

Spatial covariation of competing species in a fluctuating environment

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Citation: Lee, A. M., B.-E. Sæther, and S. Engen. 2020. Spatial covariation of competing species in a fluctuating environment. Ecology 101(1):e02901. 10.1002/ecy.2901

Abstract. Understanding how stochastic fluctuations in the environment influence population dynamics is crucial for sustainable management of biological diversity. However, because species do not live in isolation, this requires knowledge of how species interactions influence population dynamics. In addition, spatial processes play an important role in shaping population dynamics. It is therefore important to improve our understanding of how these different factors act together to shape patterns of abundance across space within and among species. Here, we present a new analytical model for understanding patterns of covariation in space between interacting species in a stochastic environment. We show that the correlation between two species in how they experience the same environmental conditions determines how correlated fluctuations in their densities would be in the absence of competition. In other words, without competition, synchrony between the species is driven by the environment, similar to the Moran effect within a species. Competition between the two species causes their abundances to become less positively or more negatively correlated. The same strength of competition has a greater negative effect on the correlation between species when one of them has a more variable growth rate than the other. In addition, dispersal or other movement weakens the effect of competition on the interspecific correlation. Finally, we show that movement increases the distance over which the species are (positively or negatively) correlated, an effect that is stronger when the species are competitors, and that there is a close connection between the spatial scaling of population synchrony within a species and between species. Our results show that the relationships between the different factors influencing interspecific correlations in abundance are not simple linear ones, but this model allows us to disentangle them and predict how they will affect population fluctuations in different situations.

Key words: environmental stochasticity; interspecific competition; Lotka-Volterra competition model; Moran effect; population synchrony; spatial distribution; spatial pattern formation.

INTRODUCTION

Understanding and predicting the dynamics and distribution of populations or species and how they are affected by fluctuations in the environment is one of the major goals of ecology. Over recent years, it has become clear that studying single species in isolation is not sufficient to predict responses to perturbations (Kinzey and Punt 2009, Legović and Geček 2010, McCarthy 2011). Populations are embedded in larger communities and ecosystems, and it is therefore necessary to understand the dynamics of interacting species and how they collectively respond to environmental fluctuations. In addition, it is crucial to account for spatial processes, as these are known to play an important role in shaping population dynamics (Tilman and Kareiva 1997).

One striking pattern that has often been seen in spatial population dynamics is population synchrony.

Synchrony in the abundance of single species has been observed in a wide range of taxa, often over large geographic areas (Liebhold et al. 2004, Ranta et al. 2006), with populations that are close together tending to show more synchronous dynamics than those that are further apart (Liebhold et al. 2004, Walter et al. 2017). Understanding the drivers behind such synchrony is of particular importance because synchronized population dynamics have been shown to increase the global extinction risk of populations (Heino et al. 1997, Earn 2000, Engen et al. 2002).

Moran (1953) showed that population synchrony can be caused by correlated environmental fluctuations, and that the spatial scale of the synchrony depends on the spatial scale of the environmental fluctuations (“the Moran effect”). More recently, it has been shown that several other factors also influence this relationship. Lande et al. (1999) derived a simple equation showing that the spatial scale of population synchrony increases with the spatial scale of environmental correlations and with the spatial scale and rate of dispersal or individual movement, and decreases with the strength of local

Manuscript received 29 April 2019; revised 10 July 2019; accepted 3 September 2019. Corresponding Editor: Allison K. Shaw.

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density dependence in the population dynamics. These general relationships have been supported by several empirical studies (Powney et al. 2012, Cavanaugh et al. 2013, Martin et al. 2017).

Interspecific synchrony in abundance or growth rates (i.e., synchrony among populations of different species) has also been observed in several taxa (fish [Tedesco et al. 2004], insects [Raimondo et al. 2004a, b], birds [Ranta et al. 1995, Robertson et al. 2015], mammals [Stephens et al. 2017], and plants [Tredennick et al. 2017]). If different species in a community can be expected to show correlated fluctuations in abundance, this has implications not only for predictions of single species dynamics, and the possibility of using fluctuations in one species as a proxy for the dynamics of another species, but also for our understanding of the characteristics of the whole community.

Synchrony in the abundance of multiple species has mainly been found among species with similar foraging or breeding behavior that causes them to experience similar environmental fluctuations (Raimondo et al. 2004a, Robertson et al. 2015), whereas several other species have shown no significant correlation (Raimondo et al. 2004b, Robertson et al. 2015), or even negative correlation in abundances (Raimondo et al. 2004a, Mutshinda et al. 2009). Intuitively, one might expect competing species to show negative correlations in abundance, since an increase in the abundance of one species is expected to increase the competition experienced by the other species (Tilman 1999). A theoretical model developed by Loreau and de Mazancourt (2008) showed that the synchrony among stationary organisms should indeed be decreased by the strength of interspecific competition but increased by the synchrony of species responses to the environment. However, the spatial dynamics of interspecific synchrony have received little attention.

Movement and spatial processes increase the complexity of studying synchrony in population fluctuations. Interspecific synchrony has two major components; the degree of synchrony among species in a single point, and the distance over which this synchrony persists. Both of these are influenced by spatial processes. Most studies of interspecific synchrony to date have ignored the spatial aspect, simply reporting the correlation between the total abundance of different species. However, populations actually exist as a pattern of abundances across space, and there is good reason to believe that movement plays a role in interspecific synchrony as well as intraspecific synchrony. This is particularly important when studying effects of environmental fluctuations and interspecific interactions, because organisms experience different environmental conditions depending on their spatial location at a given time, as well as different levels of local competition.

In this paper, we quantify interspecific population synchrony in a model with movement of individuals and spatially correlated environmental fluctuations. The

model incorporates density dependence within the dynamics of each species and utilizes a very flexible noise term allowing us to control multiple aspects of the environmental fluctuations and their effect on the species' growth rates. Using analytical results we show how the correlation between the density of two competing species, driven by correlation in how they experience the environment, is decreased as the strength of competition between them increases. We show that the effect of competition is lessened when individuals can move around in space, and strengthened when the species show differences in the variability of their intrinsic growth rates. Finally, we demonstrate how these factors influence the distance over which the species show synchronized fluctuations.

MODEL AND METHODS

Consider populations of two competing species with density $n_1(x)$ and $n_2(x)$ at location $x = (x_1, x_2)$. The populations have an intrinsic growth rate, β_i , defined as birth rate minus density-independent death rate, with temporal fluctuations $\sigma_{\beta_i} dB_{\beta_i}(x)/dt$ (where $i = 1, 2$ refers to species 1 and 2, respectively, and dB_{β_i} is the temporal increment during time dt of a standard Brownian motion). Individuals disperse at rate m_i and move a distance described by a two-dimensional distribution, $g_i(u)$. Note that dispersal here simply refers to movement in space, not necessarily natal dispersal. The populations are subject to both intraspecific and interspecific competition, such that the realized growth rate of species i is decreased by a density-dependent term $v_i n_i(x)$ that increases linearly with the density of species i (i.e., a standard logistic model for density dependence), as well as by a term $\gamma_{ij} n_j(x)$ that increases linearly with the density of species j ($i \neq j$). Then, assuming the populations are large enough for local demographic stochasticity to be ignored (Engen and Sæther 2016), the dynamics of species n_i can be expressed as

$$\begin{aligned} dn_i(x) = & \beta_i n_i(x) dt - v_i n_i^2(x) dt - \gamma_{ij} n_j(x) n_i(x) dt \\ & - m_i n_i(x) dt + m_i dt \int n_i(x-u) g_i(u) du \\ & + n_i(x) \sigma_{\beta_i} dB_{\beta_i}(x). \end{aligned} \quad (1)$$

The three-first terms on the right-hand side describe (expected) changes in dynamics due to birth and death (density-independent, intraspecific density-dependent, and interspecific density-dependent terms). Next, we have a term describing movement away from the point x at rate m_i , and one describing movement to x from all other points in the spatial field being considered. Finally, the environmental noise term controls fluctuations in the density-independent growth rate. This noise can be correlated in space as a function of distance, both within and between species, expressed as $\rho_{ij}(y) = E[dB_{\beta_i}(x) dB_{\beta_j}(x+y)]/dt$, with $(i = 1, 2; j = 1, 2)$.

Here, we will assume that this correlation is driven by a common environmental correlation, $\rho_e(y)$, such that $\rho_{11}(y) = \rho_{22}(y) = \rho_e(y)$ and $\rho_{12}(y) = \rho_{12}(0)\rho_e(y)$. For simplicity of notation when reporting results, we write $\rho_{12}(0) = \rho_0$.

The deterministic part of the growth model (i.e., the first three terms in Eq. 1) follows the form of a standard Lotka-Volterra competition model (Volterra 1928, Lotka 1932, Begon et al. 2006). Comparing our notation to the notation used by Chesson (2000) in a Lotka-Volterra equation with population size N_i , intrinsic growth rate r_i , and absolute intraspecific and interspecific competition coefficients α_{ii} and α_{ij} , respectively,

$$\frac{dN_i}{dt} = r_i N_i (1 - \alpha_{ii} N_i - \alpha_{ij} N_j), \quad (2)$$

we see that $r_i = \beta_i$, $\alpha_{ii} = v_i/\beta_i$, and $\alpha_{ij} = \gamma_{ij}/\beta_i$. Chesson (2000) showed that species coexistence is expected in this model when $\alpha_{ij}/\alpha_{ji} < 1$, i.e., when intraspecific competition is greater than interspecific competition. We introduce a metric $\alpha_i = \gamma_{ij}\beta_j/v_j\beta_i$, which describes how strong the interspecific competition is in relation to the intraspecific competition in our model, and note that coexistence is expected as long as both α_1 and α_2 are less than one.

We are going to analyze the model in Eq. 1 when the two fields n_1 and n_2 fluctuate in a stationary way in space near their deterministic equilibrium values, Q_1 and Q_2 . We find these values by ignoring the noise term and solving the equation $\beta_i Q_i - v_i Q_i^2 - \gamma_{ij} Q_i Q_j = 0$, which gives

$$Q_i = \frac{\gamma_{ij}\beta_j - v_j\beta_i}{\gamma_{ij}\gamma_{ji} - v_i v_j}. \quad (3)$$

Setting $(i = 1, j = 2)$ and $(i = 2, j = 1)$ then gives Q_1 and Q_2 , respectively. The two populations will stabilize at lower densities when they have to compete with each other than they would in isolation. If we remove interspecific competition effects from the dynamics of species i by setting $\gamma_{ij} = 0$ (i.e., species i does not experience any negative effect from the presence of species j), Eq. 3 collapses to $Q_i = \beta_i/v_i$, which is the carrying capacity of species i in the absence of other species (K_i).

Following Lande et al. (1999) and Engen et al. (2018), we assume small fluctuations and linearize the equation around the deterministic equilibrium. Thus, we approximate the density in the noise term by the equilibrium density, Q_i , and study relative deviations from this density, $z_i(x) = n_i(x)/Q_i - 1$. It has previously been shown that approximate results based on a small noise assumption and linearization in models similar to this one are remarkably accurate under moderate and even fairly large population density fluctuations (Engen et al. 2017). The linearized version of Eq. 1 becomes (see Appendix S1)

$$\begin{aligned} dz_i(x) = & \beta_i z_i(x) dt - 2v_i Q_i z_i(x) dt - \gamma_{ij} Q_j z_j(x) dt \\ & - \gamma_{ij} Q_j z_i(x) dt - m_i z_i(x) dt \\ & + m_i dt \int z_i(x-u) g_i(u) du + \sigma_{\beta_i} dB_{\beta_i}(x). \end{aligned} \quad (4)$$

From this model, we aim to derive the spatial covariance functions $c_{ij}(y) = \text{Cov}[z_i(x), z_j(x+y)]$. Following Engen et al. (2018), we achieve this by utilizing the fact that under stationarity the spatial covariances do not change through time. This means that

$$\begin{aligned} \text{Cov}[z_i(x), z_j(x+y)] = & \text{Cov}[z_i(x) + dz_i(x), z_j(x+y) \\ & + dz_j(x+y)]. \end{aligned} \quad (5)$$

Inserting $(i = 1, j = 1)$, $(i = 2, j = 2)$, and $(i = 1, j = 2)$, and then inserting dz_1 and dz_2 from Eq. 4 and dividing through by dt , gives us three balance equations that can be solved using Fourier transforms (Appendix S2). Thus, for any set of parameters, the covariance functions, c_{11} , c_{22} , and c_{12} can be computed numerically.

Using the above model, we have studied how two species covary in space depending on the strength of competition between them. To facilitate comparison between models with different parameter sets and make it easier to interpret results, we present our results in terms of the correlation between changes in density of the two species (where $C_{12}(y) = \text{Corr}[z_1(x), z_2(x+y)] = c_{12}(y)/\sqrt{\text{Var}[z_1(x)]\text{Var}[z_2(x+y)]}$). For convenience, we will call this ‘‘density correlation.’’ We first focus on the correlation between two species at a single point within the field studied (i.e., at zero distance) and study how this is affected by the strength of competition between species, the environmental correlation between species at zero distance, ρ_0 , the difference between species in how much their growth rate fluctuates in response to environmental noise, $\sigma_{\beta_1}/\sigma_{\beta_2}$, and finally dispersal rate. The environmental correlation, ρ_0 , can be interpreted as how correlated the two species are in their response to the environment. Next, we look at the distance at which the correlation between two competing species levels off, and compare this to the changes in population synchrony within species at the same distance, again studying systems with different rates of dispersal, m_i , and different levels of environmental correlation, ρ_0 . The relative deviations from equilibrium density (z_1 and z_2) for five illustrative systems are simulated using the method described in Appendix S3. Python code for calculations and simulations can be found in Data S1: Competition_covariance_code.py.

RESULTS

Competition has a negative effect on the correlation between density fluctuations of two species, both at a single point in space (Fig. 1) and at moderate distances

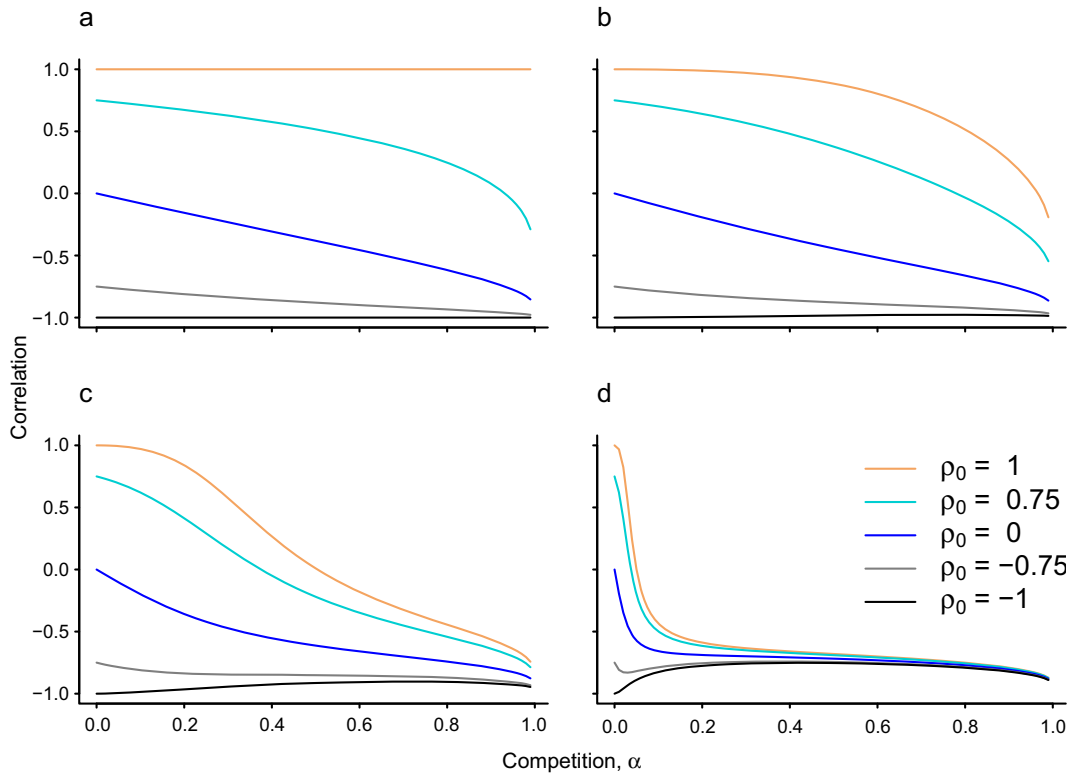


FIG. 1. Correlation between the density of two species at distance zero (i.e., at a single point within the spatial field studied) as a function of the strength of competition between them ($\alpha_1 = \alpha_2 = (\gamma_{12}\beta_2)/(\nu_2\beta_1) = \gamma_{12}/\nu_2 = \gamma_{21}/\nu_1$). The correlation between the environmental noise experienced by the two species, ρ_0 , is 1 (orange lines), 0.75 (turquoise), 0 (blue), -0.75 (gray), and -1 (black). The ratio $\sigma_{\beta_2}/\sigma_{\beta_1}$, which indicates how much the growth rates of the two species differ in their variability, is set to (a) 1, (b) 0.5, (c) 0.2, and (d) 0.02. Other parameters are population growth rates $\beta_1 = \beta_2 = 0.2$, variance in growth rate of species 1, $\sigma_{\beta_1}^2 = 0.01$, dispersal rates $m_1 = m_2 = 0.5$, and spatial scale of the common environmental factor, $l_e = 50$.

(Fig. 2). As competition becomes stronger, density fluctuations of the two species become less positively correlated and/or more negatively correlated (Figs. 1, 2). The shape of this relationship depends on several other factors.

First, the environmental correlation between the species at zero distance, ρ_0 , determines how correlated fluctuations in the density of the two species would be in the absence of competition between them, driven solely by fluctuations in the environment. Two species that are independent in their response to the environment ($\rho_0 = 0$) and do not compete with each other will show uncorrelated density fluctuations (Fig. 1a, dark blue line at $\alpha = 0$; Fig. 3a), but any level of competition between the two species will cause their density fluctuations to become negatively correlated (Fig. 1a, dark blue line), such that areas with a high density of one species tend to have a low density of the other species (Fig. 3b). Species that respond in a positively correlated manner to environmental fluctuations ($\rho_0 > 0$), such that the same sets of environmental conditions tend to have a positive effect on the growth of both species, will demonstrate positively correlated density fluctuations in the absence of competition. In other words, the density of the two

species will tend to be synchronized in space, with local areas with high density of one species also tending to have high density of the other species. Competition between the species will counteract this effect, weakening the positive correlation between their density fluctuations (Fig. 1a, turquoise line; Fig. 3c,d). If the competition is strong enough in relation to ρ_0 , it can cause them to have negatively correlated fluctuations in density despite the synchronizing effects the environment. Negative correlations in density fluctuations caused by $\rho_0 < 0$ will be even more negative when species compete (Fig. 1a, gray lines).

The relative magnitude of growth rate fluctuations experienced by one species compared to a competing species ($\sigma_{\beta_1}/\sigma_{\beta_2}$) also influences how strongly competition affects the correlation in their density fluctuations (Fig. 1). The same strength of competition between species has a greater negative effect on the correlation between them when one species has a more variable growth rate than the other (Fig. 1).

An increase in dispersal or movement causes competition to have a weaker effect on the correlation (Fig. 4). As the dispersal rate becomes extremely high (basically going toward infinity), it completely counteracts the

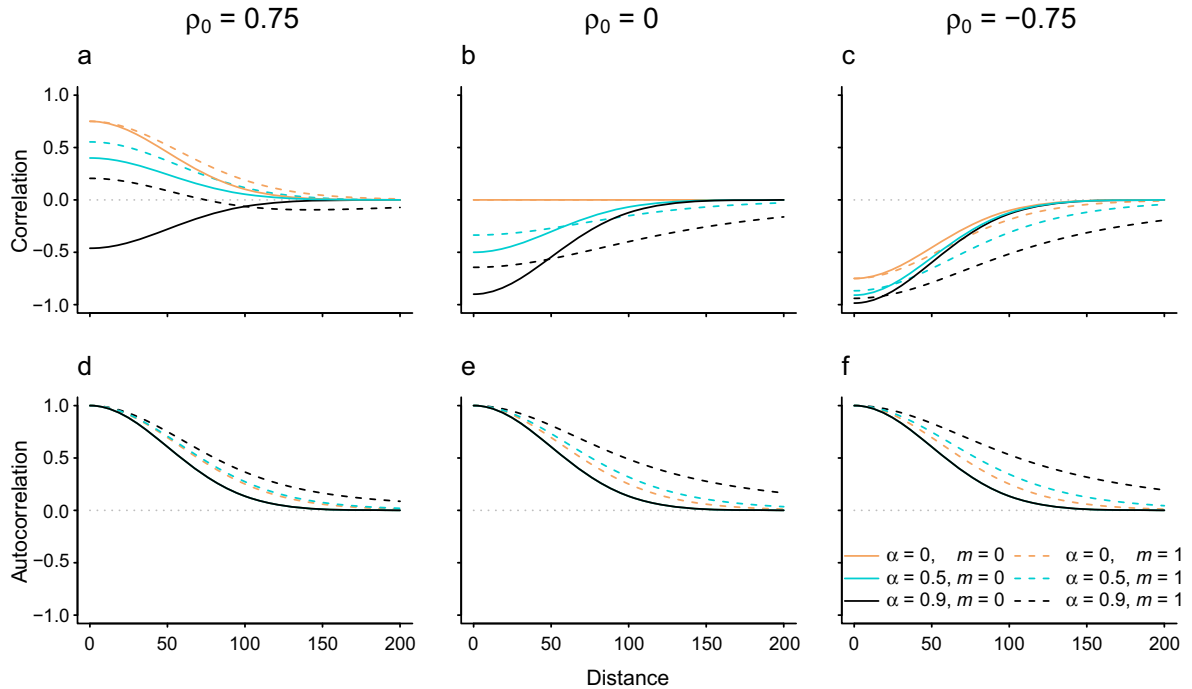


FIG. 2. Correlation between the density of two species (a–c) and autocorrelation in density within each species (d–f) as a function of distance. The strength of competition between the two species, $\alpha_1 = \alpha_2 = (\gamma_{12}\beta_2)/(\nu_2\beta_1) = \gamma_{12}/\nu_2 = \gamma_{21}/\nu_1$, is 0 (orange lines), 0.5 (turquoise), and 0.9 (black), and the dispersal, $m_1 = m_2$, is 0 (solid lines) or 1 (dashed). The correlation between the environmental noise experienced by the two species, ρ_0 , is (a) and (d) 0.75, (b) and (e) 0 and (c) and (f) -0.75 . Other parameters are population growth rates $\beta_1 = \beta_2 = 0.2$, variance in growth rates, $\sigma_{\beta_1}^2 = \sigma_{\beta_2}^2 = 0.01$, spatial scale of the common environmental factor, $l_e = 50$, and spatial scale of the distribution of dispersal distance, $l_{g1} = l_{g2} = 20$.

effect of competition and the correlation between density fluctuations in the two species stays at ρ_0 even when competition becomes nearly as strong as the density dependence within each species.

In the absence of dispersal, competition has no apparent effect on the distance at which the population dynamics of two species become independent (i.e., the distance at which the correlation between small changes in density of the two species approaches zero, Fig. 2a–c). However, dispersal increases the distance over which density fluctuations in the two species are (positively or negatively) correlated, and this effect is stronger when the two species are competing (Fig. 2a–c). This is also reflected in the intraspecific population synchrony (or autocorrelation of density fluctuations within each species): dispersal increases the distance over which density fluctuations are synchronized (Fig. 2d–f). In certain cases, a combination of competition and dispersal can cause the correlation between species to switch from positive to negative at increasing distances before finally reaching zero (Fig. 2a), although this is not very common.

As already seen in Fig. 4, competing species are more positively (or less negatively) correlated at distance zero when there is dispersal or movement in the system. At the same time, dispersal increases the distance over which density fluctuations are dependent between

species. Thus, when competition causes negative correlation between the two species at distance zero, systems without dispersal will tend to show more negative correlations between competing species at short distances (than those with dispersal), but at longer distances the correlation will tend to be less negative in the presence of dispersal than in its absence (Fig. 2b,c).

DISCUSSION

Understanding and predicting the dynamics of populations and communities and how they respond to environmental fluctuations is a major challenge in ecology and of great importance for the management of species (Lande et al. 2003). Correlation among the dynamics of interacting species is an important aspect of this which has received increased attention recently (Raimondo et al. 2004a, Robertson et al. 2015). The model presented here allows us to examine how different factors interact and influence the correlation between the population dynamics of two competing species (“density correlation”). This density correlation describes how the two species are distributed in relation to each other in space. When the density correlation is positive the spatial distribution of density of the two species is similar, with coinciding areas of high density. When the density correlation is negative the two species partially exclude

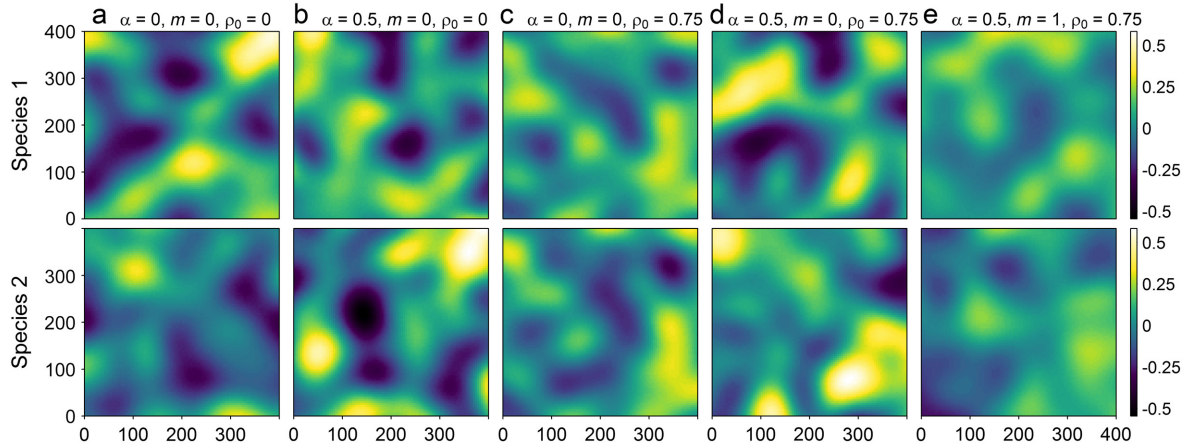


FIG. 3. Simulations of two competing species' deviations from equilibrium density (z_1 and z_2) over a 400-unit square spatial field. Simulations were run over a 800-unit square spatial field, and the center 400-unit square was extracted, to avoid edge effects. Systems correspond to the five points shown on Fig. 2. Levels of competition (α), dispersal ($m_1 = m_2 = m$), and the correlation between the environmental noise experienced by the two species (ρ_0) are shown above each panel. Other parameters are population growth rates $\beta_1 = \beta_2 = 0.2$, variance in growth rates, $\sigma_{\beta_1}^2 = \sigma_{\beta_2}^2 = 0.01$, spatial scale of the common environmental factor, $l_e = 50$, and spatial scale of the distribution of dispersal distance, $l_{g1} = l_{g2} = 20$.

each other in space such that there tends to be little overlap between areas of high density of the two species.

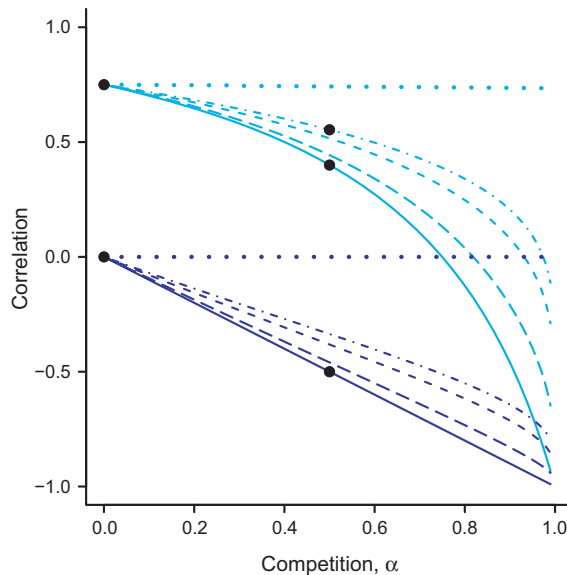


FIG. 4. Correlation between the density of two species at distance zero (i.e., at a single point within the spatial field studied) as a function of the strength of competition between them ($\alpha_1 = \alpha_2 = (\gamma_{12}\beta_2)/(\nu_2\beta_1) = \gamma_{12}/\nu_2 = \gamma_{21}/\nu_1$). The correlation between the environmental noise experienced by the two species, ρ_0 , is 0.75 (turquoise lines) and 0 (blue), and the migration rate is 0 (solid lines), 0.1 (long-dashed), 0.5 (short-dashed), 1 (dot-dashed). Other parameters are population growth rates $\beta_1 = \beta_2 = 0.2$, variance in growth rates, $\sigma_{\beta_1}^2 = \sigma_{\beta_2}^2 = 0.01$, spatial scale of the common environmental factor, $l_e = 50$, and spatial scale of the distribution of dispersal distance, $l_{g1} = l_{g2} = 20$. The dots indicate specific systems that are simulated in Fig. 3.

Results from our model showed that in the absence of competition the density correlation at distance zero was determined solely by ρ_0 (i.e., by responses to a common environment). In other words, spatial synchrony between the species was driven only by synchrony in their responses to the environment. This can be thought of as an across-species Moran effect (Ranta et al. 2006), with a shared environment synchronizing species. As competition was added and the strength of competition was increased the density correlation became less positive (or more negative), so that the species showed less spatial synchrony. This is as expected from basic theory, since competitors have negative effects on each other's density. However, the shape of this relationship is harder to predict intuitively. Our results show that it is not a simple linear relationship (Fig. 1). In fact, the shape of the relationship depends on additional factors, such as the dispersal rate (Fig. 4) and the relative variability of the population growth rates (Fig. 1). Thus, quantifying the strength of competition between two species exposed to the same environment is not in itself enough to predict how they will covary in space. Conversely, the same correlation in abundance can be produced by several different underlying processes (Figs. 1, 4). Our results show that in order to understand the interspecific synchrony (or lack thereof) observed in empirical studies, or to predict density correlations in various systems, we need to quantify species' responses to the environment, the strength of competition between them, and their mobility. Our model provides simple predictions for the relative contribution of these different factors (Figs. 1–4).

Our results clearly show that spatial processes, and in particular dispersal, play an important role in the local dynamics of interacting species (Fig. 4). Thus, even if we are only interested in the population dynamics in a single

point, we may often need to account for the spatial processes around that point. Scale is of fundamental importance in processes of pattern formation (Levin 1992), and it has previously been shown that the spatial scale of environmental fluctuations and of dispersal both influence the spatial scale of population processes (Lande et al. 1999). Our model accounts for both of these parameters, although they are held constant in the results presented in this paper. In addition to the effect of dispersal on interspecific density correlation (Fig. 4) and on the scale of population synchrony both within (Fig. 2d–f) and between (Fig. 2a–c) species, we note that simulation of a system with dispersal (Fig. 3e) shows smaller fluctuations in abundance than an equivalent system without dispersal (Fig. 3d). This is in accordance with previous theoretical studies on effects of dispersal (Engen et al. 2002, Walter et al. 2017). Underlying spatial structure, caused by, for example, heterogeneity in resource availability, can have an additional impact on how organisms distribute themselves in space (Cohen and Levin 1991, Vallespir Lowery and Ursell 2019), which we have not considered in the spatially homogeneous model presented here.

Studies from several taxa have shown that environmental fluctuations can have a synchronizing effect on population dynamics of different species (Myers 1998, Post and Forchhammer 2002, Hansen et al. 2013, Lahoz-Monfort et al. 2013). This implies that the dynamics of the species have positively correlated responses to the environment, an assumption that seems appropriate among competing species, as these will tend to have similar niches. Therefore, systems of biological interest should commonly have non-negative values of ρ_0 . However, negative correlations driven by the environment have also been demonstrated in some systems (Mutshinda et al. 2009). Our model is general enough to handle both these situations, and our results show that systems with $\rho_0 < 0$ follow the same general patterns as those with $\rho_0 \geq 0$.

Differences in the variability of growth rates between competing species also affected the density correlation (Fig. 1). In natural systems, this difference is probably unlikely to be as extreme as some of those shown in Fig. 1, but given the high level of variation seen in natural systems (Pimm and Redfearn 1988, Lande et al. 2003) this effect could contribute substantially to observed density correlations.

Scale is an important consideration when studying spatial pattern formation, both in terms of the scale on which underlying mechanisms and processes function, and the scale of generated patterns (Levin 1992). It has recently been shown that interspecific competition tends to increase the spatial scaling of intraspecific population synchrony within each of the competing species (Jarillo et al. 2018). This pattern is reflected in output from our model as well (Fig. 2d–f). We found a very close connection between the scale of this autocorrelation within each of the species and the scale of density correlation

between the dynamics of the two competing species (Fig. 2). When ρ_0 is positive, there will tend to be synchrony among species over the same distances as we see population synchrony within species. This is reflected in the patterns created by our simulations (Fig. 3), as the spatial scale of changes in abundance are similar within and among populations, regardless of the correlation between them. Population synchrony within species is known to affect extinction risk (Heino et al. 1997). When population sizes of competing species within a community also fluctuate in synchrony this could have implications for the coexistence and extinction risk at the community level.

Communities consist of an (often large) number of directly or indirectly interacting species. Understanding the factors that allow these species to coexist and how communities are structured has been of major interest in ecology for many years. In this paper, we have examined a linearized version of our model which therefore follows the standard result that there is stable (global) coexistence between the two species as long as the interspecific competition (γ_{ij}) is weaker than the intraspecific competition (ν), i.e., as long as $\alpha < 1$ (Chesson 2000). We have therefore focused on systems within this parameter space when presenting our results. Thus, although we show how competition influences the local coexistence patterns of species, or how their density is distributed in relation to each other in space, we have not considered systems where one species outcompetes and excludes the other across the whole field. However, an interesting future step would be to study coexistence in the nonlinearized version of the model, which might allow us to expand the parameter space studied. Both temporal and spatial heterogeneity have been suggested to promote coexistence of species through niche partitioning (Chesson 1986, 2000), particularly in the presence of dispersal (Chesson 1986), allowing for coexistence in a broader range of systems. A nonlinearized version of this model could allow us to study the criteria for coexistence in such systems.

In addition to coexistence, the stability of abundance or biomass in communities of competing species and how this is affected by properties of the interacting populations and of the community as a whole is a major topic of interest (Loreau and de Mazancourt 2013). Fluctuations in the total abundance of a community are of course driven by the fluctuations and dynamics of the individual species. Thus, an understanding of the mechanisms underlying correlations in fluctuations of interacting species, such as those studied here, have direct relevance to such community level studies. It has previously been shown that asymmetries in the intrinsic growth rate and carrying capacities of competing species can affect the stability of communities (Fowler 2009, Loreau and de Mazancourt 2013). Here, we found that when the intrinsic growth rate (β_i) of one species was more variable than the intrinsic growth rate of the other, competition had a stronger effect on the density

correlation (Fig. 1). Compensatory dynamics among species can play an important role in stabilizing communities by allowing the total community biomass to stay quite constant despite fluctuations in the abundance of individual species (Tilman 1999, Lamy et al. 2019). Thus, factors that influence the density correlation of pairs of species could scale up to influence the stability of whole communities. Asymmetry in the strength of interspecific competition has been shown to have a destabilizing effect on the total biomass of communities (Hughes and Roughgarden 1998, Loreau and de Mazancourt 2013). A natural future step is therefore to examine how asymmetry in the strength of competition, as well as in other parameters of our model, influences the density correlation between pairs of competing species.

ACKNOWLEDGMENTS

This work was supported by the Research Council of Norway (SFF-III 223257/F50 and KLIMAFORSK project 244647) and the Norwegian University of Science and Technology (NTNU).

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