

RESEARCH ARTICLE

Generation time and seasonal migration explain variation in spatial population synchrony across European bird species

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Abstract

1. Spatial population synchrony is common among populations of the same species and is an important predictor of extinction risk. Despite the potential consequences for metapopulation persistence, we still largely lack understanding of what makes one species more likely to be synchronized than another given the same environmental conditions.
2. Generally, environmental conditions in a shared environment or a species' sensitivity to the environment can explain the extent of synchrony. Populations that are closer together experience more similar fluctuations in their environments than those populations that are further apart and are therefore more synchronized. The relative importance of environmental and demographic stochasticity for population dynamics is strongly linked to species' life-history traits, such as pace of life, which may impact population synchrony. For populations that migrate, there may be multiple environmental conditions at different locations driving synchrony. However, the importance of life history and migration tactics in determining patterns of spatial population synchrony have rarely been explored empirically. We therefore hypothesize that increasing generation time, a proxy for pace of life, would decrease spatial population synchrony and that migrants would be less synchronized than resident species.
3. We used population abundance data on breeding birds from four countries to investigate patterns of spatial population synchrony in growth rate and abundance. We calculated the mean spatial population synchrony between log-transformed population growth rates or log-transformed abundances for each species and country separately. We investigated differences in synchrony across generation times in resident ($n=67$), short-distance migrant ($n=86$) and long-distance migrant ($n=39$) bird species.
4. Species with shorter generation times were more synchronized than species with longer generation times. Short-distance migrants were more synchronized than long-distance migrants and resident birds.

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5. Our results provide novel empirical links between spatial population synchrony and species traits known to be of key importance for population dynamics, generation time and migration tactics. We show how these different mechanisms can be combined to understand species-specific causes of spatial population synchrony. Understanding these specific drivers of spatial population synchrony is important in the face of increasingly severe threats to biodiversity and could be key for successful future conservation outcomes.

KEYWORDS

avian ecology, demography, Moran effect, seasonal migration, slow-fast continuum

1 | INTRODUCTION

Spatial population synchrony, that is the correlated fluctuation of population abundances in different places, is common between populations of the same species and an important predictor of extinction risk, since metapopulations composed of synchronized populations are more likely to go extinct (Heino et al., 1997). Synchrony has been identified between populations in a wide number of taxa including insects, fish, birds and mammals (e.g. Chevalier et al., 2014; Hansen et al., 2019; Hanski et al., 1995; Ims & Andreassen, 2000; Jones et al., 2007; Koenig, 2006; Koenig & Liebhold, 2016; Marquez et al., 2019; Raimondo et al., 2004; Ranta et al., 1995; Sæther et al., 2007). Despite the potential consequences for species persistence and the importance for conservation, we still largely lack understanding of which traits make one species more likely to be synchronized than another. We hypothesize that traits that determine the environments individuals are exposed to and traits that influence their sensitivities to those environments play an important role in determining their spatial population synchrony.

Spatial population synchrony has three main causes: Correlated fluctuations in the environment acting through demographic mechanisms (i.e. the Moran effect; Moran, 1953; Morrison et al., 2022), individual movement (i.e. dispersal) between populations (Lande et al., 1999; Paradis et al., 1999) and interactions of individuals through spatially linked populations, such as a shared predator (Ims & Andreassen, 2000; Myrberget, 1973). These three mechanisms can impact both the scaling (i.e. the relationship between synchrony and distance) and mean spatial population synchrony (Engen & Sæther, 2005; Kendall et al., 2000). Stochastic variability over time and space in population dynamics is caused by environmental stochasticity, acting on all individuals similarly, and demographic stochasticity, defined as the random variation in survival and reproduction among individuals (Lande et al., 2003). Nearby populations experience more similar fluctuations (i.e. stochasticity) in the environment, and therefore higher population synchrony, than those populations which are further apart (Ellis & Schneider, 2008; Lande et al., 1999; Sæther, 1997). Species whose dynamics are more sensitive to environmental stochasticity would be expected to be more synchronized than other species in the same habitat because they tend to have more immediate responses to environmental

stochasticity. Unlike environmental stochasticity, demographic stochasticity is not autocorrelated in space, resulting in a decoupling of species' dynamics from the environment in the presence of high demographic stochasticity (Engen & Sæther, 2016). The relative importance of environmental and demographic stochasticity for population dynamics is strongly linked to species' life-history traits (Lande et al., 2002; Sæther et al., 2013), and understanding the relationship between species traits and synchrony can help to understand differences in synchrony among species.

Life-history traits can be roughly organized along a slow-fast continuum, with high reproduction on one end and high survival on the other (Stearns, 1999). Generation time is often used as a proxy for multiple correlated traits along this slow-fast life-history continuum, such as age at first reproduction, fecundity and survival (Gaillard et al., 2005), and has successfully been used to describe patterns in population fluctuations (Marquez et al., 2019). Species with short generation times typically have high reproductive rates, low survival and are on the fast end of the slow-fast life-history continuum (MacArthur & Wilson, 1967), whereas species with longer generation times typically have low reproductive rates, higher survival and are on the slow end of the slow-fast life-history continuum (MacArthur & Wilson, 1967; Sæther & Bakke, 2000). Theoretical and empirical examples show that species with different generation times have different sensitivities to environmental variation (Bjørkvoll et al., 2012; Chevalier et al., 2014; Sæther et al., 2013; Tedesco & Hugué, 2006), and that environmental stochasticity has a greater effect on population dynamics for species with shorter generation times (Sæther et al., 2005, 2013). Some studies found evidence that generation time was related to the scaling of spatial population synchrony, where species with longer generation time had more synchronized dynamics over greater distances than those of species with shorter generation time (Marquez et al., 2019). Furthermore, species with different generation times have different sensitivities in their abundances and population growth rates to demographic stochasticity (Marquez et al., 2019; Sæther et al., 2013). Species with longer generation times typically have smaller population abundances, which can result in a larger effect of demographic stochasticity on their dynamics (Ferguson & Larivière, 2002; Oli, 2004; Sæther & Bakke, 2000; Sinclair & Pech, 1996). Investigating whether there is a relationship between contrasting life histories—and associated

sensitivities to demographic and environmental stochasticity—with variation in spatial population synchrony is an important next step in understanding causes and implications of such synchrony.

Space use and movement are important causes of spatial population synchrony. Because individuals tend to move, the environment experienced varies not only because of temporal environmental stochasticity. Most studies on individual movement effects have focused on dispersal, finding that frequent dispersal, defined as a one-way movement which links population dynamics in spatially separate populations (e.g. Engen et al., 2002), synchronizes populations (Sutcliffe et al., 1996; Swanson & Johnson, 1999). However, two-way movement such as seasonal migration between different locations is a common phenomenon in nature that complicates studies of population dynamics but has huge implications for biodiversity and ecosystem functioning (Bauer & Høye, 2014). Seasonal migration, the regular and reversible movement between locations across seasons typically between a non-breeding ground and breeding ground (Somveille et al., 2021; Webster et al., 2002), often goes overlooked when considering causes of spatial population synchrony. Migration strategies vary within and among species according to how populations make collective decisions regarding when and how to leave the breeding grounds and where to go (i.e. migratory connectivity; Newton, 2008; Webster et al., 2002). There are many parallels between the study of migratory connectivity and spatial population synchrony, but the connection between the two are rarely explored empirically. Migrating populations are exposed to several different environments through migratory routes and non-breeding grounds (Newton, 2008), and these different environment and climate patterns are known to impact vital rates (Bogdanova et al., 2011; Rakhimberdiev et al., 2018; Selonen et al., 2021), either immediately or in the future, for example as reversible state carryover effects (Harrison et al., 2010; Senner et al., 2015; van Gils et al., 2016). Species' life history and sensitivity to environmental and demographic stochasticity may modify the consequences of such variation in migratory tactic on synchrony by rendering some species more sensitive to the different environments experienced through migration.

In this study, we explored the implications of two key life-history traits—generation time and migration tactic—for spatial population synchrony across 94 bird species from four countries in Europe. Given known differences in sensitivities to environmental and demographic stochasticity among species with different life-history traits, we expected higher synchrony between populations of a given species with fast versus slow life histories, that is short versus long generation times, due to higher and lower sensitivities to environmental and demographic stochasticity, respectively. We also expected that populations of a given species that spent less time in correlated environments on the breeding ground, travelled further, and were exposed to more environmental stochasticity (i.e. long-distance migrants) would be less synchronized than populations of a given species that spent more time in one constant environment (i.e. resident species). We expected to see a gradient in increasing synchrony from long-distance migrants to short-distance migrants and resident species.

2 | MATERIALS AND METHODS

2.1 | Study area and data

We used population abundance data of breeding birds from four long-term monitoring programmes in Norway, Sweden, Switzerland and the United Kingdom. While the data collection protocol for these data varied from country to country, generally similar methods were used across countries following point or line transects, and the quality and rigour of survey protocol is known to be high. Data from these countries were publicly available for download (Norway, Sweden), or free to use with data sharing agreements (Switzerland, United Kingdom). All surveys were conducted during the breeding season, between spring and mid-summer (Figure 1).

2.1.1 | Norway

Data were downloaded in September 2021 from the Global Biodiversity Information Facility (GBIF) with supplemental location and survey information provided by the Norwegian Institute for Nature Research (Kålås et al., 2022). Data were collected as a part of the Norwegian TOV-E Bird Survey and spanned years 2006–2021. The survey methodology involved conducting 5-min point count surveys within a 2 km by 2 km square (Kålås et al., 2022). Observers recorded all pairs of individuals seen during the transects. A total of 494 unique survey points were surveyed over 19 years (Figure 1d).

2.1.2 | Sweden

Data were downloaded in March 2021 from GBIF (Lindström & Green, 2021). Data were from the *Swedish Bird Survey standardrut-terna* (i.e. standardized fixed routes) line survey transects published by the Department of Biology at Lund University, and spanned years 2006–2019. The survey methodology involved conducting a fixed route survey of eight 1 km-line transects within a 2 km by 2 km square (Lindström & Green, 2021). Observers recorded all birds seen or heard during the transects. A total of 716 unique locations were surveyed (Figure 1b).

2.1.3 | Switzerland

Data were provided in September 2020 by the Swiss Ornithological Institute Sempach. Data were from the *Monitoring Häufige Brutvögel MHB* program, a common breeding bird survey (Schmid et al., 2001). The data spanned years 1999–2020. The survey methodology involved skilled birdwatchers conducting annual repeat transect surveys across 267 individual 1 km × 1 km squares laid out as a grid across Switzerland. Transect routes and squares did not change between years. Observers record all birds seen or heard during the

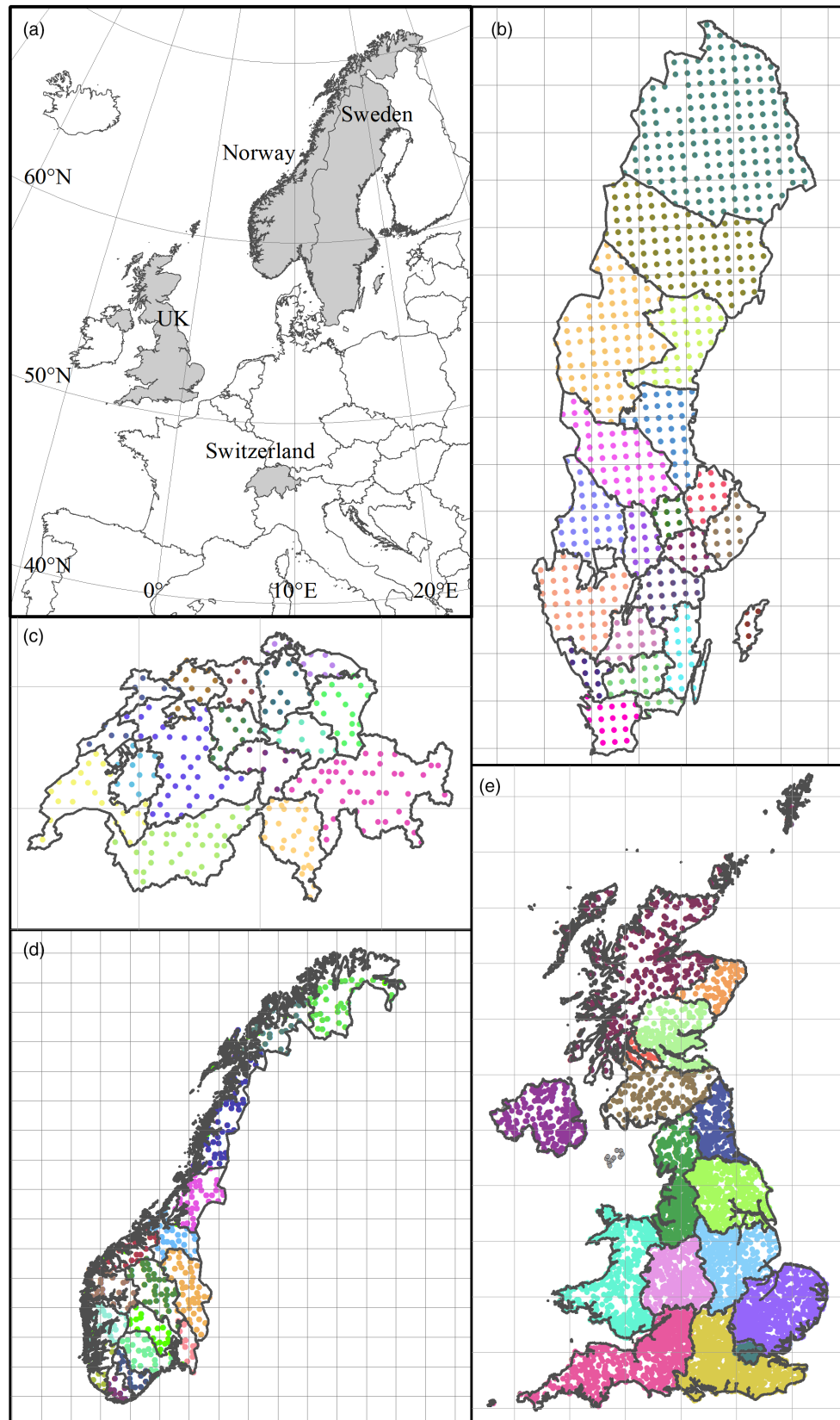


FIGURE 1 (a) The four study countries. Survey locations in each country presented in (b–e). Administrative units were clustered with next nearest neighbour with fewest survey points to achieve a minimum of 8 sample locations. Black boundaries represent aggregated administrative unit boundaries. The grids in the country maps are 100 × 100 km. Dots are survey locations, and the dot colour represents which survey points are aggregated within each administrative unit. (b) Sweden, (c) Switzerland, (d) Norway and (e) the United Kingdom.

transects. A total of 267 unique points were surveyed over 21 years (Figure 1c; Schmid et al., 2001).

2.1.4 | United Kingdom

Data were provided in December 2021 from the British Trust for Ornithology. Data were from the *BTO/JNCC/RSPB Breeding Bird Survey (BBS)* and spanned years 1994–2015. This survey consisted of two repeat visits at the beginning and end of the breeding season of 1-km transects within an allocated 1-km square, recording all birds seen or heard (Gregory & Baillie, 1994). We took the maximum count from these two surveys for all detected distances from the transect line to represent the annual count at each survey point. Between years, a stratified random sample of survey squares was selected, where stratification was representative of habitats and regions. A total of 5810 unique locations were surveyed over 16 years (Figure 1e).

Within each country, we aggregated point- or transect-level count data into regional population indices. We used country-level administrative boundaries which resulted in summing our data across 16 counties in Norway, 20 counties in Sweden, 15 cantons in Switzerland and 16 local administrative units (Nomenclature of Territorial Units for Statistics, NUTS-2) in the United Kingdom (Figure 1). Aggregating point counts into one value for the sum of all surveyed points in a region allowed us to reduce the noise (i.e. any random fluctuation) that was present in the data and improve our ability to assess regional-level population dynamics, which was our main interest. For the United Kingdom, we took the average value of the aggregated points to account for methodological variation in the density of sample units (Link & Sauer, 2002). Small administrative units were merged to secure a minimum number of sampling locations per administrative unit and the abundances from each survey location within the administrative units were added together (Figure 1). From these aggregated population indices, we excluded species that were absent from at least 25% of the aggregated regions. We also excluded regions in which a species was not observed for at least 10 years of the survey duration. We checked all synchrony calculations with different aggregation schemes of 100 km × 100 km hexagonal grids and 50 km × 50 km hexagonal grids to ensure that there was no underlying structure in relation to the municipality boundaries used.

Directional, temporal trends in abundance impact the strength of correlation between populations (Loreau & de Mazancourt, 2008). These directional trends can be accounted for in spatial population synchrony analyses by estimating synchrony of population growth rates instead of abundances (Loreau & de Mazancourt, 2008), effectively diminishing the impacts of increasing or decreasing population abundance (Tredennick et al., 2017). Here, we calculate synchrony on both population growth rate (instantaneous rate of increase, $\log(N_{t+1}/N_t)$) and abundance ($\log(N_t)$), but focus our interpretation of results on log population growth rate to consider synchrony not impacted by trends.

We classified each species along the slow–fast life-history continuum using generation time as a proxy (Bird et al., 2020). Species' generation times are defined as the average age of parents of a current cohort (IUCN, 2019) and are a common tool to distinguish species life-history traits (Gaillard et al., 2005). Species-specific generation time was taken from Bird et al. (2020), which classified the world's birds using derived generation times from proxies based on age of first reproduction, maximum longevity and annual adult survival (Appendix 1). Where species-specific generation time was unavailable, we used generation time of the species' next closest phylogenetic relative (2 out of 94 instances; Appendix 1).

We classified each species within each country as a resident, short-distance migrant or long-distance migrant (Appendix 1). Migratory avian species are typically classified by the distance that they move between breeding grounds and overwintering areas (Rappole, 2013). Residents were defined as non-migrants that made no seasonal movements outside their country of residence (Eyres et al., 2017; Newton, 2008). Short-distance migrants were defined as species that had documented non-breeding areas within Europe, but outside the country that contained the breeding ground (Rappole, 2013). Long-distance migrants were defined as species that had documented non-breeding areas outside of Europe (Rappole, 2013). To assign each species one of the three migration tactics (i.e. residents, short- or long- distance migrants), we used an available avian life-history trait database (Storchová & Hořák, 2018). We next confirmed country-specific species migration tactics by consulting country-specific avian information platforms (Bird Life International and the Royal Society for the Protection of Birds [UK], Swiss Ornithological Institute Swiss Breeding Bird Atlas [Knaus et al., 2020], Swedish Bird Ringing Atlas/Svensk Ringmärkningsatlas [Fransson & Hall-Karlsson, 2008] and Norwegian Bird Ringing Centre [Bakken et al., 2006]). When country-specific avian information platforms were inconclusive, we consulted The Eurasian African Bird Migration Atlas (Franks et al., 2022) to reclassify species given their country of origin based on ringing recoveries and satellite tagging data (Franks et al., 2022; Kays et al., 2015).

2.2 | Calculating synchrony

From the aggregated abundances, we calculated the mean spatial population synchrony in two ways: either between log-transformed population growth rates ($\log(N_{t+1}/N_t)$) or between log-transformed abundances ($\log(N_t)$) for each species and country separately. We log-transformed the abundance data and species' generation times to reduce the correlation between the mean and variance. In program R (R Core Team, 2020), we used a parametric Gaussian cross-correlation function to estimate synchrony between pairs of regions. Mean synchrony for each species within each country was then calculated as the mean of these estimates between pairs of regions for a given distance interval. Given the known relationship of decreasing synchrony at increasing distances between pairwise populations, most species had higher synchrony at short

distances between populations, but we emphasize that we present the average synchrony calculated between pairs of populations within the given distance intervals. Distances between populations were calculated as the Euclidean distances in kilometres from the centroid projected coordinate (EPSG:3035) of each aggregated administrative unit for each pair of regions. All estimates of synchrony were calculated between pairs of regions within country boundaries, meaning data from one country was not used to estimate synchrony in another. We conducted the above analyses accounting for phylogenetic relatedness between species by fitting a univariate linear mixed model incorporating a correlated random effects structure (EVOLVABILITY package; Almer function) and concluded that our results and conclusions were unaltered by the inclusion.

Distance over which populations are sampled is known to influence estimated average spatial population synchrony (Bjørnstad et al., 1999; Hanski & Woiwod, 1993; Sutcliffe et al., 1996). This comes from the general negative relationship between population synchrony and distance between populations (Lande et al., 1999). Accordingly, for a given species, the mean synchrony would be lower if populations are sampled over large distances, compared to a smaller focal area. Our main objective was to present comparable differences in average synchrony. Given the large differences in pairwise population distances among the four countries analysed (e.g. max distance between aggregated points in Switzerland of 223 km, max distance between aggregated points in Norway of 1553 km; Figure 1a, Table 1), we ran all tests on mean spatial population synchrony calculated between all pairs of populations within distance thresholds 0–350 km, 0–500 km, 0–1000 km and 0–max distance interval. Statistical analyses were run separately for the four distance intervals.

2.3 | Statistical analyses

To quantify the contribution of generation time and seasonal migration tactic to spatial population synchrony, we used linear mixed models. Using species as a random factor, we accounted for the non-independence in species which were present in multiple datasets and the potential for within-species differences in migration tactic. The fixed factors in the global model included migration tactic, generation time, country, as well as all two-way interaction terms (for global model, see Table 2). We included country as a parameter to control

for differences in sampling methods, survey efforts and the variation in size of the aggregated administrative units between countries. We assumed that the environmental autocorrelation that the species experienced within countries did not differ in a meaningful way to cause species-specific differences in synchrony within each country. We included two-way interactions between country and generation time as well as country and migration tactic to test for a different effect across sampled countries for both parameters. In this two-way interaction, country could be acting as a proxy for weather or environment and any differences detected could be of interest to correlate with synchrony. We also included a two-way interaction between generation time and migration tactic, as we were interested in testing if species with the same migration tactic, but different generation times were more or less sensitive to variability in environments throughout the year. We expected that resident species would experience similar variability in overwintering conditions while migrants may diverge and experience different variability in their overwintering conditions, and that species with different generation times would have different sensitivities in their responses to these similar or dissimilar environmental variabilities. We used Akaike information criterion adjusted for small sample size (AIC_c) to rank models (Burnham & Anderson, 2002). We assessed model uncertainty by computing simulated distributions of all parameters in the model (Knowles & Frederick, 2020). All residuals were tested for normality.

3 | RESULTS

We analysed population abundances for spatial population synchrony in 192 country-specific birds, yielding estimates of synchrony calculated for a total of 94 unique species: 36 species from Norway, 59 from Sweden, 47 from Switzerland and 50 from the United Kingdom (Figure 2a, Appendix 1). Most species were present in more than one country (Figure 2a). All countries except the UK had more short-distance migrants than residents or long-distance migrants (Figure 2b).

Log generation time ranged from 0.53 (absolute scale: 1.69) to 2.83 (absolute scale: 16.9; Figure 2c). Long-distance migrants had the shortest mean log generation time (1.06, standard deviation [SD]=0.36), followed by resident species and short-distance migrants (1.24 [SD=0.38] and 1.30 [SD=0.51], respectively). Other life-history traits associated with placement on the slow-fast

TABLE 1 Number of paired regions for each distance interval per country. Minimum distance (min distance) calculated as the smallest distance (km) from the centroid of one aggregated administrative region to another. Maximum distance (max distance) calculated as the largest distance (km) from the centroid of one aggregated administrative unit to another.

Country	Min distance (km)	Max distance (km)	0–350 km	0–500 km	0–1000 km	0–max distance (km)
Norway	63	1553	59	74	99	120
Sweden	78	1263	99	139	182	190
Switzerland	32	223	105	105	105	105
United Kingdom	42	748	71	95	120	120

TABLE 2 Top model results for estimates of spatial population synchrony in log population growth rate and log abundance at four distance intervals (0–350 km, 0–500 km, 0–1000 km and 0–max distance). The inclusion of parameters of log generation time (GT), migration tactic (MT), country and interactions between parameters designated with an 'X' when present in the model. We relied upon Akaike's information criterion with a small sample size correction (AIC_c) for model selection and used Akaike model weights (AIC_c wt) and ΔAIC_c to identify the top model. Number of parameters in model indicated by column k. Top five models in each distance interval are presented. Bold models in 0–Max distance interval were used for figures and results interpretation.

Log population growth rate	Distance (km)	Model number	GT	MT	Country	GT X country	GT X MT	MT X country	Log-likelihood	AIC_c wt	ΔAIC_c	k
0–350		1	X	X	X				180.22	0.39	0	9
		2	X		X				177.14	0.16	1.77	7
		3	X	X	X			X	186.03	0.13	2.14	15
		4	X	X	X	X			182.39	0.12	2.43	12
		5	X		X	X			179.48	0.06	3.71	10
0–500		3	X	X	X			X	195.29	0.29	0	15
		1	X	X	X				188.24	0.24	0.69	9
		2	X		X				185.29	0.11	1.66	7
		6	X	X	X	X		X	197.93	0.11	2.01	18
		4	X	X	X	X	X		190.69	0.079	2.87	12
0–1000		3	X	X	X			X	205.49	0.44	0	15
		1	X	X	X				198.06	0.25	1.11	9
		6	X	X	X	X		X	207.24	0.07	3.74	18
		2	X		X				194.53	0.07	3.77	7
		7	X	X	X	X	X		205.86	0.06	4.06	17
0–max distance		1	X	X	X			X	176.13	0.49	0	9
		3	X	X	X			X	182.31	0.24	1.39	15
		8	X	X	X	X	X		176.62	0.08	3.51	11
		7	X	X	X	X	X		183.08	0.05	4.66	17
		4	X		X	X	X		177.14	0.05	4.74	12

TABLE 2 (Continued)

	Distance (km)	Rank	GT	MT	Country	GT X Country	GT X MT	MT X Country	Log-likelihood	AIC _c wt	ΔAIC _c	k
Log abundance	0–350	1	X	X	X				111.14	0.39	0	9
		2	X	X	X		X		113.22	0.33	0.32	11
		3	X		X		X	X	119.12	0.1	2.59	17
		4	X	X	X			X	116.36	0.074	3.32	15
		5	X	X	X	X			111.99	0.03	5.06	12
0–500		1	X	X	X				110.41	0.45	0	9
		2	X	X	X		X		112.4	0.35	0.5	11
		3	X	X	X		X	X	117.44	0.047	4.49	17
		4	X		X				105.82	0.037	4.8	7
		5	X	X	X	X		X	114.78	0.034	5.02	15
0–1000		1	X	X	X				109.71	0.46	0	9
		2	X	X	X			X	111.77	0.38	0.37	11
		3	X	X	X		X		110.86	0.05	4.46	12
		4	X	X	X	X		X	112.81	0.03	5.2	14
		5	X		X				104.7	0.03	5.65	7
0–max distance		1	X	X	X		X		90.11	0.5	0	11
		2	X	X	X				87.54	0.36	0.65	9
		3	X	X	X	X		X	91.3	0.051	4.52	14
		4	X	X	X	X	X		88.87	0.046	4.4	12
		5	X	X	X	X		X	93.97	0.02	6.35	17

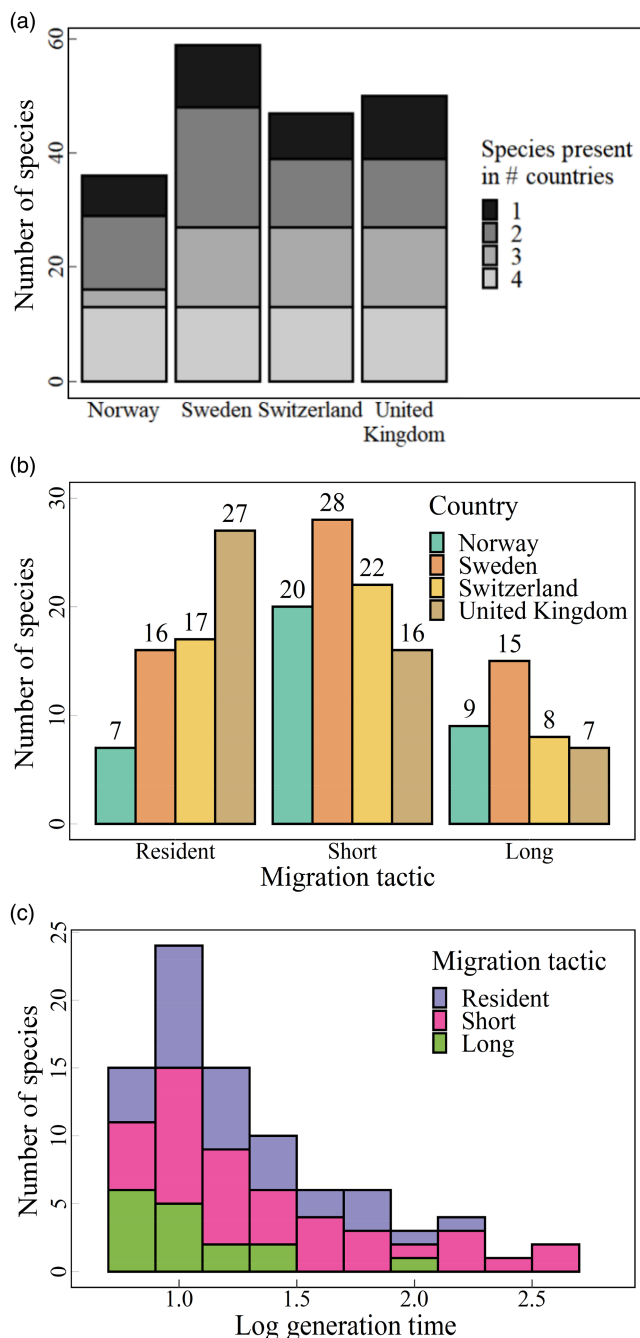


FIGURE 2 Summary of data used to estimate spatial population synchrony (i.e. pairwise correlation in population growth rate and abundance). (a) Number of species per country and number of species shared across multiple countries, (b) number of migration tactics per country and (c) distribution of log generation time separated by migration tactic. Log generation time ranged from 0.53 (absolute scale: 1.69) to 2.83 (absolute scale: 16.9).

life-history continuum such as survival, fecundity and life span were highly correlated with generation time (Pearsons corr=0.87, 0.84, 0.88, respectively; estimates for life-history traits from Bird et al., 2020; Eyres et al., 2017).

Overall, mean synchrony decreased when populations at greater distances were included in analysis to estimate mean spatial population synchrony (Figure 3). However, this relationship was weak for

both growth rate (Figure 3a, Appendix 2) and abundance (Figure 3b, Appendix 3) and did not influence the structure of the highest ranked model, and thus the conclusions are valid over all distance classes (Table 2). Figures and results presented hereafter are generated using data from 0 to max distance intervals.

Across all distance intervals for synchrony in population growth rate, the highest ranked models included the main effects of country, migration tactic and generation time, and in some cases an interaction between migration tactic and country (Table 2). The top two models across all distance intervals remained consistent and had similar support ($\Delta AIC_c \leq 1.39$ and Akaike model weights ≥ 0.24 ; Table 2). Parameter estimates for all top models for population growth rate across the four distance intervals were similar which suggested that our conclusions were not sensitive to the distance range at which synchrony was calculated (Appendix 4). After further exploration, the interaction between country and migration tactic evident in a top performing model in two distance classes (0–500km and 0–1000km) was driven by one bird species (*Sylvia communis*) which had notably high synchrony in population growth rate in the United Kingdom data compared with other countries and synchrony estimates (Appendix 2). There was also large uncertainty associated with the corresponding parameters for the interaction (Appendices 4 and 5).

Across all distance intervals for abundance, the top performing models for synchrony included the main effects of country, migration tactic and generation time (Table 2), and, in one case, an interaction between migration tactic and generation time (Table 2). Across all distance intervals, the top two models remained consistent and had similar support ($\Delta AIC_c \leq 0.65$ and Akaike model weights ≥ 0.33). Like the parameter estimates for population growth rate, parameter estimates for all top abundance models across the four distance intervals yielded similar parameter estimates (Appendix 4). In one distance interval, the strength of the relationship between synchrony and generation time depended on the migration tactic (Table 2, Appendix 5). This interaction appeared in only one distance interval as top model for abundance (0–max distance [km]), and there was large uncertainty associated with all of the corresponding parameters (e.g. [Short-distance migrant \times Log Generation Time: estimate = -0.13 SE = 0.06], [Long-distance migrant \times Log Generation Time: estimate = -0.03 SE = 0.09]).

The highest ranked models suggested that spatial population synchrony decreased with increasing generation time both for population growth rate (-0.12 [CI = -0.16 to -0.08]) and abundance (-0.14 [CI = -0.19 to -0.08], Figure 4). Moreover, short distance migrants in general had the highest synchrony (population growth rate: 0.25, [95% confidence interval (CI) = 0.19 – 0.32]; abundance: 0.48 [CI = 0.39 – 0.57]), followed by resident species (population growth rate: 0.22 [CI = 0.15 – 0.28]; abundance: 0.42 [CI = 0.33 – 0.51]), and finally long-distance migrants (population growth rate: 0.18 [CI = 0.11 – 0.24]; abundance: 0.37 [CI = 0.28 – 0.46]). Estimates of synchrony in short-distance migrants were not different from estimates of synchrony in resident species but were different from estimates of synchrony in long-distance migrants (Figure 4).

FIGURE 3 Mean synchrony (i.e. pairwise correlation in population growth rate and abundance) of all species per distance interval. Results shown for (a) log population growth rate and (b) log abundance. Number of pairs of populations per distance interval per country available in Table 1. Bars show the standard deviation.

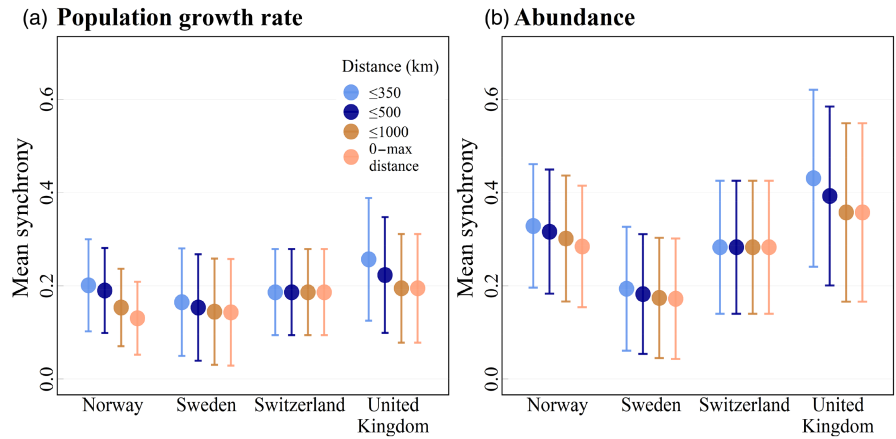
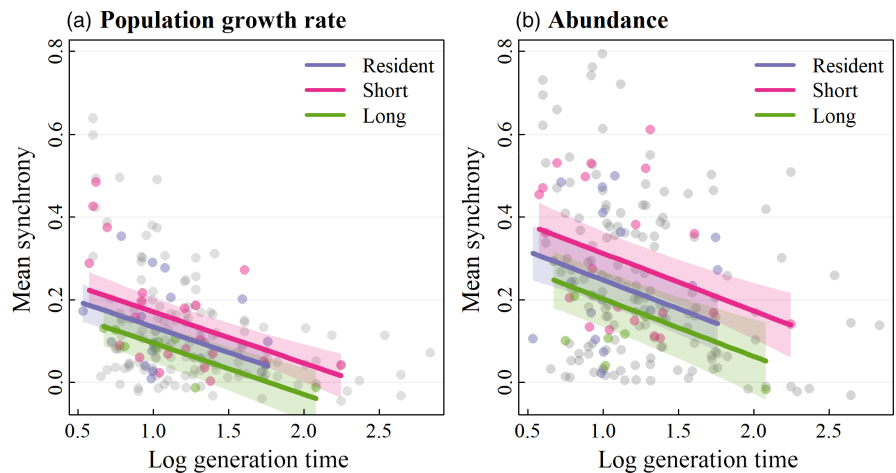


FIGURE 4 The effects of log generation time and migration tactic on mean synchrony (i.e. pairwise correlation in population growth rate and abundance) in (a) log population growth rate and (b) log abundance. Data for Switzerland in colour, all other countries in grey. Slopes are predicted for Switzerland from the top performing model: Country + Migration Tactic + Log Generation Time, see Table 2. 95% confidence intervals presented as shaded colours.



Country was an important predictor of spatial population synchrony. However, there were no interactions between country and generation time or migration tactic, so the slopes and relationships between migration tactic and generation time remained the same across countries. Synchrony in growth rate was highest in the United Kingdom, followed by Switzerland, Sweden and Norway (Appendix 4). In abundance, the highest spatial population synchrony was in the United Kingdom, followed by Norway, Switzerland and Sweden (Appendix 4).

4 | DISCUSSION

Despite the need to identify patterns of spatial population synchrony in nature, current understanding remains more theoretical and general than species specific or trait specific. Here we make use of available long-term monitoring data to investigate synchrony across countries and species to identify life-history traits that can explain why some species are more synchronized than others. We show that the same trend in spatial population synchrony and generation time was found across countries which span large geographical and environmental gradients across Europe. While the data collection protocol for the data used in this analysis varied from country to country, generally similar methods were used across countries

following point or line transects, and the quality and rigour of survey protocol is known to be high. Since the same relationship between synchrony and life-history traits was observed across all four datasets analysed, we expect this pattern to hold for other European countries as well, particularly given the high likelihood of shared species across countries. Similar studies in other parts of the world would be useful to discover how general these patterns are on the global scale.

Our top models confirmed that spatial population synchrony was related to species' generation time: Species that had shorter generation times were more synchronized (Figure 3), regardless of the spatial scale at which mean synchrony was estimated (Table 2). We also identified differences in synchrony for different migration tactics (Figure 4). Short-distance migrants had higher synchrony in both population growth rate and abundance than long-distance migrants (Figure 4). These results help to bridge a notable gap by linking known drivers of synchrony, environmental and demographic stochasticity, to species life-history traits and show how these different mechanisms can be combined to understand species-specific patterns of spatial population synchrony.

We found that population synchrony was highest for species with short generation times. Theoretical and empirical examples suggest that the impact of environmental stochasticity is greater for population dynamics of species with shorter generation times

(Sæther et al., 2013) and stronger density regulation, which is typically correlated with species at the fast end of the slow-fast life-history continuum (Boyce, 1984; MacArthur & Wilson, 1967). Accordingly, species with shorter generation times are more sensitive to environmental stochasticity that often has a high spatial autocorrelation (Herfindal et al., 2022), and thus more synchronized than species with long generation times. At the same time, the slower dynamics of species with longer generation times can mean that fluctuations in population size have more time to spread out in space, causing synchrony over larger distances. This was found in a study of marine fish, where species with longer generation times had longer spatial scaling in synchrony, that is a greater distance at which spatial synchrony was below a certain value given the standard deviation, than fish with shorter generation times (Marquez et al., 2019). While spatial scaling of population synchrony has not been the focus of our current study, an interesting future question would be whether this pattern found in fish also holds for birds.

Migration is a complex phenomenon which has considerable interspecific and intraspecific variation (Newton, 2008). The great diversity of migratory tactics seen in nature makes it challenging to form generalizable conclusions applicable to all migrant species. Here, we attempt to distil a complex migratory system into three generalizable categories—resident species, short-distance migrants and long-distance migrants—to understand the influence of seasonal environments and environmental stochasticity on population synchrony. We expected to find highest synchrony in resident species because two resident populations are more likely to experience the same or similar seasonal changes in environmental conditions compared to two migratory ones. We also expected to find lower synchrony for short-distance migrants than for residents, but we found no detectable difference. This lack of difference in synchrony between short-distance migrants and residents may be due to the fact that few of the species classified as residents were true residents with little or no movement. It is possible that residents exhibited altitudinal migration or within-country movement, which resulted in lower synchrony than expected. In these cases, variation in environment was not accounted for and could be a potential cause of the lower synchrony seen in resident birds. Furthermore, it is possible that short-distance migrants were not more synchronized than resident species because the short-distance migrant species exhibited a telescopic migration tactic, where they were clustered on the wintering grounds, and thus experienced a stronger synchronizing environment on the wintering grounds (e.g. songbirds species [Beauchamp, 2011; La Sorte et al., 2016]). The seasonal differences experienced by resident species could reflect large seasonal differences in the scaling of environmental stochasticity on the breeding ground. In nature, there are distinct seasonal differences in environmental synchrony, particularly in terrestrial systems (Herfindal et al., 2022). This varying seasonality on the breeding grounds could have a large impact on the scaling of spatial population synchrony. As expected, long-distance migrants had the lowest spatial population synchrony. In our study, we did not investigate the cause of

this lower spatial population synchrony. However, we know that long-distance migrants tend to spend the shortest amount of time on the breeding grounds before migrating across different migratory stop-over sites and wintering sites (Knaus et al., 2018). Furthermore, the differences in sensitivity to environmental stochasticity could be driving the differences that we see between short- and long-distance migrants and residents: long-distance migrants tend to be more severely affected by environmental stochasticity (Knaus et al., 2018).

An important consideration when interpreting these results is the role of carryover effects, including the concepts of different types of carryover effects (e.g. irreversible or reversible state effects) and sequential density dependence. Carryover effects link events between the breeding and non-breeding season and can impact population parameters such as survival and fecundity at subsequent stages in the circannual cycle (Senner et al., 2015). Irreversible carryover effects, such as natal conditions, can have long-term impacts, while many carryover effects are reversible, meaning that there can be compensation over time for the negative effects of a poor season on one population parameter (Norris & Marra, 2007). Similarly, sequential density dependence also results in compensation for poor conditions in one season by good conditions in another (Rakhimberdiev et al., 2015). We would expect differences in spatial population synchrony on the breeding ground when different compensatory processes are occurring. Migrant populations that exhibit reversible state effects or sequential density dependence are expected to have more synchronized dynamics on the breeding ground as they compensate for conditions experienced during time spent apart on the non-breeding ground (Rakhimberdiev et al., 2015). However, investigating the types of compensatory dynamics occurring within species is challenging, as it requires observations and tracking of individuals at multiple points in the circannual cycle (e.g. Gibson et al., 2018). Nonetheless, such investigations could yield important, species-specific insights into the nature of spatial population synchrony.

The pairwise distance of regions at which spatial population synchrony is estimated can change the average calculated synchrony (Dungan et al., 2002; Pearson & Carroll, 1999). Given the known relationship between increasing distance between pairs of regions and decreasing synchrony, we therefore analysed our data at four different biologically relevant maximum pairwise distances to ensure that we captured all patterns in spatial population synchrony across local and larger regional scales. Across all countries except Switzerland, synchrony decreased when including larger distances, but the results and support for the top models were not affected by the distance intervals. Given the large discrepancies in the range of maximum distances between countries, comparisons between countries should be done at the 350km scale because this is the maximum distance between pairs of populations in Switzerland. Even when accounting for this difference in the size of countries, country still was an important predictor of average spatial population synchrony for populations up to 250km away from one another. This effect could be a methodological effect

because of the different survey methods used between different countries, or it could be caused by differences in environmental conditions across countries.

Population growth rate yielded lower estimates of synchrony than abundance. This is unsurprising, as calculating synchrony on raw census data tends to reflect not only the synchronizing effect of regional environmental fluctuations, but also the synchronizing effects of common long-term trends (Koenig, 1999). If trends exist, either negative or positive, there will be higher synchrony in abundance than in growth rate. There are known trends in abundance of many European bird species, particularly migratory birds (Harris et al., 2022; Knaus et al., 2020; Ottvall et al., 2009), and this directional, temporal trend in population abundance could explain why synchrony in abundance is higher than in population growth rate (Tredennick et al., 2017).

There may, however, be some biological relevancy for the weakly supported interactions which should be considered. The interaction between generation time and migration tactic seen in the abundance model may result from differences in species traits and their responses to environmental and demographic stochasticity. For example, two species with different generation times could experience the same migratory and overwintering conditions, yet respond differently. We would expect migratory species with low sensitivity to environmental fluctuations (typically long-lived species) to be less affected by wintering ground environmental conditions than short-lived species, resulting in different effects of migration (Appendix 5). It is also possible that this interaction manifested in the abundance model set and not the population growth rate model set because of different population trends among groups of birds, which would affect synchrony in abundance but not necessarily population growth rate. Given that migratory species' abundances are declining more than other species, estimating synchrony on abundance would pick up these trends in the data (Gilroy et al., 2016).

Furthermore, there may be country-specific variation in synchrony across migration tactics, as seen in the population growth rate top model set. We would expect to see different synchrony for different migration tactics across countries when there is a large difference in maximum distances within each country (Norway: 1553 km, Sweden: 1263 km, Switzerland: 233 km, UK: 748 km). This large distance could be failing to uniformly capture within-country seasonal movement which could impact estimates of synchrony.

Count data used herein to understand trends in spatial population synchrony is not adjusted to account for imperfect detection or other sources of sampling error. Unfortunately, with the relatively short time series we have available and the diversity of species in the analysis with no duplicated sampling, it is difficult to identify and correct for such a relationship in a rigorous way. When studying population synchrony, the most likely impact of sampling error on estimates is to reduce the ability to detect synchrony (i.e. bias synchrony results downward Yoccoz & Ims, 2004), and underemphasize the role of extrinsic factors (i.e. Moran effect and life history traits) in causing population synchrony (Santin-Janin et al., 2014). This could mean that our results are underestimates of the real effects but would not cause us to find spurious

effects. Here, we can assume that sampling error is not systematically related to the traits we are studying, thus the main effect of sampling error would therefore be to lower the power to detect the effects we are studying.

The higher spatial population synchrony we identified for European short-distance migrant species should alert managers to the susceptibility of these populations to stochastic events on shared breeding or non-breeding grounds. Given their higher synchrony and known sensitivities to environmental stochasticity, these non-migratory or short-distance migrants' population dynamics are expected to be more susceptible to anthropogenic or climatically induced changes in environments. Understanding these trait-specific drivers of spatial population synchrony is important in the face of increasingly severe threats to biodiversity and could be key for successful future conservation outcomes. In this manuscript, we show that general trends can be detected across species, using life-history traits to capture some specific ecological factors in a general sense. Further testing of the impact of life-history traits on spatial population synchrony across taxa and environments is encouraged to uncover important ecological patterns.

AUTHOR CONTRIBUTIONS

Ellen C. Martin, Brage Bremset Hansen, Aline Magdalena Lee and Ivar Herfindal conceived the ideas and designed the methodology. Ellen C. Martin collated, cleaned and formatted data. Ellen C. Martin and Ivar Herfindal provided code for analysis of data. Ellen C. Martin led the writing of the manuscript with contributions from Ivar Herfindal. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Novel data code available from the FigShare <http://doi.org/10.6084/m9.figshare.23617197> (Martin et al., 2023). Datasets publicly available for download on GBIF:

Norway: June 2021, from GBIF DOI: <https://doi.org/10.15468/6jmw2e>.

Survey unit centroids provided by John Atle Kalas/NINA [personal communication].

Sweden: March 2021 from GBIF DOI: <https://doi.org/10.15468/hd6w0r>.

Data available upon request to listed point of contact:

Switzerland: Swiss Ornithological Institute [data share agreement], Data from the regular territory mapping for the atlas of breeding birds 2013–2016 (Knaus, P., S. Antoniazza, S. Wechsler, J. Guélat, M. Kéry, N. Strebel & T. Sattler (2018): Swiss Breeding Bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and Liechtenstein. Swiss Ornithological Institute, Sempach. 648 p.), Point of contact: Hans Schmid.

United Kingdom: British Trust for Ornithology [data request EF1599224671889842], Point of contact: Dario Massimino.

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SUPPORTING INFORMATION

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

Appendix 1. Bird species in analysis and corresponding migration tactic (resident, short-distance migrant [short] or long-distance migrant [long]) indicated in country column where species was present and analysed (Norway, Sweden, Switzerland and United Kingdom). Species noted by asterisk (*) had different migration tactics between two or more countries. Generation time presented from Bird et al. (2020). Generation times are defined as the average age of parents of the current cohort. Asterisk in generation time column indicates species for which generation time was unavailable; value given is from closest phylogenetic relative. Total of residents, short-distance migrants and long-distance migrants per country given at bottom of table.

Appendix 2. Estimated mean spatial population synchrony in log population growth rate for each species by country. NA indicates that the species was not included in the country's data.

Appendix 3. Estimated mean spatial population synchrony in log abundance for each species by country. NA indicates that the species was not in the country associated with the column. Species names in Latin and English common names provided.

Appendix 4. Parameter estimates and standard errors (parentheses) for all chosen models across all distance intervals for log population growth rate (A) and log abundance (B). Max distance varied by country, for max distance values see Table 2.

Appendix 5. Interaction terms between migration tactic and country (log population growth rate) or migration tactic and generation time (log abundance) appeared in the top model. Mean synchrony is estimated from the log population growth rate top model (Country *Migration Tactic + Log Generation Time) and 0-max distance interval log abundance top model (Country + Migration Tactic *Log Generation Time). 95% confidence intervals are presented as shaded colours.

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