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Review and synthesis

The Moran effect revisited: spatial population synchrony under global warming

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The world is spatially autocorrelated. Both abiotic and biotic properties are more similar among neighboring than distant locations, and their temporal co-fluctuations also decrease with distance. P. A. P. Moran realized the ecological importance of such 'spatial synchrony' when he predicted that isolated populations subject to identical log-linear density-dependent processes should have the same correlation in fluctuations of abundance as the correlation in environmental noise. The contribution from correlated weather to synchrony of populations has later been coined the 'Moran effect'. Here, we investigate the potential role of the Moran effect in large-scale ecological outcomes of global warming. Although difficult to disentangle from dispersal and species interaction effects, there is compelling evidence from across taxa and ecosystems that spatial environmental synchrony causes population synchrony. Given this, and the accelerating number of studies reporting climate change effects on local population dynamics, surprisingly little attention has been paid to the implications of global warming for spatial population synchrony. However, a handful of studies of insects, birds, plants, mammals and marine plankton indicate decadal-scale changes in population synchrony due to trends in environmental synchrony. We combine a literature review with modeling to outline potential pathways for how global warming, through changes in the mean, variability and spatial autocorrelation of weather, can impact population synchrony over time. This is particularly likely under a 'generalized Moran effect', i.e. when relaxing Moran's strict assumption of identical log-linear density-dependence, which is highly unrealistic in the wild. Furthermore, climate change can influence spatial population synchrony indirectly, through its effects on dispersal and species interactions. Because changes in population synchrony may cascade through food-webs, we argue that the (generalized) Moran effect is key to understanding and predicting impacts of global warming on large-scale ecological dynamics, with implications for extinctions, conservation and management.

Keywords: climate change, density regulation, generalized Moran effect, nonlinear dynamics, population dynamics

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Introduction

Almost a century ago, Elton (1924) described how the fluctuations in population sizes of snowshoe hare *Lepus americanus* were spatially autocorrelated across North America. He proposed that this phenomenon was caused by a common environmental factor influencing hare population dynamics over large areas, and that this in turn caused corresponding cycles in the hare's main predator, Canada lynx *Lynx canadensis*. This was one of the first times spatiotemporal ecological patterns were described and analyzed in a scientifically rigorous way. Revisiting these data a few decades later, Moran (1953) formulated a very simple mathematical relationship between the spatial autocorrelation in weather (or other environmental conditions) and the synchrony in the dynamics of spatially separated populations (Box 1). From both a mathematical and ecological point of view, the logic behind and results from Moran's work are quite straightforward, predicting that the dynamics of two populations having the same log-linear density dependence and same directional effect of environmental variation should display similar synchrony in their dynamics as the synchrony seen in their environment.

Despite its implications for large-scale population dynamics, Moran's theorem did not receive much attention until Royama revisited it in his seminal book on population dynamics (Royama 1992). This, in turn, initiated a decade of substantial theoretical (Ranta et al. 1995, Haydon and Steen 1997, Heino et al. 1997, Lande et al. 1999, Kendall et al. 2000, Ripa 2000, Engen et al. 2002, 2005, Engen and Sæther 2005) and empirical (Hanski and Woiwod 1993, Myers et al. 1995, Grenfell et al. 1998, Myers 1998, Paradis et al. 1999, Ims and Andreassen 2000, Benton et al. 2001, Koenig 2002, Peltonen et al. 2002, Grøtan et al. 2005) efforts to study population synchrony, in particular environmentally driven spatial population synchrony, often termed the 'Moran effect' (reviewed by Bjørnstad et al. 1999, Hudson and Cattadori 1999, Koenig 1999, Liebhold et al. 2004; see also Box 1).

These rapid scientific developments led to several major insights; 1) the pairwise population synchrony (i.e. correlation in fluctuations) tends to decrease with increasing distance between populations (Box 2) (Lande et al. 1999); 2) it is often difficult to disentangle the effects of environmental synchrony from other potential drivers of synchrony, notably dispersal and species interactions (Kendall et al. 2000); 3) Moran's strict assumptions of no dispersal and identical log-linear density dependence between populations (Box 1) seem rarely, if ever, met in the wild (Lande et al. 1999, Engen and Sæther 2005, Liebhold et al. 2006); 4) a more 'generalized Moran effect' (easing its original assumptions; Engen and Sæther 2005) is, however, theoretically expected – and often observed – to characterize spatiotemporal population dynamics across life histories and ecosystems (Liebhold et al. 2004); 5) strong spatial population synchrony is expected to increase species-level extinction risk (Heino et al. 1997); and, importantly, 6) patterns of spatial environmental autocorrelation, and thereby population synchrony, can change over time (Koenig 2002, Post and Forchhammer 2002, 2004). Accordingly, Post and Forchhammer (2002) pointed out that the influence of environmental factors on population synchrony could become important under climate change.

In more recent years, substantial effort has gone into identifying the weather patterns and variables that have a

Box 1. The Moran effect

In 1953, P. A. P. Moran proposed a model to explain how correlations in local meteorological conditions between two regions could explain observed correlations in population fluctuations between the two regions. He showed that if two populations follow dynamics defined by

$$x_t = ax_{t-1} + bx_{t-2} + \varepsilon_t$$

$$z_t = az_{t-1} + bz_{t-2} + \eta_t$$

(where x and z are on the log scale) the correlation between x_t and z_t will be equal to that between ε_t and η_t. In other words, if the external forces, ε_t and η_t, are correlated, the populations, x and z, will fluctuate in synchrony with the same level of correlation. This assumes

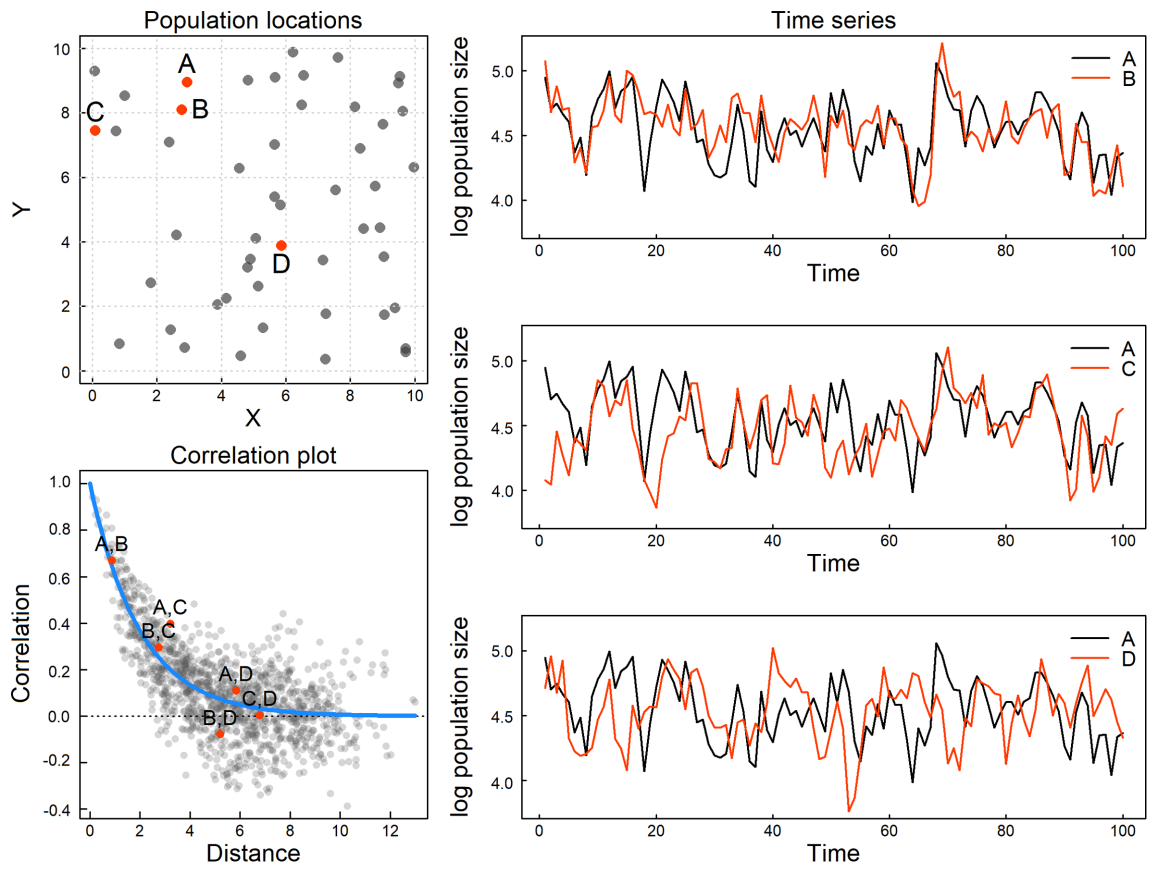
- log-linear density dependence
- identical structure between the two population processes
- no dispersal between the populations.

Note that ε_t and η_t represent the environmental noise affecting each of the populations, which is a combination of the environment itself and the way in which the environment affects the population dynamics. In real populations, the correlation between these two terms rarely, if ever, equals the correlation in the environment.

Systems that fulfil all of the above assumptions are rare, but synchronizing effects of a common environment have been demonstrated in a wide range of systems (see Introduction). It has therefore become quite common to use the term 'Moran effect' when referring to any population synchrony caused by environmental effects, even when the dynamics do not strictly follow 'Moran's theorem' presented above (Ranta et al. 2006), but this usage has not become ubiquitous. In this paper, we therefore consistently use the term 'generalized Moran effect' when considering the general synchronizing effect of correlated environments.

Box 2. What is population synchrony?

The environment fluctuates in time, contributing to fluctuations in population size. Populations that are closer to each other in space are expected to experience more similar environmental fluctuations than those that are further apart. Because of this, temporal population fluctuations are expected to be more closely correlated (i.e. more synchronous) among populations that are near each other in space than those which are further apart. Population synchrony is often measured as the correlation of temporal fluctuations in (log) population size, ranging from −1 (perfectly negatively correlated fluctuations) to 0 (independent fluctuations) and 1 (perfectly positively correlated fluctuations). Other measures of synchrony also exist (Post and Forchhammer 2002, Sheppard et al. 2016), however, their main principle is often similar as described here. Both the spatial and temporal component of the environment are often assumed to follow a spatial autocorrelation function such as the exponential function, causing a decrease in correlation with increasing distance. This is demonstrated in the figure below, where time series of log population size from near populations (e.g. A and B, top right panel) are more correlated than those of more distant populations (e.g. A and D, bottom right panel). Pairwise correlations between populations at different distances reveal the spatial pattern in synchrony (bottom left panel).



synchronizing effect on population dynamics in specific systems. This covers species from a wide range of taxa, such as feral sheep *Ovies aries* (Grenfell et al. 1998), roe deer *Capreolus capreolus* (Grøtan et al. 2005), caribou and reindeer *Rangifer tarandus* (Post and Forchhammer 2002, 2004, 2006, Hansen et al. 2019a), passerine birds (Sæther et al. 2007), fishes (Cattanéo et al. 2003, Tedesco et al. 2004), moths (Allstadt et al. 2015), aphid pests (Sheppard et al. 2016), plants (Koenig and Knops 1998, 2013, Defriez and Reuman 2017), giant kelp *Macrocystis pyrifera* (Cavanaugh et al. 2013), zooplankton (Defriez et al. 2016) and phytoplankton (Sheppard et al. 2019). Still, almost two decades after Post and Forchhammer (2002) first pointed out the potential importance of climate change, only a handful of studies have attempted to look at how changes in the climate, weather variables and environment over time might influence spatial population synchrony (Post and Forchhammer 2004, Jepsen et al. 2009, Allstadt et al. 2015, Defriez et al. 2016, Koenig and Liebhold 2016, Sheppard et al. 2016, Shestakova et al. 2016, Defriez and Reuman 2017, Kahilainen et al. 2018). This is concerning for two reasons. First, there is now compelling evidence that ongoing and anticipated future global warming might cause dramatic changes in both the mean, variability and spatial autocorrelation of the weather and environment (Koenig 2002, IPCC 2013). Second, and linked to this, there is an accelerating number of studies from different types of

ecosystems reporting climate change impacts on local population (and community) dynamics. This includes, in particular, effects of changes in mean local weather, i.e. climate trends (Walther et al. 2002, Parmesan and Yohe 2003, Hansen et al. 2019a), but also changes in weather variance and frequency of extreme events (Parmesan et al. 2000, Thompson et al. 2013, Bailey and van de Pol 2016, Vázquez et al. 2017, Hansen et al. 2019b), and in regional weather patterns (e.g. El Niño events or the North Atlantic Oscillation, NAO; Stenseth et al. 2003).

Here, we address the important question of how climate change will affect population synchrony. We review the empirical evidence and outline some pathways for how global warming can significantly alter patterns of spatial population synchrony, either directly through climate effects on population dynamics, or indirectly through effects on dispersal and species interactions, in turn influencing spatial patterns of population dynamics (Fig. 1). In particular, we address the implications of relaxing the strict assumptions of Moran's theorem (a 'generalized Moran effect'; Engen and Sæther 2005). Based on this, we argue that the generalized Moran effect is key to a predictive understanding of large-scale ecological outcomes of global warming.

Relaxing the assumptions: a generalized Moran effect

Moran's theorem (Box 1) assumes log-linear density dependence that does not vary among populations. However, population dynamics are inherently nonlinear because of an upper limit on the maximum growth rate (Royama 1992, 2005, Grenfell et al. 1998), and different populations often show different strengths of density dependence (Liebhold et al. 2004, Engen and Sæther 2005). Most empirical studies suggest that correlations in abundance are smaller and decline faster with distance than the corresponding correlation structure of key environmental variables (Liebhold et al. 2004, 2006, Liebhold 2012). This has spurred several studies investigating the effects of violating assumptions of the original Moran's theorem. Hugueny (2006) studied the effect of variation in log-linear density dependence among populations, and Royama (2005) and Engen and Sæther (2005) demonstrated how parameters in nonlinear density-dependent models influence the synchronizing effect of the environment. One key finding from these studies is that, when assuming no synchronizing effect of dispersal or trophic interactions, deviations from assumptions in Moran's theorem cause the correlation in abundance to be less than that of the environment (but see Desharnais et al. 2018). Thus, the presence of nonlinear dynamics means that population synchrony observed in nature may often be the result of a much stronger underlying environmental correlation than one would predict from the original Moran theorem (Grenfell et al. 1998). It is therefore crucial to consider the more generalized version of the Moran effect if we are to understand how climate, and in particular climate change, affects population synchrony.

Spatial population synchrony under global warming

In this section we first look at how different types of environmental change can affect population synchrony directly by influencing aspects of population dynamics, and then discuss less direct effects mediated through dispersal and species interactions.

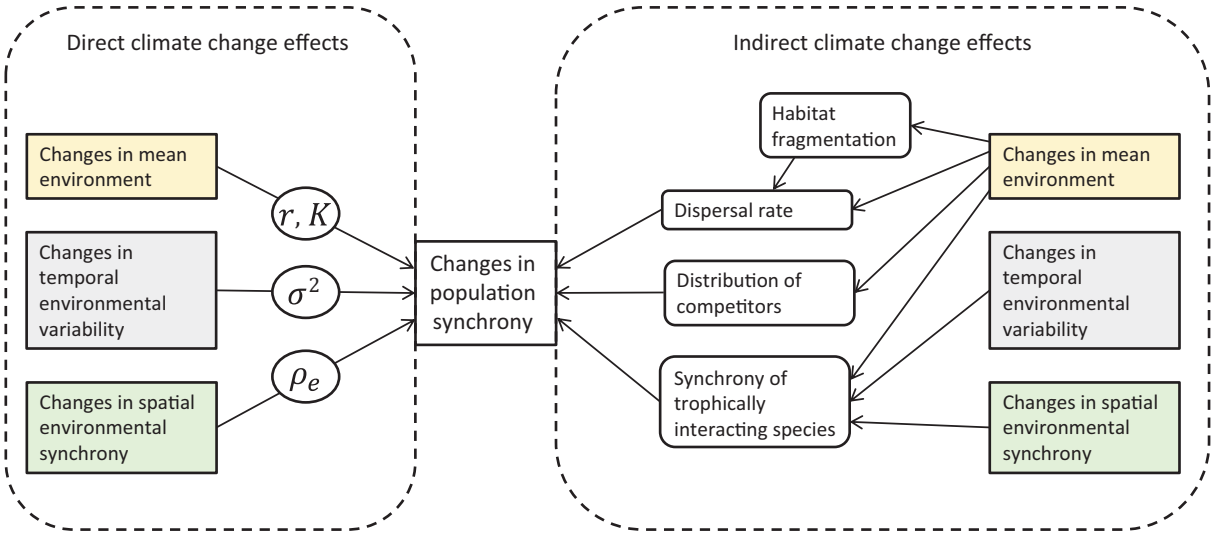


Figure 1. Direct and indirect pathways discussed in this paper through which climate change can affect population synchrony. Parameters in ovals on direct pathways relate to the model in Box 3, with intrinsic population growth rate r, carrying capacity K, environmental variance σ^2 and correlation in environmental noise ρ_e. Differences among populations in density dependence and current environment will influence responses along many of these pathways (as discussed in the main text).

Changes in the environment can influence the correlation of abundances by changing various components of the local population dynamics or by changing the correlation of the environmental noise among populations. In a hypothetical system that fulfills the assumptions of Moran's theorem, only changes in the correlation of the environmental noise are expected to influence population synchrony, but in systems with spatially variable nonlinear dynamics, as expected in the wild, the picture is more complicated (Box 3). We therefore focus on the more realistic nonlinear dynamics in the following.

The environment inhabited by a species often has an underlying spatial structure, such as along latitudinal and altitudinal gradients. The effect on populations of changes in a weather variable might depend on this underlying structure and the associated habitat heterogeneity (Sæther 1997, Engen and Sæther 2005, Anders and Post 2006, Post et al. 2009a, Hansen et al. 2019a). For example, population responses to a small increase in temperature will likely differ between populations currently experiencing temperatures in the lower range of their thermal tolerance, compared to populations that are already close to the upper limit of their thermal tolerance (Sunday et al. 2011, 2012). Then, a temperature increase that has a positive effect on the growth rate of the former population, might have a strong negative effect on the latter. Similarly, the effects of a change in winter precipitation amounts might differ between areas where the precipitation falls as snow and those where it falls as rain, such as along coast-inland gradients (Hansen et al. 2019a). Such habitat heterogeneity can cause populations to have different patterns of density regulation, and will also decrease the correlation in environmental noise affecting the populations (Box 1), both of which will tend to decrease population synchrony as well (Box 3). Population differences of this type are most striking when they cause systems to approach or cross a threshold of some sort (sometimes even a 'tipping point', causing sudden changes that are difficult to reverse; Scheffer et al. 2009), but even small differences in responses to environmental variables, which are likely to be widespread (Stenseth et al. 2002, 2004), could have important implications for predictions of how environmental change will influence population synchrony.

Changes in the mean environment

Annual or seasonal measures of precipitation and temperature are environmental variables often suggested to synchronize vital rates (Mallory et al. 2018), abundance proxies (Defriez et al. 2016, Shestakova et al. 2016) or population dynamics (Liebhold et al. 2004). Mean global land and ocean surface temperatures have increased over the past hundred years and are expected to continue to rise in most regions (Hansen et al. 2006). Similarly, mean levels of precipitation are also expected to shift, although the direction of this shift will likely differ among and even within regions (such as within the Arctic; AMAP 2019), with some areas becoming wetter and others drier (IPCC 2013). Can overall changes in mean environmental drivers like temperature and precipitation influence population synchrony? Changes in the mean environment can be expected to influence the intrinsic growth rate and/or the carrying capacity of populations. In Box 3 we show an example system in which a change in the environment causes a reduction in r. We see that, given our simple population model, such a change can have quite a dramatic influence on population synchrony (Box 3, Fig. b), especially when there is a difference in density regulation between populations. This implies that expected changes in mean environmental variables might well have important effects on patterns of population synchrony, and that this possibility deserves more attention.

Changes in temporal environmental variability

While ecological impacts of changes in average weather conditions have been quite extensively studied over many years (Walther et al. 2002, Sæther et al. 2004, Post 2013), less attention has been paid to the potential effects of changes in weather (or climatic) variability (Bailey and van de Pol 2016, Vázquez et al. 2017). However, observations suggest, and climate models predict, larger weather variability and more frequent extreme events in many regions under future global warming (Easterling et al. 2000, Goodkin et al. 2008, Cai et al. 2014, Moore 2016, Diffenbaugh et al. 2017), which can have profound influences on biological processes (Vázquez et al. 2017, Pearse et al. 2017), including local population and community dynamics (Parmesan et al. 2000, Holmgren et al. 2006, Hansen et al. 2013, 2019b). Here, we show that an overall increase in temporal environmental variability is likely to decrease population synchrony (Box 3, Fig. a, b). Note that the shape of this relationship will depend on other factors, particularly on whether the change in the environment also alters the way populations are affected by the environment (i.e. how a certain level of the environmental variable influences population growth). As for changes in the mean environment (see above), we are not aware of any studies that have attempted to demonstrate this relationship empirically.

One special case of increased temporal environmental variability is when extreme weather events, such as heatwaves, droughts or flooding, become more common. The long-term and large-scale ecological impacts of more frequent extreme events are still not well understood (Bailey and van de Pol 2016). An extreme climatic event can indeed force different populations impacted by the same perturbation into immediate population synchrony (e.g. a simultaneous population crash), possibly with a long-term effect due to a common recovery phase. However, the spatial extent of such synchronization will of course depend on the extent of the event. In fact, because some types of events, such as extreme amounts of precipitation, may occur rather locally, a desynchronizing effect on population dynamics can sometimes be expected during and following the event. The population synchrony implications of an increase in extreme climatic events due to global warming are therefore likely to be very case-specific.

Box 3. How climate change may affect population synchrony

The model

The Moran theorem (Box 1) is based on the unrealistic assumption of log-linear density dependence that does not vary among populations. To illustrate some key ways in which climate change can affect population synchrony in a more realistic population model, we will adopt a simplified version of the model described by Engen and Sæther (2005).

The stochastic log-linear model and the (moderately) nonlinear logistic model of population growth both contain the parameters N (population size), r (intrinsic population growth), K (carrying capacity) and σ^2 (environmental variance). Using the transformation $g(N) = \ln N^{-1}$ and $g(N) = 1 - N^{-1}$ for the log-linear and logistic form of density dependence respectively, the dynamics of the transformed variable X can be written as a stochastic differential equation

$$dX = (\alpha - \beta X)dt + (1 - \theta X)\sigma dB$$

where $\theta = 0$ and $\theta = 1$ for loglinear and logistic dynamics respectively, and dB is the infinitesimal increment of a Brownian motion so that $E(dB) = 0$ and $\mathrm{Var}(dB) = dt$. Furthermore, $\alpha = r - (1/2)\sigma^2$, $\beta = r/g(K) - (1/2)\theta\sigma^2$. We will here consider two populations (subscript 1 and 2) with correlation ρ_e in environmental noise. Following Engen and Sæther (2005) we can for a given set of parameters $(r_1, r_2, K_1, K_2, \sigma_1^2, \sigma_2^2, \rho_e)$ calculate the population synchrony measured as correlation of abundance ρ_x by using equations

$$\rho_x = \mathrm{corr}(X_1, X_2) = \rho_e \frac{\sqrt{4\beta_1\beta_2}}{\beta_1 + \beta_2}$$

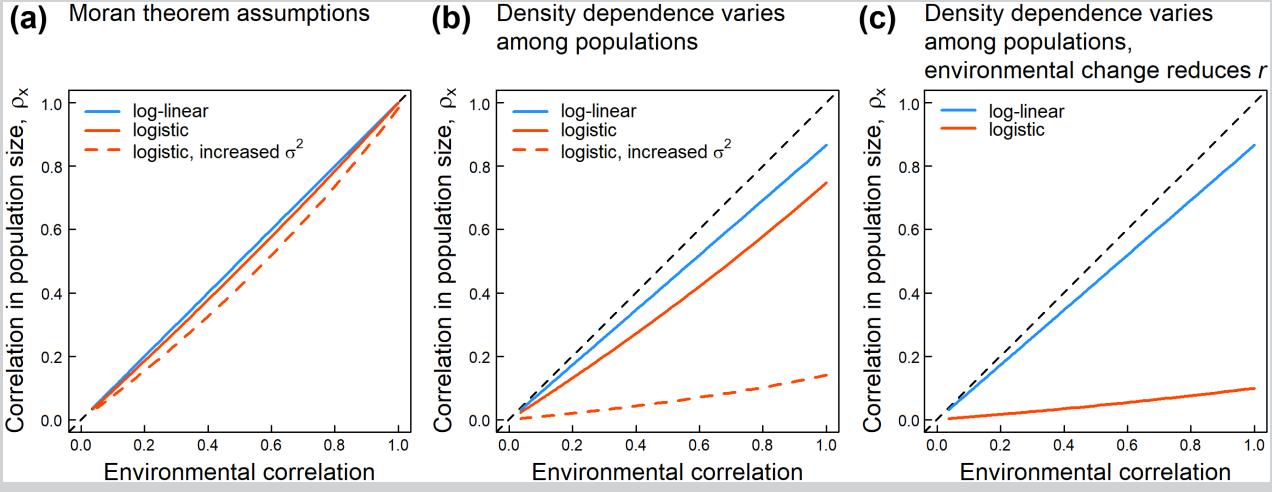
(see also Hugueny 2006 for a detailed analysis), and

$$\rho_x = \mathrm{corr}(X_1, X_2) = \rho_e \frac{\sqrt{(2\beta_1 - \sigma_1^2)(2\beta_2 - \sigma_2^2)}}{\beta_1 + \beta_2 - \rho_e\sigma_1^2\sigma_2^2}$$

for the log-linear and logistic form of density dependence respectively.

Generalized Moran effect

From this model we see, in accordance with Moran's theorem, that given equal log-linear density dependence in the two populations, the correlation in abundances (i.e. population synchrony) will be equal to correlation in the environment (panel a). For nonlinear dynamics, the correlation in abundances is always less than that of the environment (panels a, b, c). With variation in density dependence among populations in the nonlinear logistic model, the magnitude of this reduction will depend on β_1, β_2, σ^2 and environmental correlation ρ_e (panel b).



Example of a change in the mean environment

One possible effect of a change in the mean environment over large spatial scales would be a shift in r across all populations. A reduction in r causes reduced correlation of abundances for both log-linear and nonlinear dynamics, but the change is much larger in the nonlinear logistic model (panel c).

Example of a change in environmental variability
A change in the variability of the environment will influence the environmental variance (σ^2) component of population dynamics. For a given set of parameters, increased environmental variance leads to less correlation in abundances (panels a, b). Note that the relationship between the variability of the environment and the environmental variance depends on how the environment affects population dynamics.

Example of a change in spatial environmental synchrony
Increasing the environmental correlation is always expected to increase the correlation in abundance (panels a, b, c). However, the shape of this relationship depends on multiple factors, including the type and variation in density dependence (panels a, b), the environmental variance (panels a, b), the intrinsic growth rate (panel c), as well as other population dynamic parameters.

Changes in spatial environmental synchrony

Perhaps the most intuitive mechanism through which climate change can alter population synchrony is when the spatial synchrony of the environmental driver itself changes. If the level or spatial scaling of synchrony of the environmental driver of population dynamics increases or decreases, one should expect the spatial population synchrony to increase or decrease similarly (Box 3). This holds, both in the simple log-linear model used in Moran's theorem, and in the more realistic nonlinear model presented in Box 3. However, the magnitude of the change depends on the type and strength of density regulation in each of the populations (Box 3).

Several empirical studies have suggested that observed changes in population synchrony could be linked to changes in environmental synchrony. Post and Forchhammer (2004) showed that spatial autocorrelation in local weather in Greenland increased toward the end of the 20th century, and suggested that the spatial synchrony in number of harvested caribou, assumed to reflect fluctuations of distinct populations, changed due to this. Koenig and Liebhold (2016) also demonstrated a temporally increasing spatial synchrony of many North American bird species and linked these trends with a parallel increase in the spatial autocorrelation in temperature, assumed to affect the local dynamics of the bird populations. Likewise, several studies on insect abundances have identified temporal changes or trends in the level or spatial scaling of synchrony, which could be linked to climate change. An increase in metapopulation synchrony in the Finnish butterfly species *Melitaea cinxia* (Hanski and Meyke 2005, Tack et al. 2015) was likely driven by a parallel increase in the synchrony of weather conditions (Ojanen et al. 2013, Kahilainen et al. 2018), and a study of 20 aphid species in Britain showed that changes in the synchrony of winter temperatures caused large changes in the synchrony of the aphid's first flight day (Sheppard et al. 2016). Because different weather drivers acted on different time scales in this latter system, synchrony on long time scales (more than four years) was shown to decrease due to changes in winter climate, whereas synchrony on shorter time scales increased. Allstadt et al. (2015) demonstrated both theoretically and empirically, using data on North American gypsy moths *Lymantria dispar*, that temporal variation in weather synchrony can cause related changes in population synchrony, and Jepsen et al. (2009) suggested that changes in climate explained changes in synchrony of birch defoliation due to outbreaks of Fennoscandian moths. Although not strictly related to population dynamics per se, Defriez et al. (2016) suggested that a long-term change in the spatial synchrony (including in the scaling) of sea surface temperatures in the North Sea may have affected the synchrony of zooplankton. A climate induced change in the spatial autocorrelation of primary productivity has also been indicated in terms of forest growth patterns across Eurasia (Shestakova et al. 2016) and western North America (Black et al. 2018).

Most of these empirical studies relating temporal changes in the spatial synchrony of population dynamics or biomass – in highly different taxa and ecosystems – to global environmental change reported positive trends, suggesting increasing levels or spatial scaling of synchrony over time. However, the proposed links between changes in population synchrony and environmental change were, in most of these studies, either qualitative or based on correlation between time-averaged values (e.g. smoothed synchrony/correlations over decades), which restricts causal inference (but see Sheppard et al. 2016).

Different weather variables can act on different scales, both temporal, as shown in the study by Sheppard et al. (2016) mentioned above, and spatial. One important example of this is that fluctuations in precipitation amount are less strongly synchronized over long distances but more strongly synchronized over short distances than temperature (Koenig 2002). Predicted changes in the level and spatial scaling of population synchrony will then depend on which variable we study (or which is the most important for population dynamics), and must be the outcome of a combination of effects.

Indirect climate change effects through dispersal and species interactions

Besides the potential impact of direct climate change effects on the species' population dynamics, there are several likely pathways through which global warming can indirectly impact the spatial population synchrony of a species.

Dispersal among populations is one of the mechanisms expected by theory to increase population synchrony (Maynard Smith 1974, Ranta et al. 1995, 2006, Lande et al. 1999, Ripa 2000). In empirical systems it has proven quite difficult to disentangle the role of dispersal from environmental effects, partly because the effects of dispersal can cause time-lagged population synchrony (Martin et al. 2017), and

partly because effects of dispersal and the environment may interact (Kendall et al. 2000). However, dispersal as a mechanism for population synchrony is supported by results from microcosm studies (Holyoak and Lawler 1996, Fox et al. 2013), and by indirect evidence from studies that have linked dispersal ability or distance to population synchrony in natural populations (Paradis et al. 1999, Chevalier et al. 2014, Anderson et al. 2018, Vindstad et al. 2019). Climate induced changes in dispersal rates or distances could therefore be expected to alter the spatial scaling or level of population synchrony.

Climate change may alter dispersal in several ways. For example, several studies have shown that temperature is an important factor determining dispersal rates in butterflies, with higher temperatures causing more dispersal (Cormont et al. 2011, Legrand et al. 2015, Kuussaari et al. 2016). However, a recent study indicates that climate change is actually expected to decrease dispersal rates for butterflies that are already close to their thermal optimum (Evans et al. 2019). In a metapopulation of house sparrows *Passer domesticus* the effect of climate on dispersal was found to vary spatially (Pärn and Sæther 2012). In addition, climate change can influence habitat fragmentation, which will also disrupt dispersal patterns. For instance, climate warming is causing sea ice loss, which is fragmentating Arctic island ecosystems (Post et al. 2013) and causing barriers that reduce dispersal rates among (sub-) populations of e.g. the Arctic fox *Vulpes lagopus* (Geffen et al. 2007) and reindeer and caribou (Jenkins et al. 2016). Fragmentation of the snow-covered landscape under global warming also increases the geographic isolation of wolverines *Gulo gulo* in North America (McKelvey et al. 2011), and tropical mountain salamander populations may face increased isolation due to the loss of connected habitats suitable for their extremely narrow thermal tolerance range (Velo-Antón et al. 2013). Also, in aquatic ecosystems climate change is contributing to reduced connectivity among coral-reef dependent fish populations because of fragmentation effects (Munday et al. 2009), and reduced hydrological connectivity linked with regional warming is suggested to restrict dispersal in American freshwater fish species (Jaeger et al. 2014).Thus, there is considerable potential for climate change to have indirect effects on population synchrony through dispersal.

Climate change effects on population synchrony may also be mediated through species interactions (Post 2013). Strong trophic interactions with other species that are themselves spatially synchronous or mobile may generate spatial population synchrony (Ims and Andreassen 2000, Liebhold et al. 2004). In particular, in some systems predation by mobile predators is the main correlated external factor driving spatial synchrony in prey populations (Ims 1990, Ims and Andreassen 2000). Climate effects that influence the spatial distribution or mobility of predators will then also have the potential to influence the spatial synchrony of their prey. Interestingly, Ims and Andreassen (2000) suggested that dispersal among northern root vole *Microtus oeconomus* populations may have caused a 'feedback loop' enhancing the synchronizing effects of their avian predators. In other words, effects of dispersal and trophic interactions are not necessarily independent.

In addition to the directly synchronizing effect of mobile predators, synchrony may percolate through food webs (Liebhold et al. 2004, Liebhold 2012, Sheppard et al. 2019). For instance, the observed changes in the spatial synchrony of plankton dynamics in the North Sea, apparently linked with climate change and ocean warming (Defriez et al. 2016), may have cascading effects on the spatiotemporal dynamics further up the food-chain (Sheppard et al. 2019). Likewise, climate-induced changes in the spatial synchrony of alternative, non-competing prey may indirectly influence a species' spatiotemporal dynamics through their shared predator ('apparent competition'; Holt 1977). Because of the complexity of many food webs it can be difficult to identify the specific factors connecting two populations, and thus formulate predictions of how population synchrony will be affected by environmental changes (Liebhold 2012). However, the potential complicating role of such indirect influences of climate change are important to keep in mind when making predictions, and deserve more attention in future work.

For competing species, theoretical models have shown that interspecific competition tends to increase the spatial scaling of population synchrony within one or both of the competing species (Jarillo et al. 2018, Lee et al. 2020), while decreasing the spatial synchrony between species (Lee et al. 2020). The magnitude of the effect is dependent on the dispersal capacity of the species (Jarillo et al. 2018). Climate change is likely to influence the distribution of species, both expanding, contracting and shifting ranges (Parmesan 2006, Chen et al. 2011, Bellard et al. 2013, 2018), alter the transport of invasive species (Hellmann et al. 2008), and also cause species extinctions (Parmesan 2006). As species are introduced to or removed from communities, we could expect to see shifts in the population synchrony of competing species.

Overall, synchronized environmental effects appear to be the most important driver of observed synchrony in population dynamics (Liebhold et al. 2004) (i.e. the generalized Moran effect). However, the influence of dispersal, species interactions, and interactions between these different drivers cannot be ignored. As shown here, climate changes can be expected to influence population synchrony through a combination of direct and indirect effects involving all three drivers.

The generalized Moran effect: key to understand global warming impacts

We have shown that the theoretical and empirical work investigating global warming impacts on spatial population synchrony is still in its infancy. However, the growing evidence that environmental changes – irrespective of their temporal scale and underlying mechanisms – indeed influence synchrony, deserves immediate attention. This is especially

important against the backdrop of compelling evidence for population-dynamic effects of climate change at the local level (Sæther et al. 2000, 2004, Thompson and Ollason 2001, Post et al. 2009b, Barbraud et al. 2012, Jenouvrier 2013), extensive documentation of the synchronizing effect of the environment across systems (Liebhold et al. 2004), and potentially huge implications of population synchrony at the species and community level (Elton 1924, Post and Forchhammer 2002, Haynes et al. 2009, Liebhold 2012). Because the effects of environmental autocorrelation on population synchrony can influence species extinction risks (Heino et al. 1997) and spatial community dynamics (Haynes et al. 2009), our progress in analyzing and understanding the generalized Moran effect can be key to a predictive understanding of the large-scale ecological outcomes of global warming, with implications for conservation, management and harvest strategies (Post and Forchhammer 2004, Engen et al. 2018a, b).

To achieve this understanding, several methodology and knowledge gaps must be filled. First, we need a better mechanistic understanding of how climate change can impact population synchrony indirectly through dispersal and species interaction effects, and how these effects may interact with the Moran effect (Kendall et al. 2000). Second, one major open challenge when studying climate change effects on population synchrony is how to avoid simple correlations (or just qualitative comparison) of 'smoothed' or averaged timeseries of population versus environmental synchrony. This 'analytical deficiency' characterizes the empirical literature so far and has restricted the ability to make actual causal inferences linking temporal changes in synchrony to the environment. Although a few studies have made some progress towards overcoming this challenge (Sheppard et al. 2016, 2019), improved methodology on this front is crucial. Third, realistic population-dynamic assumptions (Engen and Sæther 2005) must be acknowledged and incorporated to disentangle and quantify the different drivers of population correlation (or to understand a puzzling lack of correlation) and, in turn, predict their impact. Moran's theorem should and will remain a baseline for research on spatial population synchrony, but some of his assumptions are not met in the wild (Lande et al. 1999, Engen and Sæther 2005, Liebhold et al. 2006). Nonlinear dynamics and spatial variation in parameters of population dynamics – consistent with a more generalized Moran effect – is probably the rule rather than the exception. One complicating implication of a shift from the paradigm of log-linear dynamics (as in Moran's theorem) to assuming more realistic nonlinear dynamics (a generalized Moran effect) is that the effects of changes in one population-dynamic component will then depend on the values of other components. Reliable predictions of changes in synchrony will not only require parameter estimates of local dynamics across spatially distributed populations, but also an understanding of how the joint set of parameters is likely to respond to climate change. Tackling the important and urgent challenge of understanding and predicting how impacts of climate change will affect population synchrony, and vice versa, will therefore require a joint effort involving theoretical work, methodological developments and empirical studies.

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