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Decomposing trends in bird populations: Climate, life histories and habitat affect different aspects of population change

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Abstract

Aim: Despite the complexity of population dynamics, most studies concerning current changes in bird populations reduce the trajectory of population change to a linear trend. This may hide more complex patterns reflecting responses of bird populations to changing anthropogenic pressures. Here, we address this complexity by means of multivariate analysis and attribute different components of bird population dynamics to different potential drivers.

Location: Czech Republic.

Methods: We used data on population trajectories (1982–2019) of 111 common breeding bird species, decomposed them into independent components by means of the principal component analysis (PCA), and related these components to multiple potential drivers comprising climate, land use change and species' life histories.

Results: The first two ordination axes explained substantial proportion of variability of population dynamics (42.0 and 12.5% of variation in PC1 and PC2 respectively). The first axis captured linear population trend. Species with increasing populations were characterized mostly by long lifespan and warmer climatic niches. The effect of habitat was less pronounced but still significant, with negative trends being typical for farmland birds, while positive trends characterized birds of deciduous forests. The second axis captured the contrast between hump-shaped and U-shaped population trajectories and was even more strongly associated with species traits. Species migrating longer distances and species with narrower temperature niches revealed hump-shaped population trends, so that their populations mostly increased before 2000 and then declined. These patterns are supported by the trends of total abundances of respective ecological groups.

Main Conclusion: Although habitat transformation apparently drives population trajectories in some species groups, climate change and associated species traits represent crucial drivers of complex population dynamics of central European birds. Decomposing population dynamics into separate components brings unique insights into non-trivial patterns of population change and their drivers, and may potentially indicate changes in the regime of anthropogenic effects on biodiversity.

KEYWORDS
anthropogenic impact, bird decline, conservation, drivers of change, multivariate analysis, non-linearity, population change, population trajectory

1 | INTRODUCTION

Long-term population time series offer a unique opportunity to understand drivers of species population dynamics and the consequences of ongoing global changes (Koleček et al., 2020; Magurran et al., 2010; Silvertown et al., 2006). This is crucial for both a deeper insight into species ecology and evidence-based conservation (Wauchope et al., 2021). Correlations between parameters of population dynamics and species traits may help to identify factors that limit population growth and those which are responsible for population change (Agardy et al., 2019; Brereton et al., 2011; Gregory et al., 2005; Jørgensen et al., 2016; Sæther et al., 2008).

The key traits associated with population trends of European birds include habitat affinities (Morelli et al., 2020), diet (Bowler et al., 2019), nest location (Gregory et al., 2007), climate niche (Jiguet et al., 2010), migration strategy (Howard et al., 2020) and life-history strategy (Reif et al., 2010). Previous studies showed that woodland birds have more positive population trends than farmland birds (Gregory et al., 2019), insectivorous species have undergone larger decreases than herbivorous species (Bowler et al., 2019), birds nesting on woody vegetation declined less than the ground-nesting species (McMahon et al., 2020) and species that breed in colder regions and migrate over long distances have more decreasing population trends than species breeding in warmer areas, climatic generalists and short-distance migrants or residents (Gilroy et al., 2016; Jiguet et al., 2006; Koleček et al., 2018; Stephens et al., 2016). The relationships between life-history strategies and population trends are more complex (Sæther et al., 2005), and include effects of generation time (Ducatez et al., 2020), annual fecundity (Jiguet et al., 2007) or body size (Díaz et al., 2015). However, more positive trends of species with slower life histories seem to represent a general pattern for European birds (Koleček, Schleuning, et al., 2014).

Factors underlying the abovementioned relationships are broadly attributed to land use changes (agricultural intensification, land abandonment, alteration of forestry practices and urban sprawl) and climatic changes (warming temperatures and changes in the temporal distribution of rainfall) (Jørgensen et al., 2016). Assessment of their relative contributions to bird population trajectories may be challenging (Eglington & Pearce-Higgins, 2012; Howard et al., 2020), but it is important for setting appropriate management and conservation policies to mitigate their negative impacts (Christie et al., 2020). Moreover, the trends–traits relationships may indicate that there are important interspecific differences in population dynamics which may illuminate potential fate of bird populations under various scenarios of future changes in climate and land use.

Though a plethora of studies have related species traits to population trajectories, the vast majority of them fitted a linear model to estimate the average rate of population (index) change over a given period (see Amano et al., 2018; Morelli et al., 2020, for review see Reif, 2013). While this leads to an estimate of the direction and magnitude of change over the focal time period (Wauchope et al., 2019), population dynamics often show more complex patterns than a linear trend. These patterns may contain additional information such as velocity and timing of changes (Rigal et al., 2020), which may be crucial for conservation purposes (Mace et al., 2010; Sanderson et al., 2016). Additionally, patterns that go beyond a linear temporal trend may reveal periods in which the drivers of population trends themselves change. In a recent study, Rigal et al. (2020) fitted a second-order polynomial in order to account for non-linearity in trajectories of population change. However, the complexity of population dynamics may require a more refined approach to characterize complex patterns of population change.

Here we introduce a simple method based on multivariate analyses to decompose long-term population dynamics into several independent components. One aim of our study is to compare these components with traditional metrics widely used to describe bird population changes: the slope of linear regression of population trajectory and population growth rate. Additionally, we link these measures to a comprehensive suite of species traits to judge the relative importance of various environmental drivers for different components of bird population dynamics. We apply this approach to the long-term bird population data collected in the Czech Republic, a country in Central European with a long history of bird monitoring, as a case study.

2 | METHODS

2.1 | Population trajectories

Data on population changes of 111 common species were collated within the Breeding Bird Monitoring Programme (BBMP) in the Czech Republic from 1982 to 2019 (the programme is still running). BBMP is a large-scale monitoring scheme based on standardized point counts conducted by voluntary observers (for further details see, e.g., Reif et al., 2010). All localities were not covered in all years, which is usual in such voluntary-based long-term monitoring schemes (Nakagawa & Freckleton, 2008). To control for this temporal turnover of localities, we calculated annual population indices for every species following a standard protocol, using log-linear models with Poisson error distribution in TRIM (Pannekoek & van Strien, 2001). This approach takes overdispersion and serial correlation into account (see Jørgensen et al., 2016, for additional information). For each species, we used its population index in a given year as a measure of its relative abundance (in %). The index value for the first year (1982) was set to 100%.

We used principal component analysis (PCA) to infer major components of species' population trajectories. The matrix of logarithms of population indices of all species was used as an input to the analysis, which resulted in a set of principal components (PCs) that, consecutively, represent major directions of population change shared among the species. The scores of the PCA represent the positions of individual years, and when we plot them along respective principal components, the overall shape corresponds to the prevailing population trajectory that is characterized by given PC. The loading (position) of each species along the ordination axes then reveals to which extent a given component represents its population trajectory – in other words, how accurately is given species trajectory represented by the respective principal component. We used species loadings along the first four axes (PC1–PC4) for further analysis (Figure 1). Note that the indices (which represent relative species abundances in each year) were logarithmized because the multiplicative nature of population growth leads to their very asymmetric frequency distribution; after logarithmization, the distribution is close to normal.

Then, we calculated two additional measures of population change. First, we estimated the slope of a linear regression across logarithmized annual population indices of each species as a measure of overall population trend. Second, the mean population growth rate for each species was calculated as a mean of interannual growth rates r_t, $r_t = log\frac{N_t}{N_{t-1}}$, where N_t is the population index of year t and N_{t-1} is the index in the previous year.

2.2 | Species traits

We related the abovementioned characteristics of population trajectories (the four PCs, slope of the trend and annual growth rate) to a wide array of species traits. Based on the results of previous studies (e.g. Agardy et al., 2019; Brereton et al., 2011; Gregory

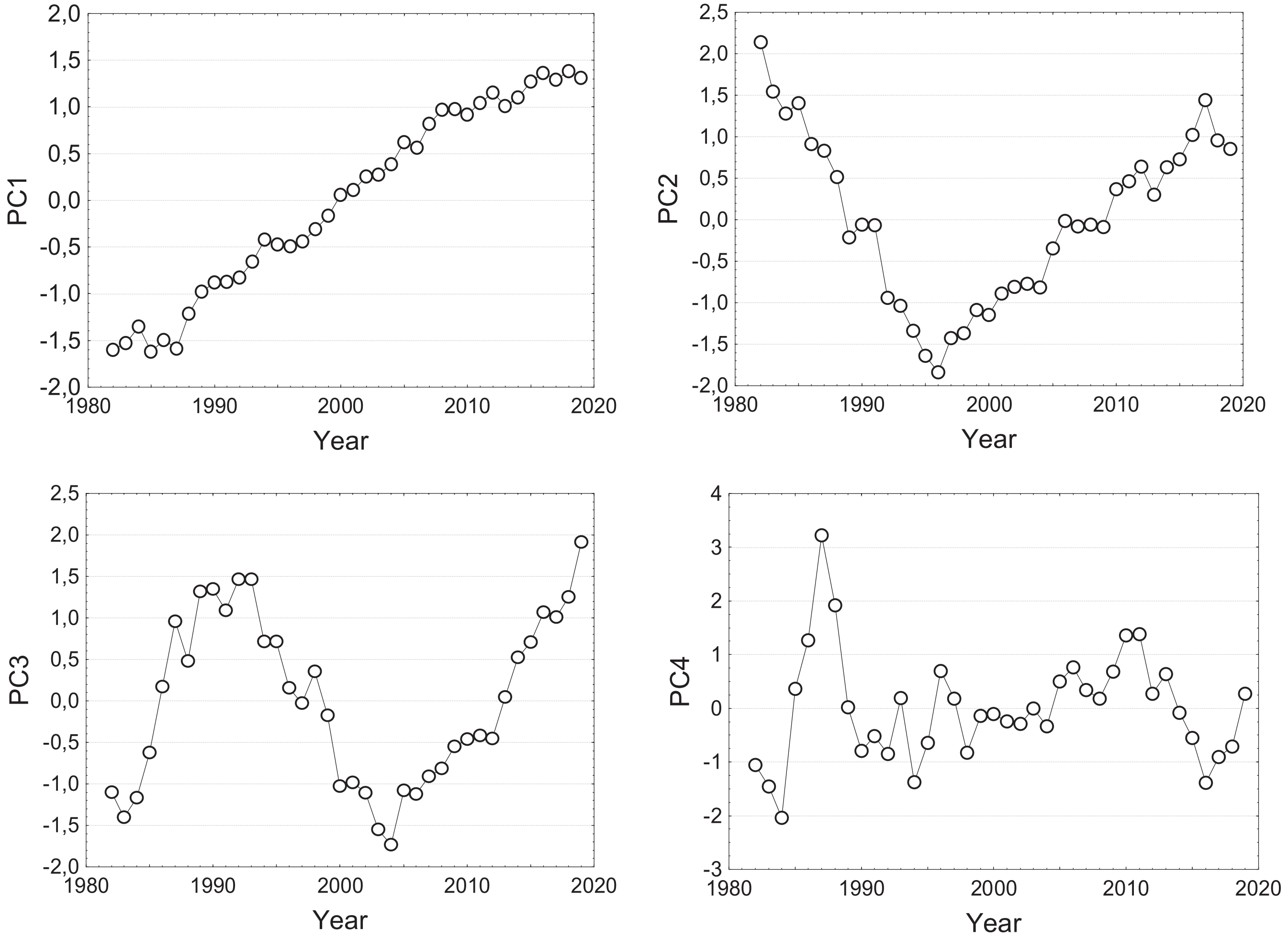


FIGURE 1 The PCA scores of four most important ordination axes (PC1, PC2, PC3 and PC4) revealed by a principal component analysis of the matrix of population trajectories of 111 common bird species breeding in the Czech Republic between 1982 and 2019. PC1 reveals increasing trend, so that populations of species with positive PC1 generally increase, while those with negative PC1 decrease. PC2 reveals U-shaped trend, which means that species with positive PC2 would have a tendency to reveal U-shaped trajectories, in contrast to the species with negative values of PC2 that have tendency to show hump-shaped trajectories. PC3 and PC4 are more complex, but generally, species with positive values on respective axis reveal trajectories that are similar to those depicted in the panels, whereas species with negative values on these axes reveal the opposite trajectories.

et al., 2005; Jørgensen et al., 2016), we selected 16 traits which included life-history traits, breeding habitat, diet, temperature niche (position and breadth), migration distance and regional abundance (see Appendix S1).

Habitat requirements of individual species were based on the information in Storchová and Hořák (2018), updated and slightly modified using our own field experience and regional literature (Hudec & Šťastný, 2005; Šťastný & Hudec, 2011, 2016) and expressed as species presence/absence in the following six habitats during the breeding season: urban, open vegetation mosaic (comprising non-forest habitats with sparse trees or shrubs), farmland, wetland, coniferous forest, deciduous forest. Each species could be assigned to one or more habitats. According to this assignment, a species classified in a single habitat was considered as a specialist in this habitat, whereas a species classified in more habitats was considered as a generalist in these habitats. Additionally, we categorized species as (1) insectivorous or (0) non-insectivorous based on data on species' diet provided by Storchová and Hořák (2018). In principle, it would be possible to distinguish more food categories, but it could cause problems with the interpretability of the results, as there are no clear hypotheses on how different food could affect different population trajectories. In contrast, there are good reasons to assume that insectivory may be associated with particular population trajectories (namely declining ones; Bowler et al., 2019; Reif & Hanzelka, 2020). For five life-history traits, namely, body mass, number of broods per year, clutch size, incubation period and life span, we used the species-specific mean values from Storchová and Hořák (2018).

The information on species temperature niches was excerpted from Hanzelka et al. (2019) for most species. In the remaining species, we followed the protocol of Hanzelka et al. (2019). Specifically, we considered mean temperatures in the main species-specific 3-month breeding season (in most cases April, May and June) for the period 1961–1990 based on temperature data obtained from Haylock et al. (2008), following Jiguet et al. (2010). Temperature niche position was then the mean breeding season temperature over the breeding range of given species within Europe (taken from Hagemeijer & Blair, 1997). Temperature niche breadth was calculated as the difference between minimum and maximum temperatures across the breeding range in Europe. Migration distance was extracted from Hanzelka et al. (2019). Again, for species not covered by Hanzelka et al. (2019), we reproduced their approach. We calculated this trait using species' geographic range maps in BirdLife International and NatureServe (2014) considering species' breeding and non-breeding ranges, as well as residential areas defined as the areas of overlap between the breeding and non-breeding range. As breeding areas, we considered those situated in European part of the Greater Western Palaearctic (Mitchell, 2017), i.e., we excluded Asian areas not relevant to the region we focus on in our analyses. Non-breeding ranges did not include areas where species fly over or stop during migration. Migration distance was the distance (km) between the centroids of species' breeding and non-breeding ranges, calculated using QGIS 2.16.3 (QGIS Development Team, 2016). For the purpose of some specific analyses (the trends in total abundance, see below), we used national bird migration atlas (Cepák et al., 2008) and classified each species according to their migration strategy into discrete categories of long-distance migrants (those wintering in sub-Saharan Africa or India), short-distance migrants (wintering in Europe or the Mediterranean region) and residents (wintering in Central Europe).

Finally, species abundance in the Czech Republic was expressed using extrapolations from point count data (calculated as the number of bird pairs). Birds were counted five times in April–June 2004 and 2005 on 768 census points across the whole Czech Republic, and for the calculation of regional abundance, the density of each species within each habitat class was taken into account together with the data on total areas of habitats within the Czech Republic (Reif et al., 2008, 2013). Alternative data of regional abundances were represented by the estimates taken from the Breeding Bird Atlas of the Czech Republic (Šťastný et al., 2006), but since the results were similar, and the atlas estimates seem less reliable (as they are based on the expert opinion of volunteers and not on systematically collected data; Reif et al., 2013), only the results based on the former data are presented in the main text, while the atlas estimates have been used for calculation of the confidence intervals of total group abundances presented in Appendix S2 (Figure S2.1).

2.3 | Statistical analysis

We used two complementary approaches – linear models (LM) and random forests (RF) – to relate characteristics of population trajectories (responses) to species traits (predictors). LMs represent a familiar technique that provides statistical power, interpretability of parameters and possibility to make probabilistic statements (e.g. *p*-values), but they are sensitive to over-simplification or model misspecification, particularly in complex observational data with many predictors. In contrast, RF (Hastie et al., 2009) is a non-parametric method that can fit non-linear relationships and complex interactions, without the need to specify these a priori, and can estimate relative importance of predictors; the disadvantage is, however, the lack of interpretable parameters and difficulty in calculating P-values. We will thus interpret a convergence in results between the two approaches as an indication that the LM is reasonably specified and robust.

We related all the characteristics of population trajectories, i.e., the four PC axes, annual population growth rate and the slope of the linear regression, as response variables to their predictors using LMs, i.e., the simplest form of the general linear model with the Gaussian error structure and the identity link function. All variables were checked for intercorrelations using pairwise Spearman correlations, ensuring that correlation coefficients among the resulting set of variables were always lower than 0.3. The variables were scaled to zero mean and unit variance to make their statistical effects directly comparable (Schielzeth, 2010), ensuring that model residuals did not indicate any violation of assumptions for LMs. For each analysis, we composed a full model containing all explanatory variables and assessed the performance of all possible combinations of predictors using an information-theoretic approach. We defined the main-effects models only and restricted the maximum number of parameters (k) in each candidate model following $n/k \geq 10$ (n being the number of samples, i.e., number of bird species involved) to prevent overfitting and to obtain conclusive inference (Burnham & Anderson, 2002). For each model, we expressed its relative performance using Akaike Information Criterion corrected for small sample sizes (AICc) and calculated accompanying measures – i.e. ΔAICc, the number of model parameters (k) and model weight. For the inference, we used a subset of the models with ΔAICc <2 (Burnham & Anderson, 2002) and expressed the statistical effects of particular explanatory variables by averaging their estimates using weights of the models containing respective variables (Johnson & Omland, 2004). We performed full averaging, i.e., we used the weights of all the models, as this is generally considered to be more conservative than conditional averaging. In addition, we expressed 95% confidence limit (CL) and relative importance (RI, sum of weights of all models where a given variable appeared) of each variable to judge the precision of the estimate of its effect. All models were run in R version 3.4.1 (R Core Team, 2017) using the R-package 'MuMIn' (Bartoń, 2018) for multimodel inference based on information-theoretic approach.

We complemented the analyses above with phylogenetically controlled regression (PGLS, Freckleton et al., 2002). We used a consensus tree (see Figure S2.2 in Appendix S2) of 500 trees ("Hackett trees" based on 9993 OTUs) downloaded from BirdTree.org (Jetz et al., 2012), calculating a strict consensus using function *consensus* in R package 'ape' (Paradis & Schliep, 2019) and function *consensus.edge* in the R package 'phytools' (Revell, 2012). For the PGLS, we used the same set of predictors that were selected by the model averaging approach mentioned above. We also tested for the phylogenetic signal in the raw values of the response variables as well as in the residuals from the full LM using Blomberg's K.

For a better understanding of the comparative importance of individual traits in explaining variation in the response variables, we additionally fitted random forest models (Hastie et al., 2009) with the same variables as in LMs. We used the *randomForest* function (R package 'randomForest', Liaw & Wiener, 2002) with all RFs produced using 50,000 trees and the default settings: one-third of predictors sampled in each tree, sampling with replacement of the entire dataset and terminal node size of five. To assess the relative importance of species traits in RF explaining the shapes of population trajectories, we calculated the following important metrics (Loecher, 2022): For each tree in the RF, the mean squared error (MSE) on the out-of-bag portion of the data was recorded. Then, the same was done after permuting each predictor variable. The difference between the two was then averaged over all trees, and normalized by the standard deviation of the differences.

To further evaluate our results based on LM and RF, we additionally explored the dynamics of composite total abundances of species groups delimited using above analyses, and visually checked the trajectories of these total group abundances. To express changes in abundance of ecological groups defined by individual traits, we recalculated species' population indices into absolute abundances using the estimate of absolute abundance for the year 2004, mentioned above. Then, we plotted trajectories of recalculated total abundances for these groups. Note that this was possible only for the groups delimited by a qualitative (categorical) criterion, namely, the presence in particular habitats and the category of migration (residents, short-distance migrants, long-distance migrants).

3 | RESULTS

3.1 | Measures of population trajectories

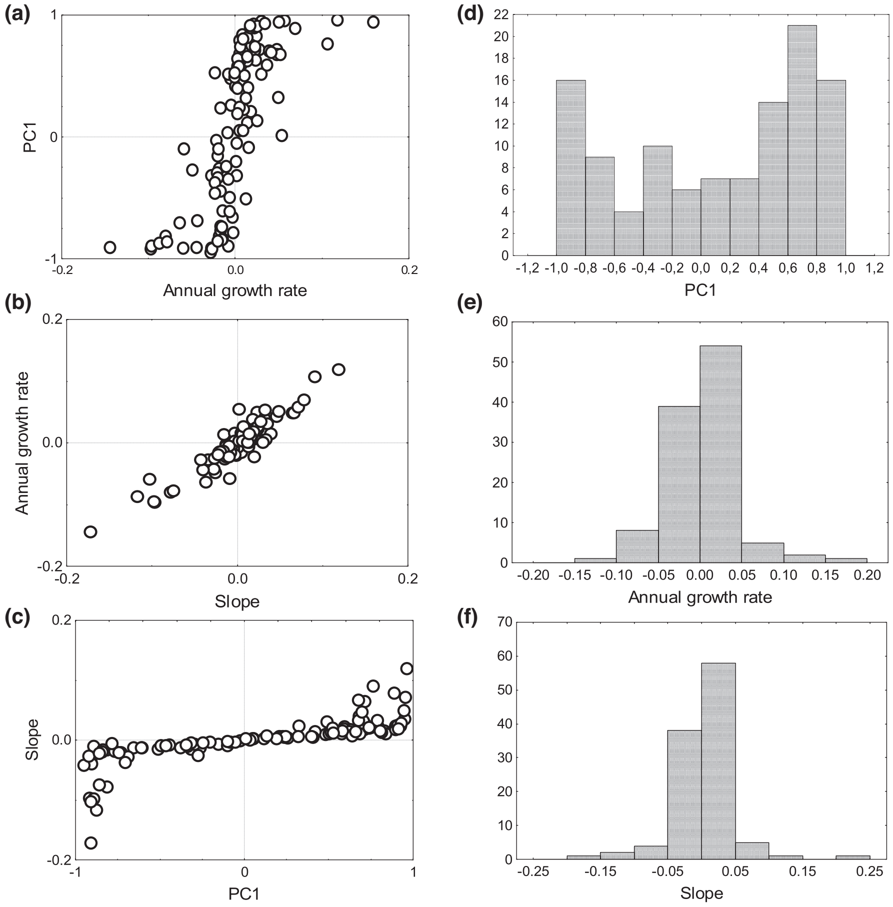
Different aspects of population trajectories obtained by the PCA axes can be revealed by plotting PC scores (pointing to the position of each year) against time (Figure 1). The first ordination axis (PC1, explaining 42.05% of the variability among species population trajectories) expressed a roughly linear gradient distinguishing species with decreasing and increasing population trends (populations of species with low values consistently decreased, and those with high values increased). The second axis (PC2, explaining 12.47% of variability) depicted an independent gradient, distinguishing species whose trends were U-shaped (i.e. decreasing in the beginning and then increasing; positive values) from those with hump-shaped trends (i.e. increasing in the beginning and then decreasing; negative values). The third axis (PC3, explaining 6.31% of variability) revealed a gradient from the species with increasing–decreasing–increasing trajectory (N-shaped) to the species with the opposite (decreasing–increasing–decreasing trajectory). Finally, the fourth axis (PC4, explaining 4.3% of variability) described even more complex dynamics with multiple peaks and troughs (Figure 1).

All principal components characterize mutually orthogonal properties of population trajectories, and thus they are uncorrelated by definition. In contrast, the other measures (the slope of the linear regression and population growth rate) are positively correlated, and also positively correlated to the PC1 (Figure 2a–c). However, the correlations between population growth rate and both the slope and PC1 are relatively weak. For instance, there are species with extreme (high or low) values of PC1, indicating a consistent trend (either increasing or decreasing) which at the same time reveal population growth rate close to zero. This means that these measures capture different facets of population dynamics, namely the consistency or stability of the trend (PC1), in contrast to its magnitude (growth rate).

3.2 | Predictors of major components of species population trajectories

In the LMs that related PC1 to individual explanatory variables, 9 out of 63,019 candidate models met the ΔAICc <2 threshold. The association with farmland and deciduous forest, the position of

FIGURE 2 Bivariate relationships and frequency distributions for three measures of population trends across species: PC1 (see Figure 1), mean interannual population growth rate and the trend expressed as the slope of the linear regression on abundances over time. (a) Relationship between growth rate and PC1, (b) relationship between trend slope and growth rate, (c) relationship between PC1 and trend slope, (d) frequency distribution of PC1, (e) frequency distribution of growth rate, (f) frequency distribution of the trend slope.



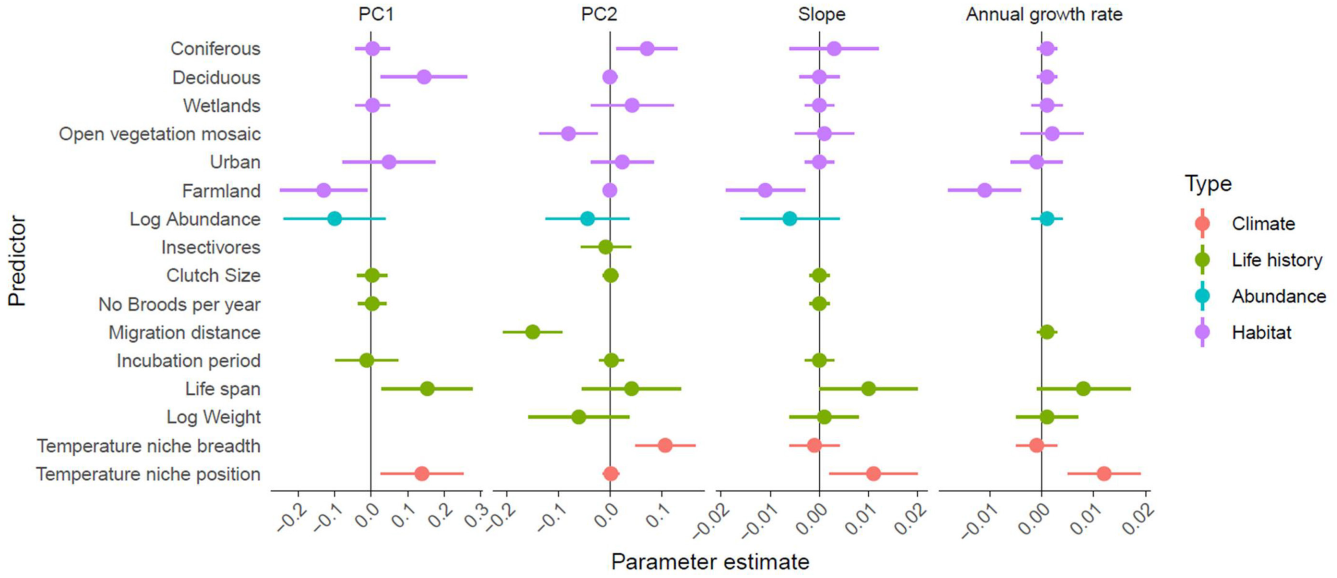


FIGURE 3 The averaged coefficients (including 95% CI) from linear models assessing the relationships between the measures of the trajectories of population changes (PC1, PC2, slope of the linear regression on abundances over time and mean interannual population growth rate) and individual explanatory variables in 111 common bird species breeding in the Czech Republic in 1982–2019. The variables whose confidence intervals do not overlap zero are also those retained in all the selected models; the variables whose effects are not depicted in the plot did not appear in the selected models. Note the different scaling of the parameter estimate axes which indicates that the effect sizes are considerably smaller (by approximately one order of magnitude) in the case of slope and annual growth rate than in PC1 and PC2. Colours refer to the grouping of the variables into four different categories/types.

temperature niche and life span were retained in all of these best models (Tables S2.1 and S2.2 in Appendix S2), and these variables were the only ones significantly related to PC1 (confidence intervals of their average estimates did not overlap zero, Figure 3). Compared to the remaining species, population trends were more negative in farmland species and more positive in species breeding in deciduous forests. Besides that, species that breed in warmer climatic conditions had more positive population trends than those living in lower temperatures, and long-lived species increased more than short-lived ones. The results of PGLS were similar (Figure S2.3 in Appendix S2), except for additional positive effect of wetlands and no detected effect of temperature niche position. PC1 revealed a significant phylogenetic signal detected by Blomberg's K ($K = 0.276$, $p = .039$ based on 100 randomizations), but the residuals from the full LM revealed no significant phylogenetic autocorrelation, indicating that the phylogenetic structure of PC1 was well explained by the traits used. The random forest model explained only 4.7% of variance of PC1 and revealed the importance of temperature niche position, while the importance of the other variables was comparatively low (Figure 4).

In the case of PC2, which distinguished U-shaped and hump-shaped population trajectories, 21 LMs fulfilled the ΔAICc <2 criterion. Coniferous forest, open vegetation mosaic, temperature niche breadth and migration distance were present in all of the best models (Table S2.2) and none of the remaining variables was significantly related to PC2 (Figure 3). Species that breed in coniferous forests and species with broader temperature niches had a tendency towards U-shaped population trajectories (positive values of PC2; Figure 1). In contrast, species that migrate long distances and species that breed in open vegetation mosaic were associated with negative values of PC2, indicating tendency towards hump-shaped trajectories, here manifested as an increase before the year 2000 and then a decrease. These results were fully confirmed by the PGLS (Figure S2.3 in Appendix S2), which is in accord with the test of phylogenetic autocorrelation that revealed non-significant Blomberg's K for both the raw values of PC2 and its residuals from the full LM. The random forest model explained 33.7% of variance of PC2 (considerably more than in the case of PC1) and also showed the high importance of migration distance and temperature niche. In accord with the results of LMs, coniferous forests and open vegetation mosaic appear as the most important variables out of habitats (indicating hump-shaped or U-shaped population trajectories of birds associated with these habitats), although their importance is much lower than migration distance (Figure 4).

As to the other two principal components, the ΔAICc <2 threshold was met by 23 LMs explaining PC3, but none of the explanatory variables significantly affected PC3. Other 59 LMs with the ΔAICc <2 were averaged to evaluate possible correlates of PC4, but only the number of broods per year remained in all candidate models. The abundance of the species with a higher number of broods followed complex dynamics with multiple peaks and troughs. However, RF did not explain any variance of PC3 and PC4, and PGLS also did not reveal any significant effects on PC3 and PC4 (phylogenetic autocorrelations tested by Blomberg's K was non-significant for raw values of PC3 and PC4 as well as for the residuals from the full LM).

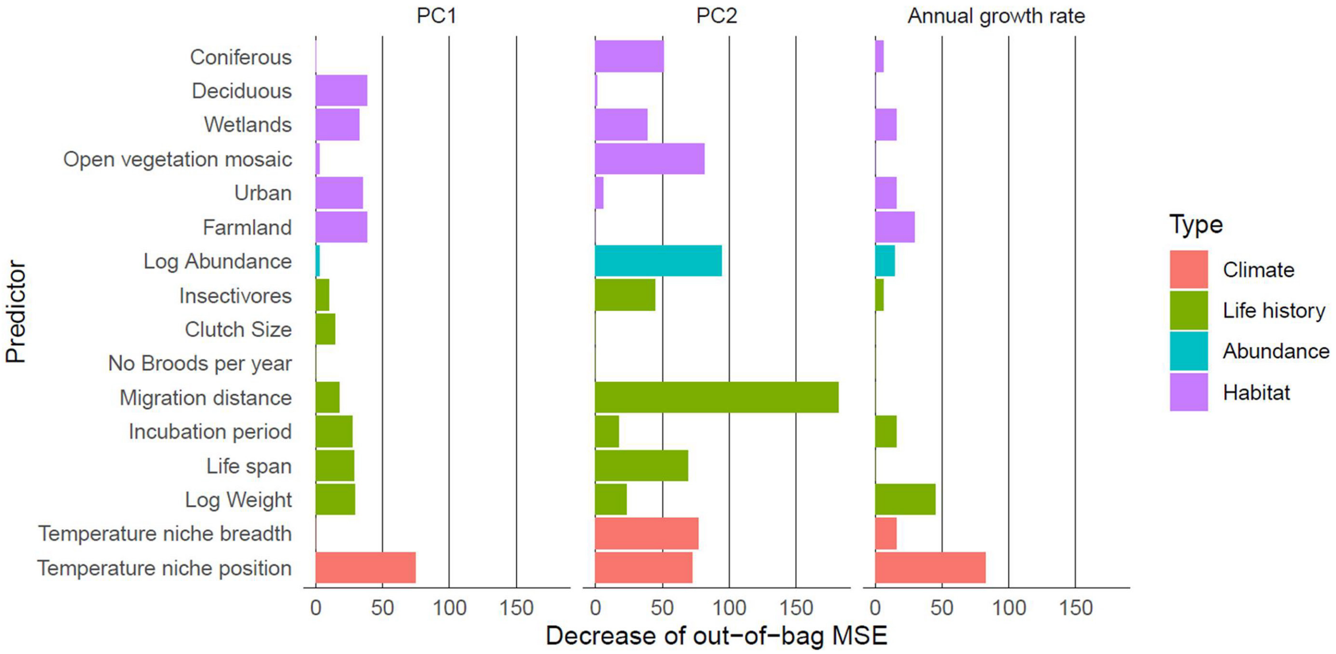


FIGURE 4 Variable importance plots for PC1, PC2 and mean interannual population growth rate generated by random forest (RF). Variable importance was measured as the decrease of out-of-bag mean square error (MSE). The proportion of variance explained by all the variables was very low in the case of PC1 (4.8%), and zero in the case of annual growth rate and the slope of the linear regression of the trend (not shown). In contrast, species traits were able to explain 33.8% variance of PC2 that distinguishes hump-shaped from U-shaped trajectories, migration distance being the most important factor distinguishing the population trajectories.

For the two other measures of population trajectories, the slope of linear regression and annual population growth rate, 27 and 16 candidate LMs with the ΔAICc <2 were selected, respectively. For both measures, and similarly to PC1, the most supported variables present in all models were farmland and the position of the temperature niche (Figure 3). Life span was contained in >90% of all models. Except for the missing effect of deciduous forest, these results agree with models to explain PC1, but the effect sizes revealed by the LM are much smaller and RF model did not explain any variance in the data. Additionally, PGLS analyses revealed only the effect of farmland on these variables (strongly declining populations of farmland birds), while the effects of all other traits are negligible (Figure S2.3 in Appendix S2); the tests for phylogenetic autocorrelation of both these variables, as well as of residuals of the full LM, revealed no significant signal. This implies that the approach that uses the decomposition of population trajectories into principal components better expresses the variation of population trajectories that are attributable to species traits than traditional measures like population growth rate and the slope of the linear trend.

3.3 | Overall trends and total abundances of species groups

Within all studied species, population trends reveal approximate balance between increasing and decreasing ones, regardless of the measure used for expressing the trajectory (Figure 2d–f). It is in accord with the trend of the total abundance of all the birds together, which reveals a slight drop at the end of 20th century, but since 2000 it is remarkably stable (Figure 5).

Despite the long-term stability of the estimated total bird abundance, some species groups reveal pronounced changes (Figure 5; for confidence intervals see Figure S2.1). Farmland birds are the most rapidly decreasing group, while the situation is more complicated for forest birds. Forest generalists (i.e. birds that can live in forests as well as some other habitats) reveal increasing trends of total abundances, and the same holds for deciduous forests specialists (even though their total abundances are much lower since only a few birds are restricted to deciduous forests, at the same time unable to live in other habitats). In contrast, coniferous forest specialists reveal pronounced drop in abundance during the last decades of 20th century leading to a slight U-shaped trajectory. Additionally, long-distance migrants reveal a hump-shaped trend of total abundance, in accord with the analyses of the second PC axis mentioned above. In contrast, residents reveal the opposite, i.e., U-shaped trajectory, while short-distance migrants approximately copy the trend of total bird abundances.

4 | DISCUSSION

We applied multivariate analysis to decompose population dynamics of birds in the Czech Republic between 1981 and 2019 into different aspects of the trajectories of population change, corresponding to the respective principal components (PCs). Even though the method is relatively simple and provides important information that can be extracted from widely reported monitoring data, we are not aware of any study that would employ such a technique for similar purposes. We have shown that in contrast to the slope of population trend and annual population growth rate, the first two PC axes were considerably well explained by species traits. This decomposition thus provides better information on possible drivers of different population trajectories than the linear approaches widely used in population ecology and conservation so far (Wauchope et al., 2021). This is best illustrated by our findings that according to the random forest models, the second PC, which captures hump-shaped or U-shaped population trajectories, is more tightly linked to species traits than the first PC and the other linear measures of population trends (i.e. the slope of population change and population growth rate).

One of the strongest results of our analyses was that the second PC axis was linked to migration distance. The pronounced hump-shaped trends in long-distance migrants were further supported by the analyses of total abundance changes for this group and may indicate an important change in their ecological situation. One possibility includes a change in the velocity of climate change on breeding grounds. Slightly more pronounced rise in spring temperature after 1990 (CHMI, 2021) may have led to the advancement of arrivals of long-distance migrants to breeding grounds (Gienapp et al., 2007; Lehikoinen & Sparks, 2010; Pearce-Higgins et al., 2014). Long-distance migrants that have not been able to sufficiently advance their spring migration and timing of breeding to keep pace with this change then may have had a fitness disadvantage, resulting in decreasing population trends (see also Kamp et al., 2021; Koleček et al., 2020). In contrast, residents and short-distance migrants have more flexible arrivals and thus are able to cope with such changes (Kamp et al., 2021; Telensky et al., 2020). In addition, more intensive competition with residents can also limit populations of migratory species (Samplonius & Both, 2019). However, the state of populations of long-distance migrants may be also related to the changing situation in their wintering grounds related to increasing anthropogenic pressures (Creswell et al., 2020; Koleček et al., 2018), and distinguishing these effects represents a promising avenue for future research.

According to the results of linear models and especially random forests, traits related to species' life histories and those characterizing species climatic preferences represent crucial determinants of population trends. Long-living species exhibited population increases more frequently than short-living ones. This agrees with reduced threat levels (Koleček, Albrecht et al., 2014) and higher success during invasions (Sol et al., 2012) in slow life-history species. Long-living species are able to wait longer until environmental conditions are suitable for reproduction, and may explore alternative strategies for coping with environmental changes during their lives. In contrast, short-living species might be more susceptible to environmental change as they might have too short life to learn and adapt to it (Jiguet et al., 2007). Additionally, large

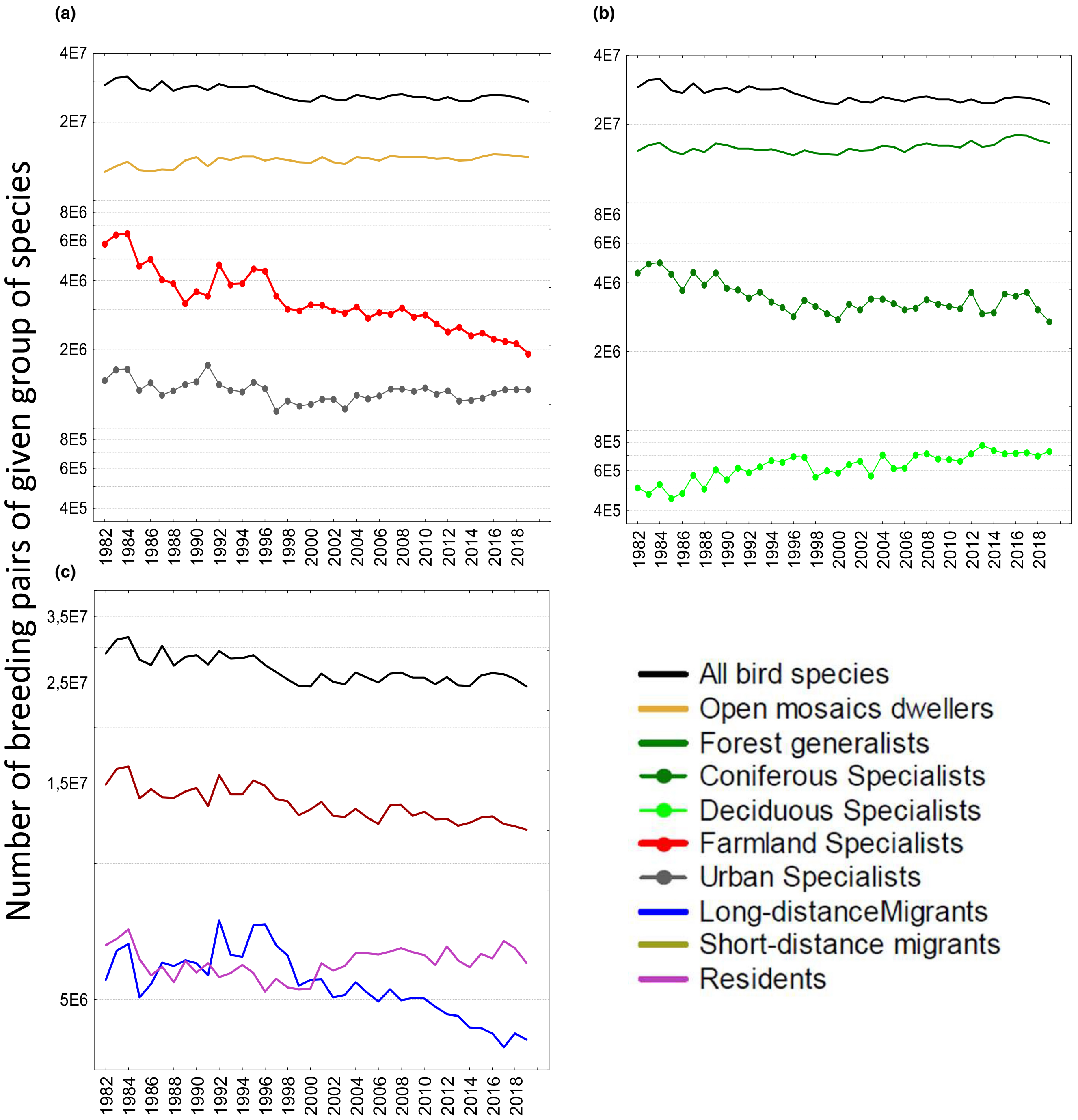


FIGURE 5 Temporal trajectories of total population abundances of species groups delimited based on selected qualitative (categorical) characteristics. The trend of total abundance of all birds (black line) is depicted in all the panels, for comparison with the trends of the subgroups. (a) Trends of three bird groups associated with open habitats: open vegetation mosaic (beige line), urban specialists (grey line) and farmland birds (red line). (b) Trends of forest birds: forest generalists (upper green line), deciduous forest specialists (bottom green line) and coniferous forest specialists (middle green line). (c) Trends of three migration categories: long-distance migrants (blue line), short-distance migrants (olive line) and residents (purple line). See Figure S2.1 for confidence intervals of these abundance estimates.

and long-living birds are not so vulnerable to short-time disturbances, and may also benefit from the increasing size of typical grain of landscape mosaics due to land abandonment and regrowth, and functional differentiation of larger regions (Brambilla et al., 2020; Sæther et al., 2005; Silva et al., 2010). Besides, the species with slow life histories are often the large-bodied birds, such as Grey Heron (*Ardea cinerea*), Red Kite (*Milvus milvus*), Marsh Harrier (*Circus aeruginosus*) and other raptors, that were hunted in the 20th century and now enjoy legal protection and hunting ban (Donald et al., 2007; Koleček, Schleuning, et al., 2014). Their population trajectories may thus reflect the recovery of once-depleted populations.

Our findings that abundances of the species that breed in warmer climates reveal more increasing trends corresponds well to the shifts in the distribution of breeding ranges for most species to northern latitudes, caused by increasing temperatures (Huntley et al., 2008; Kamp et al., 2021; Reif et al., 2010). This trend by itself is, thus, not unexpected. On the other hand, the finding that the climatic niches of species often represent more important predictors of species population change than their habitat association, as indicated by the RF results, is far from trivial. Extensive habitat transformation of most European landscapes in the last decades, including agriculture intensification, land abandonment, urbanization and the increase of landscape grain size (Kupková et al., 2021), all represent important changes that are expected to be the major drivers of population changes. Our findings may indicate that the ongoing climate change will drive changes in bird population dynamics even if we are able to mitigate the negative effects of land use change (Barnagaud et al., 2020).

Focusing on the effects of species habitat associations revealed by the linear models, very pronounced is the decrease of farmland birds, which is already well-established phenomenon (Stoate et al., 2009). It is probably related to widely reported switch from extensive to intensive agricultural practices and homogenization, along with cultivating crops with tall and dense sward (Chamberlain et al., 2000). These changes, together with land abandonment in less productive areas, may have led to reduced food availability and possibilities for nesting in farmland (Donald et al., 2001; Wretenberg et al., 2006). Land abandonment accompanied by tree and shrub encroachment (Kupková et al., 2021) could also explain the increasing trends of the deciduous forest species (Lenzen et al., 2008; Orłowski & Ławniczak, 2009; Reif et al., 2008). This trend can be additionally strengthened by the change in forest composition and spatial and age structure towards older classes with higher proportion of deciduous trees (Reif et al., 2022; Riedl et al., 2020). Similar landscape changes may be also responsible for hump-shaped trends of birds inhabiting habitat mosaics – while the development of early successional stages at the beginning of the study period was beneficial for mosaic-dwelling species, the ongoing succession led to less favourable conditions and this could result in the following population declines of these species.

In contrast to birds inhabiting deciduous forests and similar habitats, coniferous forest specialists revealed an overall decline. This could be related to the abovementioned change in forest structure towards more mixed or deciduous forests. However, both the results concerning the second PC as well as total abundances of coniferous forest specialists indicate a slightly U-shaped pattern, with the decline being prominent only at the beginning of the studied interval. This may be related to the decline of coniferous forests in some mountains due to industrial emissions (Flousek, 1989), which were strongly reduced in the early 1990s (Reif et al., 2007). In addition, species associated with coniferous stands are those breeding in colder climate (Barnagaud et al., 2013) and are adversely affected by global warming (Jiguet et al., 2010). In any case, contrasting trends of deciduous and coniferous forest specialists are illuminating, and indicate that it is misleading to treat "forest species" as a homogeneous group that responds consistently to environmental changes. This further stresses the necessity of studying more complex population trajectories.

When considering the trends for all species together, the data indicate an interesting pattern of relative stability of total abundances after 2000 following a decline in 1990s, and a balance between increasing and decreasing species. Although the loss of bird numbers likely occurred since the mid-20th century in North America and Europe (Reif et al., 2021; Rosenberg et al., 2019), our results correspond to more detailed analyses showing stabilization of overall bird abundance in Europe after 2000 (Burns et al., 2021; Inger et al., 2015). Even though this finding may be affected by our selection of studied species (note that we did not consider ca 40% of regular breeders due to their poor record in the common bird monitoring data), the sample is not expected to be biased towards species with increasing trends. For example, we did not include Anseriformes, a group with generally increasing trends (Musil et al., 2011), neither the birds which newly established in the Czech Republic and show exponential population growth. Therefore, if the sample is biased, then it is slightly biased towards decreasing species, and thus it is notable that the trends seem to be balanced or even slightly shifted towards increasing populations in this century.

The results of our LMs did not substantially differ from those obtained by PGLS. This supports the lack of phylogenetic signal in population trajectories indicated by previous studies (e.g. Morelli et al., 2020; Reif et al., 2010). However, the observed differences between LMs and PGLS in the importance of some predictors imply that some individual traits may be phylogenetically conserved and/or that they may be phylogenetically associated with some other (hidden) traits that are proximate drivers of population dynamics. An example is temperature niche position (Wiens & Graham, 2005), which appeared as a strong predictor of the linear trend only when phylogenetic autocorrelation was not accounted for. Still, the finding that the residuals from the full LM (in contrast to the raw values) do not show any significant phylogenetic signal indicates that common evolutionary history of related species generally does not affect their population trends beyond the effects given by the studied traits (Seoane & Carrascal, 2008; Westoby et al., 1995).

In summary, our approach based on the decomposition of population trajectories into mutually independent components illuminates complex causes of population change. Population trajectories can be non-linear, changing their direction abruptly (see also Kamp et al., 2021). The points of the change can be useful for evaluating biodiversity responses (e.g. signatures of improvement) to various events including a change in legislation (Koleček, Schleuning, et al., 2014; Male & Bean, 2005) that would have been overlooked using a linear trend (although they may be revealed by other methods, see Cunningham & Olsen, 2009; Fewster et al., 2000; Muggeo, 2003; Rigal et al., 2020; Smith et al., 2015). Our findings comprising the correlates of individual components of population dynamics confirm some previous results (decline of farmland species, inconsistent patterns in forest species, increase of species with slow life histories and those inhabiting warmer areas), but also reveal unexpected non-linear patterns, most prominently the hump-shaped abundance trends in long-distance migrants and slightly U-shaped trend of coniferous forest species. Moreover, our results indicate that regardless of the role of habitat transformation in the last decades and the substantial decline of some habitat specialists (namely farmland birds), the most prominent effects are those related to species' life histories and climate, highlighting climate change as a crucial driver of current bird population dynamics.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available as the Supplementary material associated with this article.

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BIOSKETCH

David Storch is interested in macroecology, biodiversity and ecological theory. He is focused especially on patterns of species diversity in space and time and biodiversity scaling. Currently, he has been developing macroecological Equilibrium Theory of Biodiversity Dynamics (ETBD) that addresses past as well as current biodiversity changes within a unifying framework.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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