

# Generalizations of the Moran Effect Explaining Spatial Synchrony in Population Fluctuations

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**ABSTRACT:** The Moran effect for populations separated in space states that the autocorrelations in the population fluctuations equal the autocorrelation in environmental noise, assuming the same linear density regulation in all populations. Here we generalize the Moran effect to include also nonlinear density regulation with spatial heterogeneity in local population dynamics as well as in the effects of environmental covariates by deriving a simple expression for the correlation between the sizes of two populations, using diffusion approximation to the theta-logistic model. In general, spatial variation in parameters describing the dynamics reduces population synchrony. We also show that the contribution of a covariate to spatial synchrony depends strongly on spatial heterogeneity in the covariate or in its effect on local dynamics. These analyses show exactly how spatial environmental covariation can synchronize fluctuations of spatially segregated populations with no interchange of individuals even if the dynamics are nonlinear.

*Keywords:* population synchrony, Moran effect, theta-logistic model, spatial population dynamics.

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In 1953, Moran published a seminal paper in which he showed that the correlation of the size of two populations located at different locations was equal to the correlation in the common environmental noise if the populations were subject to the same linear model of density regulation. This implies that the environment can cause synchronous fluctuations over time of two populations that initially were of different size (Royama 1992). Later theoretical

work has provided further support for the importance of environmental covariation as a synchronizing agent for fluctuations of spatially structured populations (Lundberg et al. 2000). It is therefore surprising that the presence of a Moran effect in the dynamics of spatially structured natural populations has been difficult to demonstrate empirically (but see Grenfell et al. 1998; Benton et al. 2002). In general, the scaling of the population synchrony is far less than the spatial scale of variation in ecologically important environmental variables (Koenig 1999, 2001; Liebhold et al. 2004), even under experimental conditions (Benton et al. 2001).

Empirical analyses of spatial synchrony in population size between two locations are based on estimates of the spatial autocorrelation in joint time series observations. Let  $X_{11}, X_{12}, \dots, X_{1n}$  and  $X_{21}, X_{22}, \dots, X_{2n}$  be observations taken at the same points in time from two locations. The correlation in population fluctuations between these two localities is estimated by calculating the product moment correlation by considering the two-dimensional observations  $(X_{11}, X_{21}), (X_{12}, X_{22}), \dots, (X_{1n}, X_{2n})$  as a sample from a bivariate distribution (for examples, see Liebhold et al. 2004). These estimates are then plotted against distance for all pairs of localities and smoothed by parametric (Buonaccorsi et al. 2001; Engen et al. 2005; Lillegård et al. 2005) or nonparametric techniques (Bjørnstad et al. 1999; Koenig 1999) to give a spatial autocorrelation function. This autocorrelation function is commonly compared with the covariation in space of some environmental variable (e.g., Koenig 1999; Koenig 2001), assuming the same local dynamics at all localities.

Population fluctuations are determined by parameters such as the specific population growth rate and carrying capacity affecting the expected values as well as by stochastic factors that at larger population size are mainly affected by stochastic fluctuations in the environment (Lande et al. 2003). Empirical analyses of spatial variation in demography and population dynamics of many vertebrate species have shown that the parameters characterizing the expected dynamics may show large spatial variation (Myers et al. 1997; Myrsetrud et al. 2000; Sæther et

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al. 2003; Williams et al. 2003; Engen et al. 2005). Furthermore, the effects of environmental covariates may vary geographically (Mysterud et al. 2000; Sæther et al. 2003; Both et al. 2004; Engen et al. 2005), resulting in spatial variation in the parameters determining these environmental effects. Writing  $\psi$  for the vector of all parameters describing the local dynamics that may vary in space, Engen et al. (2002a) pointed out that the smoothed spatial autocorrelation function actually is an estimate of the expectation of the correlations with respect to the bivariate distributions of  $\psi$  at two locations with specified distance. Our purpose here is to examine how different parameters affecting the local dynamics influence this autocorrelation function.

Theoretical analyses have shown that spatial synchrony in population fluctuations is affected by variation in parameters determining the expected dynamics, such as the strength of density dependence (Lande et al. 1999; Engen 2001; Engen et al. 2002a, 2002b) and spatial variation in carrying capacity (Engen et al. 2002a), spatial autocorrelations in the environmental noise (Moran 1953; Haydon and Steen 1997; Ranta et al. 1997b; Lande et al. 1999, 2003; Bjørnstad and Bolker 2000; Kendall et al. 2000; Lundberg et al. 2000; Engen 2001; Engen et al. 2002a, 2002b, 2005), and migration (e.g., Ranta et al. 1997b; Lande et al. 1999; Kendall et al. 2000; Engen et al. 2002a, 2002b, 2005). However, when synchrony is examined at large spatial scales, migration can be ignored, provided that density regulation is not extremely weak (Lande et al. 1999, 2003; Engen et al. 2002a). Under the assumption of no migration, we will derive an analytical expression for the spatial autocorrelation function that enables us to examine how parameters affecting the expected dynamics of local populations as well as autocorrelations in the environment contribute to the population synchrony. These analyses show that both the form of the density regulation and the spatial heterogeneity in environmental effects on the local dynamics (e.g., Ranta et al. 1999) are important determinants of the degree of spatial synchrony in population fluctuations. This provides, in two different ways, a generalization of Moran's early formulation (Moran 1953) of how environmental covariation causes synchronous population fluctuations. First, using a proper decomposition of the environmental noise into terms defined by fluctuating covariates and a residual noise term, we will demonstrate how spatial variation in covariates as well as in the coefficients determining their effects on local population dynamics will affect the spatial autocorrelation in the total noise, which again influence the synchrony in population fluctuations. Second, synchrony of population fluctuations measured by the correlation defined above will be determined by this total noise as well as the spatial fluctuations in the other parameters defining the dynam-

ics. We explore these effects by examining populations described by the theta-logistic model of density regulation (Gilpin and Ayala 1973) with spatial variation in the parameters. This is a rather general type of model with different forms of density regulation, including the familiar log-linear as well as the logistic model.

### The Theta-Logistic Model with Spatial Variation in Parameters

Here we adopt the parametrization of the theta-logistic model used by Lande et al. (2003). The expected change in population size from one year to the next conditioned on the population size  $N$  the previous year is then

$$E(\Delta N|N = n) = rn \left( 1 - \frac{n^\theta - 1}{K^\theta - 1} \right). \quad (1)$$

The parameter  $r$  is the growth rate at population size 1,  $K$  is the carrying capacity, and  $\theta$  is a parameter determining the form of the density regulation. If  $\theta = 1$ , this is the logistic model. In the limit as  $\theta$  approaches 0, the density regulation is linear in  $\ln n$ , while as  $\theta$  approaches infinity, the density regulation vanishes for population sizes smaller than  $K$  and becomes extremely large immediately above  $K$ , leading to a so-called ceiling model (Lande 1993). Here we shall consider the diffusion analogy of this model with infinitesimal mean  $\mu(n)$  equal to the above expression for  $E(\Delta N|N = n)$ . We shall assume that all local populations are large enough for the demographic variance to be ignored (see Lande et al. 2003) so that the infinitesimal variance of the diffusion, which is approximately  $\text{Var}(\Delta N|N = n)$ , takes the form  $\nu(n) = \sigma^2 n^2$ , where  $\sigma^2$  is the environmental variance (often denoted  $\sigma_\epsilon^2$ ). Hence, the total set of parameters that may vary in space is  $\psi = (r, K, \theta, \sigma^2)$ .

### Transformation to Linearity

Because the product moment correlation is a measurement of linear covariation between two variables, the spatial autocorrelation is most conveniently analyzed on a scale  $X = g(N)$ , giving linear population models at each location. For example, it is well known that for  $\theta = 0$ , the transformation  $X = \ln N$  leads to the linear model in  $X$  that is known as the Ornstein-Uhlenbeck process (Karlin and Taylor 1981; Lande et al. 2003). The spatial correlations are to the first order the same for  $X$  and  $N$ , ensuring that the spatial analysis performed on the transformed variables really is an analysis of spatial synchrony of population fluctuations.

We show in appendix A that the remarkably simple transformation

$$g(N) = \frac{(1 - N^{-\theta})}{\theta} \tag{2}$$

for  $\theta \neq 0$  and the limiting form  $g(N) = \ln N$  for  $\theta = 0$  lead to a linear model that is suitable for analyzing spatial autocorrelations in general. This transformation is depicted in figure 1 for different values of  $\theta$ . In figure 2, we show a simulated process together with the transformed process for the logistic case ( $\theta = 1$ ). We see that the patterns in the fluctuations are almost identical, although the values of  $X$  and  $N$  are very different.

We also show in appendix A that the dynamics of the transformed variable  $X$  can be expressed by the stochastic differential equation

$$dX = (\alpha - \beta X)dt + (1 - \theta X)\sigma dB, \tag{3}$$

where  $\alpha = r - (1/2)\sigma^2$ ,  $\beta = r/g(K) - (1/2)\theta\sigma^2$ , and  $dB$  is the infinitesimal increment of a Brownian motion so that  $E(dB) = 0$ ,  $\text{Var}(dB) = dt$ , and the time derivative  $W(t) = dB/dt$  is so-called white noise. The simple linear form of this equation enables us to investigate the spatial synchrony of  $X$ , which is the same as the spatial synchrony of  $N$  to the first order of approximation.

Notice that the “carrying capacity” on the  $X$  scale, which is  $\alpha/\beta$ , is not exactly the transformation  $g(K)$  of the carrying capacity of  $N$  unless  $\sigma^2 = 0$ . Generally, the growth rate of  $X$  is 0 for  $X = \alpha/\beta = \tilde{X}$ , where

$$\tilde{X} = g(K) \frac{2r - \sigma^2}{2r - g(K)\theta\sigma^2}. \tag{4}$$

For the log-linear model obtained for  $\theta = 0$ , we see in particular that  $\tilde{X} = g(K)[1 - (\sigma^2/2r)]$ , where  $g(K) = \ln K$ .

### Spatial Synchrony

In order to analyze spatial synchrony in the case of no migration, it is sufficient to consider two locations with transformed processes, say  $X_1$  and  $X_2$ , and parameters of the processes indexed by 1 and 2. The noise terms for the two locations are assumed to have correlation  $\rho_e$  called the environmental correlation, which means that the expectation  $E(dB_1 dB_2) = \rho_e dt$ . The covariance  $c_{12} = \text{Cov}(X_1, X_2)$  can now be evaluated using a technique proposed by Bartlett (1960) for analyzing properties of stationary processes. We simply require that  $\text{Cov}(X_1, X_2) = \text{Cov}(X_1 + dX_1, X_2 + dX_2)$ , where  $dX_1$  and  $dX_2$  are given by equation (3) with indices 1 and 2, respectively. It is shown in appendix B that this leads to the relatively simple ex-

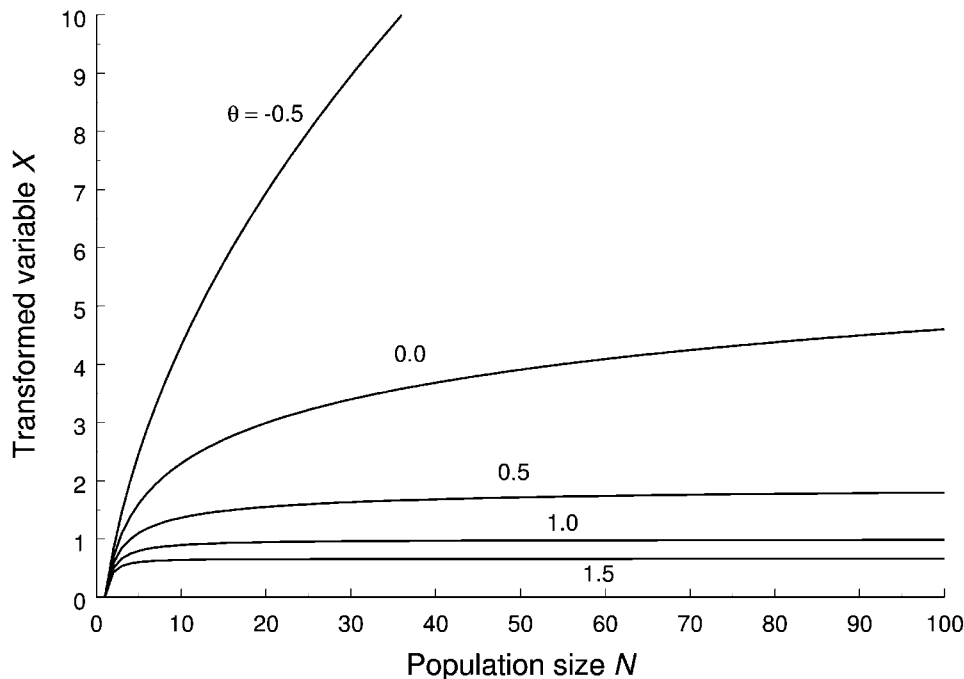


Figure 1: Transformed variable  $X = (1 - N^{-\theta})/\theta$  as a function of the population size  $N$  for some values of  $\theta$ .

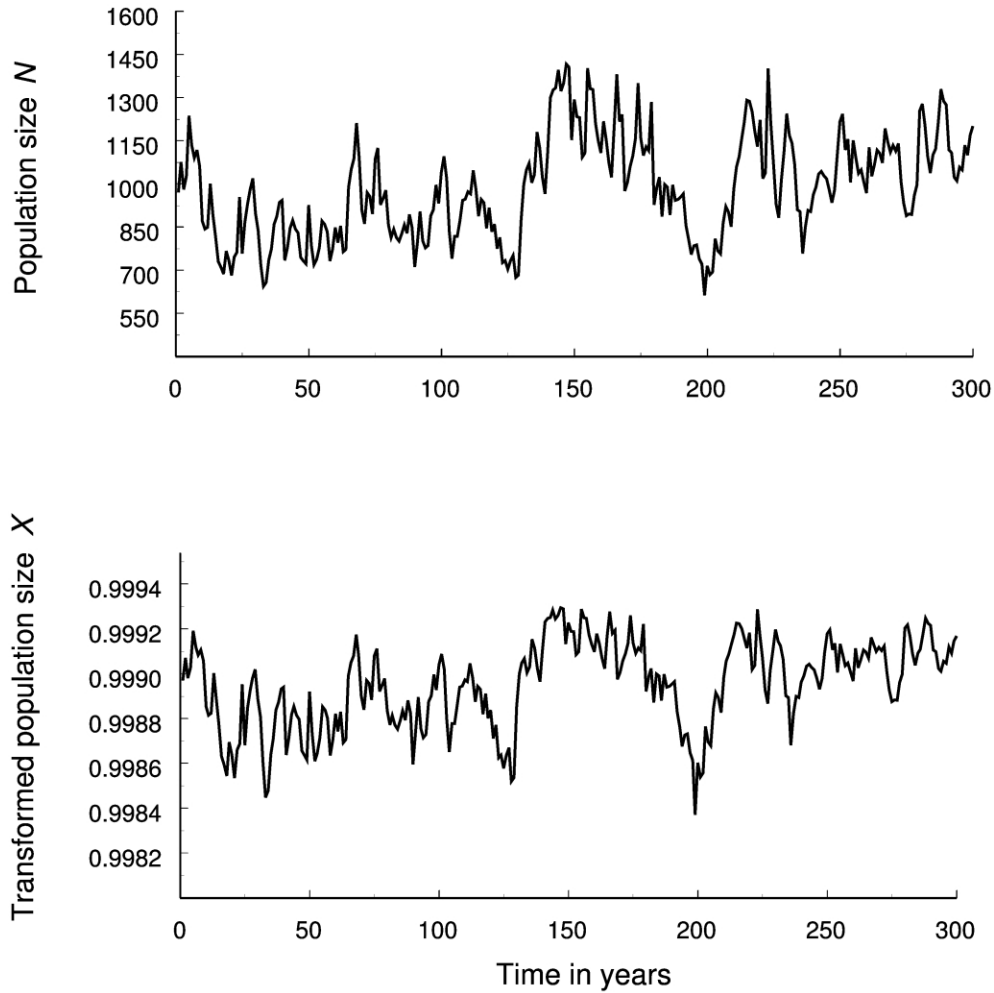


Figure 2: Simulation of a population process  $N$  (top) with parameters  $r = 0.1, K = 1,000, \theta = 1$ , and  $\sigma^2 = 0.01$ , and the corresponding transformed process  $X$  (bottom).

pression for the correlation between the transformed population sizes

$$\rho_x = \text{corr}(X_1, X_2) = \rho_e \frac{\sqrt{(2\beta_1 - \theta_1^2\sigma_1^2)(2\beta_2 - \theta_2^2\sigma_2^2)}}{\beta_1 + \beta_2 - \rho_e\sigma_1\sigma_2\theta_1\theta_2}. \quad (5)$$

For certain parameter values, the variances  $\text{Var}(X_i)$  may be infinite. In this case, the correlation is 0 as long as  $c_{i2}$  is finite. Hence,  $\rho_x = 0$  when  $2\beta_i - \theta_i^2\sigma_i^2 \leq 0$  for  $i$  equal to 1 or 2.

In order to analyze equation (5), it is convenient to write it in a different way, introducing  $u_i = \theta_i\sigma_i$  and  $v_i = \beta_i - (1/2)u_i^2$  for  $i = 1, 2$  and  $\varepsilon = (1/2)(u_1^2 + u_2^2 - 2\rho_e u_1 u_2)^2$ . Then equation (5) can be written as

$$\rho_x = \rho_e \sqrt{\frac{4v_1 v_2}{(v_1 + v_2 + \varepsilon)^2}}. \quad (6)$$

Because  $\varepsilon \geq 0$  for any correlation  $\rho_e$ , we see from equation (6) that  $\rho_x \leq \rho_e$ . The two correlations are equal only if  $v_1 = v_2$  and  $\varepsilon = 0$ , which implies that the  $\theta_i$  are 0 and  $\beta_1 = \beta_2$ . Hence, equality occurs only for the log-linear model with equal parameters  $\beta$ , which is the case discussed by Moran (1953). For all other cases, the correlation between population sizes is smaller than the environmental correlation (see also Greenman and Benton 2001).

We have now expressed the correlation between  $X_1$  and  $X_2$  by the set of parameters  $\psi_1$  and  $\psi_2$  as well as the correlation  $\rho_e$  between the noise term. The expected correlation at a given distance with respect to the spatial dis-

tribution of the parameters can then most conveniently be calculated by stochastic simulations using the mean of the correlations, given by equation (5), based on a large number of simulations of  $\psi_1$  and  $\psi_2$  for a given spatial model

### Some Special Cases

#### The Theta Effect

Assuming that the dynamics are given by the same set of parameters at each location, we can omit the indices for the parameters. The environmental correlation  $\rho_e$  is still any given environmental correlation. This leads to the simple relation

$$\rho_x = \rho_e \frac{1 - \delta}{1 - \delta \rho_e}, \tag{7}$$

where

$$\delta = \frac{\sigma^2 \theta^2}{2\beta} = \frac{\theta^2 \sigma^2 \tilde{X}}{2r - \sigma^2}. \tag{8}$$

Equation (7), depicted in figure 3, expresses exactly how

the form of the density regulation, determined by the parameter  $\theta$ , acts between the transformed time series at locations 1 and 2 together with the spatial correlation  $\rho_e$  of the environmental noise. For any stochastic model, the environmental variance  $\sigma^2$  is positive, so we obtain the Moran effect  $\rho_x = \rho_e$  only if  $\theta = 0$  (fig. 4), in which case the model is linear (the Ornstein-Uhlenbeck process; see Karlin and Taylor 1981) in  $X = \ln N$ . Otherwise  $\delta > 0$  gives  $\rho_x < \rho_e$  for positive environmental correlations (fig. 4). For the logistic model corresponding to  $\theta = 1$ , we find by inserting  $\tilde{X} = 1 - 1/K$  that

$$\delta = \frac{\sigma^2(1 - 1/K)}{2r - \sigma^2} \approx \frac{\sigma^2}{2r - \sigma^2}. \tag{9}$$

#### Spatial Variation in Strength of Density Regulation

The strength of density regulation in the model for  $X$  is  $\beta = r/g(K) - (1/2)\theta\sigma^2$ . A large value of  $\beta$  corresponds to a short return time to equilibrium (Lande et al. 2003). This parameter is approximately the same as the strength of density regulation in the theta-logistic model, which is  $\gamma = r/g(K)$  (see Lande et al. 2003).

One should expect spatial synchrony to be broken down

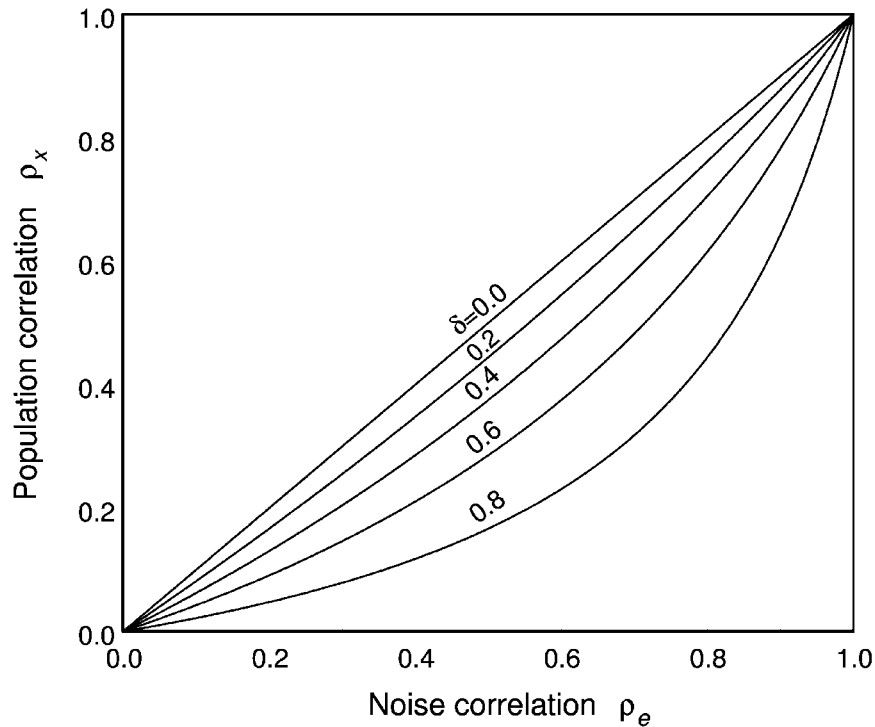


Figure 3: Population correlation  $\rho_x$  as a function of the noise correlation  $\rho_e$  for different values of  $\delta = \sigma^2\theta^2/(2\beta)$  when the population parameters are constant in space.

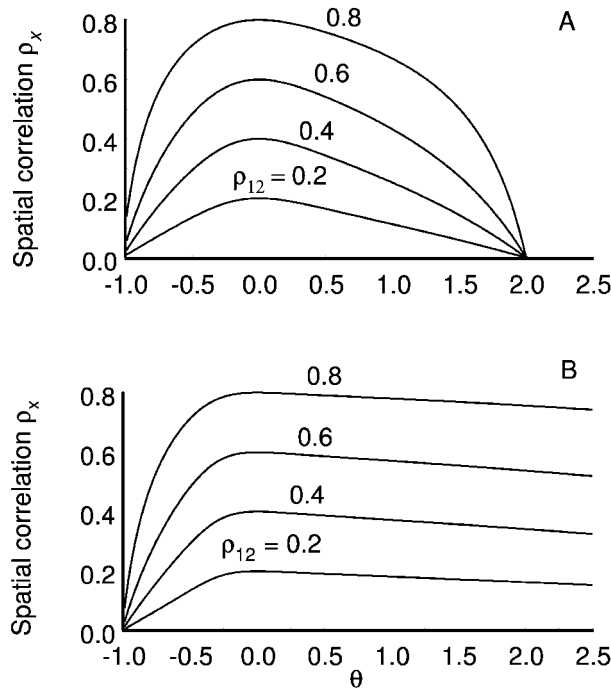


Figure 4: Correlation between population sizes at two locations with common parameters  $K = 100$  and  $\sigma^2 = 0.02$  as a function of a common  $\theta$  for different values of the environmental autocorrelation  $\rho_c$ . A,  $r = 0.03$ ; B,  $r = 0.1$ .

by spatial variation in  $\beta$ , an effect that can now be quantified using equation (5). For simplicity, let us consider the linear model on the log scale obtained by choosing  $\theta = 0$  and letting  $\alpha$  and  $\sigma^2$  be constant in space. Inserting into equation (5) then gives simply

$$\rho_x = \rho_c \sqrt{4s(1-s)}, \tag{10}$$

where  $s = \beta_1/(\beta_1 + \beta_2)$ . Since the maximum value of  $s(1-s)$  is  $1/4$  obtained for  $s = 1/2$  or  $\beta_1 = \beta_2$ , we see that stochastic spatial variation in  $\beta$  tends to break down the synchrony, making  $\rho_x < \rho_c$ .

#### Effects of Including Environmental Covariates

The environmental influence on population fluctuations has so far been modeled by the infinitesimal variance  $N^2\sigma^2$  in the diffusion for the population size  $N$ . For a discrete step with length  $\Delta t = 1$ , we then have approximately that  $\Delta N = N\sigma U$ , where  $U$  is a standard normal variate, which corresponds to how environmental stochasticity is modeled in discrete models (Engen et al. 1998; Lande et al. 2003). The noise terms, which have zero mean and variance  $N^2\sigma^2$ , are assumed to be independent between years.

In practice, however, this stochastic term may be partly

explained by some covariates that influence the dynamics (e.g., Sæther et al. 2003). Hence, the spatial properties of these covariates as well as the spatial variation in their effects may have a large influence on the spatial synchrony of the population fluctuations. We can investigate these effects by exploring the stochastic term when this term includes the effects of the covariates (Sæther et al. 2004a). We perform this analysis for a single covariate only to avoid too long and technical expressions. However, the technique can easily be applied in the case of several covariates. We write  $Z = \tau V$  for the covariate, where  $V$  is also standard, normally distributed, and independent between years, so that this has variance  $\tau^2$  and is centered to have zero mean. The noise term is then expressed as the linear function  $\tilde{\sigma}U + q\tau V$ , where  $q$  is a regression coefficient expressing the strength of the effect of  $Z$  and  $\tilde{\sigma}$  is the standard deviation of the residual noise not explained by  $Z$ . We assume that the covariate term has been defined so that the residual term defined by  $U$  is independent of  $V$ . Then the stochastic term is normally distributed with constant variance as in the model with no covariates. Thus, equation (5) can still be applied to calculate the correlations, provided that the environmental variance is interpreted as the variance of  $\tilde{\sigma}U + q\tau V$ , which is

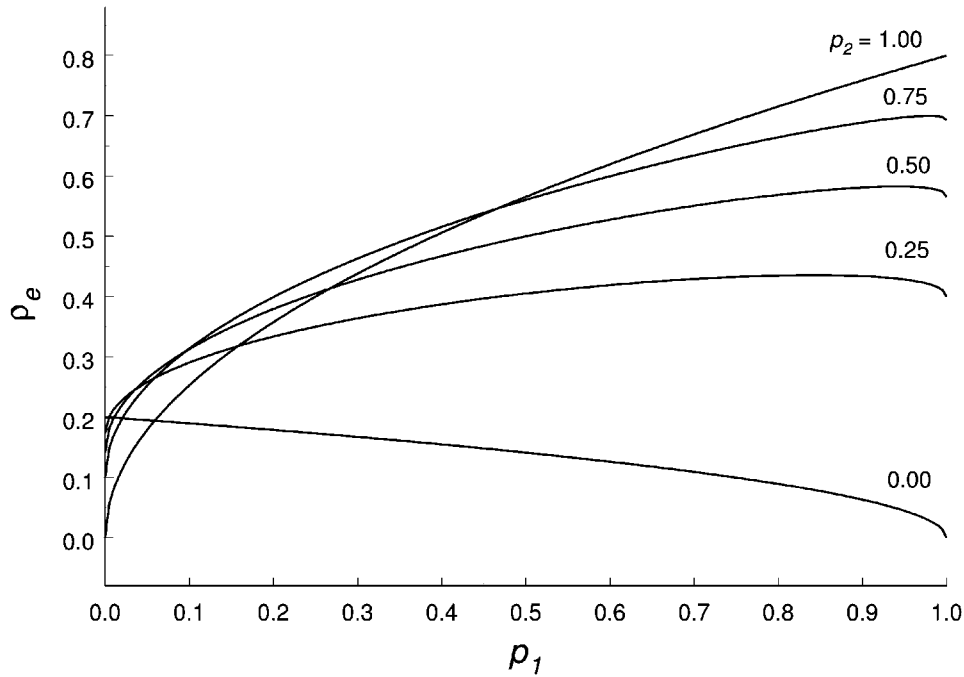


Figure 5: Total environmental correlation  $\rho_e$  as a function of the proportion  $p_1$  of the variance explained by the covariate at location 1 for different values of the same proportion at location 2. The spatial correlation for the covariate is  $\rho_z = 0.8$ , while the correlation for the residual noise is  $\tilde{\rho}_e = 0.2$ .

$$\sigma^2 = \tilde{\sigma}^2 + q^2\tau^2.$$

The environmental correlation  $\rho_e = \text{corr}(\sigma_1 U_1 + q_1 \tau_1 V_1, \sigma_2 U_2 + q_2 \tau_2 V_2)$  is then

$$\rho_e = \frac{\tilde{\rho}_e \tilde{\sigma}_1 \tilde{\sigma}_2 + q_1 q_2 \tau_1 \tau_2 \rho_z}{\sqrt{(\tilde{\sigma}_1^2 + q_1^2 \tau_1^2)(\tilde{\sigma}_2^2 + q_2^2 \tau_2^2)}}.$$

Here  $\tilde{\rho}_e = \text{corr}(U_1, U_2)$  is the environmental spatial correlation for the component of the noise not explained by the covariate and  $\rho_z = \text{corr}(V_1, V_2) = \text{corr}(Z_1, Z_2)$  is the spatial correlation of the covariate. Writing

$$p = \frac{q^2 \tau^2}{\tilde{\sigma}^2 + q^2 \tau^2}$$

for the proportion of the total environmental noise explained by stochastic fluctuations in the covariate  $Z$ , the total environmental correlation is the simple linear combination of  $\tilde{\rho}_e$  and  $\rho_z$ :

$$\rho_e = \tilde{\rho}_e \sqrt{(1-p_1)(1-p_2)} + \text{sgn}(q_1 q_2) \rho_z \sqrt{p_1 p_2}, \quad (11)$$

where  $\text{sgn}(x)$  is the sign of  $x$  (1 or  $-1$ ), which inserted in equation (5) gives the general solution for the spatial syn-

chrony. If  $q_1 q_2 > 0$ , the effects of variation in a covariate on  $\rho_e$  and synchrony  $\rho_x$  increase with increasing amount of variance in the total noise term that is explained by the covariate (fig. 5).

### Discussion

These analyses show that the correlation of fluctuations in the size of two populations at a distance so large that migration can be ignored will be less than the environmental correlation even when they have the same local dynamics (figs. 3, 4). The only exception is for a log-linear model ( $\theta = 0$ ) at both locations with the same strength of density regulation (fig. 4) that corresponds to Moran's (1953) classical results. Furthermore, spatial variation in density regulation or in the local effects of environmental covariates will also break down the population synchrony. Thus, our results represent a generalization of the Moran effect that provides an analytical tool for evaluating the relative contribution of the local expected population dynamics and environmental covariation to the pattern of spatial population synchrony.

Our analyses are based on the diffusion approximation to the theta-logistic model of Gilpin and Ayala (1973). This represents a rather general class of models that in-

cludes several types of density regulation models such as the log-linear and the logistic model (Sæther et al. 2002). A number of stochastic simulations have shown that this diffusion approximation is rather accurate for small and moderate values of the environmental stochasticity. For real populations, this parameter is often  $<0.05$  (Lande et al. 2003) but may also be larger (Sæther et al. 2004b), in which case the diffusion approximation represents only a rough approximation to the dynamics.

Several simulation studies indicate that the degree of population synchrony is influenced by the form of density regulation. For instance, nonlinearity in the density dependence typically reduces the synchronizing effect of spatially correlated noise (Ranta et al. 1995, 1997a; Bjørnstad et al. 1999; Royama 2005). Our linear transformation of the theta-logistic model given by equation (3) enables us to analyze quantitatively how variation in density dependence affects population synchrony. Strong density regulation around  $K$  (large values of  $\theta$ ) typically reduces the level of synchrony compared with what is expected for a log-linear model (fig. 4). In our case, the magnitude of the reduction in synchrony for  $\theta \neq 0$  was further dependent on the specific growth rate  $r$  (fig. 4). Thus, this extends previous modeling of spatial dynamics (e.g., Blasius et al. 1999; Haydon and Greenwood 2000; Cazelles and Boudjema 2001) that considers populations with cyclic or periodic dynamics that are often associated with strong density regulation. This represents an important extension because weak density dependence is at least common in the dynamics of many vertebrate populations (Ives and Klopfer 1997; Sæther and Engen 2002; Williams et al. 2003). Furthermore, large spatial variation in the strength of density dependence has also been recorded within the distribution area of a species (e.g., Stenseth et al. 1999; Sæther and Engen 2002; Sæther et al. 2003; Williams et al. 2003).

In general, spatial heterogeneity will reduce population synchrony. This effect can be seen directly from equation (6), which is a reformulation of equation (5). Because  $\varepsilon$  is likely to be very small, we may approximate equation (6) by ignoring this parameter in the denominator. We see that the square root factor in equation (6) then becomes the same function as the square root factor in equation (10), only with  $\beta_i$  replaced by  $v_i = r_i/g(K_i) - \theta_i^2\sigma_i^2$ . Hence, the relationship in equation (10) also represents how spatial synchrony in general is reduced by spatial heterogeneity in the parameter  $v_i$ , which is a function of all four parameters describing the local dynamics.

A central question in theoretical analyses of spatial population dynamics has been how spatial correlations in the environmental noise translate into synchrony in population size (see reviews in Ranta et al. 1998; Bjørnstad et al. 1999; Koenig 1999; Lundberg et al. 2000; Liebhold et al.

2004). Equation (5) gives the explicit relationship between the population and noise correlation as depicted in figure 4. We see that population correlation will always increase with the noise correlation because it is always a factor in this expression and, in addition, the denominator of equation (5) decreases with increasing noise correlation  $\rho_e$ . This generalizes the previous analytical results of Greenman and Benton (2001) obtained for a discrete Ricker type population model (May 1981) with the same parameter values at the two locations (fig. 3). These deviations are larger for intermediate values of  $\rho_e$  (Greenman and Benton 2001).

Spatial variation in environmental effects on the local dynamics will also influence the population synchrony (fig. 5). Writing  $p_1 = p - d$  and  $p_2 = p + d$ , equation (10) takes the form

$$\rho_e = \tilde{\rho}_e \sqrt{(1-p)^2 - d^2} + \text{sgn}(q_1 q_2) \rho_e \sqrt{p^2 - d^2}.$$

This shows that increasing differences between populations in the proportion of noise variance explained by the environmental covariate reduces both terms in the above expression for  $\rho_e$  provided that  $q_1 q_2 > 0$ . Consequently, if the effects of the covariate have the same direction, spatial heterogeneity in the environmental effects reduces the noise correlation, which in turn according to equation (5) decreases the population correlation. Accordingly, in an extensive simulation study, Ranta et al. (1999) found that spatial structures in noise strongly affected the population synchrony.

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#### APPENDIX A

##### Transformation of the Theta-Logistic Model

The transformation formulas for diffusions say that for smooth functions  $X = g(N)$  with inverse  $N = g^{-1}(X)$ ,  $X$  is also a diffusion process, with infinitesimal mean and variance  $\mu_x(x) = g'(n)\mu(n) + (1/2)g''(n)v(n)$  and  $v_x(x) = g'(n)^2 v(n)$  (Karlin and Taylor 1981). Performing the transformation  $g(n) = (1 - n^{-\theta})/\theta$  then leads to  $\mu_x(x) = a - bx$  and  $v_x(x) = (1 - x\theta)^2 \sigma^2$ , where  $a = r - (1/2)(\theta + 1)\sigma^2$  and  $b = r/g(K) - (1/2)\theta(1 + \theta)\sigma^2$ .

The model for the process  $X$  can then be written as a stochastic differential equation. Since the variance is not constant unless  $\theta = 0$ , the presentation most relevant for our calculations is the so-called Stratonovich representation (Karlin and Taylor 1981):

$$dX = \left( \mu_x(x) - \frac{1}{4} \frac{d}{dx} \nu_x(x) \right) dt + \sqrt{\nu_x(x)} dB,$$

where  $t$  denotes time and  $B(t)$  is a standard Brownian motion so that  $E dB = 0$  and  $\text{Var}(dB) = dt$  (see Karlin and Taylor 1981). This representation ensures that the parameter values that make  $N$  a stationary process are the same as those giving stationarity for  $X$ . Inserting the expressions for the infinitesimal mean and variance leads to equation (3) in the main text.

## APPENDIX B

### Correlation between Transformed Processes

Following Bartlett (1960), we now require that  $c_{12} = \text{Cov}(X_1, X_2) = \text{Cov}(X_1 + dX_1, X_2 + dX_2)$ , where  $dX_1$  and  $dX_2$  are given by the above stochastic differential equation with indices 1 and 2, respectively. Writing out these covariances using equation (3) and considering the fact that second-order terms like  $(dt)^2$  vanish in continuous models like this, we find, using the fact that  $dB_1$  and  $dB_2$  are independent of  $X_1$  and  $X_2$ , that

$$\begin{aligned} \text{Cov}(X_1 + dX_1, X_2 + dX_2) = \\ [1 - (\beta_1 + \beta_2)dt] \text{Cov}(X_1, X_2) + \omega, \end{aligned}$$

where

$$\omega = \sigma_1 \sigma_2 \text{Cov}[(1 - X_1 \theta_1) dB_1, (1 - X_2 \theta_2) dB_2].$$

The two Brownian motions  $B_1$  and  $B_2$  describing the environmental noise are correlated in space with correlation  $\rho_c$ , so that  $E(dB_1 dB_2) = \rho_c dt$ . This leads to

$$\omega = \sigma_1 \sigma_2 E(1 - X_1 \theta_1)(1 - X_2 \theta_2) \rho_c dt$$

or

$$\omega = \sigma_1 \sigma_2 \rho_c \left[ 1 - \frac{\alpha_1 \theta_1}{\beta_1} - \frac{\alpha_2 \theta_2}{\beta_2} + \frac{\alpha_1 \theta_1 \alpha_2 \theta_2}{(\beta_1 \beta_2)} + \theta_1 \theta_2 c_{12} \right] dt.$$

Requiring that  $\text{Cov}(X_1, X_2) = \text{Cov}(X_1 + dX_1, X_2 + dX_2)$  and solving for the covariance then give

$$c_{12} = \frac{\rho_c \sigma_1 \sigma_2 (1 - \alpha_1 \theta_1 / \beta_1)(1 - \alpha_2 \theta_2 / \beta_2)}{\beta_1 + \beta_2 - \rho_c \sigma_1 \sigma_2 \theta_1 \theta_2}. \quad (\text{C1})$$

From this, we find the corresponding correlation

$$\text{corr}(X_1, X_2) = \rho_e = \frac{c_{12}}{\sqrt{c_{11} c_{22}}}$$

given by equation (5) using the fact that  $\text{corr}(X_1, X_1) = \text{corr}(X_2, X_2) = 1$ .

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