening of migration routes having positive effects on reproductive success (Pulido & Berthold 2010).

While farmland birds were declining across all countries, there was some indication of geographic variation in the relative decline of farmland birds compared with non-farmland birds. Other analyses have already shown that farmland birds have been suffering ongoing declines for decades in all the countries of our analysis (Birrer, Spiess, Herzog, Jenny, Kohli et al. 2007; Busch, Katzenberger, Trautmann, Gerlach, Dröschmeister et al. 2020; Heldbjerg, Sunde & Fox 2018; Kamp et al. 2020a; Reif & Vermouzek 2019). We found the strongest effect of farmland preference in the Czech Republic, due to a combination of increases of non-farmland species and decreases of farmland species. Out of our studied countries, the Czech Republic had probably undergone the most socioeconomic change during our study period (1990-2016), including a collapse in agriculture following the Velvet Revolution in 1989 but subsequent increase in agricultural output following EU accession in 2004 (Kuskova, Gingrich & Krausmann 2008; Reif et al. 2011). Hence, our results supported our hypothesis of the largest effect of farmland preference in the region experiencing the most agricultural change. Previous analysis has already linked EU accession with negative impacts on farmland birds due to intensification of agricultural practices (Reif et al. 2019). By contrast, in the other countries, farmland birds have been already affected by on-going agricultural intensification for several decades. For instance, in Switzerland, steep decreases of formerly common agricultural species happened before the 1990s (Knaus, Graf, Guélat, Keller, Schmid et al. 2011) and some have already benefited from targeted conservation measures since then (Birrer et al. 2007). In Denmark, agriculture dominates the land, covering 62% of the area, hence both farmland and non-farmland birds might be now affected by past intensification of agricultural practices. Overall, the importance of farmland preference as a predictor of population trends probably showed some geographic variation because we compared countries that had been differently affected by large-scale intensification effects of the EU Common Agricultural Policy, e.g. Germany and Denmark since the beginning of our study time period, compared with the Czech Republic since EU accession in 2004.

Long-distance migrants were among the most likely to be an international loser since they were declining across all countries, but the magnitude of the effect of long-distance migration on population trends somewhat differed among countries. While the decline of long-distance migrants is well-recognized, multiple causes have been proposed (Howard, Stephens, Pearce-Higgins, Gregory, Butchart et al. 2020; Sanderson et al. 2006; Telenský, Klvaňa, Jelínek, Cepák & Reif 2020; Vickery et al. 2014). One hypothesis relates to environmental changes on the African wintering grounds and is supported by studies showing that variation in the decline of migrants can be partly explained by the location of their wintering grounds (Cresswell, Wilson, Vickery, Jones & Holt 2007; Ockendon, Hewson, Johnston &

Atkinson 2012). Another hypothesis relates to habitat changes on the breeding grounds (Morrison, Robinson, Clark, Risely & Gill 2013). This hypothesis is supported by, for example, a recent study showing that co-occurring species within their European breeding range have similar population trends, even if their wintering grounds differ (Morrison, Butler, Robinson, Clark, Arizaga et al. 2021). However, in Finland, long-distance migrants are declining even within protected areas, suggesting habitat loss or degradation on the breeding grounds was not the cause here (Virkkala, Rajasarkka, Heikkinen, Kuusela, Leikola et al. 2018). Hence, further work is still necessary to evaluate the relative roles of changes in the breeding and wintering grounds of species (Howard et al. 2020). Most long-distance migrants are insectivores and hence may be also affected by long-term changes in insect biomass (Bowler, Heldbjerg, Fox, de Jong & Böhning-Gaese 2019) or trophic mismatches between peak insect availability and the breeding period during the annual cycle (Jones & Cresswell 2010; Kolecek, Adamik & Reif 2020). Many of the identified international loser and migratory species, such as the tree pipit or willow warbler, prefer open habitats or open forest, hence forest maturation might have also negatively affected them (Kamp, Trappe, Dübbers & Funke 2020b). Given bird species, and species' populations of different countries, vary in their breeding grounds and often also their wintering grounds, pressures on migrants probably vary geographically, which may lead to different magnitudes of declines.

Our findings suggest that tackling declines associated with land-use change, including agricultural intensification, might be best approached by a combination of a common framework addressing the overall decline of farmland birds in Europe, for instance via greening the EU Common Agricultural Policy, as well as country-specific conservation approaches that account for the legacies of different historical contexts within each country. By contrast, a more uniform approach might be applied to mitigate climate change impacts, such as improved landscape connectivity to facilitate adaptive range shifts (Littlefield, McRae, Michalak, Lawler & Carroll 2017). Adaptive management of protected areas might be also an option in order to prevent spatial mismatches of range-shifting species and their habitats and to provide refuges for retreating species (Michalak, Lawler, Roberts & Carroll 2018; Schuster, Wilson, Rodewald, Arcese, Fink et al. 2019). However, because of interactions between climate and land-use change, climate change mitigation measures need to carefully consider possible impacts on both habitats and species. Better understanding of the regional causes of the declines of long-distance migrants is necessary to assess which declines should be jointly tackled by neighbouring countries and which declines necessitate country-specific conservation interventions.

Our analysis highlights the limitations to trait-based analysis since, despite some differences, many of the effect sizes of the associations between population trends and traits were similar across the countries. Hence, our analysis did not explain the overall tendency to increase in the bird community of Switzerland nor the decrease of the overall community in Denmark. Trait-based analyses only explain the interspecific variation in trends but not the mean trend of community (Bowler, Heldbjerg, Fox, O'Hara & Böhning-Gaese 2018). More detailed data on land-use changes and conservation measures, and analysis of relationships between environmental covariates and bird population indices, may help better understand the mean country differences. Nonetheless, trait-based analyses have been used in many previous studies to understand the compositional changes in bird communities (Jiguet et al. 2010, Bowler et al. 2018) and more broadly applied across taxa to predict which species are more or less vulnerable to different types of environmental changes. Trait-based analyses help prioritize groups and taxa for conservation and help to guide conservation policies and management at European and country level.

Our analysis was limited by its focus on the trends of the most common and widespread species. This is partly because quantitative, robust monitoring data are only available for these species across countries, but also because we restricted our analysis to species in families found in the datasets of all countries to enable a fair comparison. These steps mean that many specialists are not included, particularly affecting our ability to assess the effect of habitat breath. This calls for more efforts to develop robust monitoring schemes for rare species and approaches to integrate data from different monitoring schemes to enable comparison between rare and common species (Kühl, Bowler, Bösch, Bruelheide, Dauber et al. 2020). Our list of international winners and losers is also highly dependent on the species with available data – since we only used species with data from all countries for this part of our analysis. The Turtle Dove, *Streptopelia turtur*, is one of the most strongly declining farmland birds in Europe, but we only had data for it from three of our countries; hence it was not named as an international loser.

Despite being geographic neighbours, we found many differences in the population trends of species in different countries of central Europe. Most likely geographic differences in land cover and land-use change, especially associated with the agricultural practices, explain the differences in the trajectories of each community. We identified several species declining across our study countries in central Europe; hence, these might be considered for coordinated international conservation efforts. Currently, of all international loser species that we identified, only a management plan for Skylark and a species action plan for Lapwing have been created, but even for these there is a lack of implementation at national scales. Our comparative analysis suggests that regional approaches might add to our toolbox to appropriately tackle the adverse impacts of land-use change; however, internationally coherent conservation action for farmland bird species should be also a priority.

Acknowledgements

We thank all those involved in the data collection schemes of each country for enabling national-scale analysis of species' population trends. We also thank Corey Callaghan for comments on a previous version of the manuscript. The German bird monitoring is funded through an agreement between the German government and the federal states ("Verwaltungsvereinbarung Vogelmonitoring"). The Danish point count census survey is financially supported by the Danish Environmental Protection Agency. JR was supported by the Czech Science Foundation (20-00648S) and Charles University (PRIMUS/17/SCI/16). DB was supported by the German Research Foundation (DFG) for funding the sMon working group (Trend analysis of biodiversity data in Germany) through iDiv (DFG FZT 118).

Appendix A. Supplementary data

Supplementary data (figures and tables) associated with this article can be found, in the online version, at XXXXX."

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Tables

Table 1. Main survey features of each national monitoring scheme

Country	Survey type	Sample size	Site selection	# species in our analysis
Czech Republic	5 min point counts	20 points per transect; c. 100 transects	free choice	99
Denmark	5 min point counts	10-20 points per transect; up to 377 transects	free choice	85
Germany (1990-2010)*	5 min point counts	10-20 points per transect; up to 497 transects	free choice	88
Germany (2004-2016)*	Territory mapping	3 km line; up to 1200 plots	stratified random	
Switzerland	Territory mapping	267 1 km squares	systematic	94

* Both schemes ran parallel during 2004 to 2010 to allow the combination of population trends (that were calculated separately for both periods) into a single time series covering the full period (Kamp et al. 2020a)

Figure legends

Fig. 1. Comparison of environmental change in each country. Shown are cereal yield (as a measure of agricultural land-use intensity) and mean temperature anomalies (anomalies = differences compared to mean temperature during 1951–1980, as a measure of climate change).

Fig. 2. (A): Number of species in different population trend classes per country. Data subsets are either all species (restricted to shared families among datasets, n = 109) or the subset of shared species among countries (shared species, n = 66). (B). Multi-species indicators ('MSI') showing median and quantiles (lower and upper 2.5%) of the population indices of the 66 shared species across countries, rescaled to 100 in 1990. See Appendix A: Figs 1 & 2 for time-series plots of species.

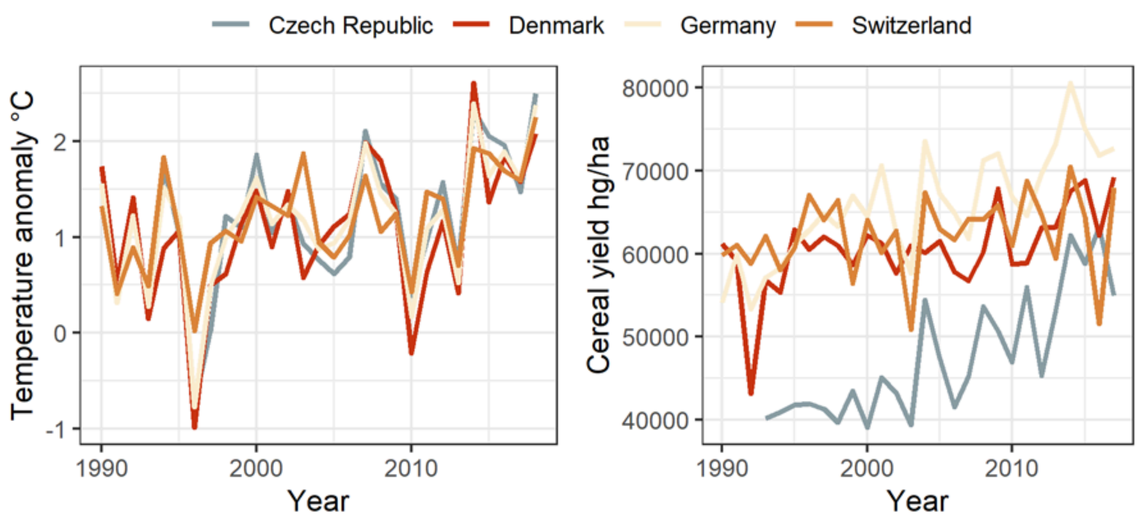
Fig. 3. Effect sizes (mean and 95% CI) of the effect of each trait on species' population trends in each country. Effect sizes represent the effect of the traits on species' trends, when tested in a simple regression model (i.e., the effect size for farmland is the mean difference in population trend between farmland and non-farmland birds). Subset is either analysis with all species (datasets restricted to shared bird families, n = 100, 85, 88, and 94 species for Czech Republic, Denmark, Germany and Switzerland, respectively) or shared species (restricted to species found in all four datasets, n = 66). "Migrant" includes only long-distance migrants. Appendix A: Fig. 3 shows boxplots of the trends in each trait group.

Fig. 4. Similarities show the mean effect sizes (and 95% CI) for each trait on species' population trends across all countries tested together in a multiple regression model. Differences show the maximum differences in effect sizes (and 95% CI) of each trait among each pairwise country comparison. Differences are presented to be positive – i.e., the difference is always the largest effect size minus the smallest effect size.

Fig. 5. Traits associated with being (left) an international loser (10 species, a negative trend estimate in all countries) – long-distance migration or farmland preference, or (right) an international winner (8 species, a positive trend estimate in all countries) – forest preference or another habitat preference. The y-axes

show the median population trend of each species across all countries and points are labelled by first four letters of the species genus and epithet see (see Appendix A: Table 6 for full names). Only species for which data from all countries were available were considered.

Figure 1



Czech Republic
Denmark
Germany
Switzerland
Temperature anomaly °C
2
1
0
-1
1990
2000
2010
Year
Cereal yield hg/ha
80000
70000
60000
50000
40000
1990
2000
2010
Year

Figure 2

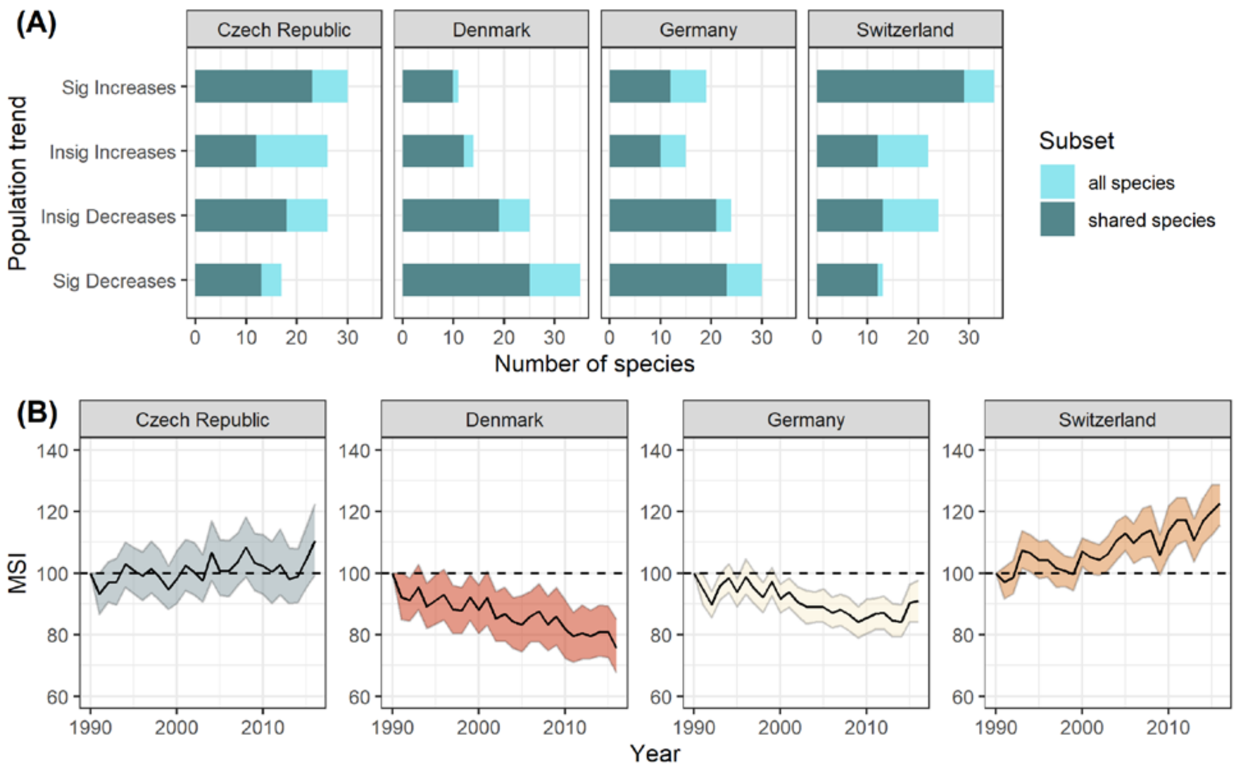

(A)
Czech Republic
Denmark
Germany
Switzerland
Population trend
Sig Increases
Insig Increases
Insig Decreases
Sig Decreases
0
10
20
30
Number of species
Subset
all species
shared species
(B)
Czech Republic
Denmark
Germany
Switzerland
MSI
140
120
100
80
60
1990
2000
2010
Year

Figure 3

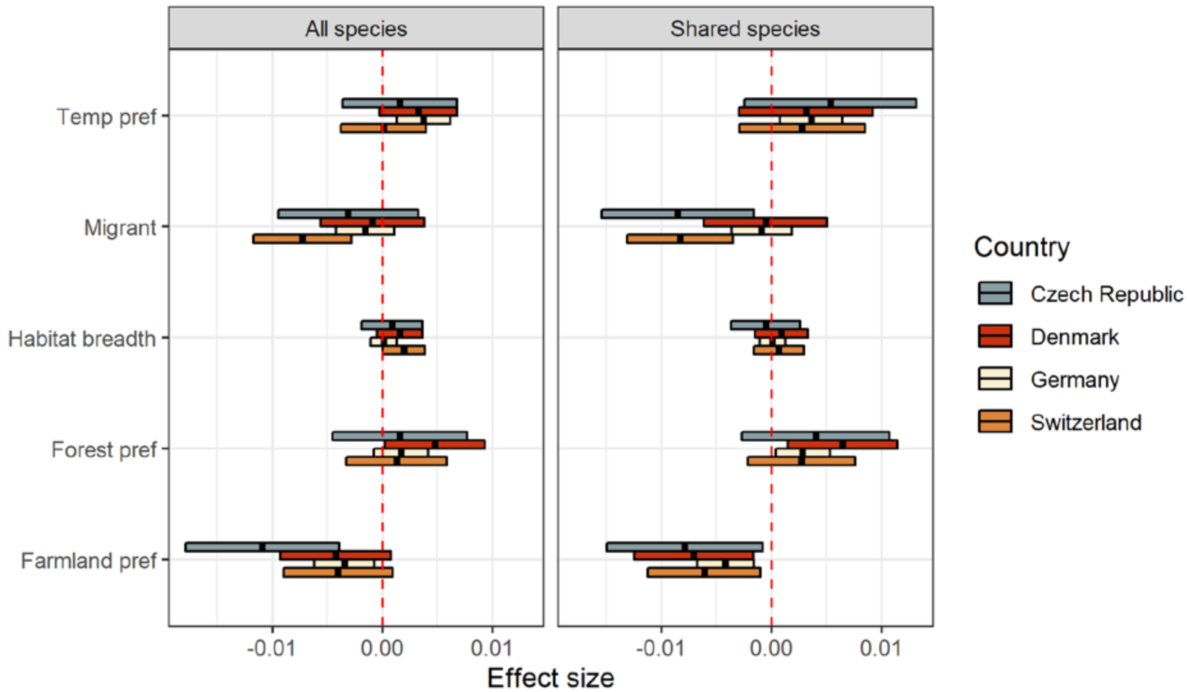

All species
Shared species
Temp pref
Migrant
Habitat breadth
Forest pref
Farmland pref
-0.01
0.00
0.01
Effect size
Country
Czech Republic
Denmark
Germany
Switzerland

Figure 4

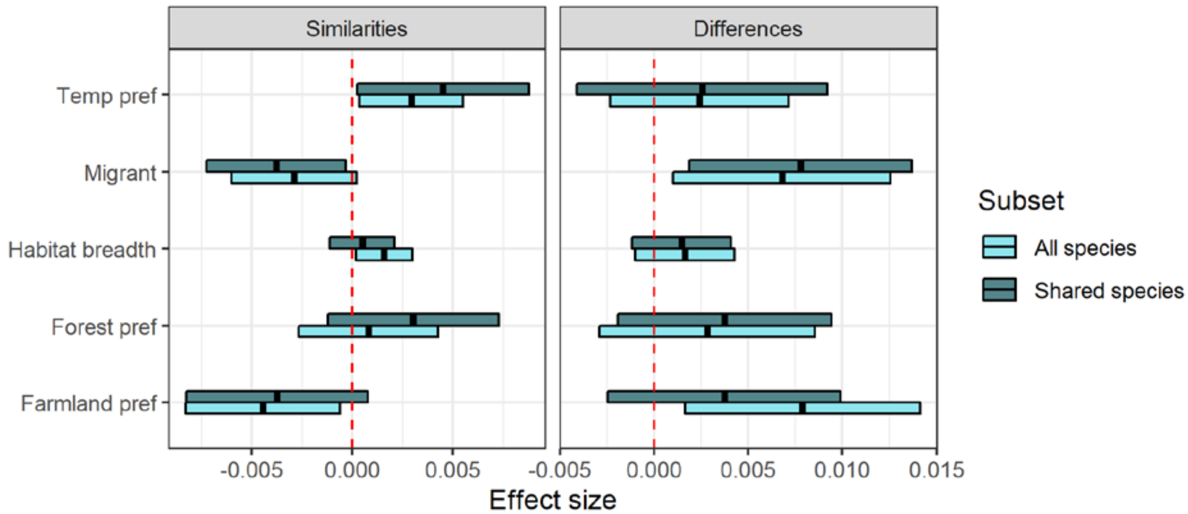
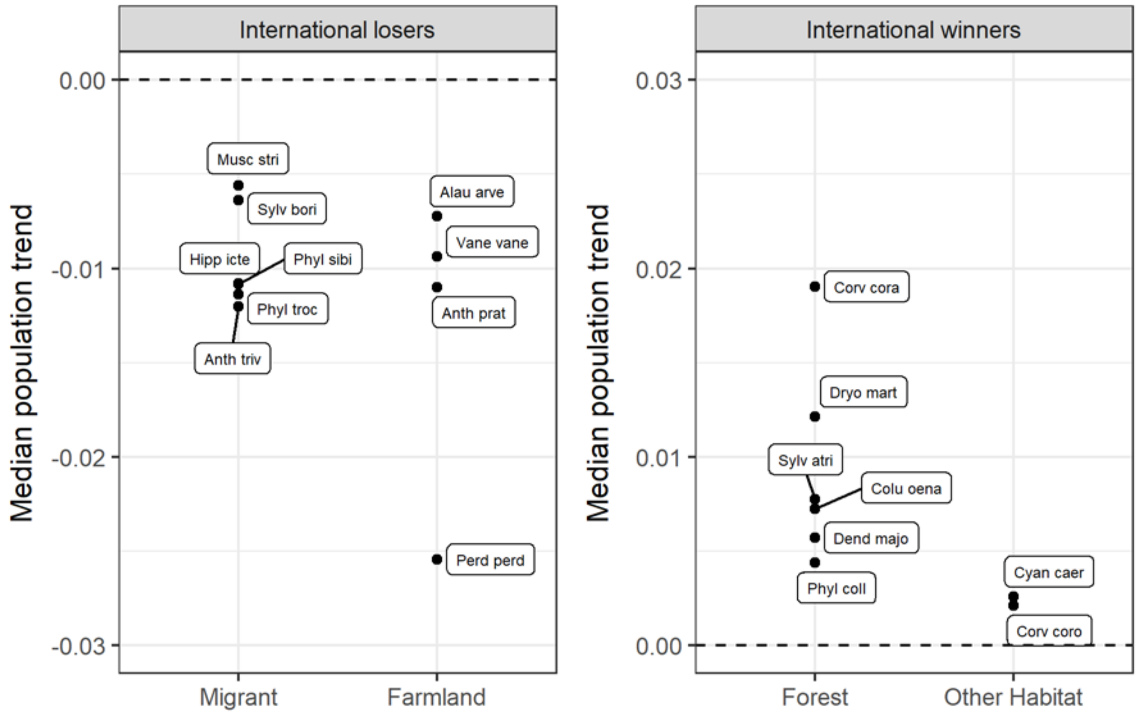

Similarities
Differences
Temp pref
Migrant
Habitat breadth
Forest pref
Farmland pref
-0.005
0.000
0.005
-0.005
0.000
0.005
0.010
0.015
Effect size
Subset
All species
Shared species

Figure 5


International losers
International winners
Median population trend
Median population trend
0.00
-0.01
-0.02
-0.03
0.03
0.02
0.01
0.00
Musc stri
Sylv bori
Hipp icte
Phyl sibi
Phyl troc
Anth triv
Alau arve
Vane vane
Anth prat
Perd perd
Corv cora
Dryo mart
Sylv atri
Colu oena
Dend majo
Phyl coll
Cyan caer
Corv coro
Migrant
Farmland
Forest
Other Habitat