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Doctoral thesis

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Summary

Spatial population synchrony, the correlated fluctuation of population abundances in different places, is common between populations of the same species and an important predictor of extinction risk. More highly synchronized populations face a greater risk of species-level extinction compared to populations with lower synchrony because synchronized local populations may collectively face low abundance periods. Synchrony has been identified between populations across a wide number of taxa including insects, fish, birds, and mammals.

Correlated fluctuations in abundances are largely caused by spatial autocorrelation in the environment acting through demographic mechanisms (*i.e.,* the Moran effect). Moran's theorem states that spatially separated populations are expected to have the same synchrony in their dynamics as that in their environment. However, species have unique traits (*i.e.,* life history traits) that influence what environments they are exposed to and how sensitive their population dynamics are to these environments. One would expect to see differences in synchrony between species that have different life history traits rendering them more or less sensitive to the environment. The literature is currently lacking a comprehensive understanding of how synchrony varies within and among species exposed to different environments.

In this thesis, I answer the following questions: How do different migration strategies influence spatial population synchrony? Are there differences between fast- and slow-lived species' spatial population synchrony that can be explained by the influence the environment has on their demographic rates? How do life history traits influence the effect of the environment on spatial population synchrony? To answer these questions, I investigate a suite of life history traits which dictate 1) the environments that different populations are exposed to via migration or dispersal and/or 2) how population dynamics are expected to respond to these environments based on life history traits linked to sensitivity of survival and fecundity, such as position on the fast-slow life history continuum. By investigating these questions, we can improve our general understanding of mechanisms causing variation in synchrony.

In ***paper I,*** I build a population dynamic model to simulate seasonal environments experienced during migration in combination with different migration tactics. I simulate the different complexities of seasonal migration to determine how they can impact spatial population synchrony. In ***paper II***, I build a stochastic population dynamic model to simulate how the strength of environmental noise acts on key vital rates to influence spatial population synchrony across life history traits in the presence of dispersal and demographic stochasticity. I model spatial population synchrony for different combinations of survival and fecundity parameters which represent slow- and fast-lived species and vary the strength of environmental noise acting on these vital rates. In ***paper III*** and ***paper IV***, I use European long-term monitoring data from birds and insects to investigate if species have certain life history traits that make them more sensitive to the environment and, consequently, more likely to have synchronized population dynamics (***paper III***). I then extend these findings in

paper IV to investigate how life history traits such as generation time and migration tactic can influence the environment's effect on spatial population synchrony.

The relationship between spatial population synchrony, life history traits, and correlated environmental conditions is complex: I find that environmental stochasticity experienced by a population may change across seasons and locations, and different species respond differently to the environment based on a suite of life history traits. In ***paper I,*** I first establish that for species that are seasonally migrant, spatial population synchrony can be strongly influenced by the environment experienced during the nonbreeding season. The degree of synchronization in population abundances depends on a variety of different components of migration, such as how populations migrate in relation to neighboring populations on the breeding ground, and how autocorrelated the environment on the nonbreeding ground is. Next, in ***paper II***, I show through simulation that variation in species' spatial population synchrony depends on the presence of dispersal and demographic stochasticity in a population, and how strong of an effect environmental noise has on individual vital rates. I also show that differences between life history traits do not follow a simple pattern and are not always going to be the same, but rather will depend on which parameter environmental noise is acting, and the strength of this environmental noise. In ***paper III*** and ***paper IV***, I link these findings to empirical examples and show e.g., that species with shorter generation times tend to be more synchronized than species with longer generation times (***paper III***, ***paper IV***), and short-distance migrants are more synchronized than long-distance migrants and resident species (***paper III, paper IV)***. Finally, I show that in some species, key life history traits influence the effect that the environment has on spatial population synchrony between populations (***paper IV)***. I show that bird species' responses to synchrony in the environment depends on generation time and movement propensity, whereas insect responses to synchrony in the environment do not depend on life history traits.

These results provide novel theoretical and empirical links between spatial population synchrony and species traits known to be of key importance for population dynamics. In this thesis, I show how species' traits can make them sensitive to environmental stochasticity and the effect that this has on spatial population synchrony. By constructing population models and using available long-term monitoring datasets, I demonstrate the importance of considering species' life history traits and the resulting different levels of sensitivity to the environment when determining a metapopulation's susceptibility to environmental variability. This is essential to understand species extinction risks under future environmental change and guide conservation and policy prioritization decision making. We can use this information to make broader predictions about species' likelihood to have synchronized dynamics based on what is known about their life histories.

Contents

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List of articles

This thesis contains the following articles:

I. **Martin, E. C.**, Hansen, B. B., Herfindal, I. & A.M. Lee. (2023) The role of seasonal migration in spatial population synchrony. *Ecology*, 104(11): e4158. https://doi.org/10.1002/ecy.4158

II. **Martin, E. C.,** Hansen, B. B., Herfindal, I. & A.M. Lee. Spatial population synchrony depends on relative impacts of environmental noise on different vital rates. *Manuscript*.

III. **Martin, E. C.,** Hansen, B. B., Lee, A. M., & I. Herfindal. (2023) Generation time and seasonal migration explain variation in spatial population synchrony across European bird species. *Journal of Animal Ecology*, 92, 1904–1918. https://doi.org/10.1111/1365-2656.13983

IV. **Martin, E. C.,** Hansen, B. B., Lee, A. M., & I. Herfindal. (2023) How do life history traits influence the environment's effect on population synchrony? Insights from European birds and insects. *Preprint*. bioRxiv doi: https://doi.org/10.1101/2023.09.08.556676

Declaration of contributions

Paper I

All authors were involved in developing the original idea for the study. ECM and AML led study conceptualization. AML developed model and code for the environmental field and dispersal function. ECM developed and coded the rest of the model and ran all simulations with input from AML. ECM wrote the original manuscript with input from AML, BBH, and IH. All authors contributed critically to the drafts and gave final approval for publication.

Paper II

AML and ECM developed the original idea for the study. AML provided theoretical computations for proportional survival calculations. ECM coded the model and ran all simulations with input from AML. ECM wrote the original manuscript with input from AML, BBH, and IH. All authors contributed critically to the drafts and gave final approval for publication.

Paper III

All authors were involved in developing the original idea for the study and designed the methodology. ECM led study design, collated, cleaned, and formatted data. ECM and IH provided code for analysis of data. ECM wrote the manuscript with contributions from IH, BBH, and AML. All authors contributed critically to the drafts and gave final approval for publication.

Paper IV

All authors were involved in developing the original idea for the study and designed the methodology. ECM led study design, collated, cleaned, and formatted data. ECM and IH provided code for analysis of data. ECM led the writing of the manuscript with contributions from IH, BBH, and AML. All authors contributed critically to the drafts and gave final approval for publication.

Introduction

Synchronized population dynamics

Species can be distributed throughout their range into multiple geographically distinct populations. Population abundances naturally fluctuate over time and space as part of normal population dynamics, influenced by various biotic (e.g., habitat) and abiotic (e.g., dispersal) mechanisms (MacArthur & Wilson, 1967, May, 1974, Lande et al., 2003). Spatial population synchrony is defined as the degree to which two or more populations have correlated fluctuations in their abundances (Bjørnstad et al., 1999, Liebhold et al., 2004). Understanding how different drivers impact these fluctuations across space is fundamental to the field of population ecology.

The spatial extent and magnitude of co-fluctuating dynamics among populations is integral to metapopulation viability. Highly synchronized populations have a higher risk of species-level extinction than populations which have lower levels of synchrony (Harrison & Quinn, 1989, Gilpin & Hanski, 1991, Burgman et al., 1993, Grenfell et al., 1995, Heino et al., 1997, Kendall et al., 2000), because if all local populations are synchronized in their dynamics, they may collectively face low abundance periods (Hanski, 2001). Asynchronous dynamics can enable high abundance populations to act as rescue patches with individuals dispersing to populations with lower abundances (Holland & Hastings, 2008, Gupta et al., 2017). Asynchronous fluctuations in population sizes across space can act as a buffer against regional extinction, and ultimately allow metapopulations to persist in a dynamic landscape through recolonizations compensating for local extinctions (Levins, 1970).

Spatial population synchrony was first introduced by Elton (1924) to describe and quantify spatially autocorrelated fluctuations in population abundances of snowshoe hares (*Lepus americanus*), lemmings (*Lemmus lemmus*), and lynx (*Lynx canadensis*). Both theoretical and empirical work on spatiotemporal fluctuations in population dynamics has since followed. Synchrony has been identified in a variety of taxa and is considered to be a common phenomenon across ecosystems and species including insects and lepidoptera, fish, small mammals, birds, and large mammals (Hanski et al., 1995, Ranta et al., 1995, Ims & Andreassen, 2000, Raimondo et al., 2004, Grøtan et al., 2005, Koenig, 2006, Jones et al., 2007, Sæther et al., 2007, Chevalier et al., 2014). While initial studies were focused on identifying the existence of spatial population synchrony in natural populations, more recent studies have focused on the work of untangling species-specific and geographic-specific mechanisms that are responsible for causing synchrony (e.g., Post & Forchhammer, 2002, Koenig, 2006, Mortelliti et al., 2015, Marquez et al., 2019).

Three possible causes of spatial population synchrony have emerged from the literature: With increased movement or dispersal, increased synchrony can occur as individuals from a population at high density move to a population with lower density, resulting in a smaller difference between the two populations (Ranta et al., 1995, Lande et al., 1999, Ripa, 2000, Abbott, 2011). The strength of the effect of dispersal on synchrony usually increases with increasing dispersal rate (Yang et al., 2022). Interactions of individuals can also synchronize populations through strong trophic interactions such as predator-prey dynamics. This can result in correlated predator dynamics causing correlation in the dynamics of their prey (Ims & Steen, 1990, Ims & Andreassen, 2000). Finally, shared spatially correlated environmental fluctuations can cause spatial population synchrony across populations in space (Elton, 1924, Moran, 1953). These three mechanisms impact both the mean spatial population synchrony and the relationship between synchrony and distance (i.e., scaling of synchrony; Kendall et al., 2000, Engen & Sæther, 2005), but there is also evidence that these mechanisms interact to produce different observed patterns in synchrony (Kendall et al. 2000).

Environment, life history traits, and spatial population synchrony

Spatially correlated fluctuation in the environment is considered to be the strongest driver of spatial population synchrony (Moran, 1953, Grenfell et al., 1995). The Moran effect is a realization of Moran’s theorem, which states that given the same density dependence, spatially separated populations are expected to show the same synchrony in their population dynamics as the synchrony in their environment (i.e., the Moran effect, Moran, 1953). In species with high spatial population synchrony, population parameters such as abundance and growth rate tend to be more correlated among closer locations than far ones (Koenig, 1999), because of the autocorrelation in the environment (Sæther, 1997, Lande et al., 1999, Ellis & Schneider, 2008). This pairwise temporal population synchrony in both population parameters and environmental correlation typically decreases with increasing distance between populations (Ellis & Schneider, 2008; Lande et al., 1999; Sæther, 1997). Environmentally driven spatial population synchrony has been observed across many taxa e.g., in birds synchronized by food availability and the North Atlantic Oscillation (NAO; Sæther et al., 2007), and in wild reindeer populations synchronized by rain-on-snow events and temperature (Post & Forchhammer, 2004, Hansen et al., 2019). Two commonly measured environmental variables that have previously been identified as important drivers of spatial population synchrony are temperature and precipitation (e.g., Post & Forchhammer, 2004, Koenig & Liebhold, 2016, Kahilainen et al., 2018, Dallas et al., 2020, Nicolau et al., 2022), with most results correlating increased synchrony in the environment with increased spatial population synchrony. These variables typically exhibit strong spatial synchrony that declines with distance (Koenig, 2002, Herfindal et al., 2022).

Species-specific responses to the environment complicate the relationship between spatial population synchrony and correlated environments as described by Moran. Different species exposed to the same environmental synchrony do not always exhibit the same degree of synchrony in their population fluctuations (e.g., Marquez et al., 2019). These different responses to the same environmental conditions are often attributed to life history traits that render different species more or less sensitive to changes in the environment (Tedesco & Hugueny, 2006, Chevalier et al., 2014, Hansen et al., 2020). Key life history traits such as e.g., a species' position on the fast-slow life history continuum (i.e., an organism's pace of life; Gaillard et al., 2005, Reif et al., 2010), or movement propensity (Howard et al., 2020) are expected to impact a species' sensitivity to the environment. Despite the potential consequences for population resilience and the importance for conservation, we are still largely lacking a good understanding of which traits make one species more likely to exhibit synchrony over another and how these traits interact with other common drivers of synchrony (e.g., dispersal and demographic stochasticity). Evaluating synchrony in population dynamics of different species exposed to the same environmental synchrony allows us to understand the role of life history traits in regulating spatial population synchrony. Investigating whether there is a relationship between contrasting life histories—and associated sensitivities to shared environments—with variation in spatial population synchrony is an important next step in understanding causes and implications of such synchrony.

Some elements of the environment (e.g., temperature) are expected to change through time under future climate change (Post & Forchhammer, 2004, Di Cecco & Gouhier, 2018). Climate change is a major threat to all wildlife populations, and species extinctions are on the rise (Møller et al., 2004, Ceballos et al., 2017, Davis et al., 2018). Scenarios of global climate change predict increased variability in weather, which can have notable impact on spatial population synchrony (Post & Forchhammer, 2004, Allstadt et al., 2015, Hansen et al., 2020). This may promote large-scale fluctuations and magnify spatial population synchrony for species that have traits rendering them more sensitive to the environment (Post &

Forchhammer, 2004, Koenig & Liebhold, 2016). Therefore, predicting species-specific responses to environmental changes is crucial for mitigating climate change impacts and aiding conservation prioritization decisions for vulnerable species. Understanding how life history traits interact with the environment to drive spatial population synchrony is vital to be able to predict different species' responses, and consequently their susceptibility to, these inevitable changes.

Research objectives

In this thesis, I aim to improve our understanding of how spatial population synchrony varies with life history traits and movement such as migration. I use theoretical and empirical methods to investigate a suite of traits that determine the environments that different populations are exposed to via migration or dispersal (***paper I, paper II, paper III, paper IV***). I also investigate how population dynamics are expected to respond to environmental conditions based on traits linked to sensitivity to the environment, such as position on the fast-slow life history continuum (***paper II, paper III, paper IV***).

The specific questions I address in this thesis are as follows:

1. How do different migration strategies influence spatial population synchrony (***paper I, paper III, paper IV***)?
2. Are there differences between fast- and slow-lived species' spatial population synchrony that can be explained by sensitivity in their demographic rates to the environment (***paper II, paper III, paper IV***)?
3. How do life history traits influence the environment's effect on spatial population synchrony (***paper IV)***?

Methods

In this thesis, I use theoretical and empirical methods to investigate the posed research questions. In ***paper I*** and ***paper II***, I build population models to simulate the effects of movement and demographic parameters on spatial population synchrony. Population-level responses to the environment are often complicated and masked by other stochastic processes that occur naturally (e.g., strength of density dependence, compensatory dynamics; Hansen et al., 2020). By simulating population dynamics, these noisy stochastic processes can be controlled and the real effects of parameter perturbations more cleanly explored. Therefore, theoretical work provides a suitable approach to fill in the existing empirical gap. Furthermore, many life history traits are complex and have proven difficult study in the wild. For example, traits related to movement such as migration, or sensitivity to seasonal environments are particularly challenging to study because they require monitoring of a species throughout its annual cycle. There are immense logistic and collaborative challenges to studying populations across their complete annual cycle in a systematic and long-term monitoring program (Bowlin et al., 2010), because these efforts require time, standardized survey methods (Marsh & Trenham, 2008) , and financial commitment (Caughlan & Oakley, 2001).

In ***paper III*** and ***paper IV***, I use empirical examples to show how different life history traits impact spatial population synchrony, and how they influence the environment's effect on spatial population synchrony. Spatial population synchrony calculation is data intensive and requires multiple-occasion surveys conducted systematically over distinct geographic locations in order to correlate abundance or growth rate fluctuations over time. Despite the challenges of monitoring a species throughout its annual cycle, there exist long-term monitoring programs established to collect abundance data for both birds and insects on their breeding grounds throughout Europe (Nadeau et al., 2017, Sevilleja et al., 2020, Brlík et al., 2021). Such long-term monitoring datasets allow us to identify not just synchrony as it is occurring, but also its drivers. Birds and insects are useful study species because of the history of long-term monitoring on their breeding grounds (Nadeau et al., 2017), and they are well-suited to a large interspecific study given their wide breadth of life history traits related to foraging behavior, survival, mobility, and reproduction (Jones et al., 2007, Shirey et al., 2022). These species are generally widely distributed, making it possible to study the same species spread out in space across areas with varying degrees of environmental synchrony (Jones et al., 2007).

Theoretical model

Here, I give a brief overview of the steps in one annual cycle of the dynamic population models used to simulate abundances of spatially separated populations through time. More details of the models can be found in ***paper I*** and ***paper II***.

When simulating migratory populations in ***paper I,*** the annual cycle in the population model consisted of four steps: dispersal (1), survival (2), and reproduction (3) on the breeding ground, and nonbreeding season survival (4). All populations were on a shared spatial field where there was spatially autocorrelated environmental noise causing populations closer together in space to experience more similar environmental conditions (i.e., causing a Moran effect; Moran, 1953). On this shared spatial field, individuals went through steps one through three of the population model (i.e., dispersal, survival, and reproduction). Populations could then remain on the same breeding ground as residents or migrate to one of several nonbreeding grounds during the "nonbreeding season". During this nonbreeding season, individuals experienced the effects of a second, different environment on survival, which represented either 1) the nonbreeding season spent on the breeding ground (residents) or 2) the nonbreeding season spent away from the breeding ground (migrants). This environment was spatially autocorrelated, as on the breeding ground, but also was governed by a parameter which allowed the environment to covary between different nonbreeding grounds.

In ***paper II***, the annual cycle in the stochastic population model consisted of three steps: survival (1), dispersal (2), and reproduction (3). Populations were nonmigratory and were subject to one environmental field with consistent variance and scaling. Like in *paper I*, all populations were on a shared spatial field with spatially autocorrelated environmental noise. Survival and reproduction were directly influenced by this environmental noise. I modeled combinations of survival and fecundity parameters which represented slow- and fast-lived species and varied the weighted effect of environmental noise acting on these vital rates. Variation in the weighted effects of this noise on vital rates represented how strong the environment was when acting on a given vital rate. I ran all parameter combinations in the presence of dispersal and/or demographic stochasticity. In both papers, I calculated spatial population synchrony (ρ) as the mean of Pearson's correlations between pairs of population abundances at given distances at the end of the breeding season.

Empirical analyses

In the first empirical analysis (***paper III***), I used data to explore the implications of two key life history traits—generation time and migration tactic—for spatial population synchrony across bird species from four countries in Europe. Population abundance data for breeding birds came from four long-term monitoring programs in Norway, Sweden, Switzerland, and the United Kingdom. Data from these countries were publicly available for download (Norway, Sweden), or free to use with data sharing agreements (Switzerland, United Kingdom). I classified each species along the fast-slow life history continuum using generation time as a proxy (Bird et al., 2020), and classified each species within each country as a resident, short-distance migrant, or long-distance migrant (Eyres et al., 2017). I calculated the mean spatial population synchrony between log-transformed population growth rates or log-transformed abundances for each species and country separately. To quantify the contribution of generation time and seasonal migration tactic to spatial population synchrony, I used linear mixed models.

In the second empirical analysis ***(paper IV)***, I extended findings from *paper III* to investigate how life history traits influenced the environment's effect on spatial population synchrony in birds and insects using abundance data from eleven long-term monitoring programs located across eight countries: Finland, France, Ireland, Netherlands, Norway, Sweden, Switzerland, and the United Kingdom. I extracted mean summer temperature and precipitation values for all survey locations included in the spatial population synchrony analysis. I characterized each bird or insect species using a range of species-specific traits: position on the fast-slow life history continuum (generation time for birds, voltinism for insects), movement propensity (migratory tactic for birds, months in flight for insects), and specialist/generalist species (dietary diversity for birds and larval dietary breadth for insects). Using the same methods as in *paper III*, I calculated the mean spatial population synchrony between log-transformed population growth rates for each species and country separately and quantified the contribution of life history traits and environmental covariates (temperature and precipitation) to spatial population synchrony using linear mixed models.

Summary of papers

Paper I: The role of seasonal migration in spatial population synchrony

The synchronizing effect of the environment is one of the strongest drivers of spatial population synchrony and causes populations closer together in space to be more synchronized than populations further from one another (Lande et al., 1999, Liebhold et al., 2004). Most theoretical and empirical understanding of this driver considers sedentary (i.e., resident) species. For migratory species, however, the degree of spatial autocorrelation in the environment may change across seasons and vary by their geographic location along the migratory route or on a nonbreeding ground, complicating the synchronizing effect of the environment. Migratory species are typically exposed to different environments throughout their annual cycle, either due to seasonal environmental variation or seasonal migration, i.e. the regular and reversible individual movement between locations across seasons, most commonly between a breeding ground and a nonbreeding ground (Somveille et al., 2015, Webster et al., 2015). Migratory species have a variety of different strategies in how they

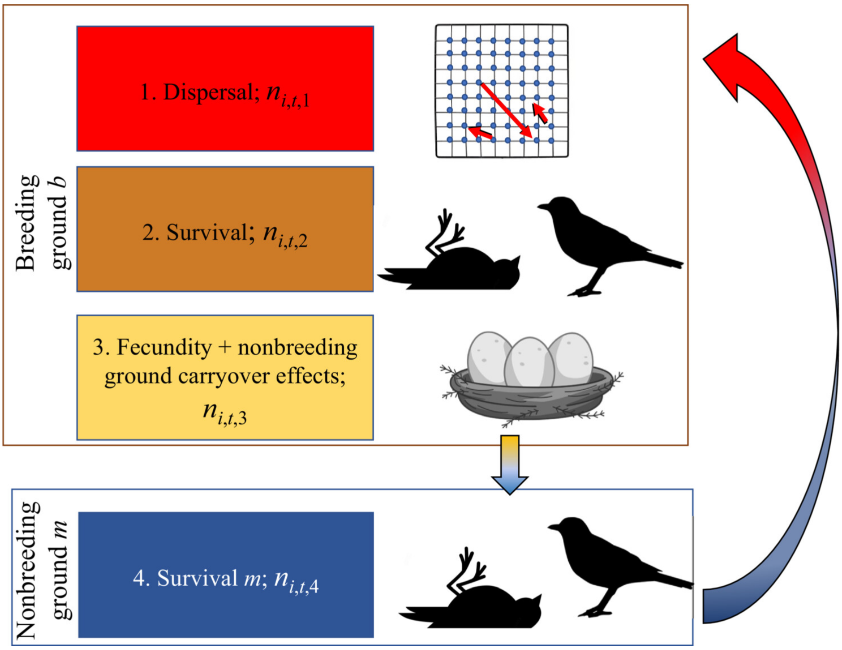

Figure 1: Schematic representing one annual cycle t for migratory populations. Populations are on one shared breeding ground b, where there is an environmental field in which populations closer together in space experience more similar environmental conditions. Here, individuals experience (1) a probability to disperse to other populations via a distance kernel, (2) a survival probability, and (3) a reproduction probability. Populations then (4) migrate to the nonbreeding ground m or remain on the breeding ground b (not shown), where they experience another survival probability. For migrants, the environment can vary between nonbreeding grounds. The abundances $n_{i,t,4}$ are passed back to breeding ground b at the beginning of the next annual cycle $t+1$.

disperse to and aggregate on nonbreeding grounds (Newton, 2008, Bairlein, 2013, Burgess et al., 2020). Depending on the sensitivity to environmental conditions off the breeding grounds, we can expect that migration and overwintering strategies will impact the spatial pattern of population synchrony on the breeding grounds.

In this paper, I used population dynamic modelling and simulations to disentangle the relationship between spatially correlated environmental conditions, migration tactics, and spatial population synchrony (Figure 1). To compare different migration tactics, I simulated three scenarios: 1) No migration, where individuals remained resident on the breeding ground for the entire annual cycle. 2) Individuals migrated to the same nonbreeding ground as their near neighbors. 3) Individuals migrated randomly, where each population had an equal probability of migrating to one of several nonbreeding grounds. The number of nonbreeding grounds to which populations could migrate varied and how similar the nonbreeding ground environments were by to one another varied.

The effects on synchrony of environmental autocorrelation experienced off the breeding ground depended on the number and size of nonbreeding grounds, and how populations migrated in relation to neighboring populations. When populations migrated to multiple nonbreeding grounds, synchrony increased with increasing environmental autocorrelation between nonbreeding grounds. Populations that migrated to the same place as near neighbors had higher synchrony at short distances than populations that migrated randomly. However, synchrony declined less across increasing distances for populations that had a random migration tactic. The differences in synchrony between migration strategies were most pronounced when the environmental autocorrelation between nonbreeding grounds was low.

In this paper, I showed that when attempting to link levels of synchrony to environmental variables, season-specific variability must be analytically accounted for. The simple relationship described by Moran (1953) between autocorrelation in the environment and spatial population synchrony does not account for seasonally changing environmental autocorrelation that most species experience through migration. These results show the importance of considering migration when studying spatial population synchrony and predicting patterns of synchrony and population viability. Climate change and habitat loss and fragmentation may cause range shifts and changes in migratory strategies (Crick, 2004, Robinson et al., 2008), as well as changes in the mean and spatial autocorrelation of the environment, which can alter the scale and patterns observed in spatial population synchrony (Hansen et al., 2020). The results presented here help to understand the consequences of environmental change on population dynamics for migratory species and can be used to understand how susceptible to extinction populations of migrating species are given where and how they migrate and the expected scaling of environmental changes.

Paper II: Spatial population synchrony depends on relative impacts of environmental noise on different vital rates

Spatially correlated fluctuations in the environment act on demographic parameters to cause spatial population synchrony. Different species can exhibit different degrees of spatial population synchrony when exposed to the same environmental fluctuations (Engen & Sæther, 2005, Sæther et al., 2007). Theoretical and empirical work has shown that a species' spatial synchrony can depend on how its life history strategy interacts with the environment, suggesting that spatial population synchrony can be influenced by key demographic processes (i.e., survival, reproduction, dispersal, and demographic stochasticity) across species. It is likely that in the presence of environmental noise, different species' demographic processes have non-identical influences on synchrony, but we lack understanding of how these processes collectively impact spatial population synchrony and vary across species.

Many differences in demographic processes between species, including spatial population synchrony, have be explained by a species' position on the fast-slow life history continuum (Gaillard et al., 1989, Marquez et al., 2019). The axis of this continuum ranges from fast-reproducing, short-lived species at one end (i.e., fast-lived) to slow-reproducing, long-lived species at the other (i.e., slow-lived; Gaillard et al., 1989, Stearns, 1999). Empirical studies have identified several patterns in spatial population synchrony across the fast-slow life history continuum (Jones et al., 2007, Chevalier et al., 2014, Marquez et al., 2019), e.g., synchrony of slow-lived species that disperse tends to be higher for populations at far distances than synchrony of fast-lived species that disperse (Marquez et al., 2019).

In this paper, I build a stochastic population dynamic model to investigate the key demographic processes driving synchrony and understand how they collectively influence synchrony for species with different life history traits. Specifically, I simulate how different weights of environmental noise act on vital rates to influence spatial population synchrony in the presence or absence of dispersal and demographic stochasticity. I model spatial population synchrony for different combinations of survival and fecundity parameters which represented slow- and fast-lived species and varied the weight of environmental noise acting on these parameters to determine the sensitivity of spatial population synchrony.

I found that variation in spatial population synchrony between life history traits depends on the presence of dispersal and demographic stochasticity, and how strong of an effect environmental noise has on individual vital rates. Differences in synchrony between life history traits are not simple and are not always going to be the same, but rather will depend on which parameter environmental noise is acting and the strength of the environmental noise: I ultimately show that different combinations of demographic processes can result in different patterns of synchrony for fast- and slow-lived species. Differences in models which included only demographic stochasticity or both demographic stochasticity and dispersal were related environmental noise, with fast-lived species' synchrony more influenced than slow-lived species' synchrony to environmental noise acting on fecundity, while slow-lived species' synchrony was more influenced to environmental noise acting on survival.

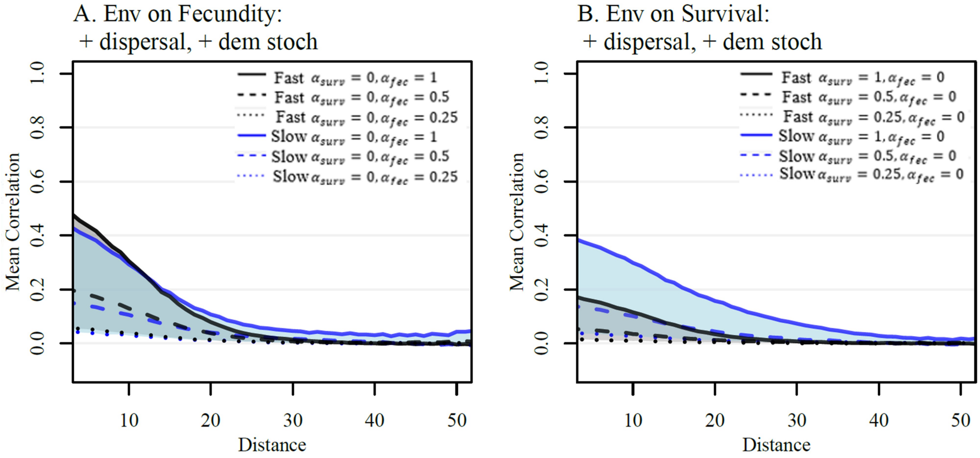

Figure 2: The effect on spatial population synchrony of variation in the weight of environmental noise acting on fecundity (A) and survival (B) in models including dispersal and demographic stochasticity. Fast- (black) and slow-lived (blue) species' ranges of spatial population synchrony are indicated with shading.

Detecting species-specific responses to environmental noise in wild populations is difficult, yet it is a critical component of successful conservation action (Davidson et al., 2012). The pattern I have shown in this paper between life history traits, vital rate responses to correlated environmental noise, and spatial population synchrony is an important step in understanding how future changes to environmental conditions will affect population dynamics. I show how a relatively simple stochastic population model can be used to investigate different processes driving spatial population synchrony through a series of simulations. I show that life history information can be used to identify vital rates that most influence spatial population synchrony under scenarios including dispersal and demographic stochasticity, and suggest that understanding these elements in interaction is key for understanding species' vulnerability to correlated environmental conditions.

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

Spatial population synchrony is common among populations of the same species and is an important predictor of extinction risk (Heino et al., 1997). 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. Generally, environmental conditions shared in space can explain the extent of synchrony, with populations that are closer together in space experiencing more similar fluctuations in their environments than those populations that are further apart (Moran, 1953). However, the same species exposed to the same environmental conditions do not always exhibit the same spatial population synchrony. The relative importance of environmental stochasticity for population dynamics is strongly linked to species' life history traits, such as pace of life, which may impact population synchrony (Sæther & Bakke, 2000). For populations that migrate, there may be multiple environmental conditions at different locations driving synchrony. In this paper, I explored the importance of life history and migration tactics in determining patterns of spatial population synchrony and species' responses to correlated environments.

I used population abundance data on breeding birds from four countries to estimate spatial population synchrony in population growth rate and abundance. I investigated differences in synchrony across generation times in resident ($n = 67$), short-distance migrant ($n = 86$), and long-distance migrant ($n = 39$) bird species. The highest ranked models suggested that spatial population synchrony decreased with increasing generation time both for population growth rate and abundance (Figure 3). Short distance migrants in general had the highest synchrony, followed by resident species, and finally long-distance migrants. 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.

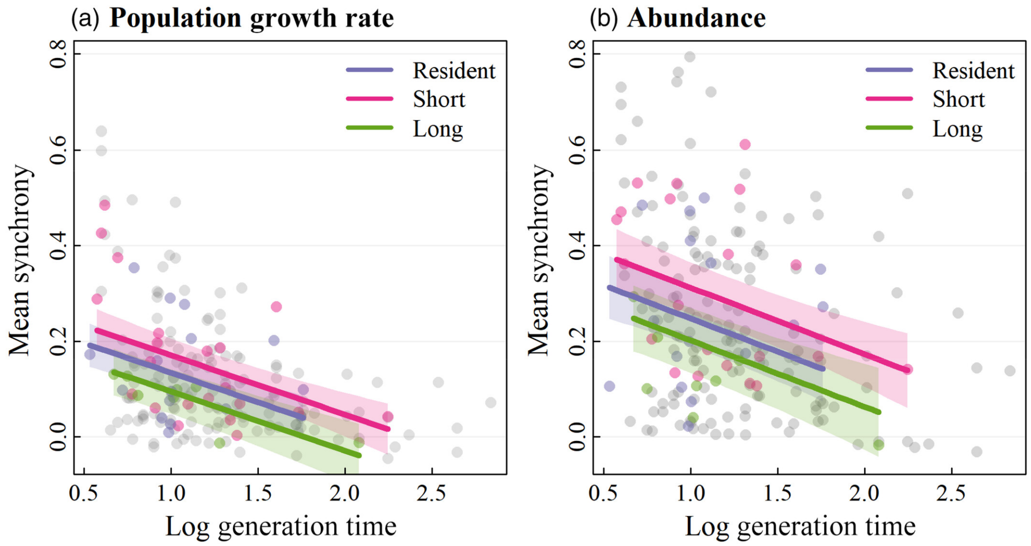

Figure 3: The effects of log generation time and migration tactic on mean synchrony (*i.e.* pairwise correlation) in (a) log population growth rate and (b) log abundance. Data for Switzerland in color, all other countries in grey. Slopes are predicted for Switzerland from the top performing model: Country + Migration Tactic + Log Generation Time. 95% confidence intervals presented as shaded colors.

These 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. I show how life history traits can be used to understand species-specific causes of variation spatial population synchrony. The higher spatial population synchrony identified for European short-distance migrant species and fast-lived species should alert managers to the susceptibility of these populations to stochastic events on shared breeding or nonbreeding grounds. Given their higher synchrony and known sensitivities to environmental stochasticity, these nonmigratory or short-distance migrants' population dynamics are expected to be more susceptible to anthropogenic or climatically induced changes in environments. 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.

Paper IV: Population synchrony across European birds and insects: do effects of environmental synchrony depend on life history traits?

Environmental conditions affect population dynamics by influencing reproductive success (Andreasson et al., 2020), survival rates (Jones et al., 2007, Hansen et al., 2013, Clarke, 2017), immigration, and emmigration rates (Pärn & Sæther, 2012). The two most commonly measured environmental variables that have been identified as important drivers of spatial population synchrony are temperature and precipitation (e.g., Post & Forchhammer, 2004, Koenig & Liebhold, 2016, Kahilainen et al., 2018, Dallas et al., 2020, Nicolau et al., 2022), with most results correlating increased synchrony in these environmental variables with increased spatial population synchrony. Temperature and precipitation typically exhibit strong spatial synchrony that declines with distance (Koenig, 2002, Herfindal et al., 2022). Moran's theorem states that spatially distinct populations of the same species are expected to show the same synchrony in their population dynamics as the synchrony in their environment (Moran, 1953), however, this is rarely the case in the wild. These species-specific variations can be due to life history traits that make some species more susceptible to environmental stochasticity, such as reduced mobility or faster pace of life (***paper III***; Tedesco & Hugueny, 2006, Chevalier et al., 2014). In this study, I extend findings from ***paper III*** to investigate if the effects of synchrony in specific environmental variables depend on life history traits.

I compiled long-term annual abundance datasets on European birds and insects (*Lepidoptera* sp. and *Bombus* sp.), mean monthly temperatures, and mean monthly precipitation for all surveyed sites. I characterized each bird or insect species using a range of species-specific traits: position on the fast-slow life history continuum (generation time for birds, voltinism for insects), movement propensity (migratory tactic for birds, months in flight for insects), and specialist/generalist species (dietary diversity for birds and larval dietary breadth for insects). I used linear mixed models on bird and insect data separately to determine if there was an effect of environmental synchrony on spatial population synchrony across species, while accounting for life history traits. I included models in the model set that included an interaction between the environmental covariate and life history traits to determine if species had different responses to environmental synchrony depending on trait differences.

As expected, the environment was a synchronizing factor for both birds and insects, as increasing spatial synchrony in precipitation and temperature had a positive effect on synchrony in annual population growth rates. Birds were more strongly synchronized by temperature, while precipitation was a stronger driver of synchrony in insects. For birds, there was strong support for an effect of environmental synchrony on population synchrony, and this synchronizing effect of the environment depended on life history traits. For birds, effects of synchrony in the environment depended on generation time and movement propensity, with a positive impact found only for short generation times (i.e., species with "fast" life histories) and for resident and short-distance migration species (Figure 4). For insects, movement propensity and dietary niche breadth influenced annual population synchrony but did not modify the effects of synchrony in the environment.

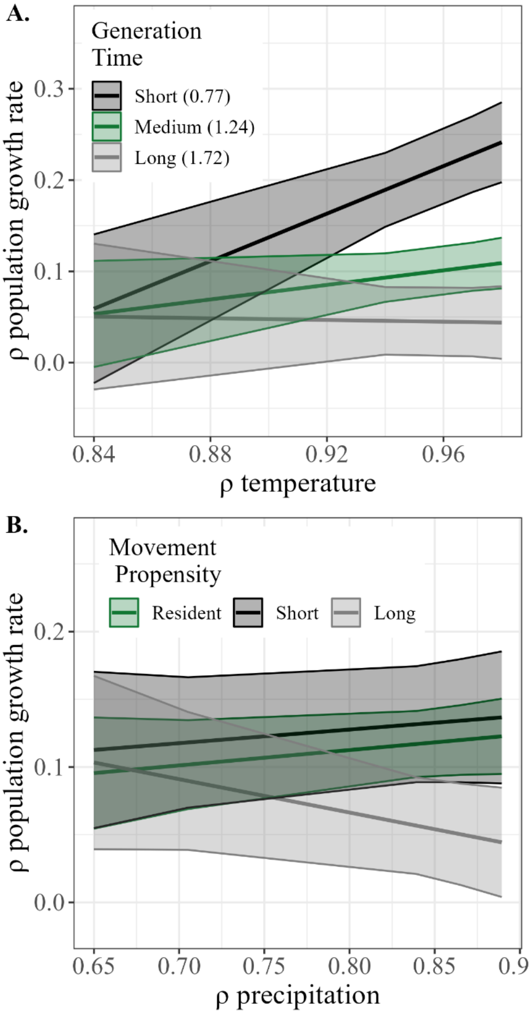

Figure 4: Effects of environmental variables and life history trait covariates included in top models for birds. A) Synchrony in temperature and generation time in birds. B). Synchrony in precipitation and movement propensity in birds.

In this paper I have documented the same effects of the environment in two quite different taxonomic groups, indicating general patterns relevant at large scales. Our study provides empirical support for the prediction that spatial population dynamics are more influenced by environmental stochasticity for life histories with lower mobility and faster pace of life, but only in birds. By quantifying spatial population synchrony across different levels of environmental synchrony and accounting for an interaction with life history traits, our study informs effective conservation strategies and improves our understanding of the factors that drive population persistence in the face of environmental change.

Discussion & Future Directions

By constructing population-dynamic models and using available long-term monitoring datasets, I have disentangled some of the complex mechanisms that cause variation in spatial population synchrony. This work emphasizes the importance of considering different species' life history traits when determining a metapopulation's susceptibility to environmental conditions, and ultimately, its probability of extinction. Overall, theoretically and empirically I have identified life history traits or environmental conditions that make species more likely to be synchronized (***paper I, paper II, paper III, paper IV***). I show how spatial population synchrony can be more influenced by the environment acting on different vital rates of species across the fast-slow life history continuum (***paper II, paper III, paper IV***). For species which migrate or move, I highlight how considering the seasonal environments experienced during the nonbreeding season is important for predicting spatial population synchrony (***paper I, paper III, paper IV***). This thesis also shows that, for some species, life history traits and environmental covariates interact (***paper IV***).

The conclusions and generalizations from this work are likely applicable across a wide variety of species and environments. For the theoretical analysis, an important consideration is that the conclusions are not species-specific. For a wide variety of species with a suite of life history traits that position it as a fast- or slow-lived species, I show how spatial population synchrony is expected to change under various scenarios (e.g., in the presence of dispersal, demographic stochasticity, and environmental effects on vital rates). Similarly, the results from the migration simulation are applicable across taxa, as the patterns explored are not limited to just avian migration, for example. In application, these conclusions should be the same regardless of if the suite of life history traits in question represent a bird, insect, or mammal. The results from the empirical analysis are also generalizable across species – I show that the same trend in spatial population synchrony and generation time was found across countries which span large geographic and environmental gradients across Europe. The same effects of synchrony in the environment were evident in two different taxonomic groups, indicating general patterns relevant at large scales.

There are many possible next steps to continue investigating mechanisms causing spatial population synchrony through both the population models developed and using the datasets compiled. First, given its construction, the theoretical population model can allow deeper exploration of the effect of changing environmental variance in addition to the strength of the environment and the impact of these parameters on synchrony. Parameters built into the model but not explored in this thesis are numerous: For example, a carryover effect from the overwintering season, variation in generation time, or differing sensitivity of wintering and summer environmental conditions. Furthering the investigations into different characteristics of migration and the impact on spatial population synchrony could also be an interesting next step. Through simulations, it can be possible to answer questions such as: How is synchrony altered if migratory species are more affected by the environment on their nonbreeding grounds, and what is the effect on synchrony of partial migration? There are many yet unexplored questions surrounding the causes of spatial population synchrony that this model can be used to explore theoretically. Further empirical work can also be done from the datasets I have compiled to answer questions surrounding life history traits and spatial population synchrony. Expanding beyond birds and insects to see if the patterns identified herein can be identified in other taxa is a logical next step. Expanding geographically to include other long-term monitoring data globally could help crystallize the relationships identified in European data used in this thesis and determine how generalizable patterns are across taxa and if they are applicable globally.

These findings fill a knowledge gap in the literature on spatial population synchrony and identify pattens that can be used to better predict how synchronized species dynamics are expected to be given their life history traits and the environments they are in. Generalizations in ecology are crucial for understanding and predicting ecological patterns and processes (Evans et al., 2013). They allow researchers to draw broad conclusions from specific studies and apply findings to a wider range of ecosystems and species, guiding conservation efforts and management strategies for vulnerable species. Climate change and other environmental challenges are intensifying, making the need for reliable generalizations increasingly critical. Most species are not intensively monitored, so either leveraging existing long-term monitoring data representative of multiple taxa and life history traits or simulating population dynamics as done here in this thesis allows us to draw conclusions about similar, but less-studied species. The patterns identified in this thesis serve as powerful tools and provide a foundation for further research and exploration in a time where data for most species are limited and conservation action is needed.

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ARTICLE

The role of seasonal migration in spatial population synchrony

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Abstract

Spatially synchronized population dynamics are common in nature, and understanding their causes is key for predicting species persistence. A main driver of synchrony between populations of the same species is shared environmental conditions, which cause populations closer together in space to be more synchronized than populations further from one another. Most theoretical and empirical understanding of this driver considers resident species. For migratory species, however, the degree of spatial autocorrelation in the environment may change across seasons and vary by their geographic location along the migratory route or on a nonbreeding ground, complicating the synchronizing effect of the environment. Migratory species show a variety of different strategies in how they disperse to and aggregate on nonbreeding grounds, ranging from completely shared nonbreeding grounds to multiple different ones. Depending on the sensitivity to environmental conditions off the breeding grounds, we can expect that migration and overwintering strategies will impact the extent and spatial pattern of population synchrony on the breeding grounds. Here, we use spatial population-dynamic modeling and simulations to investigate the relationship between seasonal environmental autocorrelation and migration characteristics. Our model shows that the effects of environmental autocorrelation experienced off the breeding ground on population synchrony depend on the number and size of nonbreeding grounds, and how populations migrate in relation to neighboring populations. When populations migrated to multiple nonbreeding grounds, spatial population synchrony increased with increasing environmental autocorrelation between nonbreeding grounds. Populations that migrated to the same place as near neighbors had higher synchrony at short distances than populations that migrated randomly. However, synchrony declined less across increasing distances for the random migration strategy. The differences in synchrony between migration strategies were most pronounced when the environmental autocorrelation between nonbreeding grounds was low. These results show

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the importance of considering migration when studying spatial population synchrony and predicting patterns of synchrony and population viability under global environmental change. Climate change and habitat loss and fragmentation may cause range shifts and changes in migratory strategies, as well as changes in the mean and spatial autocorrelation of the environment, which can alter the scale and patterns observed in spatial population synchrony.

KEYWORDS
demography, environmental autocorrelation, environmental change, Moran effect, population-dynamic model, seasonal dynamics, spatial ecology

INTRODUCTION

Spatial autocorrelation in environmental variability is one of the main drivers of spatial population synchrony, that is, the correlated fluctuation of population sizes in different locations (the Moran effect; Moran, 1953; Royama, 1992). Identifying population synchrony and its causes is key for predicting species persistence because population synchrony can inhibit recovery from low abundance periods because of a lack of dispersal and rescue effects, which has implications for population-level management strategies (Engen et al., 2002; Hanski, 1989; Heino et al., 1997; Liebhold, Sork, et al., 2004). Understanding the environmental drivers of synchrony is important for predicting how spatial population synchrony and regional extinction probability will change with continued environmental change. For instance, climate change is affecting the mean, spatial autocorrelation, and variability of weather. These changes make the relationship between climate and population dynamics less predictable (Di Cecco & Gouhier, 2018; IPCC, 2022). There has been progress in identifying the environmental drivers of species-specific synchrony across taxa (e.g., in *Lepidoptera* [Tack et al., 2015], mammals [Grenfell et al., 1995], and birds [Sæther et al., 2007]; see review in Bjørnstad et al., 1999). However, most of these studies only consider environmental conditions on the breeding ground. For migratory species, the degree of spatial environmental autocorrelation among populations may change across seasons and vary by their location along the migratory route, complicating the synchronizing effect of the environment.

The synchronizing effect of the environment is the strongest driver of spatial population synchrony (Liebhold, Koenig, & Bjørnstad, 2004). The Moran theorem states that populations with the same density dependence will have the same correlation in abundance as the correlation in their environmental stochasticity (Moran, 1953). Populations that are closer together in space experience more correlated fluctuations in the environment and therefore tend to have higher population synchrony than populations that are further apart (Ellis & Schneider, 2008; Lande et al., 1999; Liebhold, Koenig, & Bjørnstad, 2004; Sæther, 1997). Because climate change and habitat loss and fragmentation influence spatial environmental autocorrelation (Allen & Lockwood, 2021; Koenig & Liebhold, 2016), efforts to understand environmentally driven synchrony and its patterns in space and time have seen renewed interest in recent years. Current theoretical and empirical understanding of patterns of spatial population synchrony mainly considers sedentary populations. However, species are typically exposed to different environments throughout their annual cycle, either due to seasonal environmental variation or seasonal migration, that is, the regular and reversible individual movement between locations across seasons, most commonly between a breeding ground and a nonbreeding ground (Somveille et al., 2021; Webster et al., 2002). It is well documented how environmental conditions on the breeding ground impact population dynamics in general (e.g., Humphrey, 2004; Imlay et al., 2018; Newton, 2008), but less is known about the direct and indirect effects (i.e., carry-over effects) of environmental conditions experienced on nonbreeding grounds and the impact these conditions have on overall population growth rates and large-scale population dynamics (Dingle, 1996; Selonen et al., 2021; Webster et al., 2002).

Seasonal migration is complex, with large interspecific and intraspecific variations in characteristics (Bell, 2005; Dingle, 1996). 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). For example, in some species, all populations from the breeding ground migrate to one shared nonbreeding ground, where they are densely aggregated in a shared environment with high interpopulation mixing (Bell, 2005; Finch et al., 2017). This type of telescopic migration (Salomonsen, 1955), where

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populations are spatially structured independently on the breeding ground but aggregate during the nonbreeding season, is documented to occur across the animal kingdom (e.g., songbirds species [Beauchamp, 2011; La Sorte et al., 2016], wildebeest [*Connochaetes taurinus*; Mduma et al., 1999], and elk [*Cervus elaphus*; White et al., 2010]), notably with longer-distance migrants (Beauchamp, 2011; La Sorte et al., 2016). Conversely, populations on a shared breeding ground may migrate to many nonbreeding grounds, yielding a lower degree of interpopulation mixing and lower migratory connectivity (Finch et al., 2017; Gilroy et al., 2016). Such differentiated nonbreeding grounds are common in species of butterflies (e.g., *Danaus plexippus*; Chowdhury et al., 2021) and some birds (Lemke et al., 2013). Furthermore, how populations of the same species migrate in relation to neighboring populations on the breeding ground (i.e., "departure strategy") also varies among species (Newton, 2008). Some species migrate to the same place as neighboring populations on the breeding ground (Newton, 2008), whereas others migrate away from shared breeding grounds randomly, for example, along flyway margins when there are geographic obstacles, that is, migratory divides, preventing near neighbors from migrating to the same place (La Sorte et al., 2016). We do not yet know how migration characteristics and environmental stochasticity together impact synchrony.

In this paper we have studied the influence of migration characteristics on spatial population synchrony by using spatial population-dynamic modeling and simulations to investigate the relationship between environmental autocorrelation, migration characteristics, and spatial population synchrony. We expected synchrony to be higher when the strength of the environmental autocorrelation outside of the breeding ground was high, and that migration characteristics mattered for determining the strength of spatial population synchrony. We expected different spatial patterns of synchrony for different migration strategies, and that this would be dependent on both the autocorrelation between nonbreeding grounds and the degree of environmental autocorrelation within each nonbreeding ground.

MODEL AND METHODS

Population model for annual cycle

We used a dynamic population model to simulate the abundance of spatially separated populations through time. Here, we give a brief overview of the four steps of the model and below go into greater detail about the individual steps. The annual cycle in the population model consists of four steps (Figure 1), as detailed below. The population model is used to simulate local population abundances $n_{i,t,s}$ (defined as a cluster of individuals located at a given point i) for $i = 1, 2, ..., f$, $s = 1, 2, ..., 4$, where i represents coordinates at the intersections of regular grid lines evenly distributed across a spatial grid, t is year, and s is a time step within the annual cycle. All populations are contained within the same spatial grid. The grid is composed of unique populations at each i coordinate at the intersections of grid lines.

In the first step, all populations are on a shared breeding ground where there is spatially autocorrelated environmental noise causing populations closer together in space to experience more similar environmental conditions. On this shared breeding ground, individuals can disperse among populations, survive or not, and reproduce. Populations then can remain on the same breeding ground as a resident or migrate to one of several nonbreeding grounds. Here, individuals experience the effects of a second, different environment on survival: either (1) the nonbreeding season spent on the breeding ground (residents) or (2) the nonbreeding season spent away from the breeding ground (migrants). The spatial autocorrelation on the nonbreeding ground is controlled by one parameter that sets the correlation in environmental conditions experienced by two random individuals within the same nonbreeding ground (r_{within}) and one parameter that sets the correlation in environmental conditions between two separate nonbreeding grounds (r_{between}). Each step of the population model is described in greater detail below.

Breeding ground dispersal

In the first model step, all individuals have a probability d of dispersing. Dispersal is assumed to be equally likely in all directions (i.e., it is isotropic) and the distance traveled follows a normal distribution in two dimensions, $\psi(|l - i|)$. The spatial scale of this distribution is defined as the standard deviation of dispersal distance in one direction when scaled to integrate into one (l_g; following Engen et al., 2018). Individual dispersers are distributed deterministically by the dispersal distribution. The expected abundance in each population after dispersal can then be expressed as:

$$n_{i,t,1} = (1 - d)\, n_{i,t-1,4} + d\left[\sum_{l \neq i} n_{l,t-1,4}\psi(|l - i|)\right], \qquad (1)$$

where the last term represents dispersal into point i from all other points in the grid. Note that in the simulations, probabilities of dispersing to a given point are scaled over all possible points in the grid.

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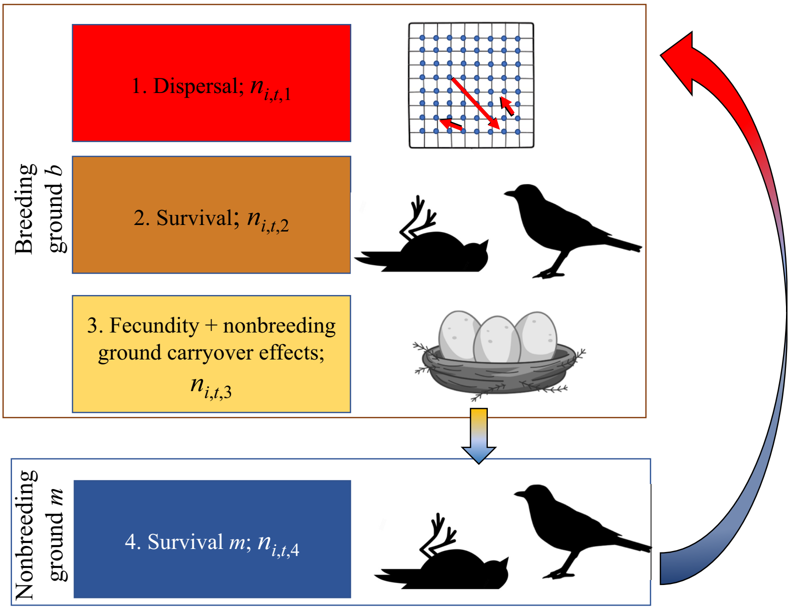

FIGURE 1 Schematic representing one annual cycle t for migratory populations. The annual cycle in the population model consists of four steps. Populations are on one shared breeding ground b, where there is environmental noise determined by an environmental field in which populations closer together in space experience more similar environmental conditions. Here, individuals experience (1) a probability to disperse to other populations via a distance kernel, (2) a survival probability, and (3) a reproduction probability. Populations then (4) migrate to the nonbreeding ground m or remain on the breeding ground b (not shown), where they experience another survival probability. For migrants, the environment can vary between different nonbreeding grounds. (3). The abundances $n_{(i,t,4)}$ are passed back to breeding ground b at the beginning of the next annual cycle $t+1$. Bird images taken from www.phylopic.org.

Breeding ground survival

In the second step of the model, abundances are updated by breeding ground survival as a function of mean survival (S_b) and realized environmental noise $(\xi_{i,t,b}$; see *Variation in environmental noise*). We use the logit distribution to ensure values between zero and one for the survival probability:

$$n_{i,t,2} = \left(\text{inv logit}\left[\text{logit}(S_b) + \xi_{i,t,b}\right]\right) \times n_{i,t,1}. \qquad (2)$$

Breeding ground fecundity

In the third step, offspring are produced from and added to the surviving adults from $n_{i,t,2}$. Fecundity is a function of mean fecundity (F_b) and realized environmental noise on the breeding ground $(\xi_{i,t,b}$; see *Variation in environmental noise*):

$$n_{i,t,3} = n_{i,t,2} + \left(\left(\exp\left[\log(F_b) + \xi_{i,t,b}\right]\right) \times n_{i,t,2}\right). \qquad (3)$$

Nonbreeding ground/overwintering survival

The fourth model step represents the nonbreeding season when populations are either (1) experiencing the nonbreeding season spent on the breeding ground (residents) or (2) experiencing the nonbreeding season spent away from the breeding ground (migrants). The abundances $n_{i,t}$ at this step is expressed as:

$$n_{i,t,4} = (\text{inv logit}[\text{logit}(S_m) + E_m + \nu(n_{i,t})]) \times n_{i,t,3}, \qquad (4)$$

where S_m is the nonbreeding ground/overwintering survival, E_m is the nonbreeding ground environmental noise (see *Variation in environmental noise*), and $\nu(n_{i,t})$ is a density-dependent term. For residents, the environmental noise term E_m is replaced by $\xi_{i,t,nb}$ the environmental noise experienced on the breeding grounds during the winter season). The density dependence is linear on the logit scale. On the nonbreeding grounds, populations are assumed to be clustered in space, such that migrants experience more similar environments than residents. At the end of this fourth

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time step, the abundances $n_{i,t,4}$ are passed back to Equation (1) as $n_{i,(t-1),4}$ to begin the annual cycle again.

Variation in environmental noise

On the breeding ground, environmental noise is captured by $\xi_{i,t,b}$ during the breeding season for both migrants and residents. Regardless of migration strategy, all populations are on the breeding ground simulated spatial field during the first three model steps and experience the same environmental noise. If populations do not migrate, they remain resident at the same location on the breeding ground simulated spatial field during the fourth step of the model. A second environmental noise parameter $(\xi_{i,t,nb})$ captures environmental noise on the breeding ground during the nonbreeding season for residents. These two environmental noise fields have an isotropic spatial distribution with a spatial scale l_e, defined as the standard deviation of the environmental correlation function in any given direction (when normalized to integrate to 1; following Lande et al., 1999) and variance σ^2. Realizations of the environmental noise fields are simulated according to the procedure described in Appendix S1.

If populations are migratory, they either all go to one common nonbreeding ground or they go to one of several nonbreeding grounds, depending on the simulated scenario. On the nonbreeding grounds at the fourth model step, populations experience environmental noise (represented as E_m) as a function of the correlation between nonbreeding grounds (r_{between}; only if populations migrate to >1 nonbreeding ground) and of correlation within each nonbreeding ground (r_{within}), depending on migration tactic. The nonbreeding ground environmental noise (E_m) depends on whether populations belong to the same migration route (r_{within}) or different migration routes (r_{between}), and is drawn from a multivariate normal distribution with a mean of zero. The within nonbreeding ground environmental autocorrelation (r_{within}) controls how similar the environment within one nonbreeding ground is for the populations that all migrate to the same place. The between nonbreeding ground environmental autocorrelation (r_{between}) controls how similar the environment in one nonbreeding ground is compared to the environment in another nonbreeding ground for populations which migrate to different places. The resulting environmental variation directly impacts survival at the fourth step of the model.

Model scenarios

Using the above stochastic population model, we simulated a grid of 150 by 150 populations (22,500 total populations) for 1000 complete annual cycles t with Python 3.9 (Van Rossum & Drake Jr., 1995). Abundances $n_{i,(0),4}$ were initialized at carrying capacity for all simulation runs. Parameters used in the population model were long-lived species (i.e., K-selected species; adult survival = 0.9, fecundity = 0.25) migrating to one, two, or four nonbreeding grounds. See Appendix S2: Table S1 for other parameter values and considerations.

The first 50 annual cycles were discarded as a burn-in period. At the end of each breeding season in the annual cycle, we saved the innermost 50 by 50 square populations of the grid to avoid edge effects. The resulting 1250 abundances per annual cycle represented a post-breeding census, a common metric used to estimate spatial population synchrony.

To compare different migration strategies, we simulated three scenarios: (1) No migration, where individuals remained resident on the breeding ground for all four time steps of the annual cycle. (2) Individuals migrated to the same nonbreeding ground as their near neighbors (i.e., proximity migration scenario, Figure 2A). For populations on the breeding grounds that had near neighbors that migrated to different nonbreeding grounds (e.g., populations on the border between two division points), we created buffer regions where population had an equal probability of migrating to either of the shared-border nonbreeding grounds (Figure 2A). (3) Individuals migrated randomly (Figure 2B), where each population had an equal probability of migrating to one of several nonbreeding grounds.

We varied the number of nonbreeding grounds to which populations could migrate from one to four. We varied how similar the nonbreeding ground environments were by changing the between nonbreeding ground environmental autocorrelation ($r_{\text{between}} = 0, 0.25, 0.50, 0.75, 1$). Finally, we ran the simulations with different within nonbreeding ground correlation ($r_{\text{within}} = 0, 0.25, 0.50, 0.75, 1$).

Quantifying synchrony

We calculated the spatial population synchrony (ρ) as the average of Pearson's correlations between pairs of population abundances $(n_{i,t,3})$ at given distances at the end of the breeding season.

RESULTS

Between nonbreeding ground environmental autocorrelation

As expected, resident species showed high synchrony at short distances with decreasing synchrony at increasing

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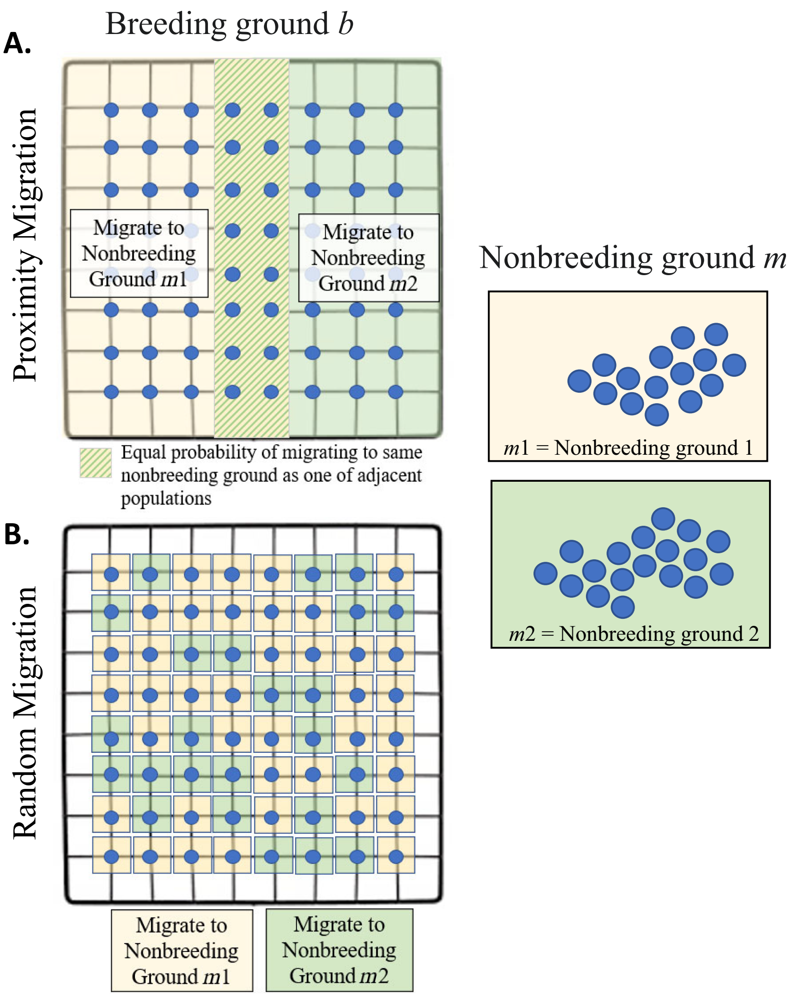

FIGURE 2 Schematic of (A) proximity and (B) random migration. Colors represent the different nonbreeding grounds to which populations migrate. (A) In proximity migration, each population migrates to the same nonbreeding ground as their near neighbors. The populations in the buffer region between nonbreeding grounds have an equal probability of migrating to one or the other nonbreeding ground. (B) In the random migration scenario, every population has an equal probability of migrating to each of the nonbreeding grounds.

distances (Figure 3). For migrant species, when all populations from the breeding ground migrated to the same nonbreeding ground, spatial population synchrony between populations at the breeding ground was high and decreased only slightly more than larger distances (Figure 3). When populations migrated to multiple nonbreeding grounds, spatial population synchrony increased with increasing environmental autocorrelation between nonbreeding grounds (r_{between}) (Figure 3). The decline in population synchrony with distance was more pronounced when nonbreeding grounds had less correlated environments between them.

Within nonbreeding ground environmental autocorrelation

For all migration strategies, average synchrony was not only determined by the environmental autocorrelation between nonbreeding grounds (r_{between}), but it was also a function of environmental autocorrelation within nonbreeding grounds (r_{within}; Figure 4). Higher within nonbreeding ground environmental autocorrelation yielded higher synchrony. When combining the within nonbreeding ground environmental autocorrelation with the between nonbreeding ground

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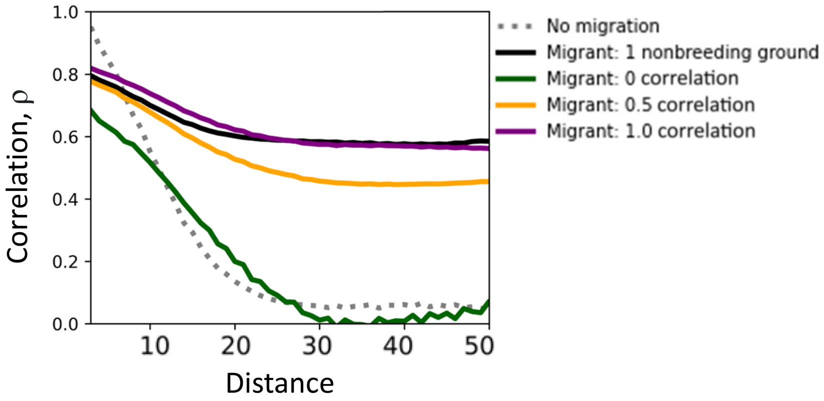

FIGURE 3 Average correlation in abundances (ρ) for a given distance between two populations on the breeding ground when there was no migration ("no migration") and when migrants went to one or multiple (i.e., four shown here) nonbreeding grounds with varying correlation between them. Within nonbreeding ground correlation = 0.75. Migrants experienced different between nonbreeding ground environmental autocorrelations (r_{between}), ranging from 0 ("0 correlation") to 1.

environmental autocorrelation, high r_{between} yielded higher spatial population synchrony than low r_{between}, regardless of how low or high r_{within} was (Figure 4). Results throughout the rest of the paper are presented using $r_{\text{within}} = 0.75$.

Migration characteristics

The type of migration impacted the average spatial population synchrony (Figure 5A). Proximity migration yielded higher synchrony at short distances than random migration. However, synchrony declined less across increasing distances with random migration (Figure 5A). The differences in synchrony between migration strategies were most pronounced when the environmental autocorrelation between nonbreeding grounds was low (Figure 5A).

Spatial population synchrony was lower when populations migrated to four nonbreeding grounds than when they migrated to two (Figure 5B). Like the results for proximity versus random migration, differences in synchrony between two versus four nonbreeding grounds were most pronounced at lower correlations of between nonbreeding ground environmental stochasticity (r_{between}; Figure 5B). We also varied the number of populations on the breeding ground that went to the same nonbreeding grounds by dividing the simulated population grid on the breeding ground horizontally and vertically into different-sized sections and sending these different-sized sections to different nonbreeding grounds (Appendix S3: Figure S1). We found that the environmental conditions from nonbreeding grounds that had more populations aggregated on them drove the observed patterns of synchrony at low between nonbreeding ground environmental correlations (Appendix S3: Figure S1).

DISCUSSION

Existing theory shows us what patterns of spatial population synchrony to expect when considering sedentary populations in a common environment. However, when attempting to link levels of synchrony to environmental variables, season-specific variability must be analytically accounted for (White & Hastings, 2020). The simple relationship described by Moran (1953) between autocorrelation in the environment and spatial population synchrony does not account for seasonally changing environmental autocorrelation that most species experience through migration. Here, we show that the spatial synchrony of populations of seasonal migrants was no longer only determined by correlation in environmental noise on the breeding ground. We showed that the average and the scaling of spatial population synchrony estimated on the breeding ground was altered when considering more than one source of environmental stochasticity, and that the Moran effect on the breeding ground alone was not sufficient to explain synchronous or asynchronous fluctuations in population dynamics for migratory populations (Figures 3 and 4). As predicted, our model showed that the effects of environmental autocorrelation experienced off the breeding ground on population synchrony on the breeding ground depended on the characteristics of migration, such as size and number of nonbreeding grounds, and how populations migrated in

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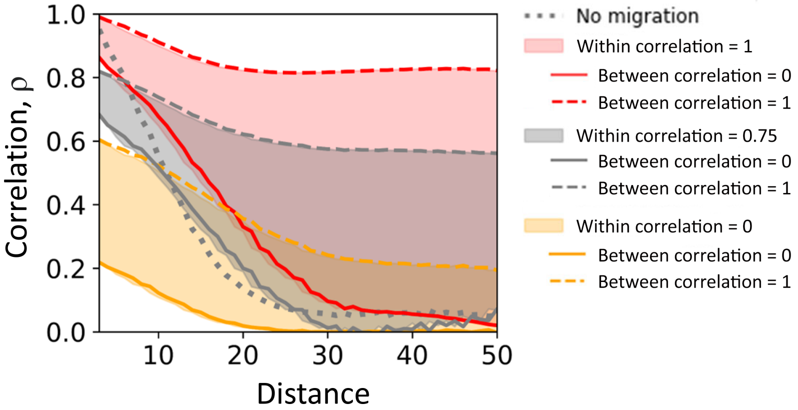

FIGURE 4 Relationship between within (r_{within}) and between (r_{between}) nonbreeding ground environmental autocorrelation and correlation in abundance (ρ). Ranges of possible average abundance correlation (ρ) for a given distance between two populations on the breeding ground are shown for different within nonbreeding ground environmental correlations (ranging 0–1). Each within nonbreeding ground correlation shows range of possible correlation (ρ) outcomes with all possible values (ranging 0–1) of between nonbreeding ground environmental autocorrelation. Upper limit of each color range represents when the between nonbreeding ground environmental autocorrelation = 1, lower limit of each color range represents when the between nonbreeding ground environmental autocorrelation = 0.

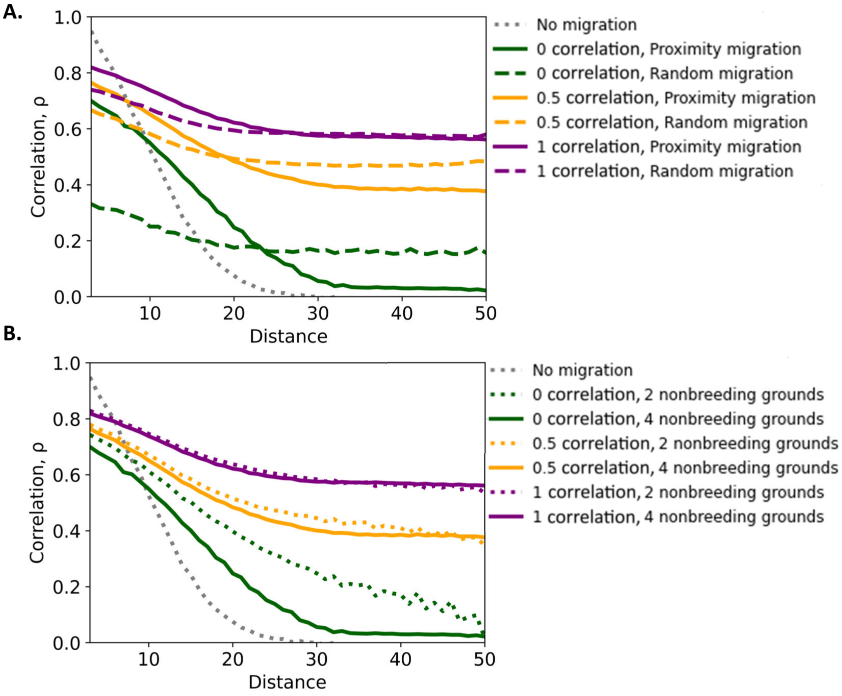

FIGURE 5 (A) Average spatial population synchrony on the breeding ground changed based on environmental autocorrelation experienced on nonbreeding grounds and the type of migration. Populations went to four nonbreeding grounds. (B) Average spatial population synchrony on the breeding ground changed based on the number of nonbreeding grounds to which populations migrated at both short and long distances: Proximity migration shown here.

relation to neighboring populations (Figure 5). Complex and diverse migration strategies have proven difficult to understand and track in the wild. There are immense logistic and collaborative challenges to studying migratory populations across their entire annual cycle in a systematic and long-term monitoring program (Bowlin et al., 2010), and so simulations and theoretical work as shown here provide a suitable approach to fill in this empirical gap.

When populations migrated to multiple nonbreeding grounds, spatial population synchrony increased with increasing environmental autocorrelation between nonbreeding grounds. Notably, the differences in synchrony between migration strategies were most pronounced when the environmental autocorrelation between nonbreeding grounds was low. There are different ways to biologically interpret the impact of environmental autocorrelation between nonbreeding grounds. High environmental autocorrelation between nonbreeding grounds could represent nonbreeding grounds that are close together in space, while lower environmental autocorrelation between nonbreeding grounds could represent nonbreeding grounds that are further from one another in space. Alternatively, high environmental autocorrelation could also represent nonbreeding grounds that are not close in space but have experienced a similar synchronizing environmental event (e.g., extreme climate event) with a large geographic impact (e.g., Hansen et al., 2013). Most climate change scenarios predict a more synchronized climate in the future (Post & Forchhammer, 2004). This will likely promote large-scale regional fluctuations in climate, which means we can also expect to see a concomitant increase in spatial population synchrony for populations whose dynamics are highly environmentally driven (Post & Forchhammer, 2002). Consequently, understanding how migratory populations respond to more synchronized nonbreeding grounds could be an important tool for predicting metapopulation dynamic-level responses to climate change (Kahilainen et al., 2018).

How populations migrated in relation to other populations on the breeding grounds and dispersal characteristics were important for determining synchrony on the breeding grounds. For populations that migrated to the same place as nearby populations, there was an increase in spatial population synchrony at short distances with a clear decrease in synchrony at the distance at which populations were far enough away from one another to follow different migratory paths and/or migrate to different nonbreeding grounds. Populations on the breeding ground that migrated to the same place were therefore expected to be more susceptible to extinction via small-scale or local events because of high local spatial population synchrony. Over the entire breeding ground, however, we could expect that proximity migrant species would likely be less susceptible to regional extinction because these populations were desynchronized at greater distances. The proximity migration strategy enhanced the already existing relationship between environmental autocorrelation and distance (i.e., Moran effect) and increased the environmental autocorrelation a population experienced in the annual cycle. In effect, we showed that in cases in which populations had the same linear dynamics and were proximity migrants, they were more likely to have more correlated population dynamics than the correlation in their environment on their breeding ground alone. Conversely, populations that migrated randomly had lower synchrony at short distances than proximity migrants, but did not experience as large of a decrease in synchrony at larger distances. At larger distances, there was higher synchrony for the random migration strategy (except when the correlation was very high). This was because these far-apart populations experiencing relatively uncorrelated environmental conditions on the breeding grounds now had on average a higher probability of sharing environments on the nonbreeding grounds than two far-apart populations in the “proximity” scenario. These patterns of migration strategy and changing synchrony with distance may ultimately have implications for species persistence. Species where populations migrate to a nonbreeding ground independent of their neighboring populations could be less susceptible to extinction via small-scale or local events, because of this lower spatial population synchrony at short distances. Conversely, they could be more susceptible to large-scale events.

In nature, there is variation in the number of nonbreeding grounds to which populations can choose to migrate. In instances in which populations migrate to many different nonbreeding grounds, changes to nonbreeding ground habitats that impact demography will have diffuse but widespread effects on synchrony because population dynamics on the breeding ground are then buffered by the environments experienced in other places (Finch et al., 2017). Loss of nonbreeding grounds could also force more populations to go to the same place, which would result in increased synchrony and thus vulnerability. Conversely, populations that migrate to few or even only one nonbreeding ground(s) are likely more susceptible to environmental variability, making them more synchronized because of the direct and indirect impacts of shared nonbreeding ground environments on the breeding ground population dynamics. Species that typically migrate to many nonbreeding grounds can be more buffered against extinction events than species that migrate to few. How species aggregate during the nonbreeding season has clear implications for species conservation and management, because adverse conditions in one location during the nonbreeding season can

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carry over and directly impact the population dynamics seen on the breeding ground.

An important consideration when interpreting the results from this modeling exercise is that the degree of spatial population synchrony is dependent upon environmental correlations both within and between nonbreeding grounds. We found that when populations migrated to nonbreeding grounds with high within nonbreeding ground environmental autocorrelation, spatial population synchrony was higher than for populations that migrated to nonbreeding grounds with lower within nonbreeding ground environmental autocorrelation. In our model, within nonbreeding ground environmental correlation dictated if spatial population synchrony was higher (if within correlation = 1) or lower (if within correlation <0.75) than the nonmigrating populations at all distances. Generally, we found that synchrony depended on the combined environments both within and between nonbreeding grounds experienced by populations throughout an annual cycle, and that migration and its characteristics were an important part of determining which environments these populations were exposed to.

Different species may have different sensitivities in their vital rates to environmental stochasticity. In the simulations presented here, the effect of the environment was identical for both survival and fecundity on the breeding ground, but varying this strength of the environmental effect on different vital rates could be of future interest and biologically relevant for particular cases in some systems. By varying the parameters that specified the strength of the environmental noise on different vital rates, we could gain knowledge about the relationship between spatial population synchrony, life-history traits, and different migration types. Different species may also be more susceptible to environmental conditions during migration or on nonbreeding grounds than on their breeding grounds (e.g., Gordo & Sanz, 2008; Harrison et al., 2010; Schaub et al., 2005). In the simulations presented here, we do not vary the sensitivity to nonbreeding ground environmental conditions in relation to the sensitivity to the conditions on the nonbreeding grounds, but this could be an important future consideration in future modeling exercises. The same is true for the effect of density dependence on observed synchrony in population dynamics. Variability in the strength and type of density dependence that can act in a population to impact spatial population synchrony was not explored here. Investigating the role of density dependence during breeding season, nonbreeding season, and its variable strength, could lead to interesting insights into how this driver of spatial population synchrony interacts with (non)breeding ground environments and sensitivities. For other considerations of parameters used in the population model, see Appendix S4.

Populations of migratory species are declining globally at alarming rates (Rosenberg et al., 2019; Vickery et al., 2014). To understand the causes of these declines and better determine appropriate conservation measures, we must first understand where populations are most sensitive to conditions experienced throughout their annual cycle (Small-Lorenz et al., 2013). There has been significant research bias toward research conducted on the breeding grounds of migratory species (Marra et al., 2015). Similarly, conservation efforts for migratory species are often targeted to habitat and environmental conditions in one location in the annual cycle, rendering many conservation actions for migratory animals inadequate and unable to critically account for different climate change sensitivities and how linked populations interact (Small-Lorenz et al., 2013). Migratory species are particularly vulnerable to climate change (Humphrey, 2004; Møller et al., 2008; Robinson et al., 2008), and full-annual cycle understanding of dynamics is critical to address climate-induced habitat loss or range shifts. Anthropogenically driven environmental change will also change habitat via loss and fragmentation, resulting in changes to the size of the wintering grounds, breeding grounds, or the connectivity between these two for many species, which can have a direct impact on spatial population synchrony (e.g., Bellamy et al., 2003).

Our results help to understand the consequence of environmental change on population dynamics for migratory species and can be used to understand how susceptible to extinction populations of migrating species are given where and how they migrate and the expected scaling of environmental changes (e.g., via small-scale or local events). Similarly, the simulations presented here could serve as a tool to identify biodiversity, conservation, or restoration priorities by indicating for which species there is a need for an increasing number of nonbreeding grounds versus increasing the size of the breeding grounds. Given that the question is no longer if environmental change will happen, but when, where, and to what degree, being able to simulate the possible consequences of this environmental change on the synchrony of populations is critical for identifying conservation or restoration steps needed for continued species' persistence.

AUTHOR CONTRIBUTIONS

All authors were involved in developing the original idea for the study. Ellen C. Martin and Aline Magdalena Lee contributed to the study conceptualization, writing code,

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and running simulations. Ellen C. Martin wrote the original manuscript with substantial input from Aline Magdalena Lee, Brage Bremset Hansen, and Ivar Herfindal.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Novel code (Martin et al., 2023) to generate figures and conclusions is available in Figshare at https://doi.org/10.6084/m9.figshare.23828877.

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SUPPORTING INFORMATION

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

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Appendix S1. Supplemental material in *Ecology* for "The role of seasonal migration in spatial population synchrony" by Ellen C. Martin, Brage Bremset Hansen, Ivar Herfindal, and Aline Magdalena Lee.

Simulation of the environmental noise field

Let $dA(x)$ be a spatial white noise process with $\mathrm{E}\ dA(x) = 0$ and $\mathrm{E}\ dA(x)^2 = dx$. The environmental field, $v(x)$, can then be written as $v(x) = \xi(u)\int dA(x-u)$ with $\xi(u) = \xi(-u)$, such that $c(y) = \mathrm{Cov}[v(x), v(x+y)] = \int \xi(u)\xi(y-u)du$. Now let g be the Fourier transform of the weighting function ξ and let f be the Fourier transform of $c(y)$. Using the fact that $c(y)$, as written above, is a convolution, we then have that $g = \sqrt{f}$.

In general, if a Fourier transform $f(\omega) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} e^{i(\omega_1 y_i + \omega_2 y_2)} b(y) dy_1 dy_2$ is isotropic with $b(y) = \tilde{b}(r)$, where $r = \sqrt{y_1^2 + y_2^2}$, it can be expressed as $f(\omega) = \tilde{f}(u)$, where $u = \sqrt{\omega_1^2 + \omega_2^2}$. Then, the inverse transformation is

$$\tilde{b}(r) = \frac{1}{2\pi}\int_0^{\infty} \tilde{f}(u) J_0(ru) u du, \tag{S1}$$

where J_0 is the Bessel function of first kind of order zero (Abramowitz and Stegun, 1972; Engen et al., 2018). If $b(y)$ has an isotropic Gaussian form, $b_0 e^{-r^2/(2\sigma^2)}$, the Fourier transform is $\tilde{f}(u) = 2\pi\sigma^2 b_0 e^{-u^2\sigma^2/2}$. Thus, we have

$$\xi(u) = \frac{l_e \sigma}{\sqrt{2\pi}}\int_0^{\infty} e^{-u^2 l_e^2/4} J_0(ru) u du, \tag{S2}$$

where l_e is the spatial scale of the environmental noise field (as defined in the main text).

The environmental field was simulated by drawing normal variates with zero mean and variance Δx for each point in the grid, as a discretization of $dA(x)$. The contribution from each square to every other square was then calculated as $\sum \xi(x-u)\Delta A(x)$. We use Euclidian distances to calculate distances from one population to all other populations. Distances were rounded to the nearest integer for computational reasons, but we checked that this did not have any major effects on the properties of the environmental field or our results.

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Appendix S2. Supplemental material in *Ecology* for "The role of seasonal migration in spatial population synchrony" by Ellen C. Martin, Brage Bremset Hansen, Ivar Herfindal, and Aline Magdalena Lee.

Table S1. Parameters used in model

Parameter	Definition	Value in base model
Nit	Number of iterations for the simulation	1,000
abundances	One-dimensional numpy.ndarray of abundances (initial size, (gridsize**2,)) All initialized at the same value	20
xi_list	Output from xi_dist function. Gives the xi-values that will produce the appropriate environmental field associated with different distances	varied
Distlist	Distlist[i] gives the distances from point i to all thinned points. All points (not just thinned ones) are included as i	varied
gridsize	Side length of spatial grid	150
Thin	Reducing number of points in grid for saving purposes (gridsize divided by thin)	2
midsection	One side length of inner grid which we are saving	50
Le	Spatial scale of environmental noise	9
Sigma	Standard deviation of environmental noise	0.10
Disprate	Dispersal rate (probability of dispersing at breeding ground)	0.02
lg	Spatial scale of dispersal distribution	5
breedsurv	Survival probability at breeding ground	1
nonbreedsurv	Survival probability at nonbreeding ground	0.9
survenv	Relative effect of environmental noise on survival	1
fec	Fecundity parameter (mean number of offspring)	0.25
fecenv	Relative effect of environmental noise on fecundity	1
Sdd	Density dependence acting on survival	0.02
Randommigroutes	Binary: 0 = not random, 1 = random	0 or 1
correlation_between ($r_{between}$)	Correlation between different nonbreeding grounds	0, 0.25, 0.50, 0.75, 1
correlation_within (r_{within})	Correlation within the different nonbreeding grounds	0, 0.25, 0.50, 0.75, 1
Weight	Weighting of the effect of migration and nonbreeding ground. Default = 1 on breeding ground	1
numbermigroutes	Different number of nonbreeding grounds in simulation	1, 2, 4
zonewidth	Width of transition zone between nonbreeding grounds where individuals have a non-zero probability of migrating in a different nonbreeding ground	8
vsplit	Location of vertical division of nonbreeding ground assignment. Used when changing sizes of nonbreeding grounds. Number refers to location in midsection	25
hsplit	Location of horizontal division of nonbreeding ground assignment. Used when changing sizes of nonbreeding grounds. Number refers to location in midsection	25
burn_in	Number of iterations at which to start saving output	50

Appendix S3. Supplemental material in *Ecology* for "The role of seasonal migration in spatial population synchrony" by Ellen C. Martin, Brage Bremset Hansen, Ivar Herfindal, and Aline Magdalena Lee.

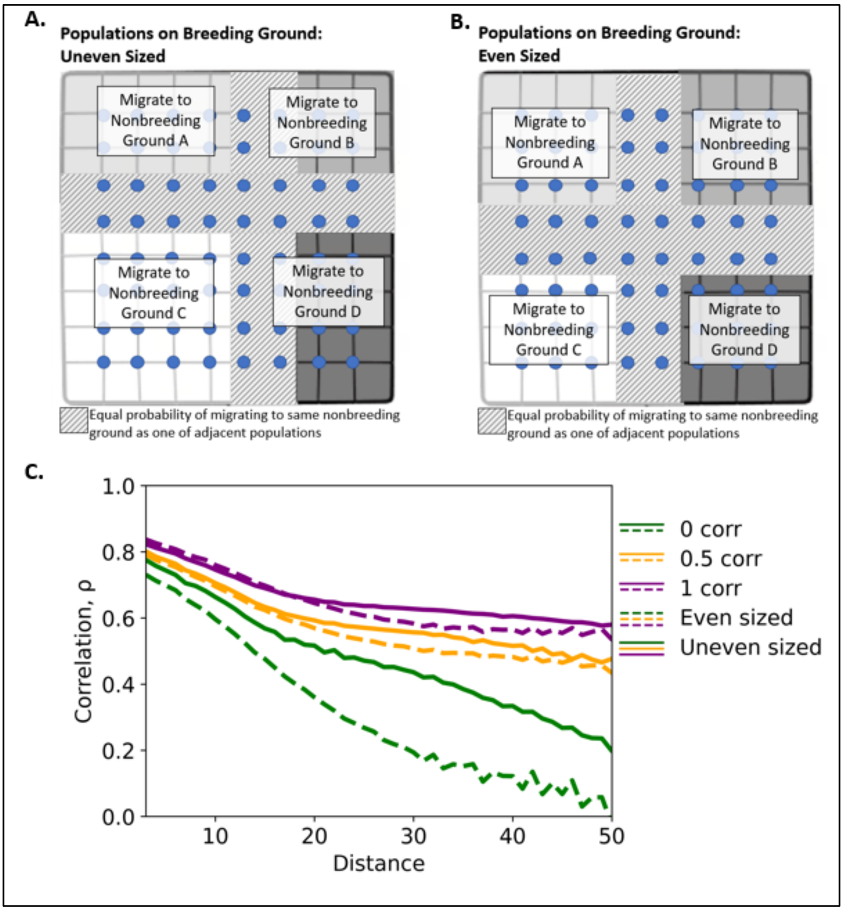

Figure S1. Schematic demonstrating how individuals on the breeding ground were assigned to different nonbreeding grounds. A) Populations on the breeding ground were sent in uneven numbers to nonbreeding grounds. B) Populations on the breeding ground were sent in even numbers to nonbreeding grounds. C) The number of breeding ground populations migrating to the same nonbreeding ground impacting the scaling of spatial population synchrony. Simulations based off proximity migration scenarios for slow-lived species (i.e., K selected species), migrating to 4 different nonbreeding grounds, with $r_{within} = 0.75$. See Appendix S2 for other parameter values.

Appendix S4. Supplemental material in *Ecology* for "The role of seasonal migration in spatial population synchrony" by Ellen C. Martin, Brage Bremset Hansen, Ivar Herfindal, and Aline Magdalena Lee.

Additional parameters used in model and further considerations

Different parameters in the model contributed to the variability in the mean and scaling of spatial population synchrony seen in the population dynamics. In natural systems, these parameters are all expected to exhibit inter- and intra-specific variation, but in our simulations the parameters were held constant to more clearly allow us to disentangle the effects of the migration parameters of interest.

Additional, non-migration related parameters impacting the scaling of synchrony include the spatial scale of environmental noise (*le),* the standard deviation of environmental noise (*sigma*), dispersal rate (*disprate*), the spatial scale of dispersal distribution (*lg),* density dependence on survival (*sdd),* the width of transition zone between nonbreeding grounds where individuals have a non-zero probability of migrating in a different nonbreeding grounds (*zonewidth),* the location of vertical and horizontal division of nonbreeding ground assignment (*hsplit and vsplit),* and if a carryover effect is applied (*carryover;* see definitions in Appendix S1). We draw particular attention to the relationship between synchrony and the spatial scale of environmental noise. This parameter (*Le)* determined the rate at which synchrony broke down across distances. Varying this spatial scale of environmental noise to be larger, for example, would result in a different shape of the synchrony-distance curve, change the mean regional synchrony, and impact the distance at which synchrony declined towards zero observed in the figures. This is also true of the spatial scale of dispersal distribution (*Lg*), wherein increasing this parameter value in the model would increase the scale at which synchrony remained high over further distances. The parameters which assign the breeding ground populations to a nonbreeding ground (*hsplit* and *vsplit*) essentially define how a patch on the breeding ground is distributed across nonbreeding grounds. We have presented in Fig. 5 only one combination of many ways to divide the breeding ground into nonbreeding ground patches, and the way in which these patches are divided will impact the scaling and mean regional synchrony observed. We present the most extreme example in Fig. 5 (*hsplit* =10, *vsplit*=40) and note that the size of the largest patch is responsible for the shape of the synchrony-distance relationship. This shape is likely to change as the way that the nonbreeding ground allocation changes.

Paper II

Martin, Ellen Claire; Herfindal, Ivar; Hansen, Brage Bremset; Lee, Aline Magdalena. Spatial population synchrony depends on relative impacts of environmental noise on different vital rates.

This paper will be submitted for publication and is therefore not included.

Paper III

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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 & Hugueny, 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

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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 & Hoye, 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 standardrutterna* (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

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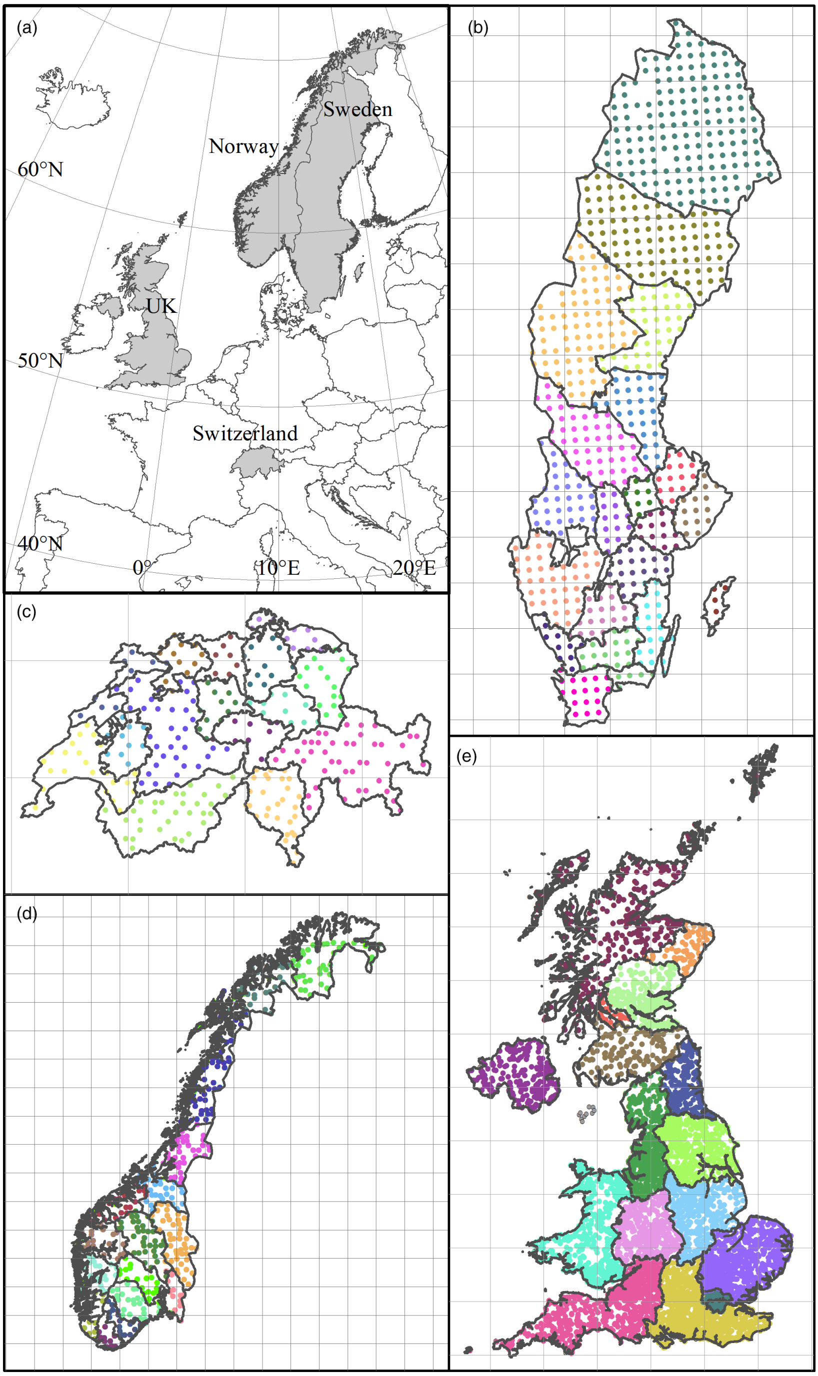

FIGURE 1 (a) The four study countries. Survey locations in each country presented in (b–e). Administrative units were clustered with next nearest neighbour with fewest survey points to achieve a minimum of 8 sample locations. Black boundaries represent aggregated administrative unit boundaries. The grids 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.

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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 $\left(\log\left(N_t\right)\right)$, 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 worlds 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 $\left(\log\left(N_t + 1 / N_t\right)\right)$ or between log-transformed abundances $\left(\log\left(N_t\right)\right)$ 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

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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

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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 intervals were used for figures and results interpretation.

	Distance (km)	Model number	GT	MT	Country	GT X country	GT X MT	MT X country	Log-likelihood	AIC_c wt	ΔAIC_c	*k*
Log population growth rate	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			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**				**176.13**	**0.49**	**0**	**9**
		3	X	X	X			X	182.31	0.24	1.39	15
		8	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			177.14	0.05	4.74	12

(Continues)

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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	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			88.87	0.046	4.4	12
		5	X	X	X		X	X	93.97	0.02	6.35	17

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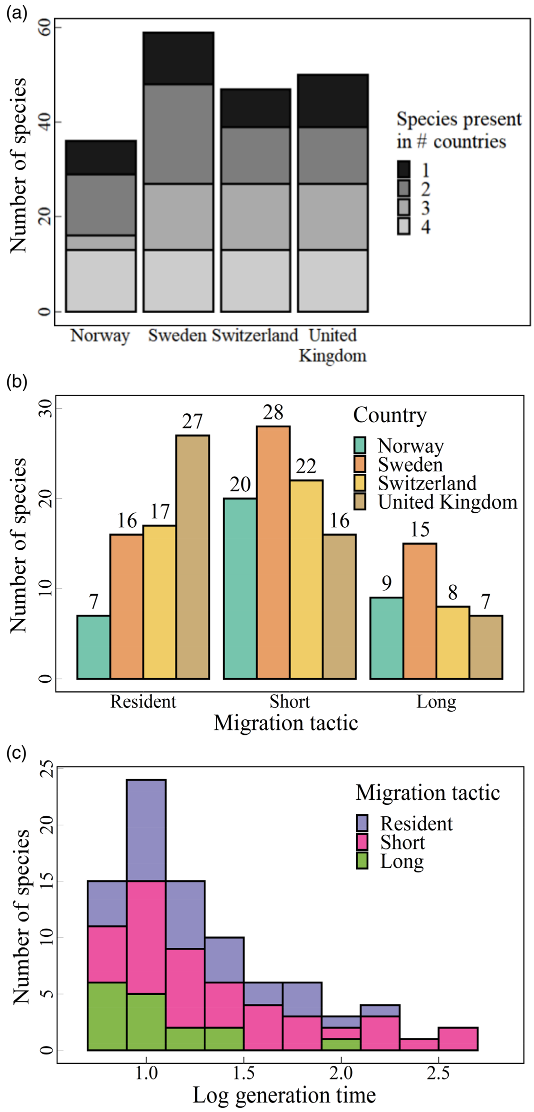

FIGURE 2 Summary of data used to estimate spatial population synchrony (i.e. pairwise correlation in population growth rate and abundance). (a) Number of species per country and number of species shared across multiple countries, (b) number of migration tactics per country and (c) distribution of log 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 ($\Delta AIC_c \le 1.39$ 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 (0–500 km and 0–1000 km) 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 ($\Delta AIC_c \le 0.65$ 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 × Log Generation Time: estimate = −0.13 SE = 0.06], [Long-distance migrant × 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).

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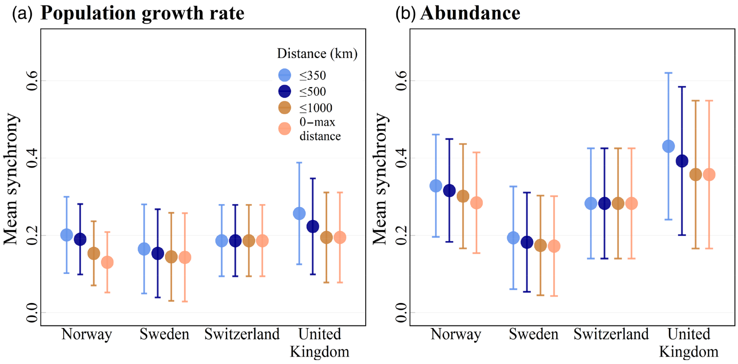

FIGURE 3 Mean synchrony (i.e. pairwise correlation in population growth rate and abundance) of all species per distance interval. Results shown for (a) log population growth rate and (b) log abundance. Number of pairs of populations per distance interval per country available in Table 1. Bars show the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

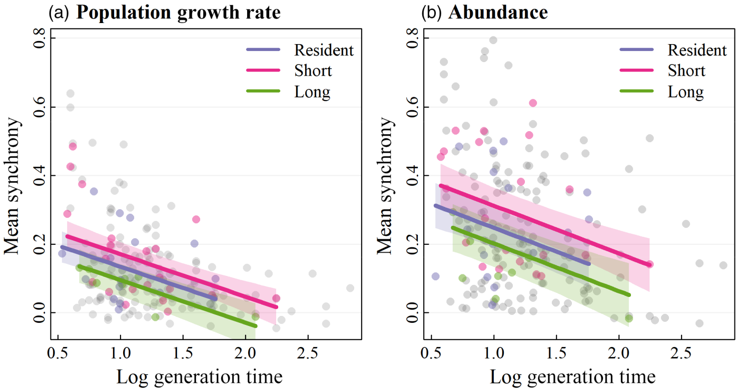

FIGURE 4 The effects of log generation time and migration tactic on mean synchrony (i.e. pairwise correlation in population growth rate and abundance) in (a) log population growth rate and (b) log abundance. Data for Switzerland in colour, all other countries in grey. Slopes are predicted for Switzerland 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

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(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 350 km 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 250 km away from one another. This effect could be a methodological effect

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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].

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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.
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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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Supplementary material

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 analyzed (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. Totals of residents, short-distance migrants, and long-distance migrants per country given at bottom of table.

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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 analyzed (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. Totals of residents, short-distance migrants, and long-distance migrants per country given at bottom of table.

	Country				
Species	**Norway**	**Sweden**	**Switzerland**	**United Kingdom**	**Generation Time**
Acanthis flammea	Short				2.59
Aegithalos caudatus				Resident	2.39
*Alauda arvensis**			Short	Resident	2.83
Anas platyrhynchos		Short		Short	4.78
Anthus pratensis	Short			Short	2.17
Anthus spinoletta			Short		2.17
Anthus trivialis	Long	Long	Long		2.11
Apus apus		Long	Long	Long	8.01
Ardea cinerea				Resident	8.88
Branta canadensis		Short			9.45
Bucephala clangula		Short			7.12
*Buteo buteo**			Short	Resident	9.45
Carduelis cannabina			Short	Short	2.20*
*Carduelis carduelis**			Short	Resident	2.53
Certhia brachydactyla			Resident		1.70
Certhia familiaris		Resident	Resident		2.05
*Chloris chloris**	Short	Short	Resident	Short	2.71
Chroicocephalus ridibundus		Short			9.85
Columba livia				Resident	3.99
Columba oenas				Resident	3.36
*Columba palumbus**	Short	Short	Short	Resident	3.72
Corvus corax	Resident	Resident			7.46
Corvus corone	Resident	Resident	Resident	Resident	5.72
Corvus frugilegus				Resident	5.59
*Corvus monedula**		Short		Resident	5.57
Cuculus canorus	Long	Long	Long	Long	2.76
Cyanistes caeruleus		Resident	Resident	Resident	2.93
Delichon urbicum		Long		Long	2.92
Dendrocopos major		Resident	Resident	Resident	2.70
Dryocopus martius		Resident			4.12
*Emberiza citrinella **	Resident	Short	Short	Resident	2.77
Emberiza schoeniclus	Short	Short			2.46

*Erithacus rubecula**	Short	Short	Short	Resident	3.60
Falco tinnunculus				Resident	4.08
Ficedula hypoleuca	Long	Long			4.12
Fringilla coelebs	Short	Short	Short	Short	4.98
Fringilla montifringilla	Short				2.99
Gallinago gallinago	Short				3.57
Gallinula chloropus				Resident	3.57
Garrulus glandarius		Resident	Resident	Resident	4.91
Grus grus		Short			17.03
Hirundo rustica		Long	Long	Long	3.13
Lagopus lagopus	Resident				2.33
Lagopus muta	Resident				2.99
Larus argentatus		Short		Short	14.07
Larus canus		Short			10.67
Larus fuscus				Short	12.62
Lophophanes cristatus		Resident	Resident		2.50
Loxia curvirostra		Short			3.16
Lyrurus tetrix	Resident	Resident			3.37
Motacilla alba	Long	Long	Long	Long	2.81
Muscicapa striata	Long	Long			2.55
Oenanthe oenanthe	Long		Long		2.25
Parus major	Resident	Resident	Resident	Resident	3.05
Passer domesticus		Resident	Resident	Resident	3.73
Passer montanus		Resident	Resident		2.72
Periparus ater		Resident	Resident	Resident	2.20
Phasianus colchicus				Resident	4.77
Phoenicurus ochruros			Short		2.41
Phoenicurus phoenicurus	Long	Long			2.31
Phylloscopus bonelli			Long		1.95*
Phylloscopus collybita	Short		Short	Short	2.00
Phylloscopus sibilatrix		Long			2.31
Phylloscopus trochilus	Long	Long		Long	2.53
Pica pica		Resident	Resident	Resident	5.81
Picus viridis				Resident	3.06
Pluvialis apricaria	Long				4.45
Poecile montanus	Resident	Resident			2.47
Poecile palustris			Resident		2.57
Prunella collaris			Resident		2.68
Prunella modularis	Short	Short	Short	Short	3.81
*Pyrrhula pyrrhula**			Short	Resident	3.35
Regulus ignicapilla			Short		1.78
*Regulus regulus**		Short	Short	Resident	1.85
Saxicola rubetra		Long			1.91

Serinus serinus			Short		2.48
Sitta europaea		Resident	Resident		2.69
Spinus spinus	Short	Short			2.78
Streptopelia decaocto				Resident	3.46
Sturnus vulgaris		Short	Short	Short	5.65
Sylvia atricapilla		Short	Short	Short	2.51
Sylvia borin		Long	Long		3.59
Sylvia communis		Long		Long	2.17
Sylvia curruca		Long			2.14
Tringa ochropus		Short			4.75
Tringa totanus	Short				4.75
Troglodytes troglodytes	Short	Short	Short	Short	1.82
Turdus iliacus	Short	Short			3.53
Turdus merula	Short	Short	Short	Short	4.03
Turdus philomelos	Short	Short	Short	Short	3.37
Turdus pilaris	Short	Short			3.43
Turdus torquatus	Short		Short		2.99
Turdus viscivorus		Short	Short	Short	3.97
Vanellus vanellus		Short		Short	6.19
Total Species:	36	59	47	50	
Residents	7	16	17	27	
Short-Distance Migrants	20	28	22	16	
Long-Distance Migrants	9	15	8	7	

* *Carduelis cannabina* generation time was taken from *Linaria flavirostris*. *Phylloscopus bonelli* generation time was taken from *Phylloscopus orientalis*

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.

Species	**Common Name**	**Norway**	**Sweden**	**Switzerland**	**United Kingdom**
Acanthis flammea	Common Redpoll	0.36	NA	NA	NA
Aegithalos caudatus	Long-tailed Tit	NA	NA	NA	0.18
Alauda arvensis	Eurasian Skylark	NA	NA	0.02	0.18
Anas platyrhynchos	Mallard	NA	0.02	NA	0.02
Anthus pratensis	Meadow Pipit	0.08	NA	NA	-0.005
Anthus spinoletta	Water Pipit	NA	NA	0.09	NA
Anthus trivialis	Tree Pipit	0.08	0.04	0.13	NA
Apus apus	Common Swift	NA	-0.003	-0.01	0.05
Ardea cinerea	Grey Heron	NA	NA	NA	0.11
Branta canadensis	Canada Goose	NA	-0.05	NA	NA
Bucephala clangula	Common Goldeneye	NA	-0.01	NA	NA
Buteo buteo	Eurasian Buzzard	NA	NA	0.04	0.04
Carduelis cannabina	Common Linnet	NA	NA	NA	0.15
Carduelis carduelis	European Goldfinch	NA	NA	0.22	0.19
Certhia brachydactyla	Short-toed Treecreeper	NA	NA	0.17	NA
Certhia familiaris	Eurasian Treecreeper	NA	0.20	0.10	NA
Chloris chloris	European Greenfinch	0.10	0.04	0.03	0.22
Chroicocephalus ridibundus	Black-headed Gull	NA	-0.02	NA	NA
Columba livia	Rock Dove	NA	NA	NA	0.05
Columba oenas	Stock Dove	NA	NA	NA	0.02
Columba palumbus	Common Woodpigeon	0.13	0.03	0.10	0.11
Corvus corax	Common Raven	0.04	0.13	NA	NA
Corvus corone	Carrion Crow	0.04	0.04	0.04	0.02
Corvus frugilegus	Rook	NA	NA	NA	-0.04
Corvus monedula	Western Jackdaw	NA	0.03	NA	0.03
Cuculus canorus	Common Cuckoo	0.12	0.06	0.08	0.12
Cyanistes caeruleus	Eurasian Blue Tit	NA	0.10	0.28	0.31
Delichon urbicum	Common House Martin	NA	-0.01	NA	0.15
Dendrocopos major	Great Spotted Woodpecker	NA	0.20	0.29	0.03
Dryocopus martius	Black Woodpecker	NA	0.12	NA	NA
Emberiza citrinella	Yellowhammer	0.02	0.06	NA	0.08
Emberiza schoeniclus	Common Reed Bunting	-0.01	-0.02	NA	NA
Erithacus rubecula	European Robin	0.26	0.23	0.19	0.30

Falco tinnunculus	Common Kestrel	NA	NA	NA	0.31
Ficedula hypoleuca	European Pied Flycatcher	0.04	0.03	NA	NA
Fringilla coelebs	Common Chaffinch	0.15	0.15	0.27	0.12
Fringilla montifringilla	Brambling	0.01	NA	NA	NA
Gallinago gallinago	Common Snipe	0.03	NA	NA	NA
Gallinula chloropus	Common Moorhen	NA	NA	NA	0.06
Garrulus glandarius	Eurasian Jay	NA	0.09	0.20	0.09
Grus grus	Common Crane	NA	0.07	NA	NA
Hirundo rustica	Barn Swallow	NA	-0.01	0.11	0.15
Lagopus lagopus	Willow Ptarmigan	0.15	NA	NA	NA
Lagopus muta	Rock Ptarmigan	0.13	NA	NA	NA
Larus argentatus	European Herring Gull	NA	-0.03	NA	0.02
Larus canus	Common Gull	NA	0.01	NA	NA
Larus fuscus	Lesser Black-backed Gull	NA	NA	NA	0.12
Lophophanes cristatus	Crested Tit	NA	0.25	0.16	NA
Loxia curvirostra	Red Crossbill	NA	0.16	NA	NA
Lyrurus tetrix	Black Grouse	-0.01	0.17	NA	NA
Motacilla alba	White Wagtail	0.08	-0.01	0.01	0.16
Muscicapa striata	Spotted Flycatcher	0.03	0.04	NA	NA
Oenanthe oenanthe	Northern Wheatear	0.03	NA	0.09	NA
Parus major	Great Tit	0.06	0.03	0.21	0.17
Passer domesticus	House Sparrow	NA	-0.01	0.06	0.17
Passer montanus	Eurasian Tree Sparrow	NA	0.09	0.10	NA
Periparus ater	Coal Tit	NA	0.11	0.35	0.16
Phasianus colchicus	Common Pheasant	NA	NA	NA	0.05
Phoenicurus ochruros	Black Redstart	NA	NA	0.16	NA
Phoenicurus phoenicurus	Common Redstart	0.04	0.04	NA	NA
Phylloscopus bonelli	Western Bonelli's Warbler	NA	NA	0.13	NA
Phylloscopus collybita	Common Chiffchaff	0.03	NA	0.38	0.39
Phylloscopus sibilatrix	Wood Warbler	NA	0.05	NA	NA
Phylloscopus trochilus	Willow Warbler	0.11	0.13	NA	0.30
Pica pica	Eurasian Magpie	NA	0.06	0.10	0.08
Picus viridis	European Green Woodpecker	NA	NA	NA	0.09
Pluvialis apricaria	European Golden Plover	0.01	NA	NA	NA

Poecile montanus	Willow Tit	0.05	0.11	NA	NA
Poecile palustris	Marsh Tit	NA	NA	0.04	NA
Prunella collaris	Alpine Accentor	NA	NA	0.01	NA
Prunella modularis	Dunnock	0.04	0.10	0.04	0.10
Pyrrhula pyrrhula	Eurasian Bullfinch	NA	NA	0.18	0.24
Regulus ignicapilla	Common Firecrest	NA	NA	0.29	NA
Regulus regulus	Goldcrest	NA	0.49	0.48	0.42
Saxicola rubetra	Whinchat	NA	0.02	NA	NA
Serinus serinus	European Serin	NA	NA	0.06	NA
Sitta europaea	Eurasian Nuthatch	NA	0.38	0.08	NA
Spinus spinus	Eurasian Siskin	0.37	0.49	NA	NA
Streptopelia decaocto	Eurasian Collared Dove	NA	NA	NA	0.01
Sturnus vulgaris	Common Starling	NA	0.01	0.05	0.13
Sylvia atricapilla	Eurasian Blackcap	NA	0.29	0.20	0.30
Sylvia borin	Garden Warbler	NA	0.19	-0.01	NA
Sylvia communis	Common Whitethroat	NA	0.17	NA	0.50
Sylvia curruca	Lesser Whitethroat	NA	0.08	NA	NA
Tringa ochropus	Green Sandpiper	NA	0.07	NA	NA
Tringa totanus	Common Redshank	0.02	NA	NA	NA
Troglodytes troglodytes	Northern Wren	0.30	0.64	0.43	0.60
Turdus iliacus	Redwing	0.02	0.06	NA	NA
Turdus merula	Eurasian Blackbird	-0.03	0.11	0.07	0.17
Turdus philomelos	Song Thrush	0.06	0.15	0.08	0.25
Turdus pilaris	Fieldfare	0.18	0.16	NA	NA
Turdus torquatus	Ring Ouzel	0.09	NA	0.07	NA
Turdus viscivorus	Mistle Thrush	NA	0.07	0.003	0.17
Vanellus vanellus	Northern Lapwing	NA	0.02	NA	0.05

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.

Species	**Common Name**	**Norway**	**Sweden**	**Switzerland**	**United Kingdom**
Acanthis flammea	Common Redpoll	0.50	NA	NA	NA
Aegithalos caudatus	Long-tailed Tit	NA	NA	NA	0.25
Alauda arvensis	Eurasian Skylark	NA	NA	0.13	0.38
Anas platyrhynchos	Mallard	NA	0.01	NA	0.17
Anthus pratensis	Meadow Pipit	0.48	NA	NA	0.01
Anthus spinoletta	Water Pipit	NA	NA	0.21	NA
Anthus trivialis	Tree Pipit	0.41	0.02	0.10	NA
Apus apus	Common Swift	NA	-0.009	-0.02	0.42
Ardea cinerea	Grey Heron	NA	NA	NA	0.30
Branta canadensis	Canada Goose	NA	-0.01	NA	NA
Bucephala clangula	Common Goldeneye	NA	-0.02	NA	NA
Buteo buteo	Eurasian Buzzard	NA	NA	0.14	0.51
Carduelis cannabina	Common Linnet	NA	NA	NA	0.27
Carduelis carduelis	European Goldfinch	NA	NA	0.28	0.76
Certhia brachydactyla	Short-toed Treecreeper	NA	NA	0.11	NA
Certhia familiaris	Eurasian Treecreeper	NA	0.27	0.49	NA
Chloris chloris	European Greenfinch	0.03	0.47	0.41	0.61
Chroicocephalus ridibundus	Black-headed Gull	NA	-0.02	NA	NA
Columba livia	Rock Dove	NA	NA	NA	0.09
Columba oenas	Stock Dove	NA	NA	NA	0.04
Columba palumbus	Common Woodpigeon	0.22	0.04	0.61	0.55
Corvus corax	Common Raven	0.17	0.10	NA	NA
Corvus corone	Carrion Crow	0.16	0.08	0.35	0.21
Corvus frugilegus	Rook	NA	NA	NA	0.06
Corvus monedula	Western Jackdaw	NA	0.07	NA	0.50
Cuculus canorus	Common Cuckoo	0.18	0.02	0.04	0.42
Cyanistes caeruleus	Eurasian Blue Tit	NA	0.10	0.50	0.36
Delichon urbicum	Common House Martin	NA	0.02	NA	0.14
Dendrocopos major	Great Spotted Woodpecker	NA	0.22	0.47	0.79
Dryocopus martius	Black Woodpecker	NA	0.15	NA	NA
Emberiza citrinella	Yellowhammer	0.08	0.43	NA	0.16
Emberiza schoeniclus	Common Reed Bunting	0.29	0.09	NA	NA
Erithacus rubecula	European Robin	0.43	0.21	0.52	0.48
Falco tinnunculus	Common Kestrel	NA	NA	NA	0.46
Ficedula hypoleuca	European Pied Flycatcher	0.38	0.18	NA	NA
Fringilla coelebs	Common Chaffinch	0.35	0.10	0.36	0.16
Fringilla montifringilla	Brambling	0.25	NA	NA	NA
Gallinago gallinago	Common Snipe	0.26	NA	NA	NA
Gallinula chloropus	Common Moorhen	NA	NA	NA	0.18
Garrulus glandarius	Eurasian Jay	NA	0.03	0.23	0.22
Grus grus	Common Crane	NA	0.14	NA	NA
Hirundo rustica	Barn Swallow	NA	0.006	0.12	0.36
Lagopus lagopus	Willow Ptarmigan	0.37	NA	NA	NA
Lagopus muta	Rock Ptarmigan	0.38	NA	NA	NA
Larus argentatus	European Herring Gull	NA	-0.03	NA	0.14

Larus canus	Common Gull	NA	-0.02	NA	NA
Larus fuscus	Lesser Black-backed Gull	NA	NA	NA	0.26
Lophophanes cristatus	Crested Tit	NA	0.21	0.17	NA
Loxia curvirostra	Red Crossbill	NA	0.23	NA	NA
Lyrurus tetrix	Black Grouse	0.006	0.23	NA	NA
Motacilla alba	White Wagtail	0.16	0.12	0.11	0.25
Muscicapa striata	Spotted Flycatcher	0.21	0.02	NA	NA
Oenanthe oenanthe	Northern Wheatear	0.24	NA	0.21	NA
Parus major	Great Tit	0.41	0.03	0.36	0.72
Passer domesticus	House Sparrow	NA	0.01	0.18	0.06
Passer montanus	Eurasian Tree Sparrow	NA	0.03	0.07	NA
Periparus ater	Coal Tit	NA	0.05	0.24	0.23
Phasianus colchicus	Common Pheasant	NA	NA	NA	0.46
Phoenicurus ochruros	Black Redstart	NA	NA	0.50	NA
Phoenicurus phoenicurus	Common Redstart	0.40	0.05	NA	NA
Phylloscopus bonelli	Western Bonelli's Warbler	NA	NA	0.29	NA
Phylloscopus collybita	Common Chiffchaff	0.47	NA	0.53	0.66
Phylloscopus sibilatrix	Wood Warbler	NA	0.07	NA	NA
Phylloscopus trochilus	Willow Warbler	0.53	0.09	NA	0.33
Pica pica	Eurasian Magpie	NA	0.07	0.27	0.04
Picus viridis	European Green Woodpecker	NA	NA	NA	0.08
Pluvialis apricaria	European Golden Plover	0.03	NA	NA	NA
Poecile montanus	Willow Tit	0.07	0.18	NA	NA
Poecile palustris	Marsh Tit	NA	NA	0.10	NA
Prunella collaris	Alpine Accentor	NA	NA	0.02	NA
Prunella modularis	Dunnock	0.33	0.11	0.11	0.35
Pyrrhula pyrrhula	Eurasian Bullfinch	NA	NA	0.15	0.20
Regulus ignicapilla	Common Firecrest	NA	NA	0.46	NA
Regulus regulus	Goldcrest	NA	0.53	0.36	0.34
Saxicola rubetra	Whinchat	NA	0.03	NA	NA
Serinus serinus	European Serin	NA	NA	0.13	NA
Sitta europaea	Eurasian Nuthatch	NA	0.26	0.20	NA
Spinus spinus	Eurasian Siskin	0.39	0.35	NA	NA
Streptopelia decaocto	Eurasian Collared Dove	NA	NA	NA	0.14
Sturnus vulgaris	Common Starling	NA	0.03	0.17	0.47
Sylvia atricapilla	Eurasian Blackcap	NA	0.29	0.53	0.74
Sylvia borin	Garden Warbler	NA	0.14	0.16	NA
Sylvia communis	Common Whitethroat	NA	0.09	NA	0.55
Sylvia curruca	Lesser Whitethroat	NA	0.30	NA	NA
Tringa ochropus	Green Sandpiper	NA	0.13	NA	NA
Tringa totanus	Common Redshank	0.18	NA	NA	NA
Troglodytes troglodytes	Northern Wren	0.69	0.73	0.47	0.62
Turdus iliacus	Redwing	0.43	0.35	NA	NA
Turdus merula	Eurasian Blackbird	0.16	0.09	0.17	0.40
Turdus philomelos	Song Thrush	0.27	0.17	0.38	0.36
Turdus pilaris	Fieldfare	0.21	0.20	NA	NA
Turdus torquatus	Ring Ouzel	0.28	NA	0.18	NA
Turdus viscivorus	Mistle Thrush	NA	0.19	0.11	0.39
Vanellus vanellus	Northern Lapwing	NA	0.06	NA	0.26

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 1.

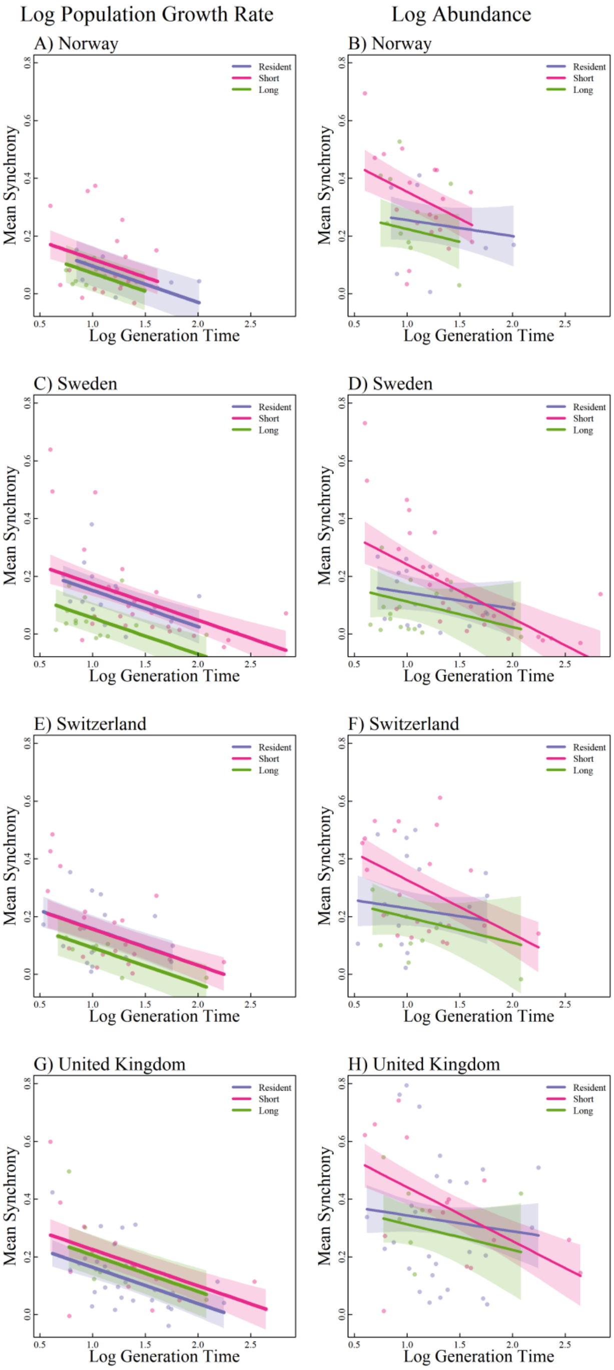
A. Log population growth rate

	Top Model			
Parameter	**0 - 350km**	**0 - 500km**	**0 - 1000km**	**0 – Max Distance**
Norway, Long-distance migrant	0.29 (0.03)	0.29 (0.03)	0.25 (0.03)	0.18 (0.03)
Norway, Short-distance migrant	0.34 (0.03)	0.32 (0.03)	0.29 (0.03)	0.25 (0.03)
Norway, Resident	0.32 (0.03)	0.32 (0.04)	0.29 (0.04)	0.22 (0.03)
Sweden, Long-distance migrant	0.27 (0.03)	0.22 (0.03)	0.21 (0.03)	0.21 (0.03)
Sweden, Short-distance migrant	0.33 (0.03)	0.32 (0.03)	0.32 (0.03)	0.29 (0.03)
Sweden, Resident	0.30 (0.03)	0.32 (0.03)	0.30 (0.03)	0.25 (0.03)
Switzerland, Long-distance migrant	0.26 (0.03)	0.28 (0.04)	0.28 (0.03)	0.22 (0.03)
Switzerland, Short-distance migrant	0.32 (0.03)	0.30 (0.03)	0.31 (0.03)	0.29 (0.03)
Switzerland, Resident	0.30 (0.03)	0.31 (0.03)	0.32 (0.03)	0.26 (0.03)
United Kingdom, Long-distance migrant	0.36 (0.03)	0.39 (0.04)	0.36 (0.04)	0.27 (0.03)
United Kingdom, Short-distance migrant	0.42 (0.03)	0.39 (0.03)	0.37 (0.03)	0.34 (0.03)
United Kingdom, Resident	0.40 (0.03)	0.34 (0.03)	0.32 (0.03)	0.31 (0.03)
Log Generation Time	-0.11 (0.02)	-0.11 (0.02)	-0.11 (0.02)	-0.12 (0.02)

B. Log abundance

	Top Model			
Parameter	**0 - 350km**	**0 - 500km**	**0 - 1000km**	**0 – Max Distance**
Norway, Long-distance migrant	0.40 (0.04)	0.39 (0.04)	0.37 (0.04)	0.37 (0.04)
Norway, Short-distance migrant	0.49 (0.04)	0.48 (0.04)	0.46 (0.04)	0.48 (0.04)
Norway, Resident	0.43 (0.04)	0.42 (0.04)	0.41 (0.04)	0.42 (0.05)
Sweden, Long-distance migrant	0.29 (0.04)	0.28 (0.04)	0.27 (0.04)	0.25 (0.04)
Sweden, Short-distance migrant	0.38 (0.04)	0.37 (0.04)	0.36 (0.04)	0.36 (0.05)
Sweden, Resident	0.32 (0.04)	0.31 (0.04)	0.31 (0.04)	0.30 (0.05)
Switzerland, Long-distance migrant	0.35 (0.04)	0.35 (0.04)	0.35 (0.04)	0.34 (0.04)
Switzerland, Short-distance migrant	0.45 (0.04)	0.45 (0.04)	0.45 (0.04)	0.45 (0.04)
Switzerland, Resident	0.39 (0.04)	0.39 (0.04)	0.39 (0.04)	0.39 (0.04)
United Kingdom, Long-distance migrant	0.54 (0.04)	0.50 (0.04)	0.46 (0.04)	0.46 (0.05)
United Kingdom, Short-distance migrant	0.63 (0.04)	0.59 (0.04)	0.55 (0.04)	0.57 (0.05)
United Kingdom, Resident	0.57 (0.04)	0.53 (0.04)	0.50 (0.04)	0.50 (0.04)
Log Generation Time	-0.12 (0.03)	-0.12 (0.03)	-0.12 (0.03)	-0.14 (0.03)

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 colors.



Paper IV

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How do life history traits influence the environment's effect on population synchrony? Insights from European birds and insects

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Abstract

Populations closer together in space are more likely to experience shared environmental fluctuations. This correlation in experienced environmental conditions is the main driver of spatial population synchrony, defined as the tendency for geographically separate populations of the same species to exhibit parallel fluctuations in abundance over time. Moran's theorem states that spatially distinct populations are expected to show the same synchrony in their population dynamics as the synchrony in their environment. However, this is rarely the case in the wild, and the population synchrony of different species inhabiting the same area is rarely similar. These species-specific differences in how the environment synchronizes populations can be due to life history traits that make some species more susceptible to environmental stochasticity, such as reduced mobility or faster pace of life. In this study, we compiled long-term annual abundance datasets on European birds and insects (*Lepidoptera* sp. and *Bombus* sp.) to identify how environmental synchrony (i.e., positively spatially correlated fluctuations in the environment, also called the Moran effect) affects species population synchrony. As expected, the environment synchronized populations of both birds and insects. Populations experiencing correlated fluctuations in precipitation or temperature had higher synchrony in annual population growth rates. Birds were more strongly synchronized by temperature, while precipitation was a stronger driver of synchrony in insects. In birds, species with short generation times had a stronger synchronizing effect of the environment compared to species with long generation times. Moreover, in birds the effects of synchrony in the environment also depended on movement propensity, with a positive impact for resident and short-distance migration species. In insects, annual population synchrony was affected by species movement propensity and dietary niche breadth, but these traits did not modify the effects of environmental synchrony. Our study provides empirical support for the prediction that spatial correlation in population dynamics is more influenced by environmental stochasticity for life histories with lower mobility and faster pace of life, but only in birds. By quantifying spatial population synchrony across different levels of environmental synchrony and life history traits, our study improves the understanding of the Moran effect as well as factors that drive population persistence in the face of environmental change.

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Introduction

Spatial population synchrony, the tendency for geographically separate populations of the same species to exhibit parallel fluctuations in abundance over time, is largely caused by correlated environmental conditions (Liebhold et al., 2004), which typically results in populations closer together in space having more synchronized dynamics (Ranta et al., 1995, Bjørnstad et al., 1999). Studies of spatiotemporal patterns in nature have long relied on the first theory of spatial population synchrony, Moran's theorem, to explain how the environment causes spatial population synchrony between these spatially separated populations (Moran, 1953, Bjørnstad et al., 1999). Moran's theorem states that given the same density dependence, populations are expected to show the same synchrony in their population dynamics as the synchrony in their environment (often called the "Moran Effect"; Moran, 1953). When populations are far enough apart for their environments to fluctuate independently of each other, we expect to see no population synchrony (Moran, 1953, Royama, 1992).

Environmental variables significantly affect population dynamics by influencing reproductive success (Lehikoinen et al., 2011, Andreasson et al., 2020), survival rates (Jones et al., 2007, Hansen et al., 2013, Clarke, 2017), immigration rates, and emmigration rates (Pärn & Sæther, 2012). The two most commonly measured environmental variables that have been identified as important drivers of spatial population synchrony are temperature and precipitation (e.g., Post & Forchhammer, 2004, Koenig & Liebhold, 2016, Kahilainen et al., 2018, Dallas et al., 2020, Nicolau et al., 2022), with most results correlating increased synchrony in the environment with increased spatial population synchrony. These variables typically exhibit strong spatial synchrony that declines with distance (Koenig, 2002, Herfindal et al., 2022).

Despite the synchronizing effect of environmental autocorrelation on population dynamics, different species present at the same locations and exposed to the same environmental synchrony do not always exhibit the same degree of synchrony in their population cofluctuations (Marquez et al., 2019, Martin et al., 2023). Different responses to the environment and, thereby, the environmental synchrony are often attributed to life history traits, rendering species-specific sensitivity to changes in the environment (Tedesco & Hugueny, 2006, Chevalier et al., 2014, Hansen et al., 2020). Key life history traits such as position on the fast-slow life history continuum (i.e., an organism's pace of life derived from generation time or age at first reproduction; Oli, 2004, Gaillard et al., 2005, Reif et al., 2010), movement propensity (i.e., migration classification or distance travelled annually; Howard et al., 2020), and dietary specialization (i.e., the number of food types in the annual diet of a given species; de Gabriel Hernando et al., 2022) are all expected to impact species' sensitivities to the environment. For example, both theoretical and empirical work shows that environmental stochasticity tends to have a greater effect on population dynamics for species with shorter generation times (Tedesco & Hugueny, 2006, Bjørkvoll et al., 2012, Sæther et al., 2013, Chevalier et al., 2014, Marquez et al., 2019). Distance traveled or migratory tactics are traits that can act as a proxy for a species dispersal ability, which has been shown to strengthen spatial population synchrony (Ranta et al., 1995, Lande et al., 1999, Kendall et al., 2000). Investigating empirically how the Moran effect is modified by such key life history traits is an important next step in understanding the implications of environmental change for spatial population dynamics and, thereby, conservation and the spatial scale of wildlife management actions.

In this study, we compiled a pan-European collection of long-term annual abundance data on birds and insects to identify how species' life history traits can modify the effects of annual

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environmental (i.e., temperature and precipitation) synchrony. Birds and insects are informative study organisms for investigating such effects of environmental synchrony on population dynamics because of their history of long-term monitoring and data availability (Nadeau et al., 2017) as well as their large variability in life histories. These taxa are also generally widely distributed, making it possible to study the same species spread across different environments (Jones et al., 2007). Based on Moran's theorem, we predicted that species of birds and insects in environments with higher synchrony would have overall higher spatial population synchrony, but that the effect of synchronized environments would depend on species' life history traits (Martin et al. 2023, Marquez et al., 2019). More specifically, we expected that species more sensitive to environmental stochasticity, such as fast-lived species (Sæther et al., 2013), or specialist species (Dumoulin & Armsworth, 2022), would be more highly synchronized and more influenced by environmental synchrony.

Methods

i. Bird and insect abundance data

We used population abundance data of breeding birds and insects from eleven long-term monitoring programs located across eight countries: Finland, France, Ireland, the Netherlands, Norway, Sweden, Switzerland, and the United Kingdom (Figure 1A, Table 1). Survey duration was variable, but all were at minimum 10 years long (Table 1). Although there were differences in data collection protocols across countries, as well as between birds and insects, all surveys used either point or line transects, with protocols known for their high quality and rigor (Voříšek et al., 2008, Sevilleja et al., 2020). For bird abundance data, all surveys were conducted during the breeding season, which spanned from spring to mid-summer. For insect abundance data, all surveys were conducted following the Butterfly Monitoring Survey (BMS) standardized protocol

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of line transects (i.e. fixed routes) repeatedly counted during the butterfly season. These datasets are representative subsets of larger data aggregates (Pan-European Common Bird Monitoring Survey [PECBMS] and Butterfly Monitoring Survey [BMS]; Sevilleja et al., 2020, Brlík et al., 2021). We assumed sampling error was the same across datasets (of birds or insects) because they followed a standardized sampling protocol and were part of a larger consortium of standardized data. Data from these countries were publicly available for download or free to use with data sharing agreements.

ii. Data cleaning and aggregation

We resolved species names across datasets using the Global Names Resolver (*gnr_resolve*) from the *taxize* package for R (Chamberlain S, 2020). Within each country, we aggregated point or transect level count data (hereafter *surveyed sites)* within hexagonal grid cells (hereafter *grid cells)* to represent regional population indices (Appendix 1; Colin et al., 2007). Hexagonal grids are the most appropriate sampling grid for sampling large areas because they reduce bias due to edge effects and have a smaller uniform average distance from the centroid of the grid compared to rectangular grid cells, an important consideration when conducting analyses using distances of grid centroids to one another as done here (Colin et al., 2007). We checked for underlying structure in relation to the size of the grid cell used by running all analyses and comparing results on grid cells with diameters (i.e., distance from one vertex to the opposite vertex) of both 100km and 50km (Appendix 2). Results presented are from grid cells with a diameter of 100km.

For each species separately, we aggregated abundances into a single value representing the sum of abundances in surveyed sites within a given grid cell to mitigate any random fluctuations caused by demographic stochasticity. We analyzed population dynamics at the grid cell level. We divided the total aggregate count of individuals per grid cell by the number of

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surveyed sites per grid cell to yield an average, which accounted for possible annual variation in the density of sample units (Link & Sauer, 2002). To ensure that only species for which there was sufficient data for synchrony calculations were included in the analysis, we excluded species that were absent from more than 25% of the grid cells that contained survey sites. Also, for each species, we excluded grid cells in which the species was not observed for at least 10 years of the survey duration. After data aggregation and cleaning, we analyzed 126 bird species and 59 insect species.

iii. Synchrony calculation

We calculated species' mean spatial population synchrony on log-transformed annual population growth rates ($\log(N_{t+1} / N_t)$) for each country separately. The strength of the correlation between populations is influenced by directional and temporal trends in their abundance (Loreau & de Mazancourt, 2008). To address these directional trends, spatial population synchrony analyses estimated as the synchrony of population growth rates instead of population abundances (Loreau & de Mazancourt, 2008). This adjustment effectively reduces the influence of changes in population abundance (Tredennick et al., 2017).

The pairwise distance between grid cells at which spatial population synchrony is estimated can change the average calculated synchrony (Pearson & Carroll, 1999, Dungan et al., 2002), with the inclusion of points at large distances reducing the estimation of average synchrony. Therefore, in order to have a standard distance at which we could compare population synchrony across countries, we limited our spatial scale for analysis to pairs of grid cells within 250km of one another. This was the shortest country-specific maximum distance between pairs of grid cells (Switzerland).

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In program R (R Core Team 2020), we calculated pairwise Pearson correlations in population growth rates. We Fisher z-transformed these correlations and took the average from pairs of gid cells within 250km of each other. Fisher z-transformation was necessary so that correlations were normally distributed (Silver & Dunlap, 1987). The mean synchrony for each species within each country was then presented as the back transformed mean of the pairwise correlations between all pairs of grid cells within 250km of one another. We measured the distances between grid cells as the Euclidean distances in kilometers from the centroid projected coordinate (EPSG:3035) of grid cell for each pair of cells. Synchrony was only estimated within country, meaning that there were not pairwise correlations across country borders.

iv. Environmental covariate classification and synchrony estimation

Mean monthly temperatures and mean monthly precipitation were taken from the Climate Research Unit (CRU) at the University of East Anglia (high-resolution gridded 0.5 by 0.5-degree (i.e., approximately 1,700 km^2 depending on latitude) data of month-by-month variation in climate; Jones, 2022). These data were based on daily or sub-daily observational data from National Meteorological Services and other external agents. We extracted mean monthly environmental covariate values for all grid cells included in the spatial population synchrony analysis. We were only interested in summer season environmental conditions, as the data available were breeding ground abundances. We defined the summer season for each country as the months across the entire study period in which average temperatures for all the grid cells were greater than 5 degrees Celsius, roughly corresponding to the meteorological vegetation growing season (Bootsma, 1994, Linderholm et al., 2008, Körner et al., 2023). Using this approach, each country was allowed different lengths of summer seasons (Appendix 3).

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Since population synchrony was analyzed for annual population growth rates, and to reduce effects of shared climate trends on estimates of environmental synchrony among pairs of grid cells, we linearly detrended temperature and precipitation across the years for each dataset and calculated synchrony on these detrended data. For mean annual summer precipitation and mean annual summer temperature separately, we calculated Pearson pairwise correlations between grid cells (Appendix 3). As with spatial population synchrony calculations on the population growth rates, we Fisher z-transformed the correlations and calculated the mean correlation for all grid cells within a 250km distance interval. The mean synchrony for each environmental covariate within each country is presented as the back transformed mean. We checked for correlations between temperature and precipitation at bird and insect surveyed sites using cross correlations.

v. Life history trait classification

We characterized each bird or insect species using a range of species-specific traits: position on the fast-slow life history continuum (generation time for birds, voltinism for insects), movement propensity (migratory tactic for birds, months in flight for insects), and specialist/generalist species (dietary diversity for birds and larval dietary breadth for insects; Table 2, Figure 2). We checked for dependencies or correlations between life history traits used in the analysis using Chi-square test of independence for categorical variables, ANOVA for categorical and continuous variables, and cross correlations for continuous variables (Appendix 4).

Fast-slow life history: We used generation time as a proxy for classification of bird species along the fast-slow life history continuum (Gaillard et al., 2005, Bjørkvoll et al., 2012, Martin et al., 2023). The fast-slow life history continuum ranges from species with short generation times that are fast-reproducing and short-lived (i.e., fast-lived) to species with long generation times that

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are slow-reproducing and long-lived (i.e., slow-lived; Stearns, 1983; Gaillard et al., 1989; Galliard et al., 2016). In this study, we used species-specific generation times from Bird et al. (2020), who derived generation times for birds worldwide using proxies such as the age of first reproduction, maximum longevity, and annual adult survival. We log transformed generation time for use in the analysis.

We classified each insect species along the fast-slow life history continuum using voltinism (i.e., the number of generations of species each year; for *Lepidoptera* species: Shirey et al. 2022, for *Bombus* species: Løken, 1973, pers. comm Sondre Dahle). Voltinism has been used to explain insects' degree of vulnerability to climatic events (e.g., Melero et al., 2016) and is a useful proxy for position on the fast-slow life history continuum in species that do not have readily available generation time information (Kőrösi et al., 2022). Fewer generations per year (i.e., univoltine) are associated with a slower-lived species, whereas more generations per year (i.e., multivoltine) are associated with faster-lived species.

Movement propensity: We classified each bird species as a resident, short-distance, or long-distance migrant (following Martin et al. 2023). Avian species that migrate are usually categorized based on the extent of their movement between breeding and overwintering regions (Rappole, 2013). In this study, resident species were defined as those that remained in their country of residence throughout the year, without undertaking seasonal movements (Newton, 2008, Eyres et al., 2017). Species considered short-distance migrants were those that has documented non-breeding areas within Europe but outside the country of their breeding ground (Rappole, 2013). Long-distance migrants were those species that had documented non-breeding areas located outside of Europe (Rappole, 2013). We used an available database of avian life

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history traits (Storchová & Hořák, 2018) to classify each bird species into one of the three migration tactics, i.e., residents, short-distance migrants, or long-distance migrants.

We classified each insect species according to their movement distance: Insects could have long-distance movement, short-distance movement, or have ‘no’ movement based on their flight duration (i.e., the number of months each year in which species were mobile; for *Lepidoptera* species: Shirey et al. 2022, for *Bombus* species: Løken 1973, pers. comm Sondre Dahle). Here, movement distance and flight duration can be considered a proxy for insect migration distance and can provide valuable information about an insect’s capability and propensity for long-distance travel. Insect migration differs from bird migration in that insects rarely complete annual circular movements between breeding and non-breeding grounds, and most movements require multiple generations to complete (Chapman et al. 2015). Following Dingle and Drake (2007), we therefore defined insect migration as the persistent, straightened-out movement typically carrying an individual away from a location where they were produced to another where they breed (Dingle & Drake, 2007). This persistent movement can be quantified as the amount of time in which a species is in flight (i.e., flight duration; Minter et al., 2018), or the distance traveled (i.e., flight distance). The two are correlated (Guo et al., 2020). We transformed the flight duration data from a continuous range of 1-12 months into 3 distinct categories: Resident species (species that moved for 1- 4 months of a year), short movement species (species that moved for 5 - 8 months of a year), and longer movement species (species that moved for 9 - 12 months of a year). One may expect that these two types of movement (bird migration and insect movement) would have a similar impact on spatial population synchrony, since, for both taxa, we assume time spent moving was time spent away from a shared breeding ground, which may have acted to disrupt synchrony.

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Specialist/generalist: We classified each bird species along a continuum of one (specialist) to nine (generalists) according to their dietary diversity (i.e., breadth). The value used in the analysis corresponded to the total number of different food types in the annual diet of a given species (Storchová & Hořák, 2018). Species could be classified as eating leaves, fruit, grains, arthropods, other invertebrates, fish, other vertebrates, or carrion. A species was recorded as eating a type of food if that food comprised at least 10% of its diet throughout the year (Storchová & Hořák, 2018).

We classified each insect species according to their larval diet breadth using a global lepidoptera trait database (Kőrösi et al., 2022). Larval diet breadth was a categorical variable with monophagous species, or species that ate only one kind of food, at the specialist end of the spectrum, with polyphagous species, or species that ate multiple kinds of food, at the generalist end of the spectrum (for *Lepidoptera* species: Kőrösi et al., 2022, for *Bombus* species: Løken 1973, pers. comm Sondre Dahle).

vi. Evaluating the impact of environmental synchrony and life history traits on synchrony in annual population growth rates

We used linear mixed models on bird and insect data separately to determine if there was an effect of environmental synchrony on spatial population synchrony across species, while accounting for life history traits. Given the collinearity between synchrony in temperature and precipitation at both bird and insect surveyed sites (correlation of 0.86 and 0.89 respectively), we built two different model sets to test the effect of these environmental covariates independent from one another. We included models that included an interaction between the environmental covariate and life history traits to determine if species had different responses to environmental synchrony depending on trait differences. In our separate global models for birds and insects

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(Table 3), we included species as a random effect and added position on the fast-slow life history continuum (continuous), movement propensity (categorical), specialist/generalist (continuous), mean synchrony in temperature or mean synchrony in precipitation as fixed effects. To account for potential bias in the distribution of survey points, we also included a covariate in the models that represented the median distance between populations at which spatial population synchrony was estimated. We used Akaike information criterion adjusted for small sample size (AIC_c) based on models fitted with maximum likelihood (ML) to rank models (Burnham & Anderson, 2002, Bolker et al., 2009). Parameter estimates and their uncertainties were based on models fitted with restricted maximum likelihood estimators (REML). Residuals were checked for normality.

Results

Of the 126 unique bird species analyzed, 13 species were present in five countries, 14 in four countries, 16 in three countries, 36 in two countries, and 47 in one country. Of the 59 unique insect species analyzed, six species were present in six countries, ten in five countries, ten in four countries, ten in three countries, seven in two countries, and 16 in one country. Average synchrony across all insect species was 0.31 (SD=0.03), while average synchrony across all bird species was 0.09 (SD=0.01; Figure 3B). Estimates of spatial population synchrony were thus generally higher for insects than for birds (Figure 3A). For bird and insect data present in the same country (i.e., in Norway, Sweden, and United Kingdom), insects had higher mean synchrony (Figure 3A). For species-specific estimates of synchrony, see Appendix 5.

There was strong support for several of the top candidate models in our model sets for insects and birds ($\Delta AIC_c < 2.0$; Table 3). The synchronizing effect of the environment, either as precipitation or temperature, was present in 9 out of ten top models for birds ($\Delta AIC_c < 1.84$; Table 3A) and in 9 out of ten top models for insects ($\Delta AIC_c < 1.83$; Table 3B). There was strong evidence that there was an environmental effect driving spatial population synchrony across the datasets analyzed.

For birds, there was strong support for an effect of environmental synchrony on population synchrony (Table 3; Figure 4A-C), and this synchronizing effect of the environment depended on life history traits. For birds, the highest ranked model which did not include an interaction between a life history trait and temperature was ranked twelfth and had a $\Delta AIC_c = 4.13$, whereas the highest ranked model which did not include an interaction between a life history trait and precipitation was ranked second and had a $\Delta AIC_c = 0.31$ (Table 3). Temperature had a stronger synchronizing effect than precipitation (Figure 4A-C, Table 3). The model with the strongest support indicated that synchrony in population growth rates increased with increasing synchrony in temperature, but only for short distance migrants (β=1.61, SE=0.34) and resident species (β=1.63, SE=0.51) compared to long-distance migrants (β=0.75, SE=0.36). Moreover, as synchrony in temperature increased, species with shorter generation times showed a larger increase in synchrony than species with longer generation times (Figure 4A). Regarding precipitation, the highest ranked model indicated that synchrony in population growth rate in birds was explained by synchrony in precipitation, movement propensity, and position on the fast-slow life history continuum (Table 3, Table 4). The effect of synchrony in precipitation depended on a species' movement propensity (resident species: β=0.29, SE=0.10, short-distance migrant: β=0.31, SE=0.12, long-distance migrant: β=0.18, SE=0.18; Figure 4C). Resident species and short-distance migrants were positively impacted by increasing synchrony in temperature and precipitation (Figure 4B-C). Position on the fast-slow life history continuum

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was an important predictor of spatial population synchrony but did not interact with synchrony in precipitation (Figure 4D).

There was also strong support for an effect of environmental synchrony in insects (Table 3; Figure 4E-F). For insects, the synchronizing effect of precipitation had a stronger effect than temperature (precipitation: β=0.35, SE=0.06, temperature: β=0.54, SE=0.27; Figure 4E-F), but both covariates were in the highest ranked models of their respective model sets (Table 3). For insects, there was weak support for that life history traits influenced the strength of the effect of environmental synchrony on population synchrony. The highest ranked model which included an interaction between a life history trait and temperature was ranked fifth and had a $\Delta AIC_c = 1.77$, whereas the highest ranked model which included an interaction between a life history trait and precipitation was ranked fourth and had a $\Delta AIC_c = 1.44$. The model which had the most support across model sets indicated that synchrony in population growth rate was explained best by synchrony in precipitation (β=0.35, SE=0.06), movement propensity (resident species: β=-0.13, SE=0.09, short-distance movement: β=0.18, SE=0.09, long-distance movement: β=0.30, SE=0.08), and classification as specialist/generalist (β=-0.05, SE=0.02; Table 3, Figure 4G-H), but no interaction between life history trait and precipitation synchrony (Table 3). The highest ranked temperature model gave the same top model, but there was weak support for all variables included (Table 3B). Synchrony in population growth rate was explained by synchrony in temperature (β=0.54, SE=0.27), movement propensity (resident species: β=-0.13, SE=0.27, short-distance movement: β=0.10, SE=0.26, long-distance movement: β=0.03, SE=0.26), and specialist/generalist, with increasing degree of generalization resulting in decreased synchrony (β=-0.05, SE=0.02; Table 3).

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Despite not being in the top model, there was also support for the inclusion of specialist/generalist classification in interaction with temperature among the bird model sets ($\Delta AIC_c = 0.33$; Table 3A). For insects, there was support for an effect of fast-slow life history traits on spatial population synchrony ($\Delta AIC_c = 0.42$; Table 3B) that was evident in all models except the top model.

We confirmed that there was some underlying structure in the data by conducting the analysis on grid cells with a diameter of 50km in addition to the grid cell diameter of 100km presented here (Appendix 2). The top models with 50km diameter grid cells resulted in a few parameter changes in the top models. For birds, the top models no longer included interactions between environmental synchrony and life history traits. However, the main strong effects of generation time and an environmental variable were still present (Appendix 2). For insects, there were fewer differences. The strong main effects of specialist/generalist classification and environmental synchrony were present in all top models for insects (Appendix 2). The loss of the interaction term with analysis at the 50km grid cell size is likely because the total number of surveyed sites within a 50km grid cell were few in some countries (e.g., Sweden averaged 1.2 survey point per 50km grid cell), adding noise to the estimates of population abundance. We also confirmed that there was no spatial bias with respect to how pairs of grid cells were distributed in space on the estimates of synchrony by testing for an effect of median distance at which synchrony was calculated (Appendix 6).

Discussion

Here, based on datasets of annual abundances of European birds and insects, we advance the empirical understanding of spatiotemporal population dynamics by showing that variation in the impacts of environmental synchrony on spatial population synchrony can depend on the species'

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life history traits. In both birds and insects, we found strong evidence that spatial synchrony in precipitation and/or temperature had a positive effect on annual spatial synchrony in population growth rates, indicating a Moran effect (Figure 4). Although synchrony in temperature and precipitation was highly correlated, population synchrony in birds appeared more strongly influenced by temperature than precipitation, and vice versa in insects (Table 3). In birds, the strength of the Moran effect depended on key life history traits. More specifically, responses to increased environmental synchrony depended on generation time and movement propensity, with a positive impact found only for short generation times (i.e., ‘fast’ species) and for resident and short-distance migration species (Figure 4). In contrast, for insects, movement propensity and dietary niche breadth influenced population synchrony but, at the temporal scale investigated here, these or other life history traits did not appear to modify the overall positive effect of environmental synchrony.

Although we do not demonstrate causality here, the synchronized environmental factors likely had a synchronizing effect on population dynamics via the Moran effect (Moran, 1953). Synchrony in the environment, either temperature or precipitation, was high at survey sites ≤ 250km apart (Figure 1B, Appendix 3). Synchrony in temperature was higher than synchrony in precipitation across all countries except Ireland, matching previously identified relationships between precipitation and temperature (e.g., Koenig, 2002, Herfindal et al., 2020). For many species, the environment experienced during the spring and breeding season is particularly important for driving fluctuations in parameters of importance to lifetime fitness and survival (Crick, 2004, Pearce-Higgins et al., 2015). Environmental conditions such as average summer precipitation and average summer temperature are known to act as important constraints on population growth rates of both birds and insects (Crick, 2004, Zipkin et al., 2012, Pearce-

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Higgins et al., 2015, Meller et al., 2018, Herrando et al., 2019). In this paper we have documented the same effects of the environment in two quite different taxonomic groups, indicating general patterns relevant at large spatial scales.

We found support for life history traits in interaction with the environment in birds, meaning that different groups of species responded differently to environmental synchrony. As far as we are aware, this is the first time interactions between life history traits and environmental synchrony have been documented to impact spatial population synchrony. Our results add knowledge about spatial population synchrony by showing that species with certain traits are more likely to respond to synchrony in the environment. Empirically, we have shown the importance of considering a species' life history traits when predicting the impacts of the environment on spatial population synchrony.

We further extend what is known about the importance of temperature to avian population dynamics by including the interaction effect with life history traits. Temperature during the breeding season interacted with avian position on the fast-slow life history continuum. Generally, for birds, species with shorter generation times had higher synchrony in population growth rates. There was no notable effect of increasing synchrony in the environment for species with long generation times, suggesting that they are less sensitive to environmental conditions. These general patterns match what is expected based on theory. Theoretical and empirical examples show that environmental stochasticity has a greater effect on population dynamics for species with shorter generation times, which tend to have more immediate responses to environmental stochasticity (Sæther et al., 2005). For example, Sæther et al. (2013) found that the stochastic influence of the environment on population dynamics of a species decreased as generation time increased, resulting in decreased overall stochasticity of population dynamics.

For movement propensity in birds, higher synchrony in temperature and precipitation was associated with higher spatial population synchrony for resident and short-distance migrants. Long-distance migrants had lower synchrony with increasing environmental synchrony. We expected to find the highest effect of synchrony in the breeding ground environment for resident species because two resident populations are more likely to experience the same or similar seasonal changes in environmental conditions for a longer duration than migrant or nomadic species, which typically spend less time on the breeding grounds. Migrants can spend as few as four months on the breeding ground before departing for wintering grounds (e.g., long-distance migrants; Knaus et al., 2018). Patterns of synchrony for short-distance migrants mirror the patterns identified in resident species. This could be occurring because short-distance migrants by our classification schema migrated within Europe, meaning that the over-wintering grounds they went to could still have environments which were synchronized with the breeding ground environmental dynamics (Butler, 2003).

Independent from environmental synchrony, insect species' life history traits were strong predictors of spatial population synchrony. Despite finding evidence for an interaction between environment and life history traits in birds, we found little support for the same interaction in insects. It is possible such an interaction exists on smaller temporal or spatial scale, and that the scales used to measure environmental synchrony in this study was too large for the scale of insect life cycles (Jan et al., 2017). Further studies testing for an interaction between life history traits and environmental synchrony in insects should consider looking at varying temporal and spatial scales. Studies which have investigated average daily temperature and precipitation during insect flight season (typically summer) found that both impacted spatiotemporal dynamics of butterfly species (Gibbs et al., 2011).

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For insects, movement propensity was an important predictor of spatial population synchrony. Species that were resident or characterized by short-distance movement had similar spatial population synchrony, which was lower than spatial population synchrony of species characterized by long-distance movement. While this is not the result we would expect if the short-distance and long-distance movement species were true "migrants", this is the expected result if long-distance movement can also encompass movement by dispersal. Insect movement is classified here as number of months a species is in flight and is expected to follow the classical theory of dispersal driving spatial population synchrony (Lande et al., 1999, Ims & Andreassen, 2005). With increased dispersal, increased synchrony occurs as individuals from a population at high density move to a population with lower density, resulting in a smaller difference in density between the two populations (Ripa, 2000). Finally, specialist species were more synchronized than generalist species. Specialist species have known higher sensitivity to environmental stochasticity than generalist species (Dumoulin & Armsworth, 2022), but linking this to spatial population synchrony has rarely been shown empirically.

While both temperature and precipitation were important predictors for the annual population synchrony in birds and insects, we found strong support showing that temperature is the more important of the two environmental variables for synchronizing bird dynamics and that precipitation is more important for synchronizing insect dynamics. Others have found that summer precipitation synchronized population dynamics (regardless of life history strategy) in *Lepidoptera* species (e.g., Glanville fritillary butterfly (*Melitaea cinxia*), a species included in this analysis; Kahilainen et al., 2018). Late spring and/or early summer precipitation is known to be important for insects as a trigger for the end of diapause (i.e., a state of arrested development), and for subsequent larval host-plant production (Wolda, 1988). The different important positively synchronizing variables for birds and insects extend the finding of Pearce-Higgins et al. (2015), who found a positive relationship between the mean effect of temperature and population size for birds, but not invertebrates, suggesting that temperature played a larger role in population dynamics for birds. Other studies have linked declining synchrony in temperature to declining bird population synchrony (Koenig, 2001, Koenig & Liebhold, 2016).

The higher spatial population synchrony we identified across bird and insect species in more synchronized environments has implications for future population stability and species persistence under climate change and intensified human use scenarios (Møller et al., 2004). Understanding general patterns in the causes of synchrony is important for predicting how spatial population synchrony and regional extinction probability will change with continued environmental change and habitat fragmentation. Recent studies indicate that global environmental change is affecting the frequency, intensity, spatial extent, duration, and timing of environmental patterns, ultimately changing the relationship between the environment and population dynamics (Di Cecco & Gouhier, 2018, IPCC, 2022). Most climate change scenarios predict a more synchronized climate in the future and a few studies have looked at the potential impact this climate change can have on spatial population synchrony (Post & Forchhammer, 2004, Defriez et al., 2016, Kahilainen et al., 2018). This will likely promote large-scale regional fluctuations in climate, which means we can also expect to see a concomitant increase in spatial population synchrony for species whose dynamics are highly environmentally driven (Post & Forchhammer, 2004, Nicolau et al., 2022). Increasing variability and severity of climatic events have been identified as the largest threat to population stability in birds (Møller et al., 2004) and insects (Harvey et al., 2023). Being able to predict species-specific responses to changes in environmental variability is an important tool in mitigating climate change impacts and avoiding

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population collapse. These sorts of generalizations shown in our results can aid managers to better make conservation prioritization decisions for species of conservation concern. 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.

Tables

Table 1. Datasets used in analysis. Datasets available either in public domain (e.g., Global Biodiversity Information Service) or through data sharing agreements.

Country	**Survey Name**	**Taxa**	**# Species**	**Years**
Finland	Finnish Butterfly Monitoring Scheme (BMS Finland)[1]	Insects- *Lepidoptera*	35	1999 - 2017
Ireland	Irish Butterfly Monitoring Scheme[2]	Insects- *Lepidoptera*	15	2008 - 2021
Netherlands	The Dutch Butterfly Monitoring Scheme[3]	Insects- *Lepidoptera*	27	1990 - 2020
Norway	Nature Index of Norway: Bumblebees and butterflies in Norway[4]	Insects- *Lepidoptera* & *Bombus*	10	2010 - 2021
Sweden	The Swedish Butterfly Monitoring Scheme (SeBMS)[5]	Insects- *Lepidoptera* & *Bombus*	40	2010 - 2021
United Kingdom	United Kingdom Butterfly Monitoring Scheme (UKBMS)[6]	Insects- *Lepidoptera* & *Bombus*	37	1995 - 2021
France	Suivi Temporel des Oiseaux Communs (STOC)[7]	Birds – Landbirds	54	2001 - 2021
Norway	Norwegian Extensive monitoring of breeding birds (TOV-E)[8]	Birds – Landbirds	39	2006 - 2021
Sweden	Swedish Bird Survey standardrutterna[9]	Birds – Landbirds	59	2006 - 2019
Switzerland	Monitoring Häufige Brutvögel MHB program[10]	Birds – Landbirds	47	1999 - 2020
United Kingdom	BTO/JNCC/RSPB Breeding Bird Survey (BBS)[11]	Birds – Landbirds	50	1994 - 2015

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[1] Finnish Biodiversity Information Facility (2023). National Finnish butterfly monitoring scheme (NAFI). Occurrence dataset https://doi.org/10.15468/imsrtd accessed via GBIF.org on 30.4.2020.

[2] Liam Lysaght. Irish Butterfly Monitoring Scheme. National Biodiversity Data Centre. Occurrence dataset https://doi.org/10.15468/7wb9as accessed via GBIF.org on 02.06.2023.

[3] The Dutch Butterfly Monitoring Scheme is run by Vlinderstichting (Dutch Butterfly Conservation) and CBS (Statistics Netherlands) as part of the Dutch Network for Ecological Monitoring (NEM).

[4] Åström S, Åström J (2022). Bumblebees and butterflies in Norway. Version 1.4. Norwegian Institute for Nature Research. Sampling event dataset https://doi.org/10.15468/mpsa4g accessed via GBIF.org on 2023-04-12.

[5] Pettersson L B (2022). Swedish Butterfly Monitoring Scheme (SeBMS). Version 1.11. Department of Biology, Lund University. Sampling event dataset https://doi.org/10.15468/othndo accessed via GBIF.org on 2023-04-12.

[6] UK Butterfly Monitoring Scheme (2021). UK Butterfly Monitoring Scheme (UKBMS). Occurrence dataset https://doi.org/10.15468/gmqvmk accessed via GBIF.org on 30.4.2020. Brereton, T.M., Botham, M.S., Middlebrook, I., Randle, Z., Noble D., Harris, S., Dennis, E.B., Robinson A., Peck. K. & Roy, D.B. 2020. UK. Butterfly Monitoring Scheme report for 2019. UK Centre for Ecology & Hydrology, Butterfly Conservation, British Trust for Ornithology and Joint Nature Conservation Committee.

[7] Jiguet F, Devictor V, Julliard R, Couvet D (2012) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecologica 44, 58-66

[8] Kålås J A, Øien I J, Stokke B, Vang R (2021). TOV-E Bird monitoring. Version 1.9. Norwegian Institute for Nature Research. Occurrence dataset https://doi.org/10.15468/qv7d3u accessed via GBIF.org on 2023-04-12.

[9] Lindström Å, Green M (2022). Swedish Bird Survey: Fixed routes (Standardrutterna). Version 1.12. Department of Biology, Lund University. Sampling event dataset https://doi.org/10.15468/hd6w0r accessed via GBIF.org on 2023-04-12.

[10] Swiss monitoring of common breeding birds, Swiss ornithological institute, https://www.vogelwarte.ch/en/projects/monitoring/monitoring-common-breeding-birds.

[11] e BTO Common Birds Census and BTO/JNCC/RSPB Breeding Bird Survey, which provided the data on which these analyses are based. The CBC was funded by the Joint Nature Conservation Committee (JNCC) on behalf of English Nature, Scottish Natural Heritage, Countryside Council for Wales and the Environment and Heritage Service in Northern Ireland, whilst the BBS is jointly funded by the BTO, JNCC and the Royal Society for the Protection for Birds (RSPB).

Table 2. Life history trait variables used in analysis. Definitions and any modifications to the variables taken from its original source are explained.

Taxa	Life History Trait	Category	Definition	Modifications	Categorical/ Continuous	Range/Categories
Birds	Log generation time[12]	Fast-slow	The average age of parents. Bird et al. (2020) classified birds worldwide using age of first reproduction, maximum longevity, and annual adult survival to derive generation times.	Log transformed generation time	Continuous	1.7 - 25.3 yr. (0.53 - 3.23 on log scale)
Insects	Voltinism[13]	Fast-slow	The number of generations each year.	N/A	Categorical	U = Univoltine, B = Bivoltine, M= Multivoltine
Birds	Migratory Tactic[13]	Movement Propensity	Resident species were defined as non-migrants with no seasonal movements beyond their country of residence Short-distance migrants had documented non-breeding areas within Europe but outside the country of their breeding ground. Long-distance migrants had documented non-breeding areas outside of Europe.	N/A	Categorical	Resident, Short-distance migrant, Long-distance migrant
Insects	Movement Distance[14]	Movement Propensity	The number of months in a given year in which mobile.	Transformed from continuous range of 1-12 months into 3 distinct categories: Resident species (moved for 1- 4 months of a year), short movement (moved for 5 - 8 months of a year), and longer movement distance species (moved for 9 - 12 months of a year).	Categorical	Resident, Short-distance migrant, Long-distance migrant

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[12] Bird, J. P., R. Martin, H. R. Akçakaya, J. Gilroy, I. J. Burfield, S. T. Garnett, A. Symes, J. Taylor, Ç. H. Şekercioğlu, and S. H. M. Butchart. 2020. Generation lengths of the world`s birds and their implications for extinction risk. Conservation Biology 34:1252-1261.

[13] *Lepidoptera* species: Shirey, V., E. Larsen, A. Doherty, C. A. Kim, F. T. Al-Sulaiman, J. D. Hinolan, M. G. A. Itliong, M. A. K. Naive, M. Ku, M. Belitz, G. Jeschke, V. Barve, G. Lamas, A. Y.Kawahara, R. Guralnick, N. E. Pierce, D. J. Lohman, and L. Ries. 2022. LepTraits 1.0 A globally comprehensive dataset of butterfly traits. Scientific Data 9:382. For *Bombus* species: Løken, A. 1973. Studies on Scandinavian Bumble Bees (Hymenoptera, Apidae). Norsk ent. Tidsskr. 20, 1–218., pers. comm Sondre Dahle, March 28, 2023.

Birds	Dietary Diversity[14]	Specialist/ Generalist	Nr. of food types composing ≥10% of the annual diet. Food type categories were no data, leaves, fruit, grains, arthropods, other invertebrates, fish, other vertebrates, or carrion.	N/A	Continuous	1 - 9
Insects	Larval Dietary Breadth[14]	Specialist/ Generalist	Diversity of larval diet breadth. Monophagous species (1) were at the specialist end of the spectrum, while multiphagous species (4) were at the generalist end of the spectrum.	Transformed categorically increasing scale from M=Monophagous, NO= Narrowly Oligophagous, O= Oligophagou, MP = Multiphagous to continuous scale 1-4	Continuous	Increasing scale from 1=Monophagous to 4= Multiphagous

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[14] Storchová, L., and D. Hořák. 2018. Life-history characteristics of European birds. Global Ecology and Biogeography 27:400-406.

Table 3. Model selection results for the analysis of spatial synchrony in annual population growth rates of (A) birds and (B) insects in Europe. Synchrony estimates are based on pairs of populations ≤250km apart, merged in grid cells of size 100km diameter. Covariates designated with a “+” were present in model. Covariates included environmental synchrony (Env; in terms of mean summer precipitation [Precip] or mean summer temperature [Temp]), movement (Mvmt), fast-slow life history continuum (Fastslow), specialist/generalist (Specgen), and two-ways interactions between environmental synchrony and the life history traits. We also included a covariate for median distance at which synchrony was calculated (Med dist). Only one environmental covariate (precipitation or temperature) was included in each model because of collinearity, resulting in two different model sets. Only the top five models are presented (rank 1-5). We relied upon Akaike’s Information Criterion with a small sample size correction (*AIC*$_c$) for model selection and used Akaike model weights (*wt*) and *ΔAIC*$_c$ to identify the top model. Number of parameters in model indicated by column k. LogLik = log-likelihood.

(A) Birds

Taxa	**Rank**	**Env. Variable**	**Env**	**Mvmt**	**Fastslow**	**Specgen**	**Mvmt x Env**	**Fastslow x Env**	**Specgen x Env**	**Med dist**	**k**	**LogLik**	**AICc**	**ΔAIC$_c$**	***wt***
Birds	**1**	Precip	+	+	+	--	+	--	--	+	**11**	**217.92**	**-412.89**	**0**	**0.13**
Birds	2	Precip	--	+	+	--	--	--	--	+	8	214.54	-412.58	0.31	0.11
Birds	3	Precip	+	+	+	--	+	+	--	+	12	218.52	-411.92	0.97	0.08
Birds	4	Precip	+	+	+	+	+	--	--	+	12	218.16	-411.19	1.70	0.06
Birds	5	Precip	+	+	+	--	+	--	--	--	10	215.92	-411.05	1.84	0.05
Birds	**1**	Temp	+	+	+	--	+	+	--	--	**11**	**219.84**	**-416.72**	**0**	**0.16**
Birds	2	Temp	+	+	+	+	+	+	+	+	12	221.53	-415.75	0.33	0.14
Birds	3	Temp	+	+	+	+	+	+	--	--	13	220.19	-415.25	0.97	0.09
Birds	4	Temp	+	+	+	--	--	+	--	--	14	216.16	-413.67	1.00	0.07
Birds	5	Temp	+	+	+	+	--	+	+	+	12	218.12	-413.29	1.47	0.06

(B) Insects

Taxa	Rank	Env. Variable	Env	Mvmt	Fastslow	Specgen	Mvmt x Env	Fastslow x Env	Specgen x Env	Med Dist	k	LogLik	AICc	ΔAIC$_c$	*wt*
Insects	**1**	Precip	+	+	--	+	--	--	--	--	**7**	**88.82**	**-162.93**	**0**	**0.18**
Insects	2	Precip	+	+	+	+	--	--	--	--	9	90.83	-162.51	0.42	0.14
Insects	3	Precip	+	--	+	+	--	--	--	--	7	88.51	-162.31	0.63	0.13
Insects	4	Precip	+	+	--	+	--	--	+	--	8	89.21	-161.49	1.44	0.09
Insects	5	Precip	+	+	+	+	--	--	+	--	10	91.26	-161.09	1.83	0.07
Insects	**1**	Temp	+	+	--	+	--	--	--	--	**7**	**61.19**	**-107.67**	**0**	**0.15**
Insects	2	Temp	+	+	--	+	--	--	--	--	9	63.12	-107.08	0.59	0.11
Insects	3	Temp	--	+	--	+	--	--	--	--	6	59.55	-106.56	1.11	0.09
Insects	4	Temp	+	+	+	+	--	--	--	--	9	62.69	-106.21	1.46	0.07
Insects	5	Temp	+	+	--	+	--	--	+	--	8	61.41	-105.89	1.77	0.06

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Table 4. Parameter estimates, standard errors, and 95% confidence intervals (CI) for the (A) bird and (B) insect top models from the model selection of spatial synchrony in annual population growth rates. Interactions indicated between variables with an “x”.

(A) Birds

Temperature

Parameter	**Estimate**	**Std. Error**	**95% CI**
Mean synchrony in temperature	1.63	0.51	1.61 – 2.65
Resident species	-1.32	0.48	-2.28– -0.36
Short-distance migration	-1.28	0.40	-2.08 – -0.48
Long-distance migration	-0.55	0.45	-1.45 – 0.35
Fast-slow life history continuum	0.76	0.31	0.14 – 1.38
Mean synchrony in temperature x Fast-slow life history continuum	-0.91	0.32	-1.55 – -0.27
Mean synchrony in temperature x Short-distance migrants	-0.02	0.34	-0.69 – 0.66
Mean synchrony in temperature x Long-distance migrants	-0.88	0.36	-1.59 – -0.15
r^2 marginal	r^2 conditional		
0.17	0.45		

Precipitation

Parameter	**Estimate**	**Std. Error**	**95% CI**
Mean synchrony in precipitation	0.11	0.10	-0.09 – 0.31
Resident species	0.18	0.09	-0.01 – 0.37
Short-distance migration	0.21	0.12	-0.03 – 0.45
Long-distance migration	0.43	0.13	-0.03 – 0.69
Fast-slow life history continuum	-0.11	0.02	-0.15 – -0.07
Mean synchrony in precipitation x Short-distance migrants	-0.01	0.17	-0.36 – 0.32
Mean synchrony in precipitation x Long-distance migrants	-0.36	0.18	-0.72 – 0.00
Median distance	-0.00	-0.00	*na*
r^2 marginal	r^2 conditional		
0.14	0.38		

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(B) Insects:

Temperature

Parameter	**Estimate**	**Std. Error**	**95% CI**
Mean synchrony in temperature	0.54	0.27	0 – 1.08
Movement propensity: Resident	-0.13	0.27	-0.67 – 0.41
Movement propensity: Short	0.10	0.26	-0.42 – 0.62
Movement propensity: Long	0.03	0.26	0.04 – 0.26
Specialist/Generalist	-0.05	0.02	-0.08 – -0.01
r^2 marginal	r^2 conditional		
0.26	0.45		

Precipitation

Parameter	**Estimate**	**Std. Error**	**95% CI**
Mean synchrony in precipitation	0.35	0.06	0.23 – 0.47
Movement propensity: Resident	0.13	0.09	-0.05 – 0.31
Movement propensity: Short	0.18	0.09	0 – 0.36
Movement propensity: Long	0.30	0.08	0.14 – 0.46
Specialist/Generalist	-0.05	0.02	-0.09 – -0.01
r^2 marginal	r^2 conditional		
0.35	0.56		

Figures

Figure 1. A) Map of European countries from which long-term abundance data were used in this analysis. We analyzed bird data from five countries (France, Norway, Sweden, Switzerland, and the UK [United Kingdom]). We analyzed insect data from six countries (Finland, Ireland, the Netherlands, Norway, Sweden, and the UK). B) Country-specific temperature and precipitation synchrony (*ρ* temperature and *ρ* precipitation) were estimated for bird and insect survey sites.

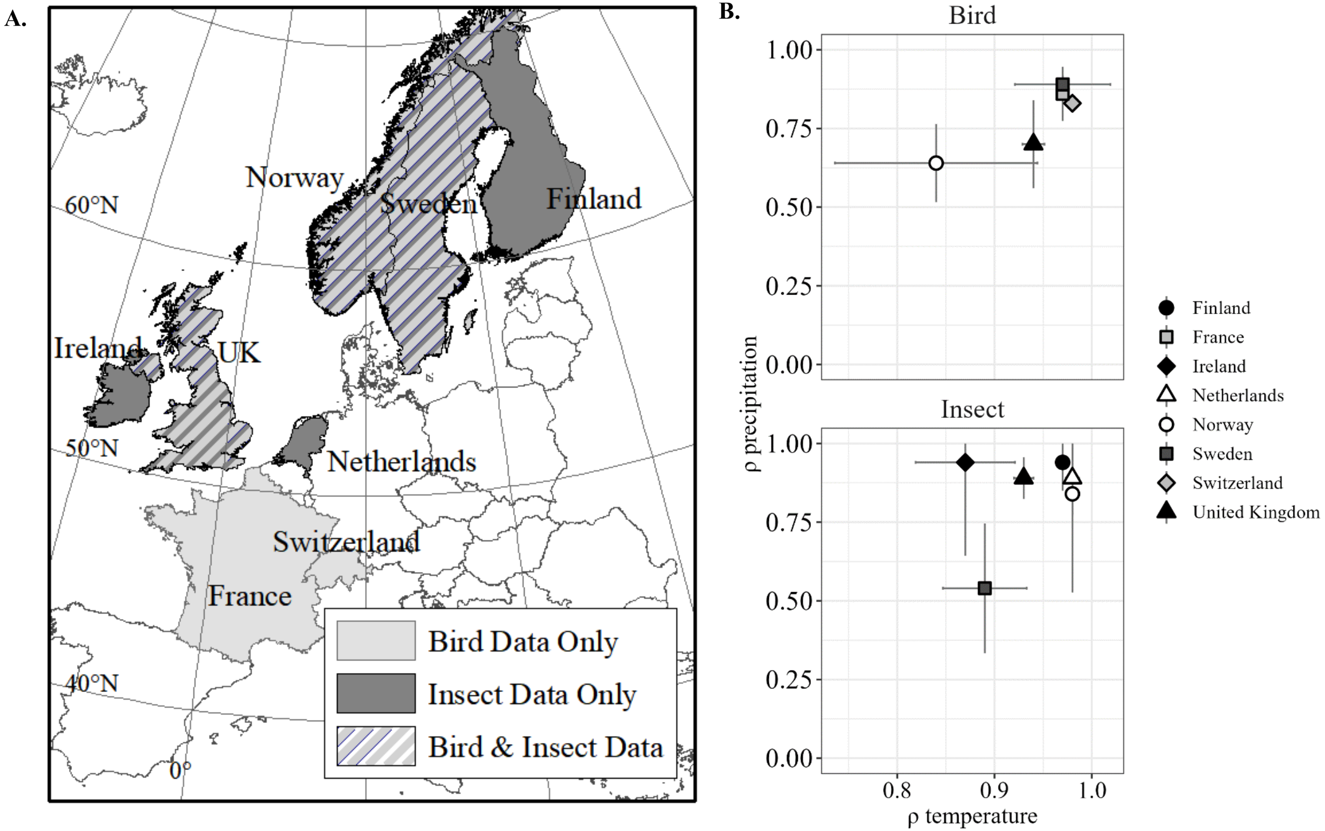


Figure 2. Distributions of the life history traits for birds (in green) and insects (in purple) are presented. (A,B) The number of species classified along the fast-slow life history continuum is presented: we used log generation time for birds, and we used voltinism for insects. Voltinism is reordered so that increasing along the voltinism axis is equivalent to increasing from fast- (multi) to slow-lived (uni) species. Log generation time ranged from 0.53 (absolute scale: 1.69 yr.) to 3.1 (absolute scale: 22.1 yr.). (C,D) The number of species classified according to their movement propensity: We used migratory tactic for birds, and we used movement distance for insects. (E,F) The number of species classified according to the specialization of their diet: We used dietary diversity for birds and we used larval diet breadth for insects. For definitions of life history traits used, see Table 2.

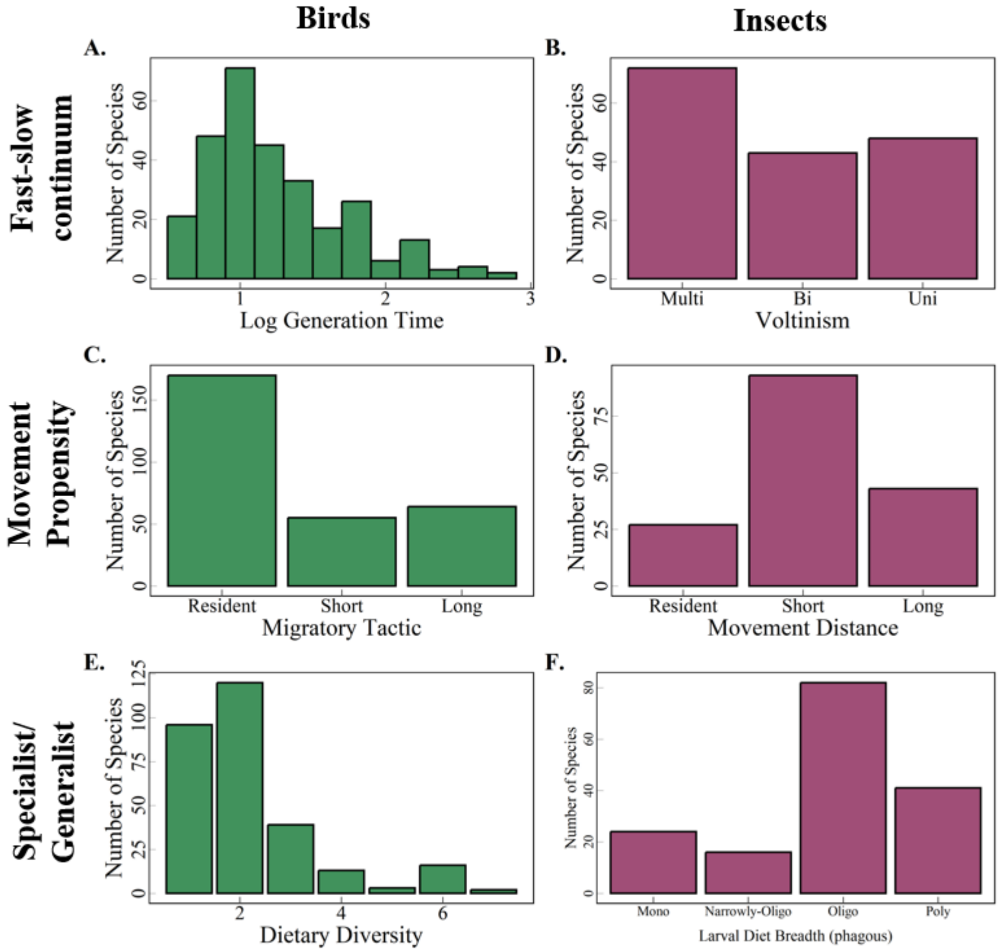


Figure 3. A) Distributions of the estimates of mean spatial synchrony in annual population growth rates for species of birds and insects, separated by country (birds shown in green, insects shown in purple). Distributions of mean synchrony are calculated from the R package *ggridges* function *geom_density_ridges*, which computes a kernel density estimate from the data. B) Distributions of the estimates of mean synchrony when combined across all countries are shown. Mean synchrony estimates are indicated by dotted line per taxonomic group.

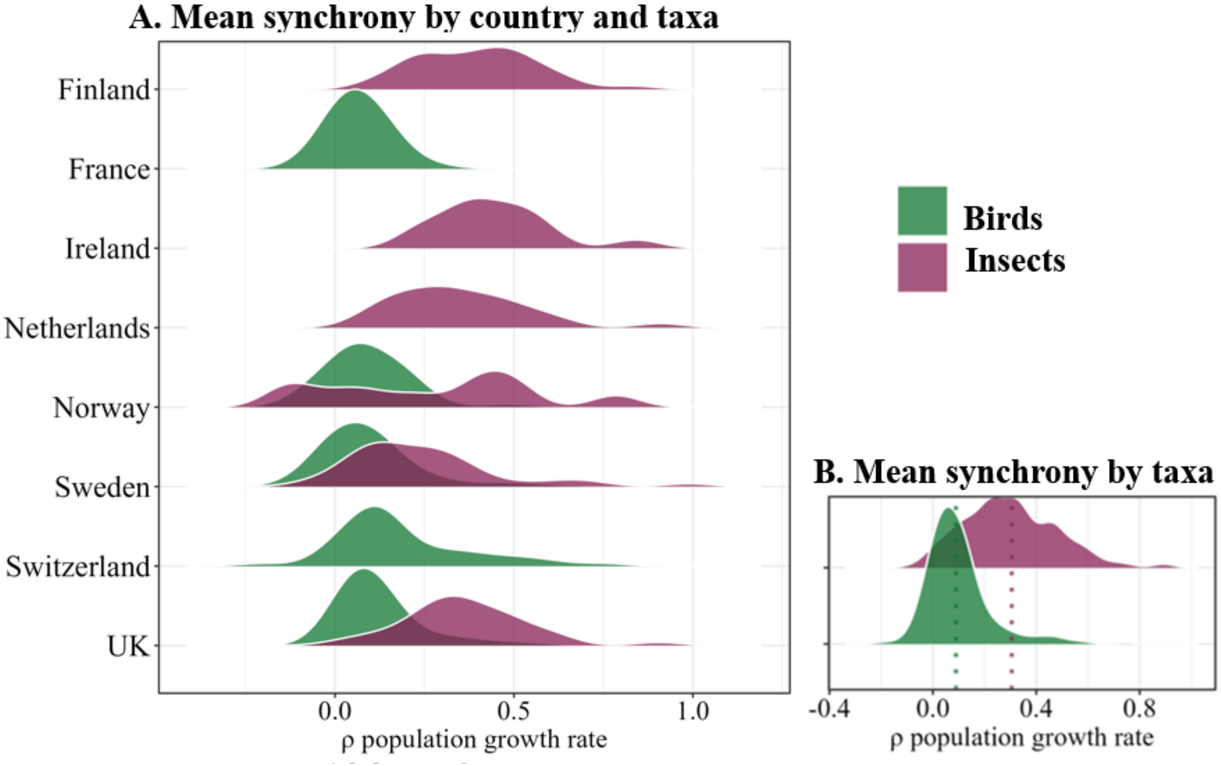
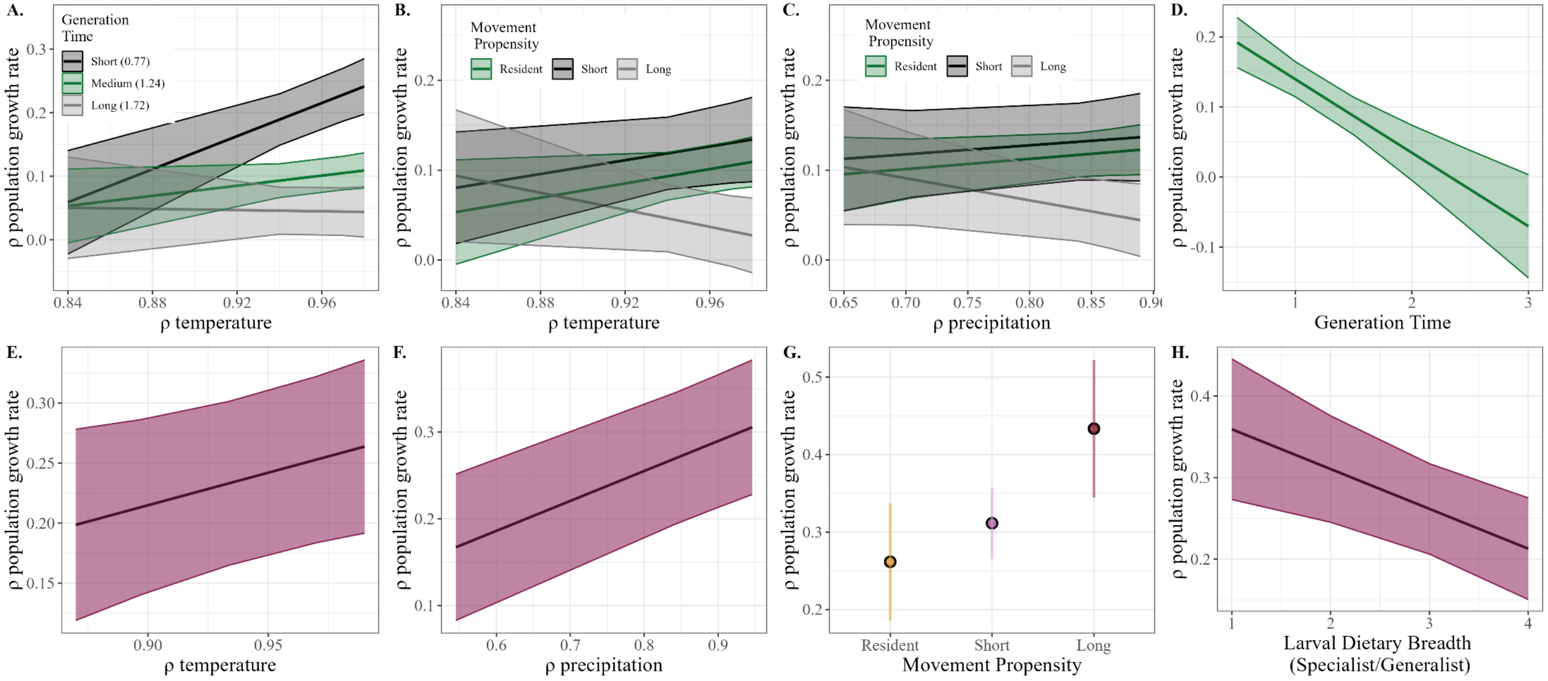


Figure 4: Effects of environmental variables and life history trait covariates included in top models for (A-D) birds and (E-F) insects. A) Synchrony in temperature and generation time in birds. B). Synchrony in precipitation and movement propensity in birds. C). Synchrony in temperature and movement propensity in birds. D) The effect of generation time on population growth rate in birds. E) Synchrony in temperature and spatial population growth rate in insects. F) Synchrony in precipitation and synchrony in population growth rates in insects. G) The effect of movement propensity on synchrony in population growth rate in insects. H) The effects of larval dietary breadth on synchrony in population growth rate in insects. 95% confidence intervals presented as shaded colors.



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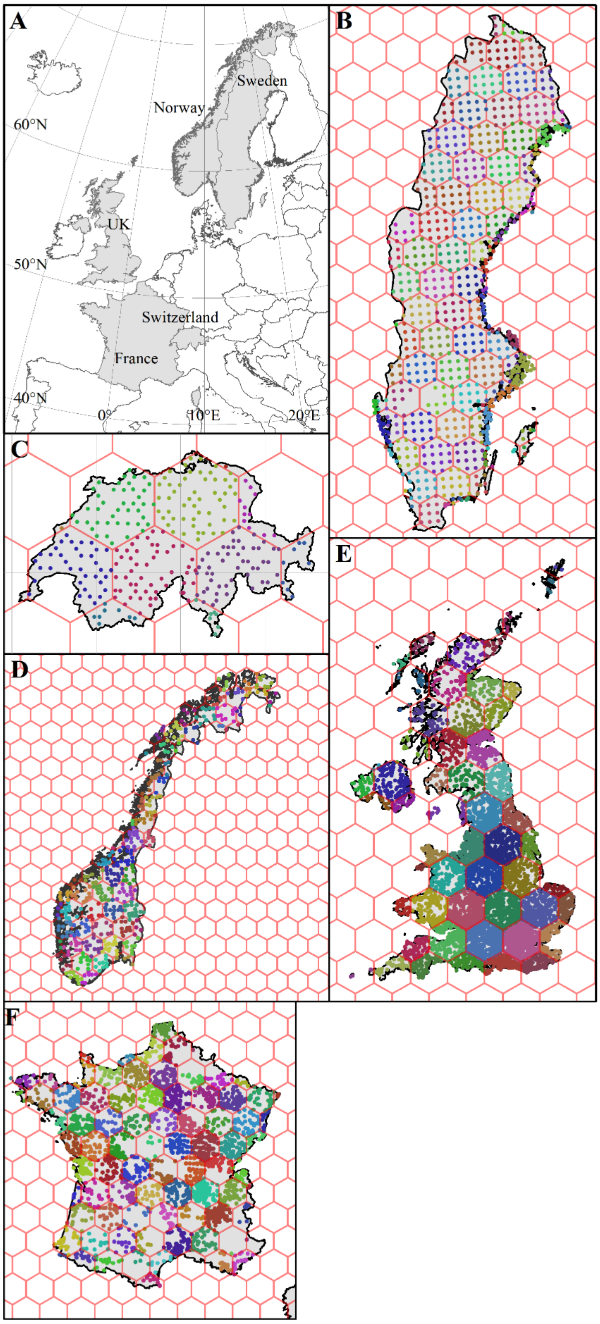
Supplemental Materials

APPENDIX 1. Figure S1. Figure of all study sites for birds in all countries. B) Sweden, C) Switzerland, D) Norway, E) the UK (United Kingdom), and F) France. 100km-diameter hexagonal grids used to aggregate survey sites shown in red.



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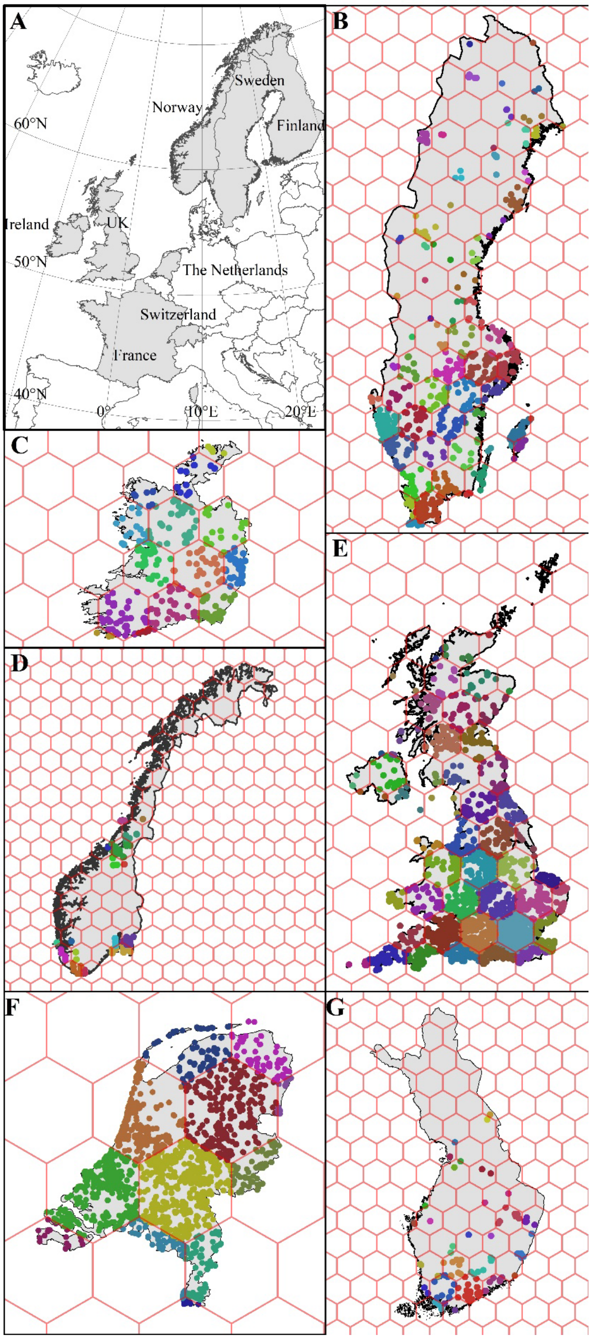
APPENDIX 1. Figure S2: Figure of all study sites for insects in all countries. B) Sweden, C) Ireland, D) Norway, E) the UK (United Kingdom), F) the Netherlands, and G) Finland. 100km-diameter hexagonal grids used to aggregate survey points shown in red.



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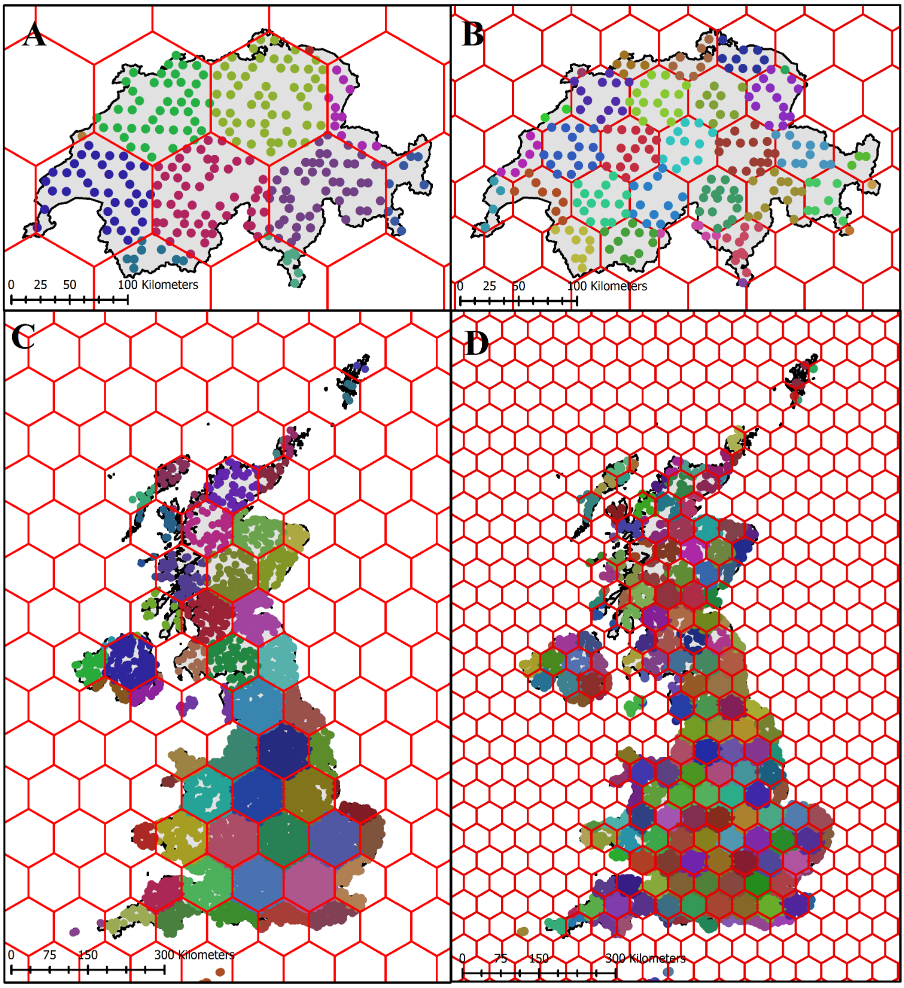
APPENDIX 1. Figure S3. Switzerland (A, B) and the United Kingdom (C, D) grid size comparison. Panels A and C show point aggregation for an overlay grid of 100km diameter per grid cell. Panels B and D show point aggregation for an overlay grid of 50km diameter per grid cell.



APPENDIX 2. Model selection results for the analysis of spatial synchrony in annual population growth rates of (A) birds and (B) insects in Europe. Synchrony estimates are based on pairs of populations ≤250km apart, merged in grid cells of size 50km diameter. Covariates designated with a “+” were present in model. Covariates included environmental synchrony (Env; in terms of mean summer precipitation [Precip] or mean summer temperature [Temp]), movement (Mvmt), fast-slow life history continuum (Fastslow), specialist/generalist (Specgen), and two-ways interactions between environmental synchrony and the life history traits. We also included a covariate for median distance at which synchrony was calculated (Med dist). Only one environmental covariate (precipitation or temperature) was included in each model because of collinearity, resulting in two different model sets. Only the top five models are presented (rank 1-5). We relied upon Akaike’s Information Criterion with a small sample size correction (*AIC_c)* for model selection and used Akaike model weights (*wt*) and ΔAIC_c to identify the top model. Number of parameters in model indicated by column k. LogLik = log-likelihood.

(A) Two top model sets for birds including synchrony in precipitation or synchrony in temperature with grid cell size 50km diameter

Taxa	Rank	Env. variable	Env	Mvmt	Fastslow	Specgen	Mvmt x Env	Slowfast x Env	Specgen x Env	k	LogLik	AICc	ΔAIC$_c$	wt
Birds	**1**	**Precip**	+	--	+	--	--	--	--	**5**	**298.42**	**-586.61**	**0**	**0.16**
Birds	2	Precip	+	+	+	--	--	--	--	7	300.00	-585.54	1.06	0.09
Birds	3	Precip	+	+	+	--	+	--	--	9	301.97	-585.21	1.39	0.08
Birds	4	Precip	+	--	+	--	--	+	--	6	298.48	-584.63	1.97	0.06
Birds	5	Precip	+	--	+	+	--	--	--	6	298.47	-584.60	2.00	0.06
Birds	1	Temp	+	--	--	+	--	--	--	4	296.14	-584.11	0	0.25
Birds	2	Temp	+	--	+	+	--	--	--	6	297.40	-582.45	1.65	0.11
Birds	3	Temp	+	--	--	+	+	--	--	5	296.18	-582.13	1.98	0.09
Birds	4	Temp	+	--	--	+	--	--	--	5	296.15	-582.05	2.06	0.09
Birds	5	Temp	+	--	+	+	+	--	--	7	297.51	-580.55	3.56	0.04

(B) Two top model sets for insects including synchrony in precipitation or synchrony in temperature with grid cell size 50km diameter

Taxa	Rank	Env. variable	Env	Mvmt	Fastslow	Specgen	Mvmt x Env	Slowfast x Env	Specgen x Env	k	LogLik	AICc	ΔAIC$_c$	wt
Insects	**1**	**Precip**	+	--	--	+	--	--	+	**6**	**58.21**	**-103.57**	**0**	**0.35**
Insects	2	Precip	+	--	--	+	--	--	--	5	57.06	-103.53	0.04	0.35
Insects	3	Precip	+	--	+	+	--	--	+	8	58.57	-.99.69	3.87	0.05
Insects	4	Precip	+	--	+	+	--	--	--	7	57.40	-99.68	3.88	0.05
Insects	5	Precip	+	+	--	+	--	--	--	7	57.19	-99.26	4.31	0.04
Insects	1	Temp	+	--	--	+	--	--	--	5	54.57	-98.57	0	0.41
Insects	2	Temp	+	--	--	+	--	--	+	6	55.35	-97.88	0.68	0.29
Insects	3	Temp	+	--	+	+	--	--	--	7	54.86	-94.61	3.95	0.06

Insects	4	Temp	+	+	--	+	--	--	--	7	54.74	-94.37	4.19	0.05
Insects	5	Temp	+	--	+	+	--	--	+	8	55.67	-93.88	4.68	0.39

APPENDIX 3. Country-specific mean (one standard error in parenthesis) within 250km of synchrony in precipitation (ρ_{precip}) and temperature (ρ_{temp}) with description of the periods included in the estimation. Months included had average temperature ≥ 5 degrees Celsius for the duration of the survey period.

Country	Avg. Start Month	Avg. End Month	Avg. Duration (months)	ρ_{precip} Birds	ρ_{temp} Birds	ρ_{precip} Insects	P_{temp} Insects
Finland	May	September	5	-	-	0.94 (0.04)	0.97 (0.00)
France	April	November	8	0.86 (0.04)	0.97 (0.00)	-	-
Ireland	April	November	8	-	-	0.94 (0.14)	0.87 (0.05)
Netherlands	April	November	8	-	-	0.89 (0.05)	0.98 (0.01)
Norway (Insects)	May	October	6	-	-	0.84 (0.13)	0.98 (0.00)
Norway (Birds)	June	September	4	0.64 (0.06)	0.84 (0.10)	-	-
Sweden (Insects)	May	October	6	-	-	0.54 (0.10)	0.89 (0.04)
Sweden (Birds)	May	September	5	0.89 (0.01)	0.97 (0.00)	-	-
Switzerland	May	October	6	0.83 (0.01)	0.98 (0.00)	-	-
United Kingdom	April	November	8	0.70 (0.06)	0.94 (0.01)	0.89 (0.03)	0.93 (0.01)

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APPENDIX 4: Correlations and dependencies between covariates used in analysis. For birds, position on the fast-slow life history continuum and mobility were not independent (chisq.test; p < 0.001). Position on the fast-slow life history continuum had a 0.35 correlation with specialist/generalist classification, while mobility and specialist/generalist classification were independent (ANOVA; p < 0.001). For insects, position on the fast-slow life history continuum was not independent from mobility (chisq.test; p < 0.001) and had a 0.21 correlation with specialist/generalist classification. Mobility and specialist/generalist classification were independent (ANOVA; p < 0.001).

A) Birds

	Specialist/generalist (continuous)	Mobility (categorical)
Mobility (categorical)	ANOVA: p < 0.001	--
Slow-fast (continuous)	corr = 0.35	chisq.test; p < 0.001

B) Insects

	Specialist/generalist (continuous)	Mobility (categorical)
Mobility (categorical)	ANOVA; p < 0.001	--
Slow-fast (continuous)	corr = 0.21	chisq.test; p < 0.001

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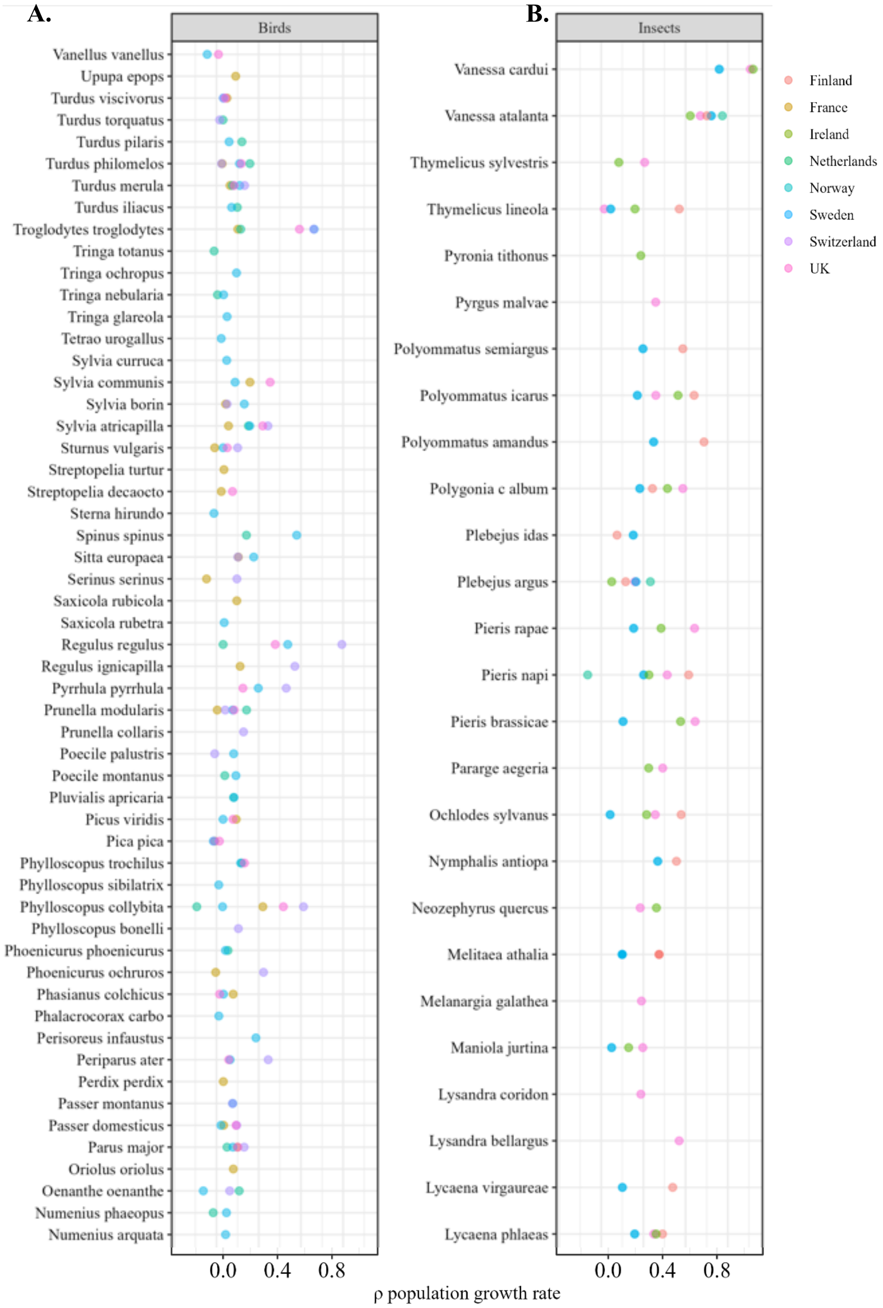
APPENDIX 5. The distribution of country-specific mean spatial synchrony for different species of birds and insects. Mean synchrony in population growth rate was calculated as the average of the pairwise synchrony estimates between all pairs of grid cells within 250km of one another. Species that had three or more estimates of synchrony have distributions shown in grey. Country from which estimate comes indicated by point color. Distributions of synchrony are calculated from the R package *ggridges* function *geom_density_ridges*, which computes a kernel density estimate from the data.



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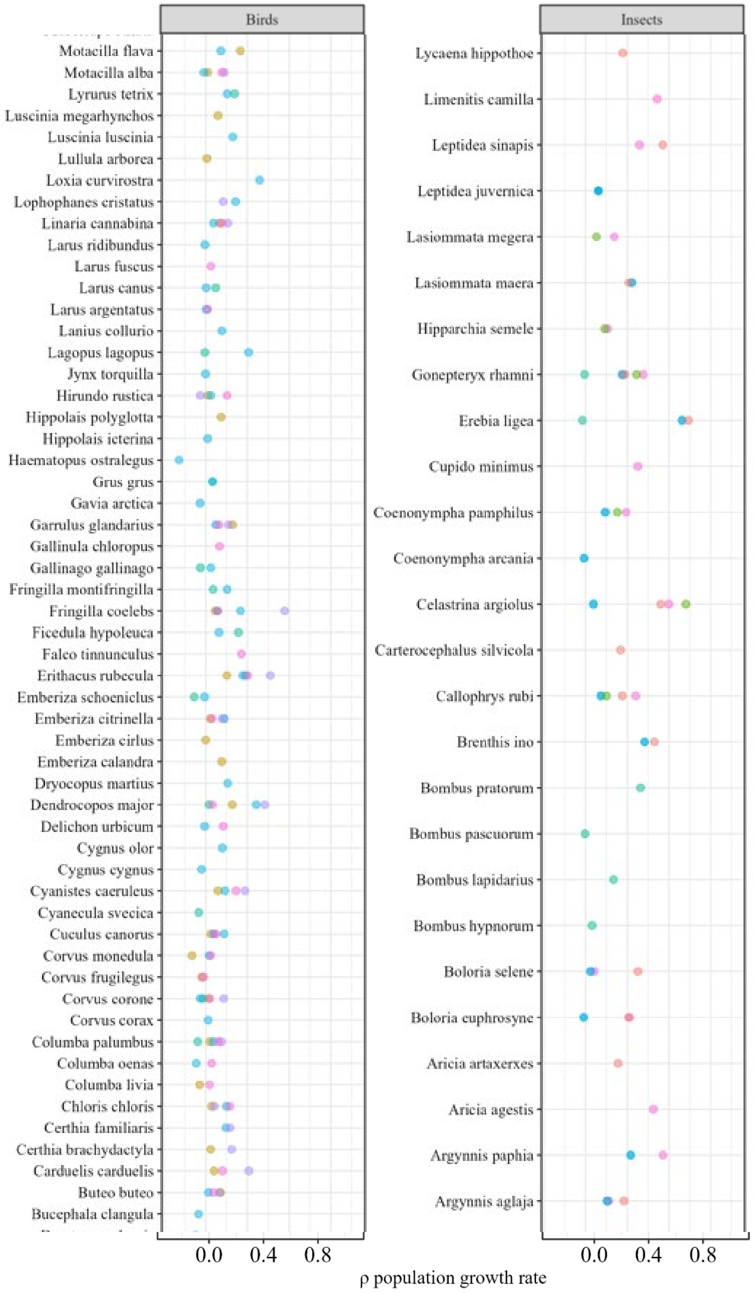

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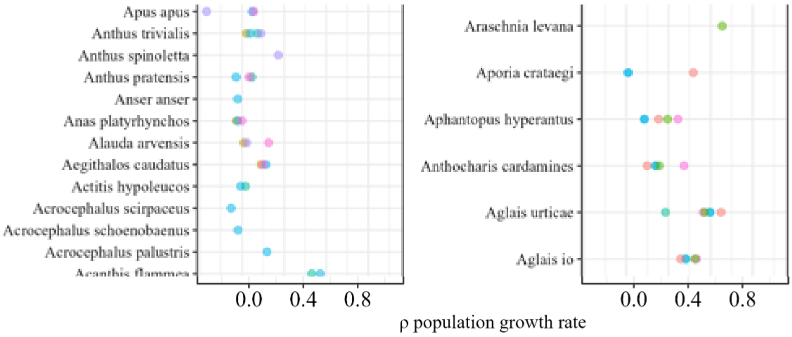

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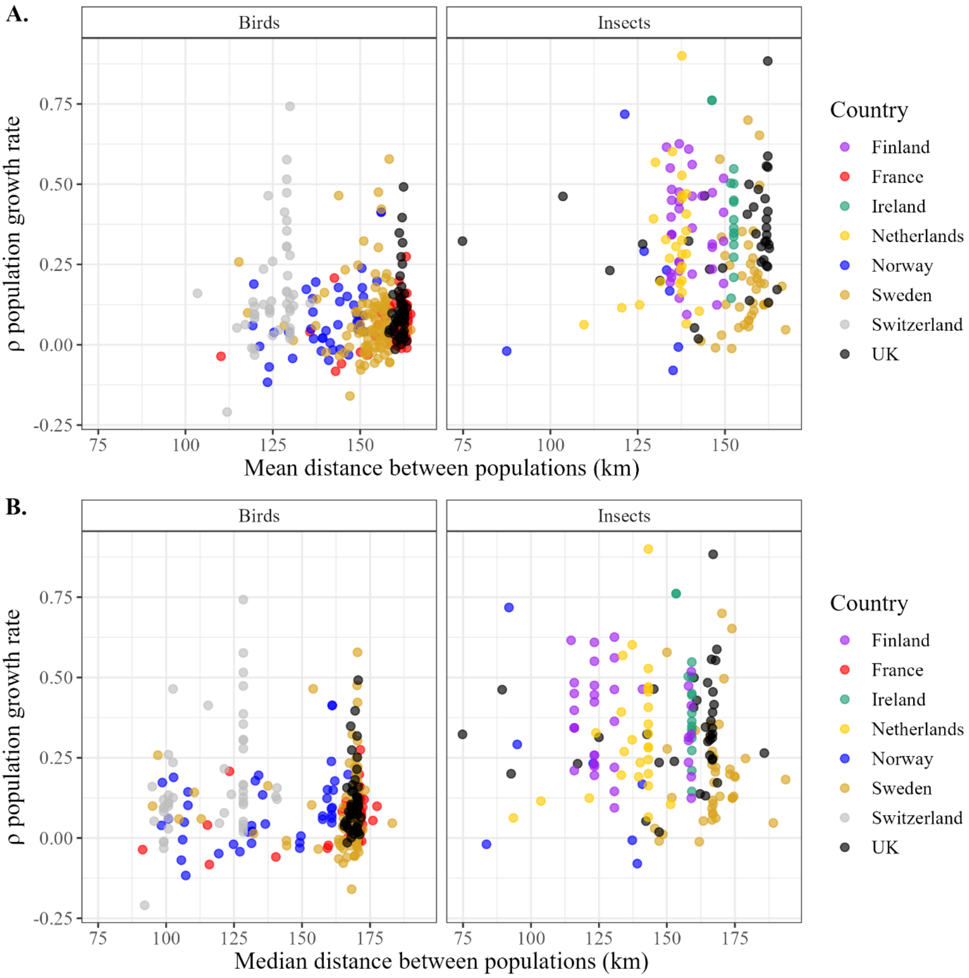
APPENDIX 6: Mean (A) and median (B) distances (km) between populations used to calculate syncrony in population growth rates for all populations within 250km. Colored dots represent individual species' mean distances separated by country and taxa.



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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer’s disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology

2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters

2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway

2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.

2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh
2019	Knut Jørgen Egelie	PhD Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	PhD Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales

2019	Kwaslema Malle Hariohay	PhD Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	PhD Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	PhD Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	PhD Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	PhD Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	PhD Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	PhD Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Emma-Liina Marjakangas	PhD Biology	Understanding species interactions in the tropics: dynamics within and between trophic levels
2019	Alex Kojo Datsomor	PhD Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (*Salmo salar L*): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	PhD Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo salar*) production and reproduction
2020	Rachael Morgan	PhD Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	PhD Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (*Salmo salar L.):* possible nutriomics approaches
2020	Haiqing Wang	PhD Biology	Utilization of the polychaete *Hediste diversicolor* (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for value adding applications'
2020	Louis Hunninck	PhD Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	PhD Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	PhD Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	PhD Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
2020	Lone Sunniva Jevne	PhD Biology	Development and dispersal of salmon lice (*Lepeophtheirus salmonis Krøyer*, 1837) in commercial salmon farming localities
2020	Sindre Håvarstein Eldøy	PhD Biology	The influence of physiology, life history and environmental conditions on the marine migration patters of sea trout
2020	Vasundra Touré	PhD Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications

2020	Silje Forbord	PhD Biology	Cultivation of *Saccharina latissima* (Phaeophyceae) in temperate marine waters; nitrogen uptake kinetics, growth characteristics and chemical composition
2020	Jørn Olav Løkken	PhD Biology	Change in vegetation composition and growth in the forest-tundra ecotone – effects of climate warming and herbivory
2020	Kristin Odden Nystuen	PhD Biology	Drivers of plant recruitment in alpine vegetation
2021	Sam Perrin	PhD Biology	Freshwater Fish Community Responses to Climate Change and Invasive Species
2021	Lara Veylit	PhD Biology	Causes and consequences of body growth variation in hunted wild boar populations
2021	Semona Issa	PhD Biology	Combined effects of environmental variation and pollution on zooplankton life history and population dynamics
2021	Monica Shilereyo	PhD Biology	Small Mammal Population Ecology and Ectoparasite Load: Assessing Impacts of Land Use and Rainfall Seasonality in the Serengeti Ecosystem, Tanzania
2021	Vanessa Bieker	PhD Biology	Using historical herbarium specimens to elucidate the evolutionary genomics of plant invasion
2021	Håkon Austad Langberg	PhD Biology	Fate and transport of forever chemicals in the aquatic environment: Partitioning and biotransformation of mixtures of Per- and Polyfluoroalkyl Substances (PFAS) from different point sources and resulting concentrations in biota
2021	Julie Renberg	PhD Biology	Muscular and metabolic load and manual function when working in the cold
2021	Olena Meleshko	PhD Biology	Gene flow and genome evolution on peatmosses (*Sphagnum*)
2021	Essa Ahsan Khan	PhD Biology	Systems toxicology approach for evaluating the effects of contaminants on fish ovarian development and reproductive endocrine physiology:A combination of field-, in vivo and ex vivo studies using Atlantic cod (*Gadus morhua*)
2021	Tanja Kofod Petersen	PhD Biology	Biodiversity dynamics in urban areas under changing land-uses
2021	Katariina Vuorinen	PhD Biology	When do ungulates override the climate? Defining the interplay of two key drivers of northern vegetation dynamics
2021	Archana Golla	PhD Biology	Impact of early life stress on behaviour and dorsal raphe serotonergic activity in zebrafish (*Danio rerio*)
2021	Aksel Alstad Mogstad	PhD Biology	Underwater Hyperspectral Imaging as a Tool for Benthic Habitat Mapping

2021	Randi Grønnstad	PhD Biology	Per- and polyfluoroalkyl substances (PFAS) in ski products: Environmental contamination, bioaccumulation and effects in rodents
2021	Gaspard Philis	PhD Biology	Life cycle assessment of sea lice treatments in Norwegian net pens with emphasis on the environmental tradeoffs of salmon aquaculture production systems
2021	Christoffer Høyvik Hilde	PhD Biology	Demographic buffering of vital rates in age-structured populations”
2021	Halldis Ringvold	Dr.Philos	Studies on Echinodermata from the NE Atlantic Ocean - Spatial distribution and abundance of Asteroidea, including taxonomic and molecular studies on Crossaster and Henricia genera- Value-chain results, including test fishery, biology, market and nutritional analysis, on Parastichopus tremulus (Holothuroidea) from the Norwegian coast
2021	Elise Skottene	PhD Biology	Lipid metabolism and diapause timing in Calanus copepods. The impact of predation risk, food availability and oil exposure
2021	Michael Le Pepke	PhD Biology	The ecological and evolutionary role of telomere length in house sparrows
2022	Niklas Erik Johansson	Dr. Philos	On the taxonomy of Northern European Darwin wasps (Hymenoptera: Ichneumonidae).
2022	Jonatan Fredricson Marquez	PhD Biology	Understanding spatial and interspecific processes affecting population dynamics in a marine ecosystem.
2022	Anne Mehlhoop	PhD Biology	Evaluating mitigation measures to reduce negative impacts of infrastructure construction on vegetation and wildlife.
2022	Malene Østreng Nygård	PhD Biology	Integrative biosystematics and conservation genomics – holistic studies of two red-listed plants in Norway
2022	Martin René Ellegaard	PhD Biology	Human Population Genomics in Northern Europe in the Past 2000 years
2022	Gaute Kjærstad	PhD Biology	The eradication of invasive species using rotenone and its impact on freshwater macroinvertebrates
2022	Stefan Vriend	PhD Biology	On the roles of density dependence and environmental fluctuations in driving eco-evolutionary dynamics of hole-nesting passerines
2022	Zaw Min Thant	PhD Biology	Anthropogenic and Environmental factors driving the Human-Elephant Conflict in Myanmar
2022	Prashanna Guragain	PhD Biology	Population analysis and structure and RNA interference to understand salmon lice biology and a review of the principles of controlling infestation in aquaculture facilities.
2022	Ronja Wedegärtner	PhD Biology	Highways up the mountains? Trails as facilitators for redistribution of plant species in mountain areas

2022	Wouter Koch	PhD Biology	Improving the citizen science data corpus for science and management
2022	Qianwen Ding	PhD Biology	Risk of Feed Additives in High-lipid Fish Diets: Effects of Propionate and Docosahexaenoic Acid on Liver and Intestinal Health in Zebrafish (Danio rerio Hamilton-Buchanan, 1822)
2022	Mingxu Xie	PhD Biology	Dietary supplementation of commensal Cetobacterium somerae ameliorates the problems associated with fish meal replacement by plant proteins in fish
2022	Sarah Louise Lundregan	PhD Biology	Impact of genetics and epigenetic processes on parasite infection dynamics in the house sparrow
2022	Stanslaus Mwampeta	PhD Biology	An assessment of field techniques to estimate lion presence and abundance
2023	Mari Aas Fjelldal	PhD Biology	Physiological and ecological challenges faced by small bats in summer
2023	Caitlin Mandeville	PhD Biology	Applications of participatory monitoring in biodiversity science and conservation
2023	Rune Sørås	PhD Biology	Energy management of heterothermic bats at northern latitudes: Understanding the physiological flexibility of bats and how this enables them to live in the northern edge of their distribution
2023	Dilan Saatoglu	PhD Biology	Spatio-temporal dispersal dynamics of a natural house sparrow metapopulation
2023	Christine Klykken	PhD Biology	Nephrocalcinosis in juvenile farmed Atlantic salmon
2023	Anna Haukedal Andreassen	PhD Biology	Mechanisms and evolution of thermal tolerance in fish
2023	Mathew Avarachen	PhD Biology	Carbon sequestration by microbial carbon pump with production of recalcitrant dissolved organic matter in different marine environments
2023	Lisa Sandal	PhD Biology	Spatiotemporal dynamics of avian communities

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