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Long-Term Trends of Adult Survival and Productivity in European Songbirds: Role of Migration Strategy and Temperature Gradient Within Species' Ranges

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ABSTRACT

Aim: To understand species population ecology, we need to study how trends of demographic drivers change over time and space, especially so under current rapid climate change. However, knowledge on long-term trends of survival and productivity, especially using multiple species over large spatial scales, is scarce. Here, we examined the long-term trends of adult survival and productivity of European songbirds, their relation to temperature gradients within species' ranges, and different traits across multiple species over large spatial scales.

Location: Ten countries in Europe.

Time Period: 2001–2021.

Major Taxa Studied: 28 songbird species.

Methods: We used bird ringing data from the European Constant Effort Ringing scheme (CES), with 1.2 million captures of birds. We investigated the long-term trends of adult survival and productivity in relation to temperature gradients within species' ranges. We also tested differences in the long-term trends of demographic measures in relation to species' migratory strategies (long-distance migrants vs. short-distance migrants and residents) and long-term population trends.

Results: There was no apparent major change in the long-term trends of either adult survival or productivity, and they did not show differences along the range gradient. Long-term trends of productivity differed between migratory strategies: long-distance migrants showed more negative trends in productivity than short-distance migrants and residents, while survival trends were similar between the two groups. Trends in both adult survival and productivity had equal positive connections with the population trends of songbirds.

Main Conclusions: The difference in long-term trends of productivity between migratory strategies highlights the importance of different conservation efforts for long-distance migrants compared to short-distance or resident birds.

1 | Introduction

Understanding the population ecology of species is important for wildlife conservation (Krebs et al. 2025). Especially, species demographics need to be studied to fully comprehend the reasons why some populations decrease while others do not (e.g., Sutherland et al. 2004). Population dynamics are affected by four main demographic parameters in animals: immigration, emigration, deaths, and births. Amongst these, deaths and births are easiest to measure (e.g., Begon and Townsend 2020), and therefore most frequently studied in scientific literature (e.g., Owen-Smith and Mason 2005; Schorcht et al. 2009; Ohlberger et al. 2022; Hanzelka et al. 2024). Here, we study deaths through apparent adult survival (i.e., probability of an adult to survive and return to the breeding site from year to year, e.g., Lebreton et al. 1992) and births through productivity (i.e., number of offspring produced per breeding season; e.g., Newton 1989).

Considerable efforts have been made to study long-term trends in demographic drivers across multiple taxa and regions. For instance, Owen-Smith and Mason (2005) showed that among nine ungulate species in South Africa, adult survival is more important for the changes in species trends than juvenile survival, whereas Schorcht et al. (2009) demonstrated that variation of survival drives the population dynamics of Leisler's bats (*Nyctalus leisleri*) in Germany. Meanwhile, in the North Atlantic, intensive fishing of Atlantic cod (*Gadus morhua*) has caused lower productivity of the populations, which is an important notion in maintaining sustainable fishing practices (Ohlberger et al. 2022). Concurrently, Hanzelka et al. (2024) researched how climate influences the breeding productivity of long-distance migratory passerines of Europe, a species group of conservation concern. Their results indicate that the responses are not uniform across different climatic variables, and that climate change does not so far have a strong effect on species productivity.

Yet as demonstrated above, despite their important findings, many of the studies on survival and productivity concentrate on only one demographic parameter, on a single species, or on one region. Therefore, there is a lack of general knowledge on the long-term trends in both survival and productivity, especially on the continental, multi-species scale. However, Morrison et al. (2022) studied the long-term demographics of 26 European songbird species and demonstrated that the productivity of the studied species is in temporal synchrony at the local spatial scale, while adult survival had similar temporal patterns across the sites. To complement these local-scale findings on survival and productivity, large-scale patterns of these demographic parameters should be studied more deeply, to support more effective conservation efforts. The spatial variation in survival and productivity has been demonstrated in several earlier studies as well (e.g., Scholer et al. 2020; Morrison et al. 2021; Nousiainen et al. 2025). However, it is not known whether productivity or survival has changed similarly within species' ranges in parallel to the observed population changes in response to climate change: i.e., increasing populations towards the cold edges (Jiguet et al. 2010; Lehikoinen et al. 2016). Alongside this potential spatial variation, long-term trends of survival and productivity should be studied with regard to species traits, to reveal whether certain species groups show different trends in their demography. For example, in birds, long-distance migrants have declined more than short-distance migrants and residents (Howard et al. 2020; Vickery et al. 2023), yet it is not well known whether the long-term trends in survival and productivity differ between these groups. In addition, often the driver behind species population trends is a change in species survival or productivity (e.g., Owen-Smith and Mason 2005; Morrison et al. 2021). Yet we lack a detailed understanding of how long-term trends of survival and productivity shape the trends, e.g., whether the roles of survival and productivity differ or whether either one is a stronger driver for declining, stable, or increasing trends.

In this study, we investigated the long-term trends of adult survival and productivity in relation to species' ranges and traits by using a multi-species, long-term, and continent-wide dataset. We used constant effort site (CES) data from the EuroCES project, which is a standardized capture-mark-recapture bird ringing dataset. Our analysis was carried out with a subset of 1.2 million captures of 28 songbird species from 10 countries, spanning from the Mediterranean to Scandinavia and covering the years 2001 to 2021. Here we define 'long-term trend' as a temporal trend spanning the 20 years of our study period, which can be considered 'long-term' for short-lived species like songbirds.

Our study questions were the following: (1) What are the long-term trends of adult survival and productivity (hereafter demographic measures) in European songbirds and do they differ from each other? (2) Do the long-term trends of demographic measures vary along the temperature gradient inside species' ranges (hereafter range gradients)? (3) Do the long-term trends of demographic measures differ between species groups of different migratory strategies? (4) Do the long-term trends of demographic measures differ between species groups with different population trends? We hypothesize that the long-term trends of adult survival and productivity are more positive in colder regions of species' ranges, as the population trends tend to be more positive in the cold range edge, mostly due to climate change-driven poleward abundance shifts (Jiguet et al. 2010; Lehikoinen et al. 2016). Due to these climate change-related differences in species trends within their ranges, we decided to use temperature as a proxy for climatic gradients inside species' ranges. We also hypothesize that long-term trends in adult survival and productivity are (more) negative for long-distance migratory birds, as they have declined during the past decades compared to residents and short-distance migrants (e.g., Howard et al. 2020; Vickery et al. 2023). Lastly, we hypothesize that long-term trends of adult survival and productivity are more negative in populations that are declining compared to populations that are stable or increasing. However, these hypothesized interactions might be compensated for and, through that, hidden by density-dependent mechanisms; therefore, we also included adult abundance as a proxy for density-dependence in our modelling.

2 | Materials and Methods

2.1 | Bird Ringing Data

We used bird ringing data from European Constant Effort Sites (hereafter CES), where birds are captured, marked, and recaptured throughout the breeding season using a standardized methodology. Since the captures are done with mist-nets, the most common species in the dataset are the small-sized songbirds, which though having on average rather short lifespans, can live up to 5–15 years (e.g., Valkama et al. 2014)—thus being a good group for demographic studies. Each bird is ringed with a metal leg ring which has a unique alphanumeric code. Besides the ring code of captured birds, the species, sex, and age are determined and noted (EURING—CES in Europe 2023).

The standardization of the CES comes from three aspects: (1) visits to sites are done regularly from April to August, (2) trapping is done during the day for the same length of time, and (3) the number of nets and their positions remain largely the same per site throughout the years. Trapping seasons vary in their length and timing across latitudes, though usually there are 7–12 visits to a site per season. Sites are commonly located on reedbeds, scrubs, or deciduous woodlands as these are ideal for mist-netting, but also a favourable habitat for many songbird species. We obtained our data in February 2023 through Euring, the European Union for Bird Ringing, which coordinates CES at the European level (EURING—CES in Europe 2023). Altogether, the data, expanding from the 1980s to the year 2021, consist of 4.5 million captures, 309 bird species, and 2070 CES sites within 19 ringing schemes in 15 different European countries, as some countries have multiple ringing schemes, referred hereafter as schemes.

2.2 | Data Selection

In our data selection, we wanted to make sure that, despite the differences between schemes, they were as comparable as possible. To guarantee this, we followed the steps used in Nousiainen et al. (2025), with small modifications:

1. We selected the years 2000–2021, as most of the schemes had been active during that period, and during those years, we selected only schemes where the sites had been in general visited 7–12 times per year, as this is the most common range of annual visits among CES schemes.
2. Within schemes, our analysis included only sites that had been continuously active for more than 5 years, visited per year at least 5–8 times (depending on scheme), and visited at least 1–3 times (depending on scheme) each half of the ringing season. This was done in order to select the most active sites with good sampling coverage throughout the ringing season.
3. Within species, we selected only sites where more than two adults (older than first-calendar year birds) and two young (first-calendar year birds) had been captured every year, and only species that had on average 50 captures per year during the time the scheme had been active. This allowed us to also include sites, years and species with lower densities, while keeping the estimates robust.

After all, 1.2 million captures from 28 species, 578 (554) sites (sites in adult survival analysis in brackets), 11 schemes, and ten countries were selected. Our chosen schemes were run between 6 and 21 years (mean 16, SD 5) during our study period (for number of individuals, species, sites, schemes, countries and time periods used in the analysis, see Tables S1 and S2). The final number of individuals, species, sites, schemes, countries, and years depended also on the filters used later in the analysis (for details, see Table S3).

2.3 | Data for Species' Range Gradients and Traits

We defined species' ranges based on our dataset; in other words, a species' range was determined based on its occurrence across our study area (i.e., across all CES schemes). Species' ranges outside of our study schemes were thus excluded. As a proxy for temperature gradients within species' ranges, we calculated the mean temperature for every scheme in our data. Average temperature data were obtained as gridded monthly averages from the CRU TS dataset at 0.5° spatial resolution (Harris et al. 2020). From this data, we calculated the country-specific temperature across the study years (2000–2021) during the breeding season months (April to August). All three Spanish schemes were assigned the same average temperature, as the temperature differences between the Spanish schemes were minimal. The scheme combining the UK and the Republic of Ireland received the average temperature of the UK, as most of the sites were situated there. All other countries had only one scheme in our analysis (for details, see Table S1). We decided to use the average temperature per country instead of finer resolutions for two reasons: first, due to sampling size limitations our data on bird survival and productivity had to be averaged per species per every scheme (see Nousiainen et al. 2025), and second, our interest was in examining variations at larger spatial scales where the country-specific temperatures give a reasonable resolution. For every species, country-specific temperature values were centred within the range to create a temperature gradient within species' ranges.

For species traits, we chose migratory strategies and scheme-specific population trends. Within migratory strategies, birds were divided into two groups: (1) long-distance migrants ($n=9$ species, including 37 scheme-specific populations), and (2) short-distance migrants and resident birds ($n=18$ species, with 73 scheme-specific populations; for species-specific migratory classifications, see Table S2). Trait information for migratory groups was gathered from the AVONET database (Tobias et al. 2022), with some modifications: chiffchaff (*Phylloscopus collybita*) and bluethroat (*Luscinia svecica*) were classified as short-distance migrants instead of long-distance migrants as the populations considered in this study were from countries where the populations of the species in question are mostly short-distance migrants (Spina et al. 2022). Population trends were calculated with a simple linear model, using adult abundance estimates from the CES data and covering the same study period from 2001 to 2021 as response variable, fitted against year. As a result, every species in each scheme had one value for its population trend over the years.

2.4 | Data Analysis

Our analysis was done in two steps, where in the first step we calculated the annual adult survival, productivity, and adult abundance estimates for each species in each scheme using the 'cesr' package (for details, see Robinson 2023) in R (R Core Team 2022). To control for the uncertainty of estimates in survival, productivity, and abundance, we decided to aggregate the site-level estimates to a scheme-level, as the uncertainty would be higher in local estimates due to the clearly smaller sample sizes at the site-level. In summary, annual adult survival was calculated by fitting the CJS model (Cormack-Jolly-Seber; Lebreton et al. 1992) in the mark program (version 9.0; White and Burnham 1999) through the 'Rmark' package (Laake 2013), where adult survival has an annual rate at the scheme level, while recapture probability is kept the same throughout years but allowed to vary between ringing sites. In the model the presence of transients is taken into account. In the end, adult survival was estimated for 427,227 individuals with 58,743 recapture occasions.

Productivity and adult abundance estimates were calculated with 'cesr' by using the function 'Index', which fits three generalized linear models (GLMs) for the CES data and, as a result, gives values for adult abundance, juvenile abundance, and productivity, from which we used the adult abundance and productivity in our analysis. In the adult abundance GLM, the response variable is the number of individuals captured per site and year, while site and year are the explanatory variables, and the error distribution is quasi-Poisson. In the productivity GLM, explanatory variables are the same, while the error distribution is quasi-binomial, and the response variable is the event-trial framework, where the trial is one capture and the success is one capture of a young bird (for details, see Robinson (2023)). Adult abundance was estimated for 485,970 individuals. Productivity was estimated for 485,970 adult individuals and for 712,823 juveniles. In total in our dataset, 1.2 million captures of birds were used in analysis (for details, see Tables S1 and S2).

During the first step, we filtered the data by using criteria explained in Table S3. In the end, we were left with 1658 species-year-scheme combinations, which resulted in a final dataset of 28 species, 11 schemes, and 10 countries.

Before the second step, to account for density-dependence in all four models, we calculated the adult abundance estimate per species-scheme combination (calculated using the 'cesr' package). We did this by using the adult abundance estimates of the year before for rows referring to adult survival, as densities in the previous breeding period should correlate with adult survival from that to the next year (Newton 1998). For adult abundance estimates referring to rows coded as productivity, we used adult abundance of the same year, as breeding densities during the breeding season affect the productivity of the same year (Newton 1998). As there is no year before the abundance estimates for the first year, the first year of every species was excluded from the data, which resulted in a final study period of 2001–2021. For our fourth study question, where we wanted to see the role of demographic measures regarding the population trends, we calculated species and scheme-specific population trends from the adult abundance estimates derived from the 'cesr' package by using a simple linear model where the response variable was the log-transformed species- and scheme-specific adult abundance, and the predictor variable was year. Before the analysis, adult survival, productivity, population trends, the two adult annual abundance estimates, and the year were standardized by using the 'scale' function in R (mean = 0, standard deviation = 1).

In a second step, we built four linear mixed models (LMMs), models M1-M4, to address our four study questions. In each model, the annual estimate of the demographic measure was the response variable (i.e., a row coded as either referring to adult survival or productivity). We assumed a Gaussian error distribution, as the model residuals were approximately normally distributed. To test whether adult survival or productivity shows different long-term trends, we included the interaction between the standardized year and demographic measure (i.e., adult survival or productivity, categorical variable) as an explanatory variable term (M1). To investigate spatial differences in adult survival and productivity trends, we fitted a three-way interaction between the scaled year, demographic measure, and range gradient (continuous variable) as an explanatory variable term (M2). However, as the three-way interaction was not significant, we removed it from the model and ran the final model with the interaction between year and range gradient, i.e., dropping the demographic measure (Zuur et al. 2009). To examine if there are differences in long-term trends regarding different migratory behaviours, we fitted a three-way interaction between scaled year, demographic measure, and migratory behaviour (i.e., long-distance migratory birds vs. short-distance migratory and resident birds, categorical variable) as an explanatory variable term (M3). To assess whether the long-term trends in adult survival or productivity differ between species with different population trends, we fitted a three-way interaction between year, demographic measure, and population trend (scaled, continuous variable) as an explanatory variable term (M4). However, as the three-way interaction was non-significant, we dropped it and ran the final model by including the interaction between year and population trend only (see Zuur et al. 2009 again). Three-way interactions were included because we hypothesized that long-term trends might differ between the demographic measures along the range gradients or in relation to species traits (i.e., interaction between year, demographic measure, and range gradient or between year, demographic measure, and species' traits).

In each model, the interaction term between demographic measure type and adult abundance estimate was included to account for adult survival- and productivity-specific density dependence patterns. Also, in each model, we allowed for species-specific random slopes on year, and included the scheme and year as random effects to account for scheme- and year-specific variation in the data (For model structures, see Table 1; for workflow of the analysis, see Supporting Information Figure S1).

In all models, the annual estimates of adult survival and productivity (i.e., the response variable) were weighted by their variance, i.e., the inverse square of their standard errors (SE, derived from 'cesr' package), so that the greater uncertainty of estimates resulted in lower weights in the models (1/SE^2). This approach guarantees that the more precise estimates get a higher importance in the models. Such inverse-variance weighting is a standard approach in many fields (Hartung et al. 2008) because it minimizes the variance of the combined estimates and appropriately accounts for differing uncertainties in each observation (e.g., see Hornstein and Greene 2012; Nakagawa and Santos 2012; Nousiainen et al. 2025). In models M1, M2 and M3, weights were defined by scheme-, species-, and year-specific SEs of adult survival and productivity estimates that were standardized by dividing every SE value by the maximum value of SEs, for adult survival and productivity values separately. For model M4, we also included the SEs of population trends, standardized in the same way, and then for every row, the average between the SE of the demographic measure (adult survival or productivity) and the population trend SE was calculated. This average was then used as a weight in model M4. The model structures are shown in Table 1. For running these models, we used the 'lmer' function from the R-package 'lme4' (Bates et al. 2015), and the 'summary' function from the R-package 'lmerTest' (Kuznetsova et al. 2017).

2.5 | Post Hoc Analysis

We also performed post hoc analyses to study the patterns of the range gradient further (models M5–M7). We were especially interested in exploring the interaction patterns of migratory behaviour and the range gradient, as we know that long-distance migrants and short-distance migrants have, in general, differing population trends in Europe (e.g., Howard et al. 2020; Vickery et al. 2023). For more detailed description, see Supporting Information: Post Hoc Analysis, for Post Hoc model structures, see Table S6.

2.6 | Model Validation

We checked the model fit by exploring normality of residuals, distribution fit, heteroscedasticity, multicollinearity, model fit (r^2), outliers and residual diagnostics of our models by using the packages 'performance' (Lüdecke et al. 2021) and 'effects' (Fox and Weisberg 2018). We validated the population trends calculated from 'cesr' by comparing them to population trends obtained from Article 12 web tool (EEA 2025) and did not find significant differences (see Figure S2).

We also tested for potential spatial autocorrelation of the model residuals by using Moran's I test with the 'testSpatialAutocorrelation' function from the 'DHARMa' package in R (Hartig 2024). We did not detect spatial autocorrelation in the model residuals in any of our models (see Supporting Information, Table S4).

Furthermore, we tested for a phylogenetic signal in the model residuals by using a phylogenetic tree of the study species from birdtree.org (Jetz et al. 2012) and the 'phylosig' function from the 'Phytools' package (Revell 2024) in R. We did not detect a phylogenetic signal in the model residuals in any of our models. The results are shown in the Supporting Information, Table S8. We also controlled for the phylogeny in the LMM analyses by fitting phylogenetic generalized linear mixed models (PGLMMs) by using the pglmm-function from the 'Phyr' package (Li et al. 2020). The results (Supporting Information, Table S8) show no phylogenetic signal.

At last, we tested our models by refitting them without using the variance as model weights, to test whether our results are driven by the chosen weighting scheme. The results (Supporting Information, Table S8) demonstrate that models without weights mostly resulted in similar outputs in both estimated direction and strength and thus confirm the robustness of our results based on models including weights.

3 | Results

3.1 | Long-Term Trends of Adult Survival and Productivity and Their Variation Along the Range Gradient

There were no significant differences between long-term trends of adult survival and productivity, and there was no significant change in their trends over time (Table 2, model

TABLE 1 | The structure of our four main models (M1–M4).

Model	Response variable	Explanatory variables	Random intercepts	Random slopes
M1	Estimate of demog. measure	Year × Demog. measure + Adult abund. estimate × Demog. measure	Species, scheme, year	Species-specific, per year
M2	Estimate of demog. measure	Year × RangeTemp + Adult abund. estimate × Demog.measure	Species, scheme, year	Species-specific, per year
M3	Estimate of demog. measure	Year × Demog. measure × Migration + Adult abund. estimate × Demog. measure	Species, scheme, year	Species-specific, per year
M4	Estimate of demog. measure	Year × Trend + Adult abund. estimate × Demog. measure	Species, scheme, year	Species-specific, per year

Note: Demographic measure ('Demog.measure') is adult survival (reference level: Productivity). Adult abund. estimate is the adult abundance estimate. RangeTemp is the range gradient (country-specific, species range-centered range temperatures across the years 2000–2021). Migration is the migratory strategy (long-distance migrants vs. short-distance migrants and residents), where long-distance migration is the reference level.

M1). However, we found a significant difference in the role of adult abundance estimates (i.e., density dependence) between adult survival and productivity (Table 2, M1, Figure 1): productivity decreased with increasing population abundance, whereas adult survival did not show a significant association with abundance. This pattern between adult abundance and the two demographic measures remained the same in the following models (Table 2, models M1–M4). The two-way interaction between scaled year and range gradient (Table 2, model M2) was not significant, indicating that long-term trends of adult survival and productivity did not differ along the range gradient.

3.2 | Long-Term Trends of Adult Survival and Productivity in Relation to Species Traits and Population Trends

In our third model (Table 2, M3, Figure 2), the three-way interaction between year, demographic measure type, and migratory behaviour was significant ($p = 0.040$), highlighting distinct long-term trends of adult survival and productivity regarding different migratory groups. This was driven by differing long-term trends in productivity between migratory groups, where long-distance migrants had a declining trend in productivity relative to short-distance migrants and residents. We quantified temporal trends for each combination of migration strategy and demographic measure using model-derived marginal slopes with the function emtrends from the R package 'emmeans' (Lenth and Piaskowski 2025). The results, found in the Supporting Information (Table S5), demonstrate that long-term trends in adult survival did not change significantly for either migratory strategy, although they both declined. Hence, the difference in productivity trends was driving the significance in the three-way interaction, although neither the productivity nor the survival trends of the migratory groups were themselves significant.

Lastly, the two-way interaction between year and population trend was significant, which showed that temporal changes of both demographic estimates differed between the different population trends. For species with increasing population trends, the estimates of both demographic measures (productivity and survival) showed increasing trends in time, and the opposite for species with declining population trends. For species with stable population trends, the demographic measures showed no change over time (Table 2, M4, Figure 3).

Annual estimates of adult survival, productivity, and adult abundance provided by the 'cesr' package (step 1) are found in the Zenodo repository (see section Data Availability Statement).

3.3 | Post Hoc Models

In our Post Hoc models, long-distance migrants showed a near significant tendency ($p = 0.06$) to have more negative population trends than the short-distance migrants and residents (see model M5; Supporting Information Table S7). Long-distance migrants also showed a significant connection between productivity estimates and range gradient, as the estimates increased significantly ($p < 0.001$) towards warmer parts of the ranges (see model M6; Supporting Information Table S7). For short-distance migrants and residents, there were no significant findings (model M7; Supporting Information Table S7). For a more detailed description of the results, see Supporting Information: Post Hoc results.

4 | Discussion

Using a multi-species, long-term, and continent-wide dataset, our study shows that there was no general pattern in the long-term trends of either adult survival or productivity of European songbirds within our study period. Further, the long-term trends in adult survival or productivity did not differ along the range gradients. However, we found a significant difference in long-term trends of adult survival and productivity between migratory groups, mainly driven by the negative long-term trend of productivity in long-distance migrants relative to short-distance migrants and resident birds. We also show that the population trends of European songbirds positively correlate with trends of both adult survival and productivity, i.e., increased populations had also more likely an increasing trend in adult survival and productivity and vice versa. Lastly, we found a significant negative connection between annual adult abundance (i.e., density-dependence) and productivity, with no significant correlation in adult survival, indicating that density-dependence processes limited productivity, but not survival at the breeding grounds.

4.1 | Long-Term Trends of Demographic Measures: Their Relation to the Range Gradient, Population Trends and Density-Dependence

We did not find long-term changes in either adult survival or productivity, which indicates that, at the temporal resolution of this study, there are no general positive or negative trends in these two demographic parameters among the study species across Europe. Furthermore, we did not find differences in long-term trends of adult survival and productivity along the range gradient although earlier studies have shown spatial variation within adult survival and productivity (e.g., Scholer et al. 2020; Morrison et al. 2022; Nousiainen et al. 2025). When considering population trends, several studies have shown that populations at the cold edge of species' ranges have been increasing (i.e., northern side in the northern hemisphere), and population trends at the warm edge of ranges have been decreasing (Jiguet et al. 2010; Lehikoinen et al. 2016). Yet we could not find evidence in our study that trends of adult survival or productivity would have varied correspondingly within ranges.

This could be because of several reasons. First, population trends of our study species might not be significantly connected with the range gradient, and thus, the likelihood of detecting range gradient signals among trends of adult survival and productivity is decreased. This is indirectly supported by our finding that population trends of species were positively connected with both adult survival and productivity change over time. In other words, a spatial gradient in demographic measures would likely translate to a spatial gradient in population trends and

TABLE 2 | Parameter estimates, their standard errors (SE), and the test values of the LMMs for the four main models M1–M4, corresponding to our four study questions. Demographic measure ('Demog. measure ') is adult survival (reference level: Productivity).

Parameter	Estimate ± SE	df	t	p
M1, Survival vs. productivity -model ($n = 3316$, where n is species-specific demographic coefficients)				
Intercept	0.0035 ± 0.140	24.290	0.026	0.980
Year	−0.014 ± 0.041	38.760	−0.356	0.724
Demog. measure (survival)	**−0.325 ± 0.027**	**3252.000**	**−12.002**	**< 0.001**
Adult abund. estimate	**−0.414 ± 0.032**	**2950.000**	**−12.961**	**< 0.001**
Year × Demog. measure (survival)	−0.010 ± 0.027	3260.000	−0.383	0.702
Demog. measure (survival) × Adult abund. estimate	**0.430 ± 0.034**	**3283.000**	**12.718**	**< 0.001**
M2, range gradient -model ($n = 3316$, where n is species-specific demographic coefficients)				
Intercept	−0.014 ± 0.131	24.716	−0.103	0.919
Year	−0.019 ± 0.038	29.376	−0.513	0.612
Demog.measure (survival)	**−0.325 ± 0.027**	**3251.270**	**−12.013**	**< 0.001**
RangeTemp	0.031 ± 0.024	28.131	1.305	0.202
Adult abund. estimate	**−0.414 ± 0.032**	**3008.952**	**−12.959**	**< 0.001**
Year × RangeTemp	0.004 ± 0.007	1188.500	0.599	0.550
Demog. measure (survival) × Adult abund. estimate	**0.423 ± 0.033**	**3282.012**	**12.816**	**< 0.001**
M3, Species migration strategy -model ($n = 3316$, where n is species-specific demographic coefficients)				
Intercept	0.017 ± 0.174	35.158	0.997	0.924
Year	−0.090 ± 0.056	66.306	−1.603	0.114
Demog. measure (survival)	**−0.333 ± 0.046**	**3243.875**	**−7.210**	**< 0.001**
Migration (SDMs & residents)	−0.022 ± 0.168	24.622	−0.133	0.895
Adult abund. estimate	**−0.423 ± 0.032**	**3062.253**	**−13.063**	**< 0.001**
Year × Demog. measure (survival)	0.070 ± 0.046	3259.112	1.517	0.130
Year × Migration (SDMs & residents)	0.111 ± 0.058	49.016	1.911	0.062
Demog. measure (survival) × Migration (SDMs & residents)	0.015 ± 0.058	3248.142	0.268	0.789
Demog. measure (survival) × Adult abund. estimate	**0.440 ± 0.035**	**3279.541**	**12.683**	**< 0.001**
Year × Demog. measure (survival) × Migration (SDMs & residents)	**−0.118 ± 0.057**	**3254.182**	**−2.092**	**0.040**
M4, Species trends -model ($n = 3316$, where n is species-specific demographic coefficients)				
Intercept	−0.033 ± 0.133	21.889	−0.252	0.803
Year	−0.022 ± 0.031	21.265	−0.720	0.485
Trend	**−0.173 ± 0.027**	**2433.454**	**−6.368**	**< 0.001**
Demog. measure (survival)	**−0.245 ± 0.026**	**3246.891**	**−9.324**	**< 0.001**
Adult abund. estimate	**−0.476 ± 0.034**	**2948.578**	**−14.208**	**< 0.001**
Year × Trend	**0.113 ± 0.019**	**118.932**	**6.102**	**< 0.001**
Demog. measure (survival) × Adult abund. estimate	**0.377 ± 0.031**	**3282.133**	**12.116**	**< 0.001**

Note: Adult abund. estimate is the adult abundance estimate, i.e., a proxy for density-dependence. MeanTemp is the temperature gradient within species' ranges. Migration is the migratory strategy (long-distance migration vs. short-distance migrants and residents), where long-distance migration is the reference level. Bolded values are significant ($p < 0.05$).

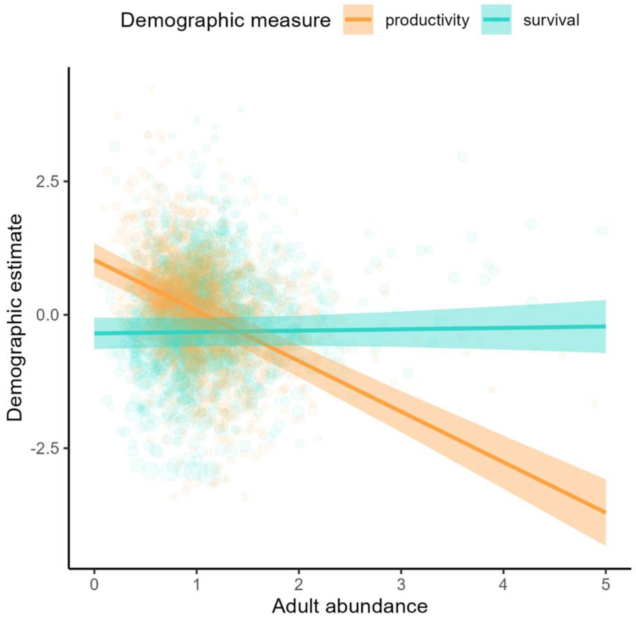

FIGURE 1 | The predicted mean scaled estimates (solid lines) of adult survival (turquoise) and productivity (orange) of European songbirds with their confidence intervals (shaded areas) in relation to adult abundance, i.e., a proxy for density dependence ($n = 3316$, $p < 0.001$) based on model M1 (Table 2). Points are the raw datapoints, where the size tells how much weight they have in the given model, e.g., a larger point indicates a smaller standard error of the estimate and thus a heavier weight.

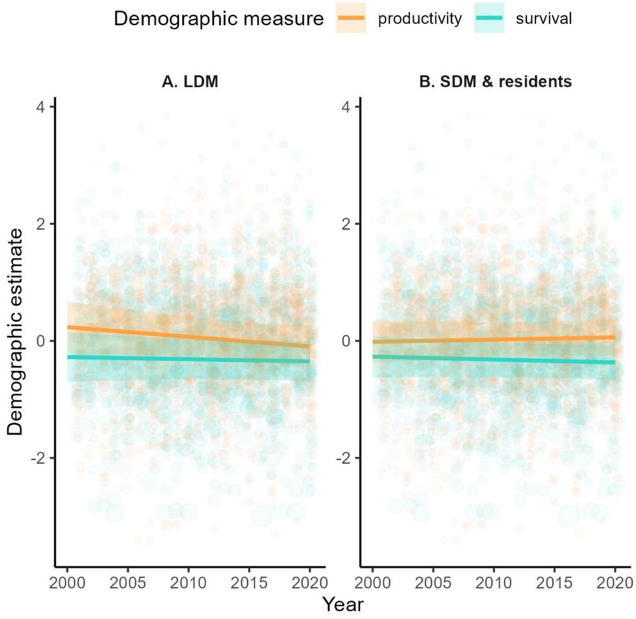

FIGURE 2 | The long-term predicted mean estimates (solid lines) of productivity (orange) and adult survival (turquoise) of European songbirds in relation to two different migratory strategies (A) long-distance (LDM) vs. (B) short-distance migrants (SDM) and residents and their confidence intervals (shaded areas). Results are based on model M3 from Table 2 (three-way interaction between year × demographic measure × migration strategy; $n = 3316$, $p < 0.001$). Points are the raw datapoints, where the size tells how much weight they have in the given model, e.g., larger points indicate a smaller standard error of the estimate and thus heavier weight.

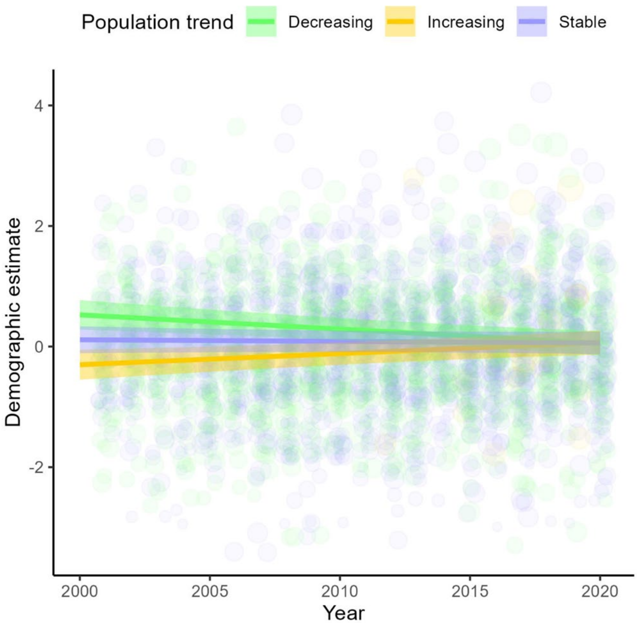

FIGURE 3 | The predicted mean estimates of adult survival and productivity of European songbirds in relation to population trend categories (solid lines), along with their confidence intervals (shaded areas). Results are based on model M4 from Table 2 (two-way interaction between year × population trend; $n = 3316$, $p < 0.001$). Points are the raw datapoints, where the size tells how much weight they have in the given model, e.g., larger points indicate a smaller standard error of the estimate and thus a heavier weight. Trend estimates are divided into three categories for visualizing purposes by dividing the full range of trend estimates into three. Green = decreasing, orange = increasing, blue = stable.

vice versa, if these two are connected. Second, it is also possible that we were not able to detect the corresponding pattern within our data: despite the standardized protocol, CES sites are situated in a non-random manner (i.e., in habitats where ringers can optimize the amount of captures), hence their demographic trends might not reflect general, large-scale patterns, which would require more and standardized data. On the other hand, despite the non-random site selection, the population trends produced through the Finnish CES scheme and common bird monitoring in Finland have produced correlated population trends (Piha et al. 2009), indicating that at least in some countries, trends from CES sites can reflect large-scale patterns. Thirdly, we should keep in mind that other drivers can also affect population trend differences than adult survival and productivity alone. For instance, immigration, emigration, or survival of first-year birds may drive the varying population trends along species' ranges.

Furthermore, we got a strong signal of density-dependence in relation to productivity, as the productivity decreased when adult abundance increased. Meanwhile, between adult survival and adult abundance, there was no such interaction. This indicates that adult survival is density-regulated elsewhere than on the breeding sites, as our proxy for density dependence did not include birds from wintering sites or during migratory routes. To understand potential density-dependent processes for survival, more research should be conducted in the non-breeding grounds together with migratory connectivity (i.e., how breeding populations are mixing during the non-breeding season; Gregory et al. 2023).

4.2 | Long-Term Trends of Adult Survival and Productivity in Relation to Migratory Behaviour

Our results point out that long-distance migrants have decreasing productivity compared to short-distance migrants and resident birds. This finding indicates that one important driver behind recent declines in long-distance migratory birds (Sanderson et al. 2006; Vickery et al. 2023, this study) could be due to decreased reproductive success. Possible reasons behind decreased productivity include habitat degradation (e.g., Reif and Hanzelka 2020), phenological mismatches (e.g., Both et al. 2006, but see e.g., Franks et al. 2018), or changes in climatic conditions in the breeding site (Hanzelka et al. 2024) or in the wintering grounds, which may have carry-over effects to the subsequent breeding (Norris et al. 2004). In addition, Morrison et al. (2021, 2022) demonstrated that population trends and productivity of species tend to correlate regardless of their migratory behaviour and that there is a strong spatial variation within productivity. Our study complements this finding, covering a continental-wide scale: despite the small-scale spatial synchrony in productivity between migratory groups (Morrison et al. 2021), at a larger spatial scale and in comparison to adult survival, long-distance migrants have declining productivity compared to short-distance migrants and residents. Furthermore, we detected a range gradient in productivity values per se for long-distance migrants, where productivity significantly increased towards warmer regions.

A study by Eglington et al. (2015) using the CES data from 1994 to 2006 corroborates our findings: they found a spatial pattern of productivity among seven songbird species, but no temporal trend. This climate-related gradient in productivity could provide a potential mechanism whereby potential surplus of birds from southern populations emigrate towards colder northern areas, leading to higher population trends at cold range edges (as seen in Jiguet et al. 2010; Lehikoinen et al. 2016). Here, especially, first-year birds could have a key role as natal dispersal distances are longer than breeding dispersal distances (Paradis et al. 1998). Our results, together with earlier work, underline the importance of reproductive success for long-distance migrants and suggest that more targeted conservation actions are needed to improve the breeding habitat quality. Although it is a common problem that the full annual cycle of a species is not well known, i.e., we lack information on long-distance migrants' non-breeding grounds and main stopover areas, our current knowledge of the problems prevailing on the breeding grounds should be enough for implementing conservation actions now (Vickery et al. 2023).

We should not, however, ignore that migration poses a risk for animals (Alerstam et al. 2003; Newton 2024). Degrading conditions on the wintering grounds have often been seen as the underlying reason for the decline in long-distance migrants (Johnston et al. 2016; Rockwell et al. 2017). Our results do not show significant changes in the long-term trends of adult survival in either long-distance migrants or short-distance migrants and residents, although their estimates indicated a (non-significant) negative trend. However, the survival of long-distance migrants may have been too low overall throughout the study period to maintain the population as stable as the decline of many long-distance migrants had started before the 2000s (Sanderson et al. 2006). Alternatively, low survival values over the study period might as well be merely a sign of low site fidelity, as in mark-recapture datasets, survival and site fidelity are difficult to separate (e.g., see Shitikov et al. 2012).

In addition, based on post hoc models, the migratory groups did not show differing population trends along species' ranges, though there was a tendency for long-distance migrants to have overall more negative population trends. We also show that long-distance migrants had higher productivity values towards the warm edge of their ranges, while for adult survival or short-distance migrants and residents, there were no detectable patterns.

Our findings add to the growing number of studies highlighting that adult survival and productivity are important drivers of species population dynamics (Owen-Smith and Mason 2005; Morrison et al. 2022) and that there are differences between migratory groups regarding the demographic drivers (e.g., Nousiainen et al. 2025; Morrison et al. 2021), which should be taken into account when planning conservation measures.

Author Contributions

I.N., L.B., P.L., M.P., and A.L. planned the study and the analysis and contributed to manuscript versions. I.N. carried out the analysis and drafted the manuscript. All other authors provided the data and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The CES ringing data were accessed through EURING, and it can be obtained through the application procedure (https://euring.org/data-and-codes/edb-application-procedure). The temperature data were downloaded from the CRY TS dataset (https://crudata.uea.ac.uk/cru/data/hrg). The trait for species migratory strategies data was downloaded from the AVONET database (https://opentraits.org/datasets/

avonet.html). The phylogeny data were downloaded from the BirdTree database (https://birdtree.org/).

The R code and the data used in the analysis can be accessed through Zenodo: https://doi.org/10.5281/zenodo.17208369.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Workflow of the analysis. From CES data with 10 countries, 11 schemes, and 28 species, we estimated adult survival, productivity, adult abundance, and population trends by species and scheme (step 1). After that (step 2), we answer our study questions by using adult survival, productivity, adult abundance, and population trend, along with the data for migratory strategies and range gradients. Q1: What are the long-term trends of adult survival and productivity in European songbirds, and do they differ from each other? Q2: Do the long-term trends of demographic measures vary along the temperature gradient inside species' ranges (i.e., range gradients)? Q3: Do the long-term trends of demographic measures differ between species groups of different migratory strategies? Q4: Do the long-term trends of demographic measures differ between species groups with different population trends? **Figure S2:** Boxplot showing how species- and scheme-specific population trends from the 'cesr' -package correlate with trends obtained from the Article 12 web tool (EEA 2025). **Table S1:** Table of ringing schemes used in the analyses, their codes, locations, years, number of sites, and number of species. DEU: Germany's three schemes (Hiddensee, Wilhelmshaven, and Radolfzell). ESP A: Aranzadi's scheme. ESP B: Schemes of the Ministry of Environment and SEO combined. ESP C: ICO's scheme (Catalonia). GBR & IRL: The UK and the Republic of Ireland. In schemes that had fewer sites in adult survival than productivity analysis due to the filtering, the number of sites in adult survival analysis is marked in brackets after the number of sites. **Table S2:** Table of species used in the analyses, their migratory strategies, number of individuals used in adult survival analysis, and number of individuals used in productivity analysis through all ringing schemes included in the study. LDM = Long Distance Migrant, SDM = Short Distance Migrant. Productivity includes both adult and juvenile birds. **Table S3:**. The filters used in the first step of the analysis. Dispersion parameter is a value that is provided by GLM models estimating productivity and adult abundance and indicates the quality of the model fit. Values less than four are considered a good model fit (after Burnham and Anderson 2002). SE: standard error that is provided by 'cesr' when calculating adult survival and productivity. **Table S4:**. Results of the spatial autocorrelation of our models using Moran's I test from the package 'DHARMa' (Hartig 2024). Models M1-M4 correspond to our four study questions. Bolded values are significant. **Table S5:** Results from the 'Emmeans' package for model M3 three-way interaction. Temporal trends for each combination of migration strategy and demographic measure using model-derived marginal slopes, giving the trend estimate, standard error (SE), lower confidence interval (LCI), and upper confidence interval (UCI). LDM = long-distance migrants, SDM = short-distance migrants. As all estimates cross zero in their CI's, none of the trends per se were significant. **Table S6:**. The structures of our Post Hoc models (M5-M7). Demographic measure ('Demog.measure') is adult survival (reference level: productivity). Adult abund. estimate is the adult abundance estimate. RangeTemp is the range gradient (country-specific, species range-centered range temperatures across the years 2000–2021). Migration is the migratory strategy (long-distance migrants vs. short-distance migrants and residents), where the long-distance migration is the reference level. SDM is short-distance migration. **Table S7:**. Parameter estimates, their standard errors, and the test values of the post hoc LMMs (M5-M7) show the differences in species trends regarding range gradient and migratory strategy. Demographic measure ('Demog.measure') is adult survival (reference level: productivity). Adult abund. estimate is the adult abundance estimate. RangeTemp is the range gradient (country-specific, species range-centered mean temperatures across the years 2000–2021). Migration is the migratory strategy (long-distance migration vs. other migratory strategies), where the long-distance migration is the reference level. SDM is a short-distance migrant. Bolded values are significant. **Table S8:** Parameter estimates, their standard errors, and the test values of the sensitivity analysis of LMMs (M1-M4) show the differences in treatments with weights, without weights and when using PGLMM. Demographic measure ('Demog.measure') is adult survival (reference level: productivity). Adult abund. estimate is the adult abundance estimate. RangeTemp is the range gradient (country-specific, species range-centered mean temperatures across the years 2000–2021). Migration is the migratory strategy (long-distance migration vs. other migratory strategies), where the long-distance migration is the reference level. SDM is short-distance migrant. Last, we also report the phylogenetic signal from the model residuals from LMMs with weights. Bolded values are significant.