Synchrony of spatial populations induced by colored environmental noise and dispersal

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ABSTRACT

Spatial synchrony of oscillating populations has been observed in many ecological systems, and its influences and causes have attracted the interest of ecologists. Spatially correlated environmental noises, dispersal, and trophic interactions have been considered as the causes of spatial synchrony. In this study, we develop a spatially structured population model, which is described by coupled-map lattices and incorporates both dispersal and colored environmental noise. A method for generating time series with desired spatial correlation and color is introduced. Then, we use these generated time series to analyze the influence of noise color on synchrony in population dynamics. The noise color refers to the temporal correlation in the time series data of the noise, and is expressed as the degree of (first-order) autocorrelation for autoregressive noise. Patterns of spatial synchrony are considered for stable, periodic and chaotic population dynamics. Numerical simulations verify that environmental noise color has a major influence on the level of synchrony, which depends strongly on how noise is introduced into the model. Furthermore, the influence of noise color also depends on patterns of dispersal between local populations. In addition, the desynchronizing effect of reddened noise is always weaker than that of white noise. From our results, we notice that the role of reddened environmental noise on spatial synchrony should be treated carefully and cautiously, especially for the spatially structured populations linked by dispersal.

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1. Introduction

In natural world, the densities of populations in different locations are frequently observed to fluctuate synchronously. Such behavior, known as spatial synchrony, has been described, for example, in small mammals (Heikkilä et al., 1994), butterflies (Sutcliffe et al., 1997), grouse (Ranta et al., 1995), various species of moths and aphids (Hanski and Woiwod, 1993), sheep (Grenfell et al., 1998), forest defoliators (Myers, 1998), and acorn crops (Crawley and Long, 1995). Spatial synchrony has been found not only in populations of same species, but also in populations of different species. The most famous example is the snowshoe hare-lynx oscillation in boreal forests of North America, which is also correlated with several other species of mammalian predators and their prey (Elton and Nicholson, 1942). Generally, there exist three principle explanations for population synchrony. First, spatially extended inter-specific interactions or trophic interactions, like predation or parasitism, may induce synchrony by imposing a common source of mortality across a region (Myers, 1998; Ims and

Andreassen, 2000). The second explanation envisages an important role for inter-population dispersal (Ranta et al., 1995; Liebhold et al., 2004), whereby the movement of individuals acts to reduce the heterogeneity of local population fluctuations. Finally, commonly known as the Moran effect (Moran, 1953), suggests that if two regional populations have the same intrinsic (density-dependent) structure, they will be correlated under the influence of common environmental variation. Such variation may include high levels of spatially correlated fluctuations in the physical environment, such as temperature and rainfall (Koenig, 2002), and independent populations can be synchronized by such spatial correlation of environmental disturbances. Moran effect has been recently rejuvenated when research in population ecology shifted focus from isolated populations to populations linked by dispersing individuals. Ranta et al. (1999) suggested that spatially auto-correlated perturbations and distance-dependent dispersal could intensify synchrony of spatial populations. Recently, Gao et al. (2007) found that the trophic correlation of environmental noise was also an important factor inducing spatial synchrony. It seems that the role of environmental noise in synchronizing spatial populations come into the view of theoretical ecologists again.

There are three traditional attributes used to describe the environmental noise: mean of the time series data, the variance

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(i.e. magnitude of variation) and power spectrum. The color is just a feature of the spectrum, which refers to the temporal correlation in time series data and is expressed as the degree of (first order) auto-correlation for auto-regressive noise (Ripa and Lundberg, 1996). The noise is said to be 'white' when no frequency dominates, 'red' when time series are dominated by low-frequency, long-term variations and 'blue' when high-frequency dominates. Earlier investigations use white noise, which assumes temporally non-correlated environmental fluctuations to characterize environmental variation (Ranta et al., 1995). However, several studies have revealed that most environmental noises in nature are not always white but often reddened, implying positive temporal correlation in the environmental fluctuations (Steele, 1985). Thus, it is conceivable that the efficacy of Moran effect may not only be related to the degree of spatial correlation of environmental fluctuations but also to the degree of temporal correlation, or the periodicity of environmental variation. The importance of noise color for population and community dynamics has been well studied (Heino et al., 1997, 2000), however, its potential impact on population synchrony has remained relatively unexplored. The methods and conclusions from these studies play an important role in our understanding and further studying of synchrony and noise color. Heino (1998) demonstrated that noise color has a major influence on both the level of synchrony in population dynamics and spatial patterns of the synchrony. However, spatial correlations among colored noises were ignored in his study. Recently, an interesting laboratory experiment showed that the color of the noise might be important in spatial synchrony (Fontaine and Gonzalez, 2005). They suggested that in the absence of dispersal only the red fluctuations induced synchrony in the population dynamics of a rotifer. In this paper, we use a novel and simple method to generate colored noises with any desired cross- (spatial) correlation. Then, we use these generated time series to analyze the influence of noise color on synchrony in population dynamics. Particularly, the complex interaction between dispersal and noise color on spatial synchrony is included.

Spatially structured populations are often modelled by partial differential equations (Okubo and Levins, 2001), coupled ordinary differential equations (Jansen, 2001; Li et al., 2005), and coupled-map lattices (Hassell et al., 1991). The first two methods usually deal with deterministic population dynamics and are difficult to incorporate stochasticity. Therefore, in this study, we choose coupled-map lattice to model spatially structured populations, which are affected by environmental noise. For any local population, the dynamics is modelled by a classical and typical discrete Maynard Smith model. Previous theoretical models predicted that spatial synchrony could be enhanced in cyclic populations due to nonlinear phase-locking (Bjørnstad, 2000), and chaotic populations were hard to synchronize (Bjørnstad et al., 1999). We know that the deterministic Maynard Smith model also can produce many complex dynamics, such as stable steady states, periodic and chaotic fluctuations. The reason selecting Maynard Smith model in this paper is for the convenience of comparing our results with the previous ones. We use spatially extended Maynard Smith model to determine the influence of environmental noise color on the operation of Moran effect on stable, cyclic and chaotic population dynamics respectively. In this paper, we focus on several factors which affect synchrony of spatial populations, including dispersal rate (the fraction of migration), distance-dependence in dispersal, noise color and spatial correlation of environmental noises.

2. Models and methods

2.1. Spatially correlated colored noises

Colored noise ψ_i is modelled as a first-order stationary autoregressive process AR_1:

$$\psi_{it+1} = \alpha \psi_{it} + \beta \varepsilon_{t+1} \tag{1}$$

where the parameter α controls the degree of temporal autocorrelation. If $\alpha = 0$, then there is no autocorrelation and the noise is 'white' (no frequency dominates). For $0 < \alpha \leq 1$, the noise is 'reddened' (low-frequency, or long-term variations dominate). While $-1 \leq \alpha < 0$ implies negatively correlated noise, the noise is 'blue' (high-frequency dominates). ε_t is a random normal deviate with zero mean and unit variance, and β determines the magnitude of environmental fluctuation. Red environmental noise is characterized by a strong dependence of expected sample variance on sample length and noise color (α) (Heino et al., 2000). This dependence has to be taken into account when assessing synchrony under red and white uncorrelated environmental noise. To facilitate a comparison between red and white noise, their expected variances can be scaled to be equal. Particularly, when $\beta = \sigma\sqrt{1-\alpha^2}$ (σ is constant), we scale the time series such that its true variance is independent of α, where σ^2 is the desired asymptotic variance of noise (Petchey et al., 1997).

Here, we introduce a method of generating sets of 'environmental' time series with desired correlations (herein referred to as ρ) and colors (referred to as α). Correlated but identically distributed colored environmental noises d_t can be constructed from a linear combination of independent identically distributed colored noises ψ_i and $cov(\psi_i, \psi_j) = 0$.

$$\begin{pmatrix} d_1 \\ d_2 \\ \vdots \\ d_n \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ b_{21} & b_{22} & 0 & \cdots & 0 \\ & \cdots & \cdots & \cdots & \\ b_{n1} & b_{n2} & b_{n3} & \cdots & b_{nn} \end{pmatrix} \begin{pmatrix} \psi_1 \\ \psi_2 \\ \vdots \\ \psi_n \end{pmatrix} \tag{2}$$

$B = (b_{ij})_{n \times n}$ is a lower triangular matrix, and $b_{ij}(j \leq i)$ are constants. d_i is environmental noise on patch i. n is the number of patches.

Given the correlation coefficients matrix of d_i:

$$C = \begin{pmatrix} 1 & c_{12} & c_{13} & \cdots & c_{1n} \\ c_{21} & 1 & c_{23} & \cdots & c_{2n} \\ & \cdots & \cdots & \cdots & \\ c_{n1} & c_{n2} & c_{n3} & \cdots & 1 \end{pmatrix} \quad c_{ij} = corr(d_i, d_j) \quad \text{and} \quad C = C^T \tag{3}$$

where C is a symmetric matrix, and c_{ij} can be obtained explicitly (see Appendix A). For simplicity, here we assume that the degrees of cross-correlations are equal ($\rho = c_{ij} = corr(d_i, d_j)$). Although the method described above is capable of generating time-series over the entire range of noise colors, the remainder of this study focuses on the impact of reddened and white environmental noise ($\alpha \geq 0$), since environmental variables of ecological interest almost exclusively take such form. In this study, we only consider ρ that located in [0,1]. When ρ equals to zero, all noises are independent and spatial correlations of environmental noises do not exist. Contrarily, $\rho = 1$ implies that all noises are the same and environmental noises are fully spatially correlated. So we can nominate the two extreme case local and global noise respectively. For intermediate ρ located in (0,1), the noise is transitional noise from local to global.

To ensure that our method of generating colored cross-correlated environmental noises is valid, it is necessary to test if the generated noises are still red noises and with desired cross-correlations. Particularly, we use two reddened noise as an example. Then the parameters are $\alpha = 0.8$, $\sigma^2 = 0.04$, $\rho = 0.7$. The power spectra of two generated noises are given in Fig. 1. Obviously, we can see that both noises show red power spectra. We do 100 replicated simulations, and then calculate the mean and variance of the cross-correlation between two generated noises. We get $mean = 0.6987$, and $variance = 0.0020$. The frequency distributions do not differ from normally distribution (Kolmogorov–Smirnov
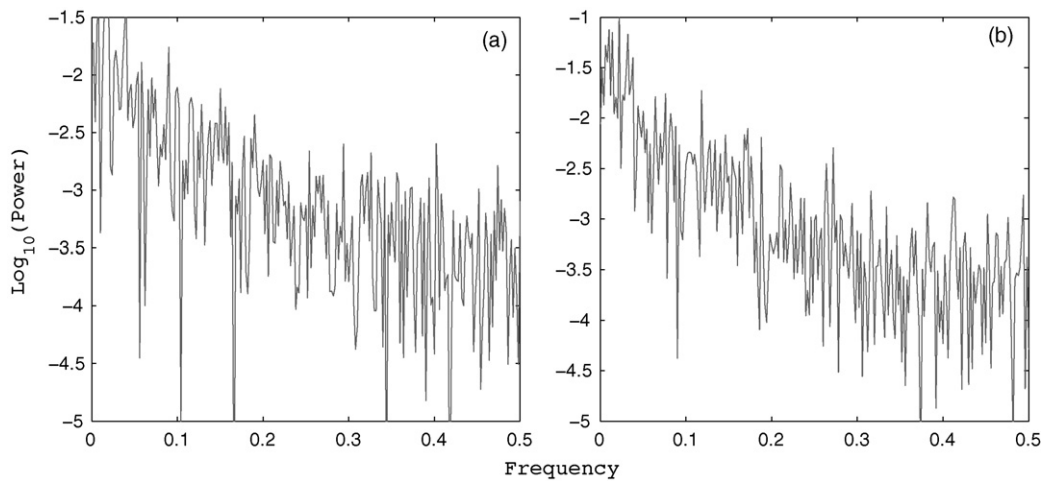
Fig. 1. Power spectra of two correlated noises. Parameter values: $\alpha = 0.8$, $\sigma^2 = 0.04$, $\rho = 0.7$..

test; $D = 0.0881$, $P = 0.4191$). Therefore, it seems that the method introduced in this study to generate spatially correlated environmental noises is reliable.

2.2. Local population model with environmental noise

We assume that local population dynamics is governed by the Maynard Smith model (Maynard Smith, 1974). In our model, the population dynamics is also affected by environmental noise of different color. The multiplicative effect of the noise yields the following population dynamics (Kaitala et al., 1997).

$$N_{t+1} = N_t \frac{r}{1 + (aN_t)^b}(1 + d_t) \tag{4}$$

where N_t is the size of the local population at generation t, r is the growth rate, a scales the carrying capacity and b describes the type and strength of density dependence. d_t is environmental noise with a desired color. Parameters r and b determine the dynamics of the Maynard Smith model. When r is constant and b increases, stable dynamics becomes firstly periodic and then chaotic in the absence of any environmental noise. Increasing r also increases the complexity of the dynamics.

2.3. The spatial model

We assume that reproduction occurs first, then dispersal, and finally census. In linking the subpopulations we apply a spatially explicit dispersal model (Ranta et al., 1995; Heino et al., 1997), in which N_{it} is given by

$$N_{it} = (1 - m)\tilde{N}_{it} + \sum_{j, j \neq i} m\tilde{N}_{it} \frac{e^{-cd_{ij}}}{\sum_{k, k \neq j} e^{-cd_{jk}}} \tag{5}$$

where i, j and k are patch indices, m is a constant, patch-independent fraction of migrating individuals, d_{ij} is the distance between patch i and j, and c is a parameter in which low values correspond to long migration distances. Migration occurs only between patches, and consequently, no boundary problems arise. Setting $c = 1$ yields a model in which a patch will receive the majority of immigrants only from the two or three nearest patches. When $c = 0.2$, distance-dependent is weak. If the distance-dependence in migration is ignored altogether $c = 0$ (parameters used in Heino et al., 1997). $\tilde{N}_{it}$ is the pre-dispersal population size in patch i at time t governed by Eq. (4). N_{it} is the post-dispersal size.

2.4. Simulation configurations

A patch system of 10 subpopulations randomly assigned in a 10×10 coordinate space is used for every simulation, and the Euclidean distances between subpopulations are calculated (Heino et al., 1997). At the beginning of a simulation, and after a global extinction, the subpopulations are initiated with $1 + U(0, 1)$. For each simulation, first 1000 iterations are discarded to eliminate transient behavior and the next 500 values of the population sizes are used for our analysis. Cross-correlations with lag zero are used as a measure of synchrony in dynamics among the subpopulations (e.g. Chatfield, 1989). We take the average of all pairwise cross-correlations calculated from the entire simulations as a measure of synchrony among the subpopulations. Then we do 100 such simulations, and report the averages of this 100 replicated simulations. Since the original population model can produce versatile dynamic behaviors, we examine the synchrony for parameters corresponding to stable equilibrium, periodic and chaotic dynamics ($b = 10$, $b = 13$, $b = 25$), respectively.

3. Results

Firstly, when local populations are governed by stable dynamics, our simulation results show that synchrony increases with increasing the cross-(spatial) correlation ρ and decreasing distance-dependence c. These results can also be obtained for periodic dynamics and chaotic dynamics, and are in line with conclusion of Ranta et al. (1999). In addition, we find that the noise color has nearly no influence on population synchrony for $m = 0.1$ (Fig. 2a and b). Synchrony decreases slightly even if distance-dependence is strong (Fig. 2b). An increase in the fraction of migration from $m = 0.1$ to $m = 0.5$ results in an increasing of synchrony (Fig. 2c and d). From Fig. 2c and d, we also find that synchrony increases with the increasing of α for relatively small ρ. This phenomenon can also be found for periodic dynamics and chaotic dynamics.

Secondly, when local populations exhibit periodic dynamics, the relationship between synchrony and noise color is much more complex. From Fig. 3b, there is a tendency for the level of synchrony in population dynamics to decrease with increasing autocorrelation of noise. This phenomenon agrees well with the conclusion draw by Heino (1998). However, strong autocorrelation of noise enhances synchrony obviously when distance dependence is weak (Fig. 3a). This phenomenon always exists when dispersal is weakly distance-dependent and the migration fraction is low. When m increases
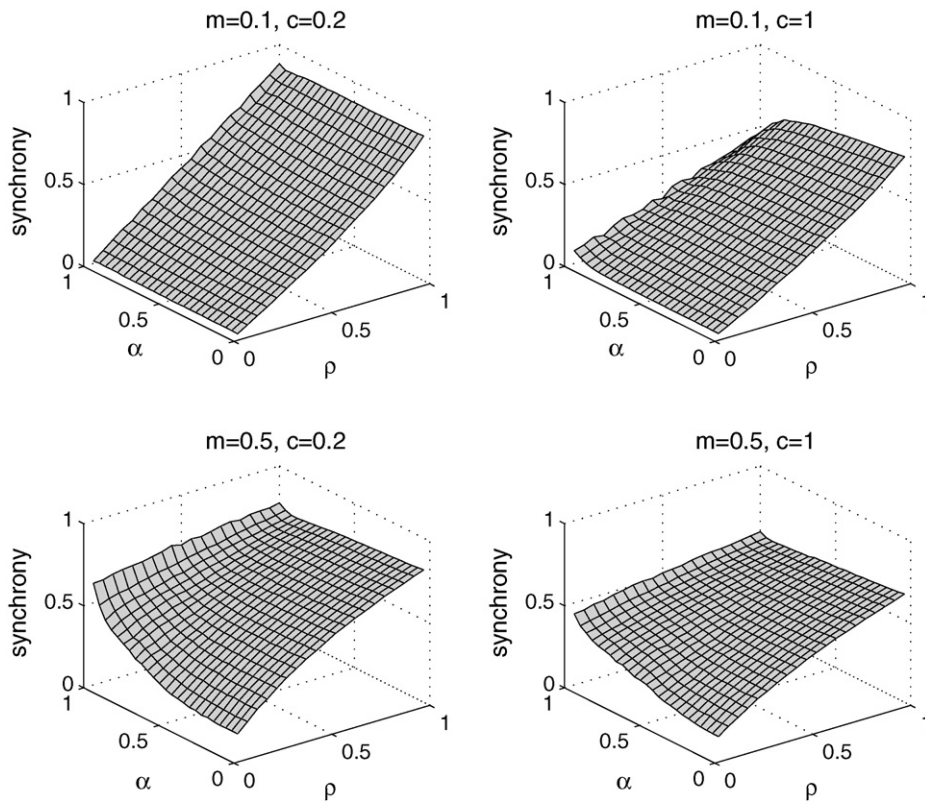
Fig. 2. Average level of synchronous dynamics (measured as the mean of all 45 cross-correlations (time lag zero) in pairs between the 10 populations). The results are the means of 100 replicated simulations in stable dynamic region. Red noises cause higher synchrony than white noises when the cross-correlations are relatively weak. Parameter values: $b = 10$. Other parameters: $\sigma^2 = 0.04$, $a = 0.5$, $r = 1.2$.
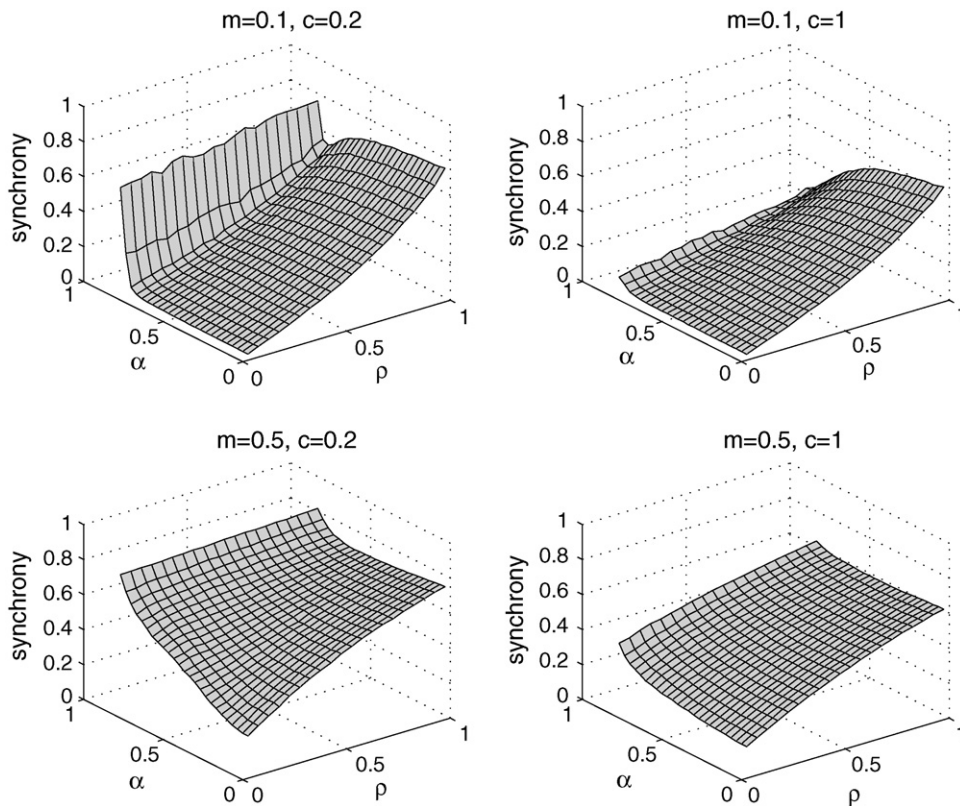

Fig. 3. Average level of synchrony of periodic dynamics (period-2). For higher correlations of noises, the changing tendencies of synchrony with increasing autocorrelation are different under various dispersal patterns. Parameter values: $b = 13$. Other details as in Fig. 2.
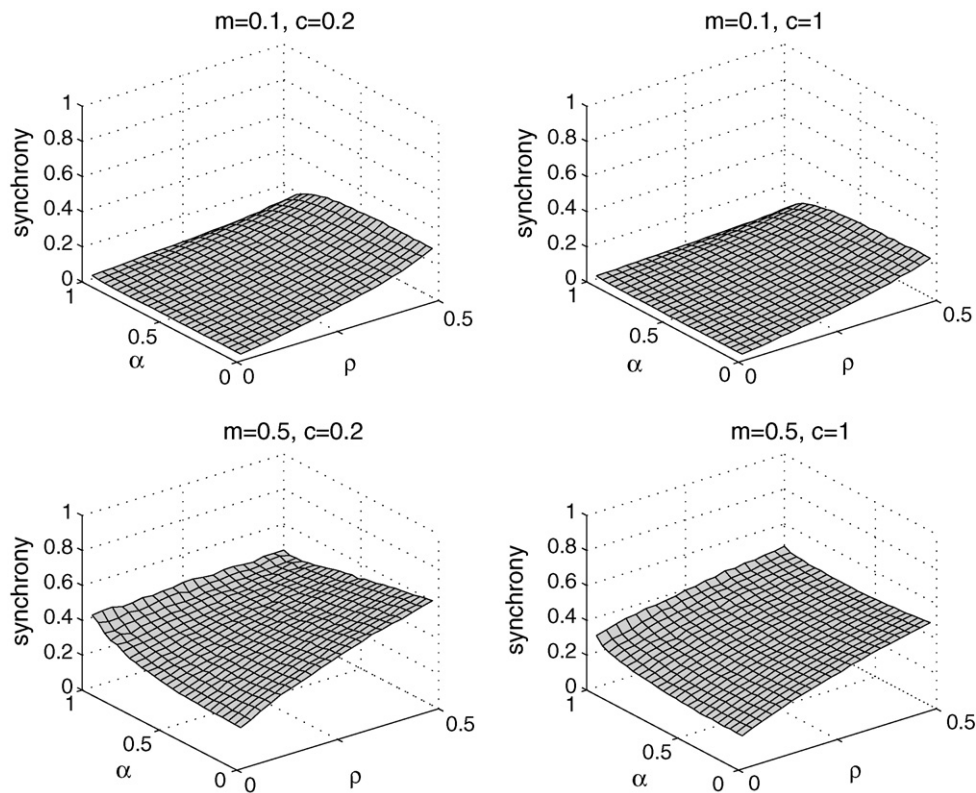
Fig. 4. Average level of synchrony of chaotic dynamics. The levels of synchrony are relatively low because of chaos, but similar changing tendencies can be found as periodic dynamics. Parameter values: $b = 25$. Other details as in Fig. 2.

from 0.1 to 0.5, we find that synchrony increases with the increasing of α for any combination of parameters (Fig. 3c and d).

Finally, we examine the synchrony when local populations exhibit chaotic dynamics. Although the surface plots are not purely smooth as the influence of chaotic dynamics, the changing tendency of spatial synchrony is clear. When fraction of migration is small ($m = 0.1$), the level of synchrony is low for any combination of parameters. However, when m becomes larger ($m = 0.5$), it is strong synchronous even if chaotic dynamics (Fig. 4c and d). This finding verifies that chaotic populations can also be synchronized in noisy environment when the dispersal is strong. This results are also consistent with the conclusion of Heino et al. (1997). For high cross-correlation, there is a tendency of correlation to decrease with increasing autocorrelation (Fig. 4a–c)—an opposite pattern to the one observed for some values of dispersal (Fig. 4d).

Overall, we conclude that reddened noise intensifies spatial synchrony only the dispersal rate is large and the cross-correlation of environmental noise is weak. Furthermore, the influence of noise color depends on patterns of dispersal between populations for high cross-correlation.

4. Discussion

In this paper, we used a spatially structured population model, in which spatially (cross) correlated noises were incorporated, to investigate the influence of environmental noise color and dispersal on spatial synchrony of populations. Although the existence of spatial synchrony is often quite clear, the mechanisms behind synchrony are often murky (Bjørnstad and Bascompte, 2001). Clarifying the mechanisms behind spatial synchrony represents a fascinating intellectual challenge for ecologists. Actually, shortage of reliable field data is the most troublesome in understanding spatial synchrony, however, theoretical research provides us another way to resolve this shortage. Given the frequent demonstration

of population synchrony, a single cause of this behavior would be attractive. However, several possible mechanisms may cause intra-specific or inter-specific synchrony, and identifying which mechanism is most important is often difficult. The causes of population synchrony thus remain an elusive ecological question (Liebhold et al., 2004).

Since Moran's (1953) inspiring work, the role of environmental stochasticity on understanding spatial synchrony has become popular. The most troublesome problem in examining the influence of environmental stochasticity on spatial synchrony is how to model stochasticity in population models. In other word, the keystone is to generate environmental noise. The first problem is about interpretation of environmental stochasticity. Generally, there are two common ways of representing environmental stochasticity in population models, corresponding to two different conceptual models for how populations respond to weather. First, populations might not be influenced much by the weather unless there is some sort of catastrophic event (Ranta et al., 1999), such as extreme cold or drought. The alternative interpretation is that populations might respond to the usual year-to-year fluctuation in average weather conditions. The second problem is related to the autocorrelation of the environmental noise. Since there are lots of studies contributed to this issue and it is also not the central focus of this study, we will not pay too much attention here. The third problem, which is also the most important problem in modelling spatial stochasticity, is to generate spatially and autocorrelated environmental noises (auto and cross correlation of environmental noise). Many authors have proposed their method that can generate colored and correlated environmental noises. Recently, Vasseur (2007) presented a method designated as 'phase partnering' to generate such sets of time series, where their color and cross-correlation were near-perfect accurate and precise. Basically, the environmental noise used in Vasseur (2007) was $1/f^\beta$-type noise, where variance at each frequency scales according to a

power law (Halley, 1996). The value of the spectral exponent β indicates the noise color, red (or pink) noise ($\beta > 0$) and white noise ($\beta = 0$). As we know, the variance of $1/f^{\beta}$ noise increases with the length of the time series (Halley, 1996), however, AR_1 noise has a finite variance. The reason that we do employ AR_1 noise but not $1/f^{\beta}$ noise is that the influence of noise variance on population synchrony is unknown. In fact, AR_1 models are commonly used to generate colored noises. It proves that our method can generate the desired cross-correlated environmental noises, where noises range from local noise to global noise through controlling spatial correlation ρ. Particularly, the generating process is so simple that can be achieved through controlling one or two parameters. In addition, for n-patch system, applying the method described by Vasseur (2007) required a modification of the 'coin toss' procedure. In fact, it is relatively complicated. Most significantly, our method can be used to generate more than two correlated environmental noise simultaneously, which is much simpler than Vasseur's method. The method described herein provides a simple framework for generating colored spatially correlated noises.

Our recent investigation showed that the trophic correlations could also affect the spatial synchrony remarkably (Gao et al., 2007). As a supplement, in this paper, we considered the relationship between the color of environmental noise and the spatial synchrony. Heino (1998) suggested that noise color had an effect on level and spatial patterns of synchrony. He concluded that the influence of autocorrelated noise on population synchrony depends strongly on the way in which environmental noise is introduced into the model. In our study, we introduced environmental noise into the carry capacity of Maynard Smith model. We also got similar results that reddened noise enhanced synchrony (not illustrated as figures). Moreover, Fontaine and Gonzalez (2005) investigated the importance of noise color on synchrony in population dynamics, and also noticed that the influence of autocorrelated noise depended on how the noise enters the model. On the one hand, our research is providing theoretically derived support for the findings of these other papers. On the other hand, our research gives some novel findings as follow:

(1) In Heino's (1998) paper, the total variance of environmental noise was the sum of the local and global noise. Therefore, he controlled local or global noise dominating through varying the ratio of the two noise variances. In this study, we employed a method of generating sets of 'environmental' time series with desired cross-correlations (herein referred to as ρ) and colors (referred to α). When ρ were of low value, environmental noise was dominated by local noise, and relatively high value corresponded to dominating of global noise. Consequently, we found that red noises caused higher synchrony than white noises when populations were subjected to weaker correlated noises and linked by migration. That is to say, reddened noise is one kind of weaker desynchronizing effect compared with white noise when the noises are not strong spatially correlated, because local noise is usually considered as a desynchronizing factor (Heino et al., 1997).

(2) Kendall et al. (2000) employed a spatially structured population model, simple enough to obtain analytic solutions for the population correlation, that incorporated both dispersal and environmental correlation. Then, they found that there was always an interaction between these two factors. In addition, Heino (1998) used a nonlinear population model that incorporated both dispersal and colored noise. However, he did not focus on the interactions between colored noise and dispersal. In this study, we discussed the interactions between noise color and dispersal using a nonlinear population model. As a

result, we found that the influence of noise color on synchrony depended strongly on the level and pattern of dispersal. When the noises were stronger spatially correlated, changing the value of m and c resulted in a different conclusion. Even if noises entered population dynamics in the same way, different effects of reddened noises were found. Synchrony increased but not decreased with the increasing autocorrelation of noises when the value of m and c are changed. From our simulation results, we conclude that there exists indecisive relation between reddened noise and synchrony. Now, our theoretical explorations lead to an increasing research topic about the environmental noise color in determining the efficacy of Moran effect.

(3) Dispersal has a dual influence on the global extinction rate. On the one hand, migration is essential for recolonization of empty patches and may thus enhance the persistence time of a spatially structured population, known as rescue effect. On the other hand, dispersal may increase the synchrony between population, which increases the global extinction risk. Moreover, we found that the role of dispersal was crucial to spatial synchrony in this study. Particularly, the combined effects of colored noise and dispersal were complex. Dispersal may either favor the reddened noise or white noise in synchronizing spatial population.

Using a spatially explicit model, we speculate that the patch number has no influence on our results about spatial synchrony of populations in stochastic perturbed environment, and the combined effects of dispersal and environmental noises are stronger. Spatially explicit models could lead to a variety of spatial self-organized patterns, such as travelling waves, crystal lattice, and spatial chaos (Bjørnstad and Bascompte, 2001). More powerful spatial statistics are needed in order to understand spatial synchrony, such as wavelet phase analysis, spatial correlated functions (SCF) and spatial cross-correlation functions (SCCF) (Liebhold et al., 2004).

The noise can interact in a complex way with the underlying population biology (Ranta et al., 2000; Laakso et al., 2001). Even when disregarding population spatial structure and time delays as potential complications, the underlying physiological processes regulating population growth may act in a nonlinear manner and consequently, buffer or amplify the effect of the environmental noise (e.g. Sinclair, 2001). Another interesting problem is that how does nonlinear noise regulate the population dynamics and affect the spatial synchrony? More detailed considerations of the spatial aspects of the study area (the sampling frame) and the spatial resolution and size of the local sampling points (the grain) could improve studies of population synchrony (Bjørnstad, 1999). In addition, temporal aspects of the frame and grain should be considered, because the pattern of synchrony may fluctuate over the long-term (Koenig, 1999). Evidence from a handful of systems suggests that synchrony may vary over time and space, due to spatial and temporal variation in the habitats, as this influences local dynamics. Spatial synchrony is just one manifestation among a broader array of space-time patterns.

Many aspects of the design of nature reserves and the effective conservation of endangered species thus hinge on the level of regional synchronization in species dynamics. The resilience of populations to manipulation, to biological control, conservation corridors construction, and to pest eradication can also be related to the degree of correlation in dynamics (Kendall et al., 2000). Therefore, the color of the noise is also a crucial factor in any attempt to manage or conserve that population. Moreover, the interaction between dispersal and noise color should not be neglected. As such, the result presented in this paper is only a starting points for understanding the influence of environmental noise, and in particular the color of noise influence spatial synchrony of population. Fur-

ther theoretical and experimental investigations in this topic are needed in the future.

Acknowledgements

Appendix A. Derivation of Matrix *B*

From Eq. (2), we obtain

$$d_i = \sum_{j \leq i} b_{ij} \psi_j \quad (1 < i \leq n)$$

If we compute $cov(d_i, d_j)\,(j < i)$,

$$cov(d_i, d_j) = cov\left(\sum_{k \leq i} b_{ik}\psi_k, \sum_{k \leq j} b_{jk}\psi_k\right)$$
$$c_{ij}\sigma^2 = \sum_{k \leq j} b_{ik}b_{jk}var(\psi_k) \tag{A.1}$$

Similarly, if we compute $var(d_i)$,

$$var(d_i) = var\left(\sum_{j \leq i} b_{ij}\psi_j\right)$$
$$\sigma^2 = \sum_{j \leq i} b_{ij}^2 var(\psi_j) \tag{A.2}$$

We firstly consider the second row, by (A.1) and (A.2), we can obtain b_{21} and b_{22}, respectively. Analogously, b_{ij} in the other rows can be obtained sequently from the third row to the *n*-th row.

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