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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

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.

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

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:

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

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.
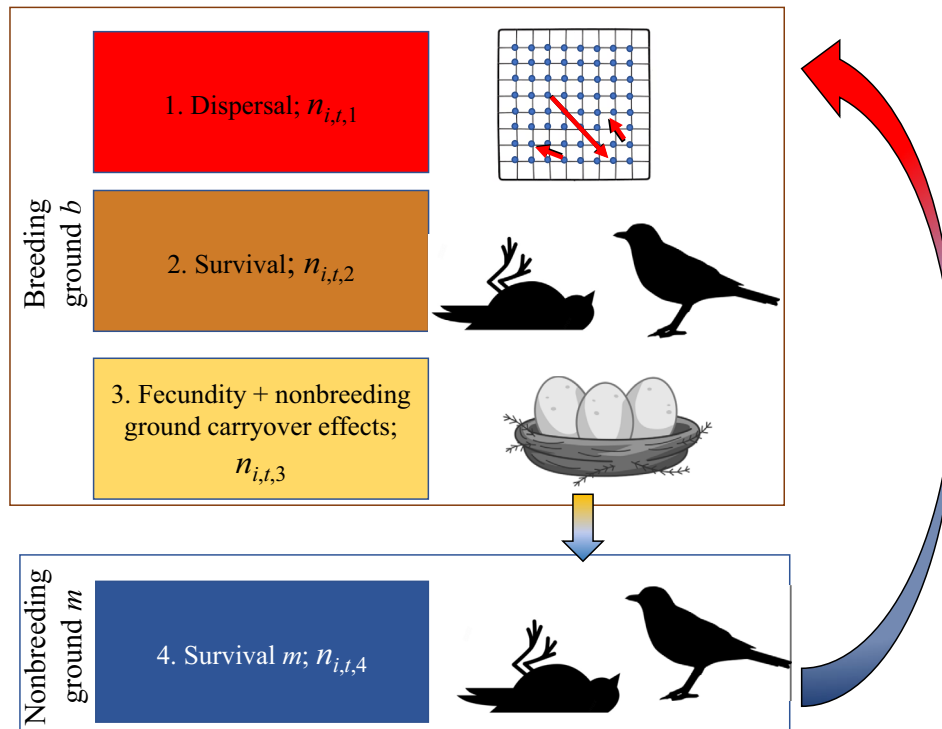
FIGURE 1 Schematic representing one annual cycle t for migratory populations. The annual cycle in the population model consists of four steps. Populations are on one shared breeding ground b, where there is environmental noise determined by an environmental field in which populations closer together 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:

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

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*):

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

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:

$$n_{i,t,4} = \left(\text{inv logit}[\text{logit}(S_m) + E_m + v(n_{i,t})]\right) \times n_{i,t,3}, \quad (4)$$

where S_m is the nonbreeding ground/overwintering survival, E_m is the nonbreeding ground environmental noise (see *Variation in environmental noise*), and $v(n_{i,t})$ 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

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 ($r_{between} = 0, 0.25, 0.50, 0.75, 1$). Finally, we ran the simulations with different within nonbreeding ground correlation ($r_{within} = 0, 0.25, 0.50, 0.75, 1$).

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
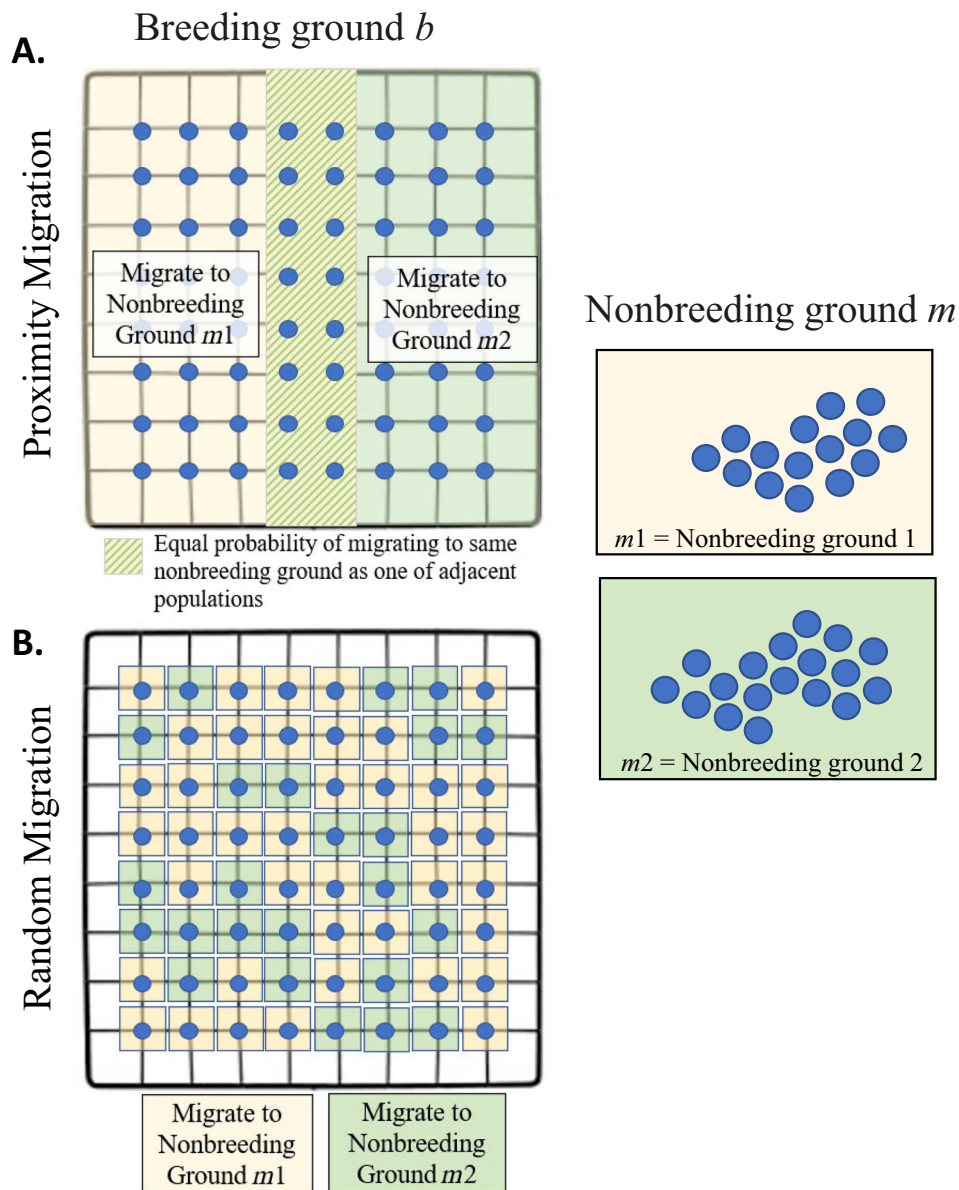
FIGURE 2 Schematic of (A) proximity and (B) random migration. Colors represent the different nonbreeding grounds to which populations migrate. (A) In proximity migration, each population migrates to the same nonbreeding ground as their near neighbors. The populations in the buffer region between nonbreeding 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
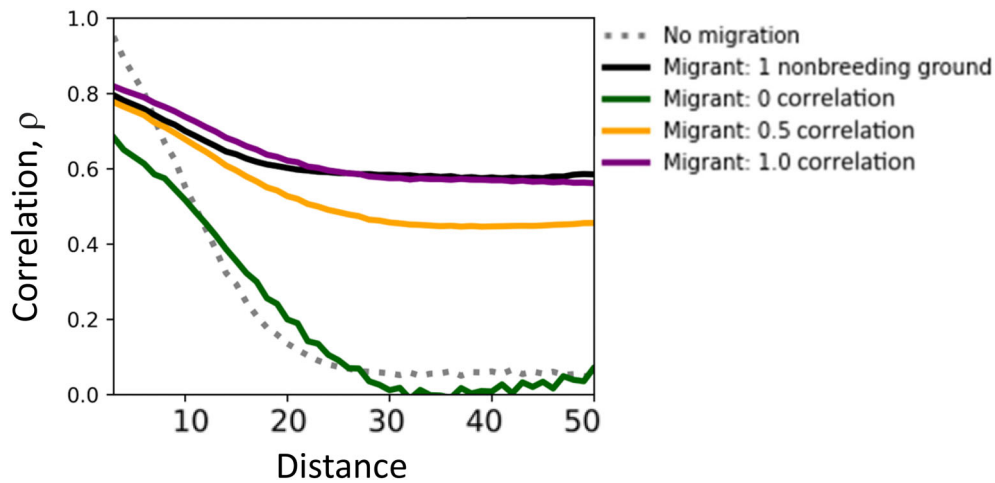
FIGURE 3   Average correlation in abundances (ρ) for a given distance between two populations on the breeding ground when there was no migration ("no migration") and when migrants went to one or multiple (i.e., four shown here) nonbreeding grounds with varying correlation between them. Within nonbreeding 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 $r_{within} = 0.75$.

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
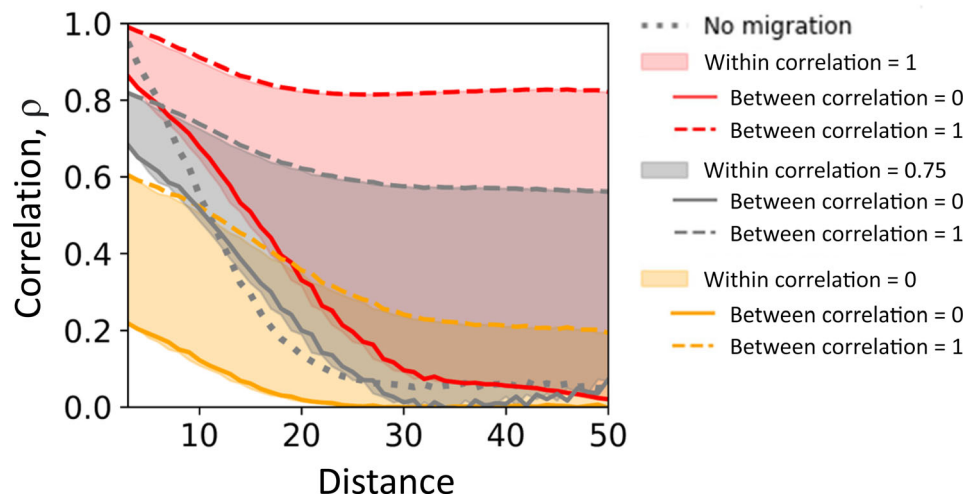
FIGURE 4 Relationship between within (r_{within}) and between ($r_{between}$) nonbreeding ground environmental autocorrelation and correlation in abundance (ρ). Ranges of possible average abundance correlation (ρ) for a given distance between two populations on the breeding ground are shown for different 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.
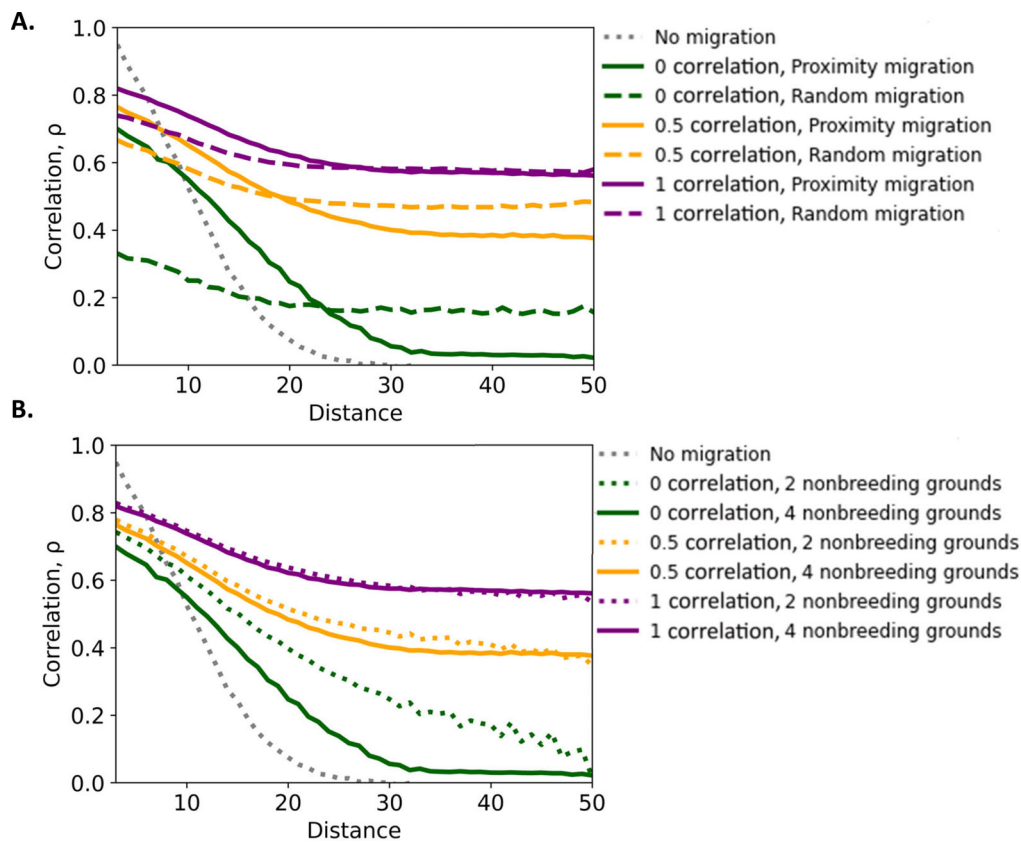

FIGURE 5 (A) Average spatial population synchrony on the breeding ground changed based on environmental autocorrelation experienced on nonbreeding grounds and the type of migration. Populations went to four nonbreeding grounds. (B) Average spatial population synchrony on the breeding ground changed based 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

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,

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

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.