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Investigating the heterogeneity within Wild bird indices in Europe

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A B S T R A C T

Biodiversity decline is monitored through a multitude of proxies. One of the most common proxies are aggregate indices constructed from time-series of species. Because of their standardised construction and simplicity of interpretation, these indices are often used as official indicators for biodiversity monitoring. However, aggregate indices hide variability among species dynamics from which they are built. Understanding this diversity is essential to interpret indices and avoid missing particular subsets of species with strong dynamics or groups of species with opposing dynamics that may result in little change in the overall index. In this study, we analyse heterogeneity within the most widely used Wild bird indices in Europe, Farmland Bird Index (FaBI) and Forest Bird Index (FoBI) in 20 European countries between 2000 and 2017. We analyse potential heterogeneity in dynamics within FaBI and FoBI of each country. We show that there is structural heterogeneity in dynamics among species as well as clusters of species with differing dynamics co-existing within aggregated indices in most countries studied. This was the case for farmland birds, even though this group shows strong general declines across Europe, and for forest birds that have less coherent long-term dynamics. We further explored whether clusters may be distinctly linked to major ecological traits, habitat specialisation, functional originality and species' thermal niche, thereby potentially indicating ecologically distinct subgroups. We however found few consistent patterns, although habitat specialisation may explains some of variability for forest birds. As new conservation objectives and policies are produced or implemented, it is important to consider the substantial heterogeneity within aggregated indices.

1. Introduction

Biodiversity is in serious decline across the globe (Habel and Schmitt, 2018; Rosenberg et al., 2019), but the decline is complex (Leung et al., 2020; Loreau et al., 2022) with species that can be considered as winners or losers to anthropogenic pressures (McKinney and Lockwood, 1999). In the face of this decline, global conservation policies have failed to meet their targets in 2010 and 2020 (Xu et al., 2021). As new strategies are negotiated and adopted, an important aim is that analyses of biodiversity decline lead to more effective protection measures.

Currently conservation strategies have at their disposal a range of tools including biodiversity indicators to assess biodiversity change as well as effectiveness of conservation policies, based in particular on well-monitored taxa like birds (Fraixedas et al., 2020). In Europe, the European Union has defined a number of indicators to "monitor, assess and report on progress in implementing the EU biodiversity strategy" (EC, 2011). Wild bird indices (Gregory and van Strien, 2010) are one set of indicators that have to be produced by each member country at their national scale, and are used to assess the health of ecosystems and to monitor changes in them (Gregory et al., 2003). These aggregated multi-species indices are constructed from geometric means of population indices across groups of focal species (common, farmland and forest birds) aimed to represent different ecosystems or habitat types (Gregory and van Strien, 2010). Wild bird indices, like other biodiversity indicators, by construction aggregate complex information from a group of species into a simple summary, useful for presenting a condensed view of change. However, aggregating masks variation among underlying taxa (Rowland et al., 2021) which makes it difficult to tell from an index whether the aggregate resembles dynamics followed by many species or if it is an average of highly heterogeneous underlying dynamics.

Given the diversity of ecological traits among the common avifauna, different bird species are led to respond in a variety of ways to human pressures, whether linked to climate change, agricultural practices or land use change (Gaüzère et al., 2020; Howard et al., 2015; Storch et al., 2023). It is therefore likely that multiple types of dynamics co-exist in an

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aggregated index (García-Navas and Thuiller, 2020; Siriwardena et al., 1998). For instance, while European indicators show broad declines in farmland birds, studies have also pointed to important differences among species such as more negative trends for resident versus migratory species (Voříšek et al., 2010) or, on the contrary, for long distance migrants versus short-distance migrants or residents (Vickery et al., 2023). For forest birds, European indicators show reasonably stable long-term trends, but there are also differences among species, e.g. specialists appearing to be declining (Gregory et al., 2019). Habitat specialisation of a species (Le Viol et al., 2012), its thermal niche (Devictor et al., 2008; Lindström et al., 2013; Tingley et al., 2009) and its functional originality (Bowler et al., 2019; Devictor et al., 2007) are among the ecological traits that most distinguish the dynamics of species undergoing global change: a species is more prone to decline if it is a habitat specialist, a cold dweller or a functionally original species (Godet et al., 2015; Jiguet et al., 2007; Le Viol et al., 2012). It can therefore be expected that the dynamics of species with similar ecological characteristics will be mainly determined by the same factors and that these dynamics will therefore share similar patterns. For example, cold-living species, specialists or functionally related species may react similarly within a given aggregated index.

Species variability in aggregated indices has mainly been explored by analysing variation in linear trend coefficients among all the species in the focal group (Bowler et al., 2021), or by analysing the sensitivity of the index to exclusion of single or a priori determined species (Leung et al., 2020). The focus then is on linear trends, ignoring other types of dynamics, or on the influence of selected species on the dynamics of the index (Fig. 1a). Dynamical Factor Analysis (DFA; Zuur et al., 2003) provides a more targeted tool for examining heterogeneity among a set of time-series. DFA is based on multivariate state-space models with the aim of representing the overall dynamics of the series using a small number dynamic factors. These factors represent the main features of the dynamics within the series and, in the context of multi-species indices, provides information about the structural heterogeneity behind the index. DFA considers dynamics that are more general than linear trends, and can be used to group species in a standardised manner without a priori classification (Fig. 1b).

In this paper, we use a toolbox combining DFA with clustering (Rigal and Knape, 2023) to explore heterogeneity in the dynamics among species in the Farmland Bird Indices (FaBI) and the Forest Bird Indices (FoBI) across European countries. Specifically, we estimate the structural heterogeneity within these indices in terms of the number latent trends needed to capture the dynamics in the indices and by identifying clusters of species sharing similar dynamics. For countries where distinct clusters are indicated, we assess whether they may be related to ecologically distinct subgroups of species. For this, we use three ecological traits: habitat specialisation, thermal niche and functional originality. These three ecological characteristic are expected to explain some of the variability in species dynamics and benefit from quantified indices that can easily be compared between the different clusters of species with shared dynamics. Our aim is to investigate how consistent the indices are both internally and across Europe, and then to understand whether clusters of species identified by the toolbox may be associated with ecologically distinct subgroups.

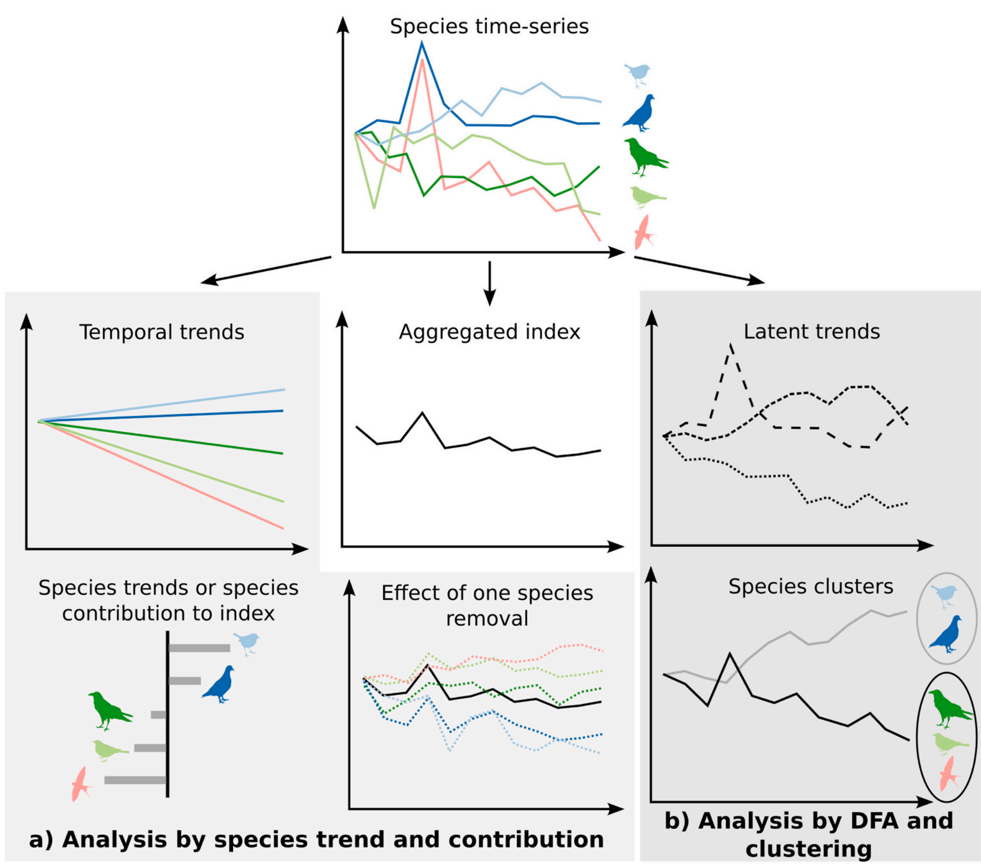

Fig. 1. Methodological approaches to assessing heterogeneity in multi-species indices. Species time-series can be used to obtain a) species temporal trends (using linear regression approaches) and the relative contribution of species to the aggregated index (e.g. using a leave-one-out method). In this case, the heterogeneity in the index is assessed at the species level. Subsequent conservation analyses focus on individual species contribution or on temporal trends of individual species or species grouped according to a given ecological characteristic. Species time-series can also be use to obtain b) latent trends (i.e. main features of dynamics) among species (using Dynamic Factor Analysis) which can serve as a basis to find clusters of species sharing similar dynamics. In that case, subsequent conservation analyses focus on the differences between groups of species with different dynamics.

2. Material and methods

2.1. Bird data

We used bird time-series collated from national breeding bird surveys coordinated by the PanEuropean Common Bird Monitoring Scheme (PECBMS) (Brlík et al., 2021). Annually, in each country, skilled volunteers carry out common breeding bird surveys using comparable standardised protocols (point counts, line transects and territory mapping). The national population indices and observation errors are then estimated from site counts using the TRIM software (Pannekoek, 2001) which processes local bird counts in a Poisson regression to determine annual indices and their standard errors. The European dataset contains these national population indices and observation errors for 170 bird species in 28 countries (the UK, Norway, Switzerland and European Union except Croatia and Malta) from the start of the national survey to 2017. To maximise the period and the number of countries covered, we focused on the 2000–2017 period for which 20 countries can be studied (see country list in Supplementary material 1). Data for Belgium were available only for Brussels and Wallonia. For Germany, data were split between former East and West entities. For each of these two countries (Belgium and Germany), abundance and uncertainty data were combined proportionally to the surface of each region. Note that for Germany, the starting dates were different for East (1991) and West (1989) and data from West Germany were therefore standardised to the value in 1991 before being combined with data from East Germany.

For each country, we extracted indices and corresponding uncertainty for the sets of species used nationally to compute the Farmland Bird Index (FaBI) and the Forest Bird Index (FoBI). The species list for each country comes from BirdLife national institutes (see source details in Supplementary material 1), and the number and selection of species differs among countries (see species lists in Supplementary material 2).

2.2. Analysing heterogeneity in dynamics among species within indices

To explore variations in species dynamics inside and among multi-species indices, we applied the toolbox in the *DFAclust R* package (Rigal and Knape, 2023) to the species used to compute the FaBI and FoBI of each of the 20 countries. The toolbox consists of three tools based on fitting Dynamical Factor Analysis (DFA) models to the data. First, latent trends summarising the general dynamics inside the set of species time-series are estimated. The number of latent trends is identified by model selection (AIC) and gives a measure of the structural heterogeneity of dynamics underlying the index. Second, an ordination biplot visualises similarities and discrepancies between species time-series, and third, a clustering algorithm is applied to detect potential clusters of species sharing similar dynamics.

To summarise the overall dynamic trend among species for each country and species group, i.e. each country's FaBI and FoBI when data were available (20 countries for FaBI and 16 countries for FoBI, Fig. 2 and Supplementary material 1), we also used the DFA to compute the geometric mean of the species latent trajectories estimated by the DFA. This can be seen as an expected trajectory of the geometric mean multi-species index, but with random noise components filtered out. Hence it is more strongly influenced by species with accurate indices and consistent dynamics, in contrast to the official European multi-species indices which are computed directly from species indices with all species weighted equally. We assess the overall trends of these multispecies indices using a dedicated analysis that take into account the error to classify the dynamics as decreasing, increasing or neither increasing or decreasing (Rigal et al., 2020).

The indices and uncertainty of the time series in the PECBMS database (Brlík et al., 2021) are relative to the first year of each survey (index equal to 100 with uncertainty 0 in the first year). This usually does not coincide with our start year (2000). As the *DFAclust* package requires that indices are relative to the first year, or relative to the mean across the whole study period, we rescaled the indices so that they reflect the abundance of the population relative the mean over 2000–2017. To also rescale the uncertainty, we used a delta-approximation (Dorfman, 1938), and assumed that the uncertainty of an unscaled index in the start year was equal to the minimum reported uncertainty (with the start year excluded). The latter assumption is conservative in that it assumes that uncertainty in the first year did not strongly inflate the uncertainty of the indices scaled relative to the first year (Knape, 2023).

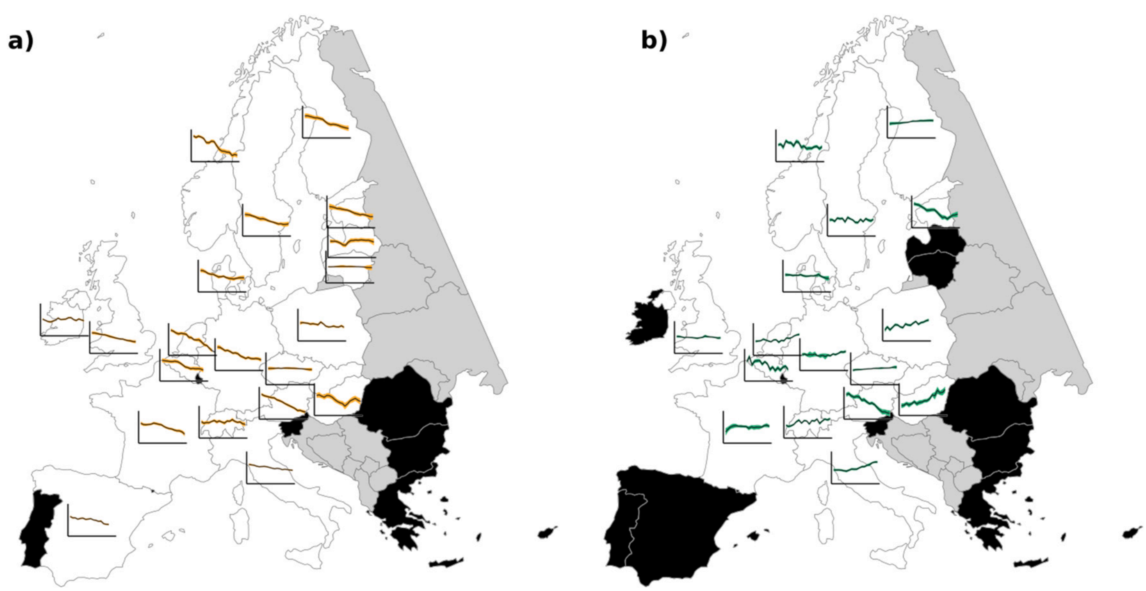

Fig. 2. Overall latent dynamics behind Wild Bird Indices in European Countries between 2000 and 2017 for: a) species in the Farmland Bird Index (FaBI) for 20 countries and b) species in the Forest Bird Index (FoBI) for 16 countries. Panels show a weighted mean of latent trends, where each weight is given by the mean of species loadings on the corresponding latent trend. The same scale is used for all countries (average log-scale dynamics between −0.4 and 0.4). 95 % Confidence Intervals are shown in yellow for FaBI and green for FoBI. Countries are displayed in white if they were PECBMS members in 2017 and data are available between 2000 and 2017, in black if they were PECBMS members in 2017 and data are not available between 2000 and 2017 and in light grey if they were not PECBMS members in 2017. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Linking species dynamics variability to ecological traits

2.3.1. Species trait indices

We investigated whether heterogeneity in species dynamics, as identified by the clustering tool, may be related species ecological traits. For this, we computed three trait indices that have been shown to be linked with species dynamics, namely Species Functional Originality Index (SFI) (Godet et al., 2015), Species habitat Specialisation Index (SSI) (Julliard et al., 2006), and Species Temperature Index (STI) (Devictor et al., 2008). SFI corresponds to the mean functional distance between one species and the other considered species. SFI therefore requires the assessment of the functional distance between each pair in a set of species. We calculated SFI based on a recent database of 34 life-history traits (measured by 85 variables) of 499 Palaearctic birds (Storchová and Hořák, 2018) using the Gower distance to handle both qualitative and continuous traits (Gower, 1971). Functional diversity is traditionally assessed with regard to resource use (Petchey et al., 2007) which encompasses (following Devictor et al. (2010)) five categories: quantity of resource needed, type of diet resources, type of nest, behaviour and migratory status. To reduce missing values and collinearity among traits, SFI was computed using 22 traits (measured by 31 variables) regrouped into these five categories (see details on traits and selection in Supplementary material 3). SSI is computed as the coefficient of variation of a species density or occupancy across a given set of habitat types. Values are available for 252 European birds (Reif et al., 2016) based on habitat occupancy across 15 habitat types obtained from Birds of the Western Palaearctic Interactive. STI is computed as the average temperature over the spatial range of a species. We used 50 × 50 km occurrence maps from the European Breeding Bird Atlas (Keller et al., 2020), and the corresponding mean temperature between 2000 and 2017 (from the E-OBS meteorological data) (Cornes et al., 2018). SFI, SSI and STI therefore reflect quantitative indices of different key ecological characteristics of species, each of them possibly able to explain species dynamics without been strongly correlated (see Supplementary material 3).

2.3.2. Discriminant analysis

We assessed links between the composition of estimated clusters and species traits using Linear Discriminant Analysis (LDA) (Izenman, 2008) via the *flipMultivariates R* package (https://github.com/Displayr/flipMultivariates). LDA is a multivariate analysis which aims at discriminating classes according to a set of explanatory variables and can be used on small sample sizes. In LDA, linear discriminatory functions are constructed from a set of explanatory variables, so that the variance between known classes is maximised, while intra-class variance is minimised. For each country and each index with at least two clusters, we ran LDA with cluster composition as classes and SFI, SSI and STI as the set of explanatory variables (see Supplementary material 3 for normality, collinearity and variance homogeneity assumptions). We recorded the percentage of inter-cluster variance for each of the species trait indices explained by the clustering, i.e. the ability of each predictor variable (SFI, SSI and STI) to separate clusters. As SSI was not available for some species, we used estimates provided by the *LDA* function to replace missing values following Von Hippel (2007). A leave-one out cross validation, using the discriminatory functions to predict the class of the left out observation, provides an estimate of the discrimination performance. However, this LDA does not account for clustering uncertainty.

3. Results

3.1. Dynamics within wild bird indices

For Farmland Bird Indices (FaBI), the overall trend has been significantly declining in 14 European countries since 2000 (Fig. 2a, see detailed results in Supplementary material 4), but shows no clear long-term trend in the remaining six countries. For Forest Bird Indices (FoBI) overall trends are less consistent across Europe with declines in five countries, increases in seven countries and no clear long-term trend in four countries (Fig. 2b, see detailed results in Supplementary material 4).

The number of latent trends identified in indices provide a measure of the structural heterogeneity of dynamics among the species in the index (i.e. an estimation of the number of different dynamic trajectories underlying the index). In most countries, the dynamic factor analysis (DFA) showed considerable heterogeneity in species dynamics with several (up to five) latent dynamic trends suggested by AIC of the DFA models (Fig. 3a and c). FaBI of 15 countries and FoBI of 13 countries contained at least two latent trends. This represents three quarter of the studied countries. Notice that the number of latent trends was not strongly correlated with the number of species (Pearson's $\rho = 0.15$), suggesting that heterogeneity is not solely a consequence of the indices containing a large number of species.

If we ignore clusters consisting of a single species, the clustering analysis suggests more than one cluster of species in 10 countries for FaBI (six countries with two clusters and four with three clusters, Fig. 3b) and 10 countries for FoBI (six with two clusters, three with three clusters and one with five clusters, Fig. 3d). This represents at least half of the countries studied. In addition, clusters from a given country may have trends in opposite directions (e.g. FaBI in Sweden, Fig. 3b and FoBI in France, Fig. 3d) and, in a few case, their dynamics are negatively correlated with the overall index (Czech Republic, Latvia and Sweden for FaBI; Czech Republic, Denmark and France for FoBI, see Supplementary material 5).

3.2. Link between underlying dynamics and species ecological traits

Analysing the variance in species traits between clusters via a Linear Discriminant Analysis (LDA, see detailed results and cross validation in Supplementary material 6) showed few consistent patterns. For the FaBI, species traits had little ability to discriminate among clusters of some countries (Norway, Poland, Spain, Sweden, Switzerland and the UK), but more in others (Ireland, Czech Republic, Latvia and France, Fig. 4). In the latter cases, the trait index with the highest ability to separate clusters differs among countries: clustering explained more than 20 % of the variance of SFI in three countries (Ireland 37 %, Latvia 31 % and Czech Republic 23 %, Fig. 4a), SSI in two countries (Czech Republic 29 % and Latvia 22 %, Fig. 4b) and STI in two countries (Ireland 45 % and France 38 %, Fig. 4c).

For FoBI, species traits in most cases had little ability to discriminate among clusters, but habitat specialisation (SSI) and niche temperature (STI) had some discriminatory ability in a few cases. Clustering explained more than 20 % of the variance of SSI in three countries (Norway 45 %, Hungary 32 %, and Italy 21 %, Fig. 4e) and STI in two countries (Sweden 24 % and Denmark 22 %, Fig. 4f), while no more than 10 % of the variance of SFI was explained by clustering for any country (Fig. 4d).

4. Discussion

Our study suggests broad heterogeneity in the dynamics of species underlying aggregated indices used in Europe to monitor the fate of avian biodiversity in agricultural and forest environments. The variability is reflected in multiple latent trends, indicating structural heterogeneity within indices, and in the presence of clusters suggested by the DFA models for Farmland (FaBI) and Forest Bird Indices (FoBI) of many countries.

The pattern of structural heterogeneity is not consistent across countries, as indicated for example by the varying species clusters, and in variation in traits related to differences among clusters. One explanation for the absence of a consistent link between structural heterogeneity in country indices and species ecological characteristics (SFI, SSI

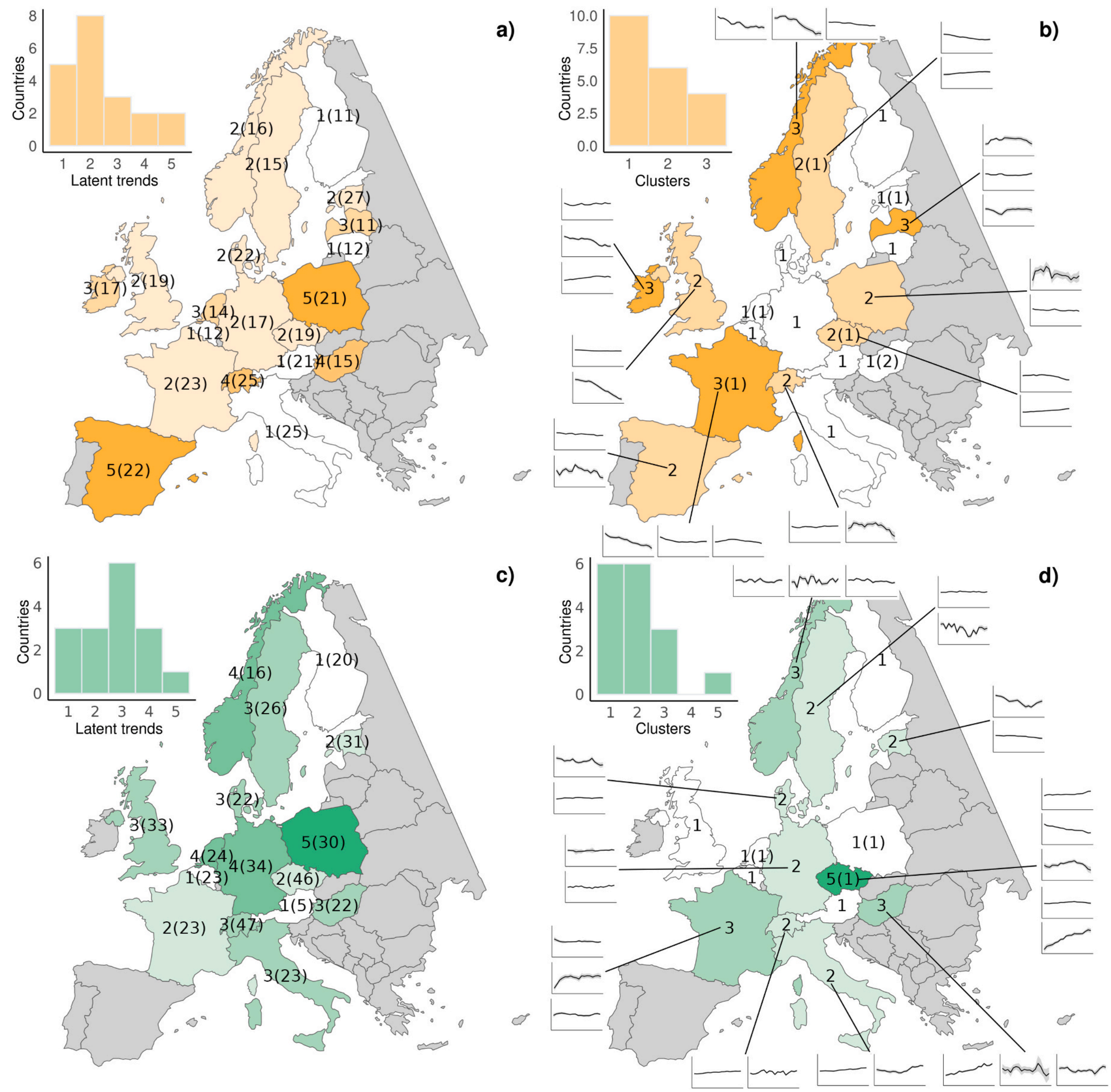

Fig. 3. Numbers of latent trends (indicating structural heterogeneity in dynamics) and clusters in Farmland Bird Indices (FaBI) and Forest Bird Indices (FoBI) in Europe between 2000 and 2017. a) Number of latent trends in national FaBI in 20 European countries. Number of species are indicated between brackets. b) Number of clusters in national FaBI in 20 European countries. Number of outliers (single species clusters) are indicated between brackets. For countries with more than one cluster, average log-scale dynamics of each cluster are shown in the side graphs. c) Number of latent trends in national FoBI in 16 European countries. d) Number of clusters in national FoBI in 16 European countries. For countries with more than one cluster, average log-scale dynamics of each cluster are shown in the side graphs. Countries are displayed in light grey when the index is not analysed or not available.

and STI) could be that the average value and variance differ across national species pools. It would in particular be the case if an increase in value or variance of ecological characteristics drives the number of clusters or the ability of those characteristics to separate clusters. However, while the number of latent trends seems related to species pool values of STI (it increases with the mean of STI in the species pool) and SSI (it decreases with the variance of SSI in the species pool), the number of clusters is not related to SSI, SFI and STI values in the species pool (see Supplementary material 8). In addition, when considering the ability of these ecological characteristics to separate clusters, only the ability of SFI (see Supplementary material 8) could be related to the variance (negatively) and the mean (positively) of this ecological characteristic in the pool of species of the index (FaBI and FoBI). This could suggest that in countries where the species pool is functionally original, but with a low range of functional originality (i.e. there are mostly original species), the clusters tend to regroup species with similar levels of functional originality (e.g. original species with other original species, less original species with other less original species). Yet, the difference in country national pools of species in terms of SSI and STI (and SFI, when the average functional originality is low or its range is wide) seems to not be related to the difference in these species ecological characteristics between clusters. This comforts the interpretation that variations in number and composition of species clusters are not solely driven by a varying effect of ecological characteristics among countries.

4.1. Farmland birds

Despite heterogeneity in dynamics, our results are in agreement with previous studies showing widespread and precipitous declines of farmland birds (Gregory et al., 2019), linked to the expansion of intensive agriculture (Gamero et al., 2017), e.g. via habitat loss such as losses of fallows and grasslands (Vickery and Tayleur, 2018), pesticide use

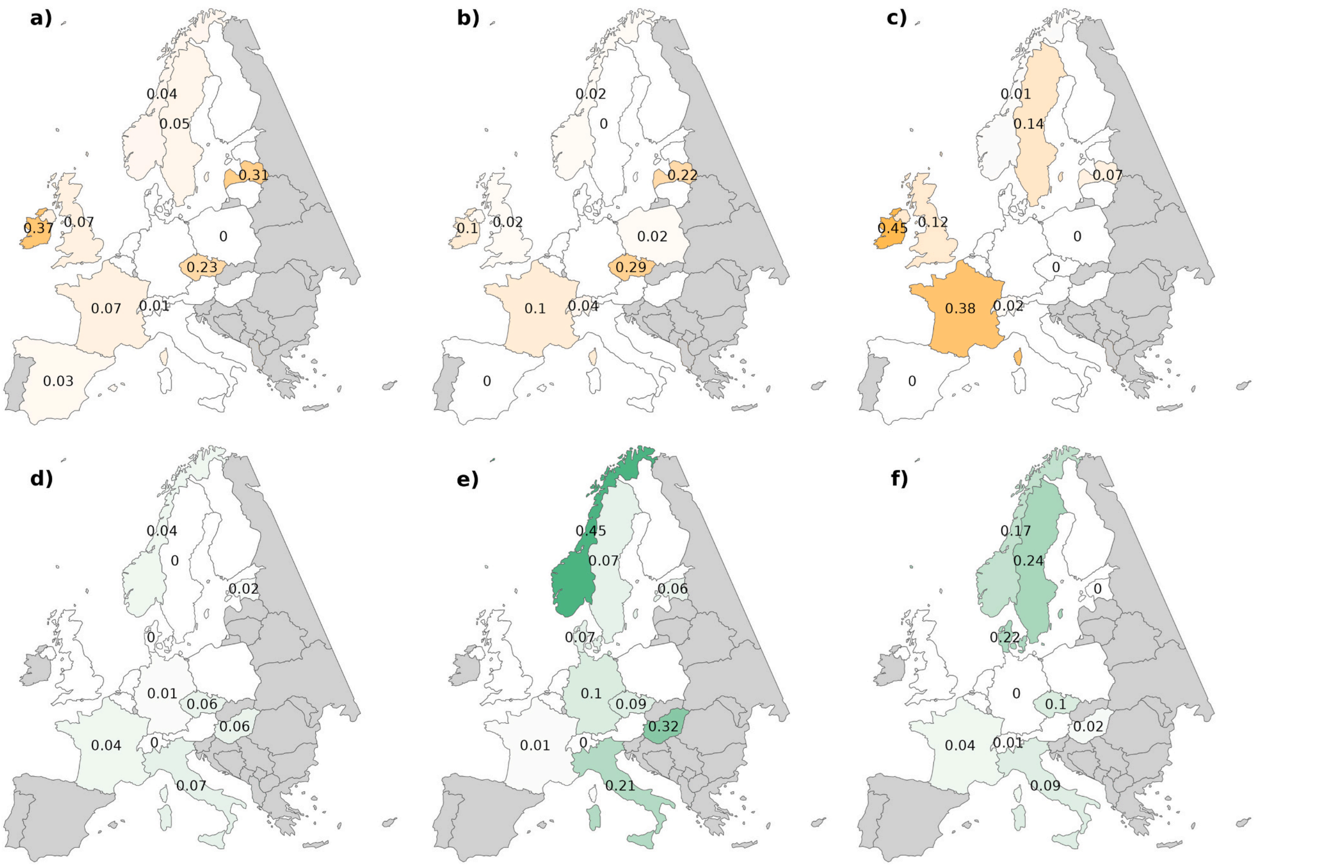

Fig. 4. Variance between clusters explained by species traits. a) Variance in Species Functional Index explained by clusters of farmland birds. b) Variance in Species Specialisation Index explained by clusters of farmland birds. c) Variance in Species Temperature Index explained by clusters of farmland birds. d) Variance in Species Functional Index explained by clusters of forest birds. e) Variance in Species Specialisation Index explained by clusters of forest birds. f) Variance in Species Temperature Index explained by clusters of forest birds. Countries with only one cluster are displayed in white, and in light grey when the index is not analysed or not available. Dark colours correspond to a high amount of explained variance (orange in the first row for farmland birds and green in the second row for forest birds). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Bowler et al., 2019), and changes in crop management (Voříšek et al., 2010). For many countries, while our model suggests multiple clusters, the geometric mean dynamics in the different clusters are all in decline, but in different ways (e.g. France, Norway). Such differences may for example be due to certain species reacting more strongly to intensive farming (Doxa et al., 2010), to differences in time lags of negative responses to changes in land-use among species (Söderström et al., 2001) or to a mitigation by another driver such as climatic change (Busch et al., 2020). However, in a few cases, clusters had trends with opposing directions (e.g. Sweden, Ireland, Switzerland), which can result in an uncertain direction of the overall trend (Ireland, Switzerland) or may reduce the overall decline (Sweden).

The exploratory trait analyses indicated that differences between clusters may sometimes be associated with species traits, thus suggesting that clusters may relate to ecologically distinct subgroups of species. In Ireland and Sweden species in clusters with increasing dynamics have on average a higher STI than species in clusters with decreasing dynamics. This might be expected as the species ability to cope with climate change and increasing temperatures could reinforce or mitigate the overall declining dynamics led by agricultural practices (Rigal et al., 2023), and it has been shown that species associated with warm temperatures may fare better than those associated with lower temperature in some farmland systems (Gaüzère et al., 2019). Moreover, farmland specialists are declining more than generalists (Heldbjerg et al., 2018). Such a pattern is consistent with differences in habitat specialisation (SSI) between clusters in Czech Republic and Latvia where the declining cluster (at least in recent years) has on average higher habitat specialisation. This pattern is also visible through differences in functional originality (SFI) in Ireland where the declining cluster has on average higher functional originality than the two other increasing clusters. However, an opposite pattern is suggested in Czech Republic and Latvia where species from the increasing cluster have on average a higher functional originality. Our study focused on the most common bird species for which the functional difference is probably too limited to detect high variability (Calba et al., 2014) and this can limit the interpretability of differences in SFI between clusters. Similar inconclusive results have been found at national scale on the change of functional originality in bird communities (Gaüzère et al., 2015). In general, differences between clusters in FaBI do not follow a consistent pattern across countries in terms of the three trait indices we used. This suggests that the general pattern of decline that is marked and consistent across most of Europe transcends the effect of these ecological characteristics, within countries and between species, on the variability of the temporal dynamics of farmland birds.

4.2. Forest birds

In contrast to farmland birds, forest birds have shown more stable populations in Europe in the past decades (Gregory et al., 2019; Reif et al., 2007). In general, they show a less coherent pattern with increases and declines over the study period in a few countries, and with strong fluctuations without clear long term trends in others. The reasons behind the more stable dynamics of forest species are not fully understood, but it has been suggested that many specialist forest species had declined before most monitoring programs started, e.g. due to the loss of old growth forests, and that remaining forest birds are to a large extent generalists that can sustain in managed forests (Fraixedas et al., 2015; Virkkala and Rajasärkkä, 2012). That said, it has been suggested that forest specialists are still not faring as well as generalists in Europe (Gregory et al., 2007), although not everywhere (Ram et al., 2017). The extent of forest cover has also increased in Europe, partially due to land abandonment, which may have benefited some forest species (Rigal et al., 2023).

The DFA identified substantial heterogeneity within FoBI across Europe. In several countries, clusters with opposite dynamics coexist (e.g. Czech Republic, Denmark, France, Hungary, see Supplementary material 5), indicating that some clusters of species have a trend clearly different than the overall index. In other countries, there were multiple clusters that all had fairly stable long-term trends but with differences in short-term dynamics (e.g. Norway, Sweden). Although variation between clusters cannot be consistently related to species traits, habitat specialisation helps to understand the difference between clusters in some cases, e.g. in Norway, even if none of the groups involved had strong long term trends. Our analyses also suggested differences between habitat specialists and generalists for Hungary where there was one increasing cluster with lower average habitat specialisation index than for a second more stable cluster. In the case of Czech Republic, previous analyses of forest species grouped into categories of specialisation indicated that generalists were increasing while trends among specialists were more variable (Reif et al., 2022). There is no strong indication that specialisation would explain the difference between the groups identified by DFA for Czech Republic in our analysis, in particular because of the high number of clusters found, suggesting that the specialisation of species is not the only factor contributing to differences among clusters. The limited ability of SFI to explain differences between clusters found for farmland birds is consistent with our results for forest birds, where the functional originality of species was even less able to distinguish between clusters.

For three northern countries (Denmark, Norway and Sweden), where temperature increase has been among the most pronounced in Europe over the past decades (Rigal et al., 2023), species thermal niche explained some of the difference between clusters. Species have on average a lower STI in the declining cluster in Denmark, consistent with previous results on forest birds impacted by climate warming (Lehikoinen et al., 2016; Ram et al., 2017; Tayleur et al., 2016). This pattern was less clear in Norway and Sweden where long term trends have been fairly stable. As for farmland birds however, there are few consistent patterns of change across Europe. One reason could be the large variability in forest management and dynamics across Europe (e.g. managed forests, natural reforestation, proportion of old forest) (Fuller and Robles, 2018).

4.3. Methodology

The DFA toolbox is useful for estimating and quantifying structural heterogeneity in dynamics and identify groups sharing similar dynamics, as well as to illustrate different trends among species in a condensed way without going into the detailed trajectories of every species. It thus allows us to simplify the full range of dynamics across species while highlighting heterogeneity within an index. However, identified groups do not necessarily consist of ecologically similar species as seen in many cases in our analysis. Any lack of clusters also does not mean that there is no heterogeneity among species trajectories. Clustering is built on identifying discrete groups of trajectories and may not find any such groups if the heterogeneity is continuous without discrete structure (Rigal and Knape, 2023). Such continuous heterogeneity is better investigated via e.g. ordination plots, which may also be computed from the *DFAclust* package (see Supplementary material 7) and particular attention should be paid to aggregated indices in countries for which several latent trends (high heterogeneity in dynamics) but only one cluster were found (e.g. FaBI of Germany and Hungary and FoBI of the Netherlands, Poland and the UK). In a few cases the DFA suggested only a single latent trend, indicating that the variability among species is of low dimension, and therefore of low heterogeneity. This may be due to coherent dynamics within those indices, which would simplify interpretation of the index, but could also partly be a result of high uncertainty in the time series of some species in these countries. In addition, the analysis of the relationship between cluster membership and species trait does not account for cluster uncertainty. The exploratory results of the LDA should therefore be taken as an indication and would need to be deepened and corroborated by further research.

Aggregate indices such as FaBI and FoBI are highly useful for conservation and monitoring by quantifying biodiversity dynamics in a simple manner. Our analyses provide a complement, not a replacement, to this simplicity by investigating internal heterogeneity among the group of species in the indices. This heterogeneity may not be the central point when the index is used to quantify or communicate an average change in the group studied, or to monitor the effectiveness of conservation policies designed to impact all the species in the group. For example, analysing the impact of a change in agricultural practices on all farmland species will logically be monitored via the FaBI. But taking heterogeneity into account can also become a central issue, for example when we expect differentiated responses among species in the group under study. For instance, understanding heterogeneity within the FoBI would be essential for studying the a priori paradoxical dynamics of forest birds, whose abundance is declining while forest cover is increasing in Europe (Rigal et al., 2023). It thus gives additional information, illuminating how coherent changes among the species are, as well as highlighting finer scale changes that the aggregated index may miss and that may warrant more in-depth study. The fact that the approach used in this study is designed for indices with a moderate number of species (Rigal and Knape, 2023) should not prevent from undertaking a more systematic analysis of the heterogeneity of aggregated indices, even those on a global scale, using complementary methods.

5. Conclusion

Indices of forest birds in Europe paint a mixed picture with stable as well as increasing and declining national trends, while farmland species show more coherent patterns with broad agreement of decline in farmland birds across countries, though not without exceptions. These differences could suggest that large scale systemic factors have been relatively more important for farmland ecosystems during the last few decades, while for forests local conditions and variation in forest management may have played a larger role. Long turnover times in forest management compared to farmland could also mean that effects of forest management on birds are only visible at longer time scales, leaving more room for local factors to play a larger role for the direction of trends over shorter time spans. However, there are complex patterns of change among species within national indices for both farmland and forest birds. These are not easily explained by single factors. It is therefore important to remember that commonly used community trait indices, while handy for highlighting overall changes in specific communities, only cover parts of community change. Until we have a better understanding of factors causing heterogeneity in biodiversity dynamics in bird and other taxa, careful investigation of changes within countries coupled with local mitigation efforts appear as important complements to large scale policy measures. Beyond national indices, a more systematic analysis of the heterogeneity of aggregated indices, including on a global scale such as the LPI, is needed to clarify their interpretation, if conservation objectives and policies are to be developed or implemented effectively.

CRediT authorship contribution statement

Stanislas Rigal: Conceptualization, Methodology, Software, Writing – original draft. **Jonas Knape:** Conceptualization, Funding acquisition, Methodology, Software, Writing – review & editing.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110452.

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