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Remarks on Metacommunity Synchronization with Application to Prey-Predator Systems

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ABSTRACT: The problem of synchronization of metacommunities is investigated in this article with reference to a rather general model composed of a chaotic environmental compartment driving a biological compartment. Synchronization in the absence of dispersal (i.e., the so-called Moran effect) is first discussed and shown to occur only when there is no biochaos. In other words, if the biological compartment is reinforcing environmental chaos, dispersal must be strictly above a specified threshold in order to synchronize population dynamics. Moreover, this threshold can be easily determined from the model by computing a special Lyapunov exponent. The application to prey-predator metacommunities points out the influence of frequency and coherence of the environmental noise on synchronization and agrees with all experimental studies performed on the subject.

Keywords: chaos, dispersal, Lyapunov exponent, Moran effect, prey-predator, synchronization.

Observations and experiments in various fields have shown that similar dynamical systems that are interconnected and subject to a common fluctuating driving force can behave in unison after a transient (Pikovsky et al. 2001). Under suitable conditions, this phenomenon, known as synchronization, can also occur if the systems are not externally driven or if they are uncoupled. In ecology, the first case corresponds to metacommunities with patches interacting

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through dispersal in a constant environment. This case is well understood (see, e.g., Jansen and Lloyd 2000): synchronization is, in general, obtainable by increasing the dispersal rate, but it can also be lost if the dispersal rate becomes too high. The second case refers to metacommunities where patches are isolated but subject to the same environmental fluctuations. Moran (1953) was the first to investigate this problem with reference to a particularly simple class of models, and his conclusion was straightforward: the metacommunities synchronize no matter how the environment fluctuates. Royama (1992) highlighted this notion in his book on population dynamics and called it the Moran effect, which has since become a synonym for "synchronization in the absence of dispersal." However, as observed by Royama, the conclusion drawn by Moran can be wrong in the context of general nonlinear dynamical systems. Indeed, we show in this article that density-dependent populations synchronize in the absence of dispersal only if the environmental fluctuations are in a suitable relationship with the dynamics of the populations. For example, we show that in prey-predator metacommunities, the Moran effect can occur for low environmental variability, but it is lost if the fluctuations of the environment become too large.

The contribution that first revealed that populations can synchronize over large distances was the study of fur returns of Canadian lynx to the Hudson Bay Company (Elton 1924). Since then, a great effort has been devoted to this case study (Elton and Nicholson 1942; Moran 1953; Bulmer 1974; Smith 1983; Sinclair et al. 1993; Ranta et al. 1997, to mention just a few), with some of these contributions supporting the idea that the synchronization of Canadian lynx is primarily a result of global environmental fluctuations. However, some recent results (Blasius et al. 1999; Lloyd and May 1999; Maggi and Rinaldi 2006) have shown that networks of tritrophic food chain models of the kind suggested for the food web of the Canadian boreal forest (King and Schaffer 2001) can easily give rise to synchronization in the absence of a common meteorological driving force, provided that there is a sufficiently high dispersal rate. This result and the discovery of a high

gene flow of the Canadian lynx over distances of 3,000 km (Schwartz et al. 2002) suggest that, most likely, both meteorology and migration contribute to the spatial synchronization of the lynx population.

In the past decades, many plant and animal populations have been shown to synchronize over large areas (Koenig 1999; Liebhold et al. 2004; see also app. A in the online edition of the *American Naturalist*). In many cases, synchronization has been attributed to the Moran effect, even if low levels of dispersal were detected (e.g., Higgins et al. 1997). Only in a few cases, for example, the sheep populations on the St. Kilda archipelago (Grenfell et al. 1998) and the caribou and musk oxen populations in Greenland (Post and Forchhammer 2002), can migration be excluded and synchronization therefore be attributed exclusively to the Moran effect.

The aim of this article is twofold. First, we make a few theoretical remarks on an extremely simple but general metacommunity model in order to obtain a sharp criterion allowing us to say (from the analysis of the model) whether the Moran effect is present or whether a certain amount of dispersal is needed in order to synchronize the metacommunity. Second, we apply our general method of analysis, based on the computation of special Lyapunov exponents (here called conditional), to the study of prey-predator systems. This extends previous studies on periodically forced prey-predator models (Kuznetsov et al. 1992; Rinaldi et al. 1993; King and Schaffer 1999) in two directions: from simple communities to metacommunities and from periodic to chaotic environments. This class of metacommunities fits with the main characteristics of many aquatic ecosystems, such as the plankton food chain (Scheffer et al. 1997, 2000), and with the characteristics of many terrestrial ecosystems in boreal and arctic regions, which, indeed, have often been studied by means of periodically forced prey-predator systems (Hanski and Woiwod 1993; King and Schaffer 1999; Hanski et al. 2001).

Any metacommunity is characterized by four basic elements: a graph in which nodes i and arcs (i, j) represent patches and dispersal flows between patches, a patch model describing the dynamics of the population vector $\mathbf{n}^{(i)}$ in patch i under the influence of an external environmental noise, an environmental noise generator, and the dispersal rates of each component of the population vector. Various forms of synchronization are possible, depending on the metacommunity model. The strongest one is complete synchronization, which occurs when a synchronous solution $\mathbf{n}^{(i)}(t) = \mathbf{n}^{(j)}(t)$ for all $i \neq j$ and for all t exists and is stable. A slightly weaker form of synchronization, called almost-complete synchronization, requires that the maximum difference between populations be small. Much weaker but quite interesting forms of synchronization are phase synchronization (Blasius et al. 1999; Lloyd and May

1999; Cazelles and Boudjema 2001), out-of-phase synchronization (Doebeli and Ruxton 1997; Ruxton et al. 1997), and intermittent synchronization (Cazelles et al. 2001; Harrison et al. 2001). In general, when the parameters of a metacommunity are not too far from the values giving rise to complete synchronization, that is, when the parameters are in the so-called presynchronization region, some weak form of synchronization is present and is revealed by various spatiotemporal patterns.

In order to derive a sharp condition for synchronization of metacommunities, we first consider only the extreme case of complete synchronization, thus avoiding the use of statistical indicators (Liebhold et al. 2004), which are useful for data processing but not for studying the stability of a synchronous solution. This implies that we can consider only metacommunities that admit synchronous solutions for any value of their parameters, and we focus our attention on the stability of such solutions. Moreover, we restrict the analysis to local stability because this allows us to extend results (Jansen and Lloyd 2000) known for the special case of a constant environment.

The metacommunity model studied in this article is composed of identical patches with interacting populations in each patch subject to a common environmental noise and dispersing at a constant rate. If one of these assumptions is slightly relaxed, for example, by introducing some degree of heterogeneity in the demography or in the environmental noise, the synchronous state ceases to exist, so that one can no longer speak of complete synchronization. However, the populations of the various patches continue to behave similarly, thus realizing a weak form of synchronization (see, e.g., Ripa 2000). In the application to prey-predator systems, we will verify the robustness of this property in order to show that the synchronization conditions derived for our metacommunity generally imply weak forms of synchronization in more realistic models. Many, if not all, metacommunity models admitting synchronous solutions discussed in previous works are particular cases of our model. For example, the first model considered by Hillary and Bees (2004) has no dispersal, while their second model, as well as the model studied by Earn and Levin (2006), has no environmental noise, a feature that precludes the possibility of discussing the Moran effect.

The article is organized as follows. In the next section, we describe the model and derive conditions for synchronization in the absence of dispersal as well as the minimal value of dispersal needed to guarantee synchronization when there is no Moran effect. The analysis is based on the notion of biological chaos, abbreviated as biochaos, and the main result is very simple: a metacommunity cannot synchronize without dispersal if there is biochaos. Technically, this is ascertained by looking at the sign of

the largest conditional Lyapunov exponent of a single patch. Then, in the next section, we apply this criterion to a prey-predator metacommunity. More precisely, we first specify the prey-predator model, then we study the effects of the noise characteristics on synchronization and discuss the role of prey and predator dispersals, and finally, we present some cases of weak synchronization. In the last section, we comment on the value and limitations of our findings and point out possible extensions to larger classes of metacommunity models as well as to other classes of prey-predator models.

Model and Method

The metacommunities considered in this article have N identical patches connected through corridors along which migration occurs in both directions. The dispersal pattern is described by an $N \times N$ matrix $\mathbf{C} = [c_{ij}]$, called the connectivity matrix, where c_{ii} is the number of corridors starting from patch i and, for $i \neq j$, $c_{ij} = -1$ if patches i and j are directly connected through a corridor, and $c_{ij} = 0$ otherwise. In order to avoid trivial cases, we assume that all pairs of patches are connected either directly or through a chain of corridors. Under this assumption, the matrix $\mathbf{C}$, which is symmetric and zero-row-sum and has non-positive off-diagonal entries, can be proved to have one 0 eigenvalue (say, $\lambda_1 = 0$) and all other eigenvalues real and positive (say, $0 < \lambda_2 \leq \lambda_3 \leq \ldots \leq \lambda_n$).

Each patch i is occupied by m populations, whose abundances are the components of an m-dimensional population vector $\mathbf{n}^{(i)}$. The abundances of the populations are influenced by an environmental noise $v(t)$ common to all patches, and local environmental variability is excluded. The continuous-time model on which we focus our attention is

$$\dot{\mathbf{w}}(t) = g(\mathbf{w}(t), \alpha), \tag{1}$$

$$v(t) = \psi(\mathbf{w}(t), \varepsilon), \tag{2}$$

$$\dot{\mathbf{n}}^{(i)}(t) = f(\mathbf{n}^{(i)}(t), v(t), \beta) - \mathbf{D} \sum_{j=1}^{N} c_{ij} \mathbf{n}^{(j)}(t), \tag{3}$$

for $i = 1, \ldots, N$, where equations (1) and (2) are the noise generator, namely, a set of m_w ordinary differential equations (ODEs; eq. [1]) generating the environmental vector $\mathbf{w}(t)$ and an output transformation (eq. [2]) transforming the vector $\mathbf{w}(t)$ into the environmental noise $v(t)$, and equation (3) is the biological component of the model, namely, a set of mN ODEs describing birth, death, and migration processes of all populations. In equations (1)–(3), α, ε, and β are constant parameters controlling some features of the environmental noise (e.g., meteorological coher-

ence) and of the populations (e.g., intraspecific competition), and $\mathbf{D} = \text{diag}[d_1, \ldots, d_m]$ is a constant diagonal matrix specifying the dispersal rates of each component of the population vector. The main difference between model (1)–(3) and most metacommunity models used in the literature (for an exception, see Hillary and Bees 2004) is that the environmental noise $v(t)$ is here described by a deterministic model (eqq. [1], [2]) and not by a suitably defined stochastic process. The advantage of model (1)–(3) is that it allows us to give a precise definition of biochaos, which is an important notion in our analysis. By contrast, the computations needed to detect whether the metacommunity synchronizes are based on equation (3) and can therefore be performed even if the environmental noise has been generated in a different way.

If all population vectors in equation (3) are identical at a specified time, they remain identical (synchronous) forever because $\mathbf{n}^{(1)}(0) = \mathbf{n}^{(2)}(0) = \cdots = \mathbf{n}^{(N)}(0)$ implies that the second term at the right-hand side of equation (3) vanishes (recall that $\mathbf{C}$ is zero-row-sum). In other words, the manifold $\mathbf{n}^{(1)} = \mathbf{n}^{(2)} = \cdots = \mathbf{n}^{(N)}$, called the synchrony manifold, is invariant. The synchrony manifold has dimension equal to m, and the dynamics one can observe in it are the dynamics one would observe in a single isolated patch described by the equations

$$\dot{\mathbf{w}}(t) = g(\mathbf{w}(t), \alpha), \tag{4}$$

$$v(t) = \psi(\mathbf{w}(t), \varepsilon), \tag{5}$$

$$\dot{\mathbf{n}}(t) = f(\mathbf{n}(t), v(t), \beta). \tag{6}$$

Model (1)–(3) is not the most general model for which the synchrony manifold is invariant. For example, one could consider patches of different sizes (Jansen and Lloyd 2000), assume that the dispersal matrix $\mathbf{D}$ depends on the environmental noise or that the migration corridors are different for different components of the population vector (e.g., avian and terrestrial predators), and still obtain a metacommunity model in which the synchrony manifold is invariant. By contrast, any perturbation of model (1)–(3) introducing some spatial heterogeneity (i.e., $\mathbf{w}$, α, β, ε, $\mathbf{D}$ replaced by $\mathbf{w}_i$, α_i, β_i, ε_i, or $\mathbf{D}_i$) would destroy the invariance of the synchrony manifold and therefore allow only weak forms of synchronization (for the case of local environmental noise, see, e.g., Haydon and Steen 1997).

If the single isolated patch (eqq. [4]–[6]) has an attractor, from now on called a patch attractor, we want to know whether that attractor is also an attractor for the metacommunity model (eqq. [1]–[3]). When this is so, we say that the metacommunity synchronizes or, equivalently, that the patch attractor is synchronous. If a patch attractor is synchronous, the metacommunity can behave

synchronously and return to the same synchronous behavior after any small perturbation.

Biochaos in an Isolated Patch

Before studying the synchronization of the metacommunity (eqq. [1]–[3]), we point out a few basic properties of the single isolated patch (eqq. [4]–[6]). First of all, the environmental submodel (eqq. [4], [5]) is not influenced by the biological submodel (eq. [6]). This means that the dynamics of the environmental variables $\mathbf{w}(t)$ are concisely captured by the so-called Lyapunov exponents (see, e.g., Turchin and Taylor 1992; Hastings et al. 1993; Strogatz 1994; Ellner and Turchin 1995; Cushing et al. 2002) of equation (1). Such exponents are m_w real numbers (depending on the parameter α) that characterize the attractor of equation (1) and describe the sensitivity of its solutions to initial conditions. They are obtained by suitably averaging the time-varying Jacobian matrix $[\partial g/\partial w]$ evaluated along a solution (Ramasubramanian and Sriram 2000). Positive Lyapunov exponents reveal the divergence of nearby solutions, typical of chaotic regimes, while negative Lyapunov exponents reveal their convergence. The sign of the largest Lyapunov exponent (LLE) identifies the nature of the attractor: strange attractors (chaotic regimes) have positive LLEs, stable cycles and tori (periodic and quasi-periodic regimes) have LLEs of 0, and stable equilibria (stationary regimes) have negative LLEs. In the following, the LLE of the environmental model (eq. [1]) is indicated by $L_{[\partial g/\partial w]}$.

The Lyapunov exponents of the single isolated patch are therefore $(m_w + m)$ real numbers that can be extracted from the Jacobian matrix

$$\begin{bmatrix} \partial g/\partial w & 0 \\ \partial f/\partial w & \partial f/\partial n \end{bmatrix}$$

evaluated along a solution $(\mathbf{w}(t), \mathbf{n}(t))$ of model (4)–(6). In view of the triangular structure of this Jacobian matrix, m_w Lyapunov exponents of model (4)–(6) are exactly those of the environmental submodel (eq. [4]), while the m remaining exponents are generated by the biological submodel, that is, by the Jacobian $[\partial f/\partial n]$. However, these m biological Lyapunov exponents depend also on the parameters α and ε because the matrix $[\partial f/\partial n]$ depends on the environmental noise $v(t)$. Thus, the largest biological Lyapunov exponent $L_{[\partial f/\partial n]}$ is actually conditioned to the characteristics (α and ε) of the environmental noise. This is why it is called conditional.

From now on, we assume that the environment is chaotic ($L_{[\partial g/\partial w]} > 0$) because the case of constant environment is well known (Earn et al. 2000; Jansen and Lloyd 2000;

Hillary and Bees 2004; Earn and Levin 2006), environmental periodicities can be eliminated through time discretization, and quasi-periodic environments are of purely mathematical interest. More precisely, we consider the following two cases: (1) $L_{[\partial f/\partial n]} > 0$ and (2) $L_{[\partial f/\partial n]} < 0$. That is, we intentionally rule out from our analysis the particular case $L_{[\partial f/\partial n]} = 0$, which does not occur generically if the environment is chaotic. In all cases, the patch is chaotic because its LLE is

$$\max \{L_{[\partial g/\partial w]}, L_{[\partial f/\partial n]}\} \geq L_{[\partial g/\partial w]} > 0.$$

In case 1, biology reinforces environmental chaos, while in case 2, biology does not contribute to the complex behavior of the populations, which is exclusively due to the environment. We can briefly say that in case 1, there is biochaos, while in case 2, there is no biochaos. The sign of $L_{[\partial f/\partial n]}$ is therefore the only information needed for detecting whether chaos is simply entrained by the environment or is, at least in part, generated by the biological processes. It is worth noting that in case 2, all techniques used for extracting the LLE from a population time series would actually give an estimate of the environmental LLE. In other words, the community is simply used as an instrument to measure a characteristic parameter of the environment, as noted by Pascual et al. (1995), who discovered that the LLE extracted from plankton time series was actually the LLE emerging from the analysis of purely oceanographic time series.

Synchronization in the Absence of Dispersal (Moran Effect)

We now focus on the possibility that model (1)–(3) synchronizes (i.e., has a synchronous attractor) in the absence of dispersal ($\mathbf{D} = 0$ in eq. [3]). As noted in the introduction to this article, this phenomenon is called the Moran effect. Restricting the analysis to the case of small perturbations from the synchronous behavior ($\mathbf{n}^{(1)}(t) = \mathbf{n}^{(2)}(t) = \ldots = \mathbf{n}^{(N)}(t) = \mathbf{n}(t)$), we can obtain the conditions for synchronization by linearizing equation (3) and studying the stability of the time-varying Jacobian matrix $[\partial f/\partial n]$ evaluated along the solution $(\mathbf{w}(t), \mathbf{n}(t))$ of model (4)–(6). The conclusion of this rather standard analysis (briefly reported in app. B in the online edition of the *American Naturalist*) is that the metacommunity synchronizes in the absence of dispersal if

$$L_{[\partial f/\partial n]} < 0, \tag{7}$$

that is, if the largest biological Lyapunov exponent of the single patch is negative.

We can therefore say that the Moran effect is present

when there is no biochaos, that is, when the complex behaviors of the populations are exclusively due to the environment. This means that two common beliefs, namely, that density-dependent processes can easily give rise to chaotic population dynamics and that metacommunity synchrony is often due to the Moran effect, are actually in conflict.

Synchronization in the Presence of Dispersal

We now consider the metacommunity model (eqq. [1]–[3]) with no restriction on **D** and assume that the single isolated patch (eqq. [4]–[6]) has a solution $(\mathbf{w}(t), \mathbf{n}(t))$ tending toward a patch attractor. Following exactly the same approach independently used by Pecora and Carroll (1998) and Jansen and Lloyd (2000) for the special case of constant environment, one can prove (for a short sketch, see app. C in the online edition of the *American Naturalist*) that if condition (7) is not satisfied, that is, if there is no Moran effect, the metacommunity synchronizes if the following $(N-1)$ Lyapunov exponents are negative:

$$L_{[\partial f/\partial n - \lambda_i \mathbf{D}]} < 0, \tag{8}$$

for $i = 2, \ldots, N$. These $(N-1)$ conditions are usually satisfied if the dispersal rates appearing on the diagonal of matrix **D** are sufficiently high. Note that condition (8) degenerates into condition (7) when $\mathbf{D} = 0$.

Condition (8) becomes particularly simple when the dispersal rates $d_1, d_2, \ldots, d_m$ are the same for all populations, that is, when $\mathbf{D} = d\mathbf{I}$ (where d is positive and **I** is the $m \times m$ identity matrix). In fact, it can be shown that in such a case,

$$L_{[\partial f/\partial n - \lambda_i \mathbf{D}]} = L_{[\partial f/\partial n]} - \lambda_i d,$$

so that the $(N-1)$ condition (8) can be replaced by a single condition, namely,

$$d > \frac{1}{\lambda_2} L_{[\partial f/\partial n]}, \tag{9}$$

where λ_2 is the smallest positive eigenvalue of the connectivity matrix. In other words, a metacommunity that does not synchronize without dispersal (because $L_{[\partial f/\partial n]}$ is positive) can always synchronize, provided all populations disperse at a sufficiently high rate. Condition (9) also says that the minimum dispersal giving rise to synchronization is proportional to the largest biological Lyapunov exponent of the single patch and that the proportionality factor $(1/\lambda_2)$ depends only on the dispersal pattern (the connectivity matrix **C**). This is useful for understanding why special dispersal patterns are particularly effective in promoting synchronization, as shown in appendix C.

Application to Prey-Predator Systems

The theory presented in the previous section is now applied to metacommunities of prey-predator systems. The model we use is the Rosenzweig-MacArthur (1963) model,

$$\dot{n}_1 = n_1 \left[r \left(1 - \frac{n_1}{K} \right) - \frac{an_2}{(1 + ahn_1)} \right],$$

$$\dot{n}_2 = n_2 \left[\frac{ean_1}{(1 + ahn_1)} - m \right], \tag{10}$$

where n_1 and n_2 are the abundances of prey and predators, respectively, while r, K, a, h, e, and m are positive parameters. Parameter r represents the intrinsic growth rate of the prey, while K is the prey carrying capacity. The function $an_1/(1 + ahn_1)$ is Holling's type II functional response (Holling 1965), where a is the attack rate and h is the handling time. Finally, e is the efficiency, namely, the number of newborn predators per unit of captured prey, while m is the predator per capita mortality rate.

The study of coupled prey-predator communities in the special case of constant environment (i.e., constant parameters in eq. [10]) has a long tradition (for the case of generalist predators also hunting on nonpreferred prey, see Vandermeer 1993; for the case of migration, see Jansen 2001; Hillary and Bees 2004) and is not surveyed here. The effect of the environmental noise on any parameter p is modeled through the function

$$p = p_0(1 + v(t)),$$

where $v(t)$ is a suitably defined zero-mean environmental noise (eq. [2]) that varies between $-\varepsilon$ and $+\varepsilon$ (with $0 < \varepsilon < 1$). Under these assumptions, p_0 corresponds to the mean value of the parameter, while ε is the variability of the parameter due to environmental randomness. In the real world, many, if not all, the parameters are affected by environmental noise, possibly in different ways, but the study of such a case would be extremely difficult to conduct. For this reason, we follow the analysis presented by Rinaldi et al. (1993), who considered six elementary seasonal mechanisms, each one giving rise to the periodic variation of only one or two parameters. A detailed description of the six mechanisms can be found in appendix D in the online edition of the *American Naturalist*, together with the corresponding results. Here we deal with only one mechanism, namely, that in which the environmental variations influence the degree of mimicry of the prey

(predator), thus facilitating the escape or the capture of the prey in some specific seasons. Obviously, such a mechanism can be modeled by assuming that the attack rate is influenced by the environmental noise $v(t)$.

In the article by Rinaldi et al. (1993), the environment was supposed to be periodic, while here we aim to model a metacommunity embedded in a chaotic environment. However, in many cases, the environment fluctuates randomly around a periodic (seasonal) pattern so that our environmental variable v must loosely resemble to an irregular sinusoid, with an easily distinguishable frequency and a certain degree of variability in the values of its maxima and minima. In order to reproduce such a behavior, we follow Hillary and Bees (2004) and model the environment with one of the most popular chaotic models, namely, the Rössler oscillator, described by the following equations (Strogatz 1994):

$$\dot{w}_1 = f \cdot (-w_2 - w_3),$$
$$\dot{w}_2 = f \cdot (w_1 + 0.2w_2), \tag{11}$$
$$\dot{w}_3 = f \cdot \left(0.2 + w_1w_3 - \frac{w_3}{c}\right),$$

where f and c are two positive parameters. Because we want to have an environmental noise $v(t)$ with a mean of 0 and an absolute value smaller than ε, we have selected the function ψ in equation (2) as follows:

$$v(t) = \varepsilon \frac{(w_1 + w_2) - \langle w_1 + w_2 \rangle}{\sup |(w_1 + w_2) - \langle w_1 + w_2 \rangle|}, \tag{12}$$

where $\langle w_1 + w_2 \rangle$ is the mean value of $(w_1 + w_2)$ and $\sup |(w_1 + w_2) - \langle w_1 + w_2 \rangle|$ is the maximum distance of $(w_1 + w_2)$ from its mean value. The environmental submodel (eqq. [11], [12]) can easily be used to mimic a wide variety of qualitatively different noises $v(t)$, as the frequency of v can be adjusted through parameter f, which appears as a multiplicative factor at the right-hand side of each differential in equation (11), while the coherence (width of the spectrum) can be controlled through c. A typical segment of a time series $v(t)$ produced by model (11), (12) is shown in figure 1A: if the time unit is in years, the graph could represent the evolution of a meteorological variable with maxima in summer and minima in winter. While the behavior of w_1 and w_2 is oscillatory, w_3 has a roughly constant (0) value with occasional high spikes, as shown in figure 1B. Therefore, by identifying $v(t)$ with w_3, it would be possible to use the same environmental model (eq. [11]) to generate rare but large and random environmental shocks to deal, for example, with
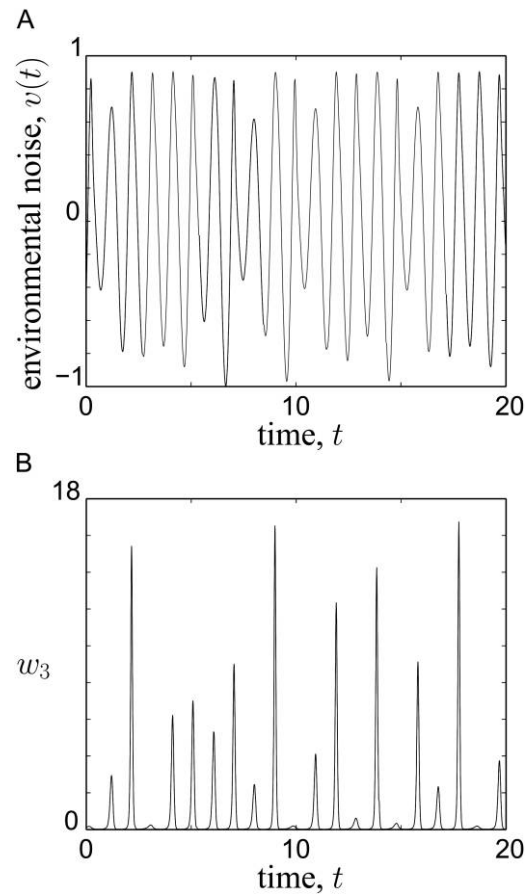

Figure 1: Two realizations of the environmental noise. *A*, $v(t)$ as in equation (12) and $\varepsilon = 1$. *B*, $v(t) = w_3$. In both realizations, $f = 6$, and $c = 1/5$.

prey-predator communities influenced by the sunspot cycle.

In the numerical analysis, we have assigned to the parameters the values used by Rinaldi et al. (1993). With these values, the attractor of the unperturbed patch is a limit cycle of period $T = 1.85$, while the environmental noise is chaotic, with central frequency close to 1. In all our simulations, we have restricted the values of ε to the range [0.1, 0.9], as very high values of ε are of little interest and small values of ε can give rise to extremely small Lyapunov exponents, so that the detection of their sign can become problematic.

Biochaos in an Isolated Patch

In the article by Rinaldi et al. (1993), an extensive analysis of the prey-predator model (eq. [10]) with periodically varying parameters was carried out. In particular, a detailed analysis with respect to ε was performed for the six
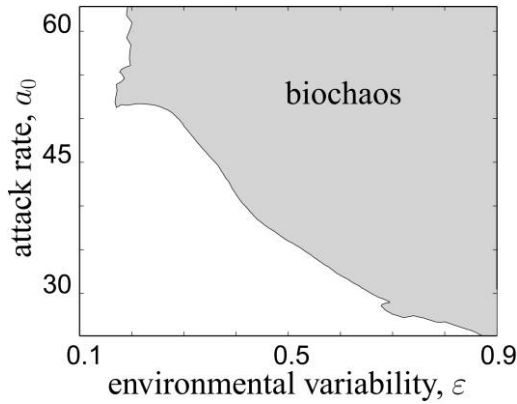
Figure 2: Region of biochaos (where $L_{[\partial f/\partial n]} > 0$) is in gray in the parameter space (ε, a_0). The parameter values are $c = 1/5$, $f = 6$, $h = 1/(4\pi)$, $e = 1$, $m = 2\pi$, $r = 2\pi$, and $K = 1$.

elementary mechanisms mentioned above. The most remarkable result was that regardless of the chosen mechanism, in any two-dimensional space (ε, p_0), there was a region of biochaos for large values of ε. In other words, the largest biological Lyapunov exponent was found to be positive for large values of ε and negative for lower values. In the case of a chaotic environment, we cannot expect exactly the same regions of biochaos, in particular when the environmental model is strongly chaotic. Nonetheless, our numerical results, reported in figure 2, show that the regions with $L_{[\partial f/\partial n]} < 0$ (*white*) and $L_{[\partial f/\partial n]} > 0$ (*gray*) resemble those reported by Rinaldi et al. (1993). As shown in appendix D, the same result holds for the other five mechanisms, so we can conclude that regardless of the parameter affected by noise, for large values of the environmental variability ε, the biological processes reinforce population chaos by adding at least one positive Lyapunov exponent to those produced by the environment. Our analysis also shows that given the environmental variability (ε), the chances of having biochaos increase with prey carrying capacity (K), predator efficiency (e), and attack rate (a) and decrease with increasing predator mortality (m).

Synchronization in the Absence of Dispersal (Moran Effect)

We now study a metacommunity composed of uncoupled patches. As explained above, in this case, the stability of the patch attractor depends solely on the sign of $L_{[\partial f/\partial n]}$. Therefore, all the information needed to determine the parameter values that guarantee that the metacommunity synchronizes without dispersal are already contained in figure 2. In particular, in the gray region (where

$L_{[\partial f/\partial n]} > 0$), the patches will not synchronize if there is no dispersal, while they will synchronize in the white region, provided that the initial perturbations from the synchronous solution are sufficiently small.

Looking at figure 2, we draw the rather surprising conclusion that in the absence of dispersal, synchronization is actually obtained for low rather than high values of ε. In a sense, this is counterintuitive, as one might expect that a strong global environmental noise is more effective than a weak one in synchronizing the patches. The reason for this is that at high values of ε, the patches produce biochaos, which, in turn, in the absence of dispersal, prevents the metacommunity from synchronizing.

In order to assess the robustness of this result, we have tested the system with noises of different frequencies and spectral coherence. In all the following plots, we show the numerical results obtained for the case of prey and predator mimicry affected by the environmental noise. Nonetheless, the same results have been checked to hold for all other mechanisms described in appendix D.

In figure 3, we show how the curve delimiting the synchronization region changes when the frequency of the noise is increased. As mentioned above, with the parameter values given in the caption of figure 2, the prey-predator model with constant environment has a period $T = 1.85$, which is comparable to the mean period of the noise (close to 1). This case corresponds to the lowest curve of figure 3. As the frequency of the noise becomes lower (red noise) or higher (blue noise), the curve moves up. In light of what we have seen above, this means that when the environmental clock is not tuned with the biological clock, there is more room for synchronization.

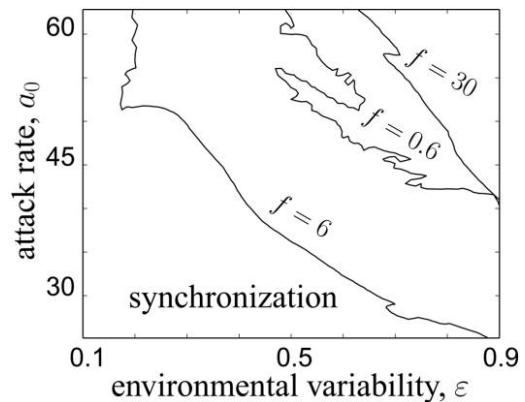The coherence of the noise also affects the tendency of

Figure 3: Synchronization regions (on the left of each curve) in the absence of dispersal for three values of noise frequency: red noise ($f = 0.6$), noise frequency close to that of the unperturbed population ($f = 6$), and blue noise ($f = 30$).

the metacommunity to synchronize. In fact, we have checked through simulation that the region of synchronization shrinks slightly when the noise becomes more coherent; that is, there is more room for the Moran effect if the environmental noise has a wide spectrum.

Synchronization in the Presence of Dispersal

We now consider a metacommunity composed of coupled patches, thus extending to the general case of chaotic environment several studies (Jansen 2001 and references therein) performed for the special case of constant environment. As we have seen, the effect of dispersal on synchronization depends both on the topology of the metacommunity (matrix C in eq. [3]) and on the dispersal rates (matrix D in eq. [3]). A detailed analysis of the metacommunity behavior for different C and D goes beyond the scope of this article, but some insights can be obtained by studying a few simple cases.

First, let us consider the case where the dispersal rates d_1 and d_2 of prey and predator are equal, that is, $d_1 = d_2 = d$, which implies that the conditions for synchronization take the simple form of equation (9). Synchronization regions obtained with equation (9) for increasing values of d in a two-patch metacommunity are shown in figure 4, and, as expected, we see that dispersal promotes synchronization. In the more general case of unbalanced dispersal ($d_1 \neq d_2$), our numerical experiments are in line with the common view that increasing dispersal rates increases the synchronization region.

What are the relative effectivenesses of prey and predator dispersal in promoting synchrony? This problem has never been systematically investigated, except for the special case of systems with highly diversified dynamics, that is, fast prey and slow predators (as in plankton food chains) or slow prey and fast predator (as in plants and insect pest systems). The main conclusion in this context (Somers and Kopell 1993; Izhikevich 2000) is that in the absence of environmental noise, the convergence to synchrony can be faster when the dispersing population is the fast one. In order to find out whether a similar result holds in the presence of environmental noise, we have computed the synchronization regions by setting the prey or the predator dispersal rates to 0. When the dispersal rates are unbalanced ($d_1 \neq d_2$), the synchronization region cannot be obtained from equation (9), namely, from $L_{[\partial f/\partial n]}$, but it can be obtained from the sign of $L_{[\partial f/\partial n - \lambda, D]}$ because the synchronization conditions are now those in equation (8). We have thus considered a two-patch metacommunity, with only prey or predator dispersing, and we have found cases (fig. 5A) where predator migration is more effective in promoting synchronization as well as cases (fig. 5B) in which the opposite is true. Note that in figure 5A, the
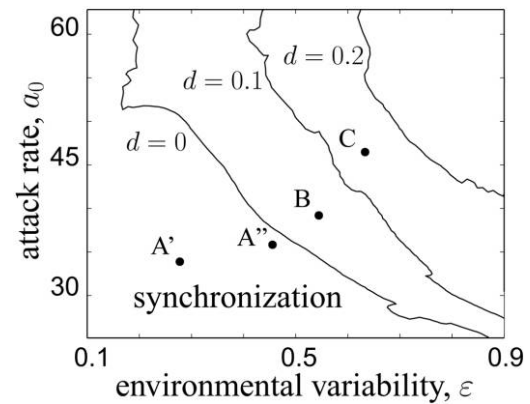

Figure 4: Synchronization regions (on the left of each curve) for increasing values of balanced dispersal $d_1 = d_2 = d$. The points A', A'', B, and C correspond to parameter sets used for generating heterogeneous metacommunities.

system is not slow-fast, and the result is consistent with a recent simulation study of a network of prey-predator systems in a constant environment (Maggi and Rinaldi 2006), while in figure 5B, the prey is fast with respect to the predator, and the result is in line with the contributions of Somers and Kopell (1993) and Izhikevich (2000).

For the dependence of synchronization on noise frequency, we have found the same result pointed out in "Synchronization in the Absence of Dispersal (Moran Effect)," namely, that red and blue noises facilitate synchronization (see fig. 3). This result is in line with the recent findings of Fontaine and Gonzalez (2005), who have shown through a series of laboratory experiments on a rotifer and its algal prey that red fluctuations promote synchrony. Moreover, the fact that reddened noise facilitates synchronization reinforces the idea that reddened noise can increase extinction risk (Lawton 1988; Petchey et al. 1997) because synchronization increases extinction risk (Earn et al. 1998, 2000). Finally, because dispersal is often adaptive and lower values of dispersal are favored by selection when the system is synchronized (Holt and McPeek 1996; Doebeli and Ruxton 1997; Johst et al. 1999; Dercole et al. 2007), on the basis of our findings, one can predict that metacommunities with red or blue environmental noise should be characterized by particularly low dispersal rates. This property has already been pointed out in the case of red noise through the extensive simulation of the evolution of a metapopulation involving a single species described by an individual-based model (Travis 2001).

Weak Forms of Synchronization

When the conditions for complete synchronization are not satisfied, weaker forms of synchronization can be present.
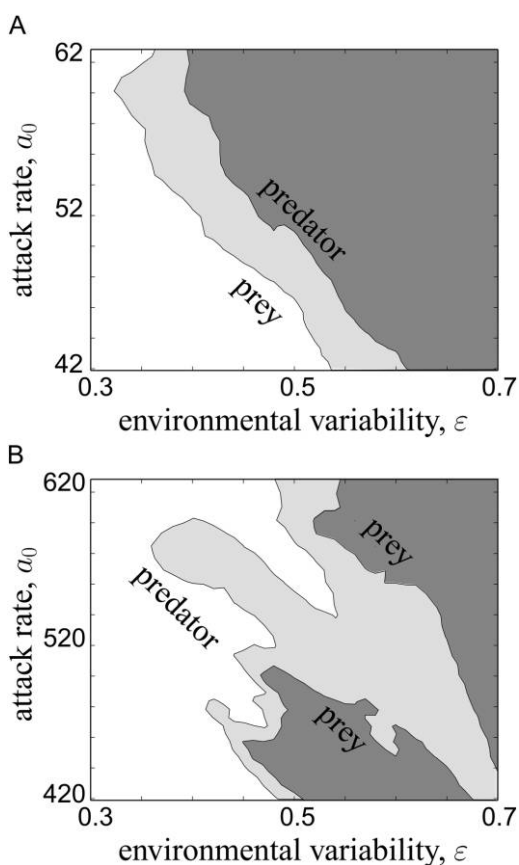
Figure 5: Synchronization with only prey or predator dispersing. In the white regions, the patches synchronize in both cases, while in the light gray regions, synchronization is obtained only with predator (*A*) or prey (*B*) dispersing. In *A*, the values of the parameters are $c = 1/5$, $f = 6$, $h = 1/(4\pi)$, $e = 1$, $m = 2\pi$, $r = 2\pi$, $K = 1$, and $d_{1,2} = 0.2$); in *B*, they are $c = 1/5$, $f = 6$, $h = 1/(40\pi)$, $e = 0.015$, $m = 0.3\pi$, $r = 20\pi$, $K = 1$, and $d_{1,2} = 0.1$.

In particular, this may happen when the metacommunity is heterogeneous because either the environmental noise or the demographic parameters are patch dependent or when the metacommunity is homogeneous but some of the Lyapunov exponents $L_{[\partial f/\partial n - \lambda, \mathbf{D}]}$ are slightly positive (see eq. [8]).

The impact of patch dependence of the environmental noise can be easily detected by taking a synchronizing metacommunity (eqq. [1]–[3]) and substituting a local noise $v_i(t) = v(t) + \delta_i(t)$ for the global noise in equation (3), where $\delta_i(t)$ is a small-amplitude, zero-mean independent noise. The result agrees with results of Ripa (2000) on a metapopulation, namely, that the correlations between all populations of the same species tend to 1 when the standard deviation of the noise δ_i tends to 0. As for the impact of the heterogeneity in the demographic pa-

rameters, consider the four points A', A'', B, and C in figure 4, together with the three values of dispersal associated with the three curves, thus identifying 12 distinct parameter sets of homogeneous metacommunities. If we assume that there are only two patches and marginally perturb each parameter set by adding 5% in one patch and subtracting 5% in the other patch from the mean values of (r, K), K, e, m, a, or (a, h) (one at a time), we obtain 72 distinct heterogeneous metacommunities, which can be simulated for each of the six mechanisms described in appendix D, for a total of 432 cases. In table 1, the correlations among predators found through simulation are shown for the case of prey and predator mimicry, depending on environmental noise (similar results are obtained for the other mechanisms). In each entry of the table, there should be six correlation values because there are six heterogeneous metacommunities associated with each entry. However, for simplicity, we have reported only the minimum of these six values.

In columns A' and A'', the correlation would be 1 if the patches were homogeneous because points A' and A'' are in the synchronization regions for all three values of dispersal. Thus, the introduction of a small amount of heterogeneity has little effect at A', which is far from the boundaries of the synchronization regions, while it is more critical at A'', which is close to the boundary, in particular for $d = 0$ (note, however, that correlation coefficients of the order of 0.4 have often been considered indicative of some degree of synchronization among populations; see, e.g., Elton and Nicholson 1942; Higgins et al. 1997; Grenfell et al. 1998). Because points B and C in figure 4 are outside the synchronization region when $d = 0$, the corresponding homogeneous metacommunities would synchronize only when the dispersal rate is sufficiently high ($d = 0.1$ for B and $d = 0.2$ for C). In the heterogeneous case, this is reflected by the fact that the correlation is extremely low for low values of dispersal in the last two columns of table 1.

A completely different form of weak synchronization is intermittent synchronization, which we have observed in homogeneous metacommunities with parameters just outside the synchronization region. In this case, the metacommunity jumps back and forth from phases where the patches behave in a highly uncorrelated way to phases where they look completely synchronized, as shown in

Table 1: Predator correlations for the case of prey and predator mimicry depending on environmental noise

d	A'	A''	B	C
0	.69	.35	.16	.18
.1	.82	.93	.77	.14
.2	.87	.92	.91	.78

figure 6. As the synchronous and asynchronous phases can be very long (see the time units on the horizontal axis in fig. 6), this represents a serious obstacle for discovering intermittent synchrony from field data.

Concluding Remarks

We focused, in the first part of this article, on a rather generic metacommunity model with N identical patches and m populations in each patch, and we derived synchronization conditions by extending results known for the special case of a constant environment (Pecora and Carroll 1998; Jansen and Lloyd 2000). Our model is composed of two compartments (environmental and biological) connected in cascade (eqq. [1]–[3]). The first compartment describes the time evolution of the environmental (e.g., meteorological) variables needed to evaluate the birth, death, and dispersal rates involved in the biological compartment. We have assumed that the environment is chaotic, and we have called the output of the environmental submodel environmental noise. Under this (realistic) assumption, populations of a single isolated patch can be chaotic only because the biological processes, being dependent on the environmental noise, cannot filter out the irregularity impressed by the environment. By contrast, the density-dependent biological processes may add extra chaos, here called biochaos. Technically speaking, this happens when the so-called largest biological Lyapunov exponent conditioned to environment is positive. This Lyapunov exponent does not depend on the dispersal rates (because it refers to the behavior of single isolated patches) and can be computed through various algorithms (Ramasubramanian and Sriram 2000) for any given parameter setting of the two submodels. Through the standard stability analysis of the linearized system, a first interesting result is obtained: the so-called Moran effect (Royama 1992), that is, the synchronization of all patches in the absence of dispersal ($\mathbf{D} = 0$ in eq. [3]), is nothing but the nonexistence of biochaos. In other words, metacommunities in which density-dependent biological processes generate biochaos cannot synchronize without dispersal. The second, and perhaps more interesting, result is that the critical (i.e., lowest) dispersal rates necessary to synchronize a metacommunity producing biochaos can be determined by computing $(N-1)$ conditional Lyapunov exponents, which also depend on the parameters characterizing the environmental noise. If the dispersal rates are the same for all populations, the result simplifies, and the critical dispersal rate becomes proportional to a single Lyapunov exponent, which is again the largest biological Lyapunov exponent conditioned to environment. Moreover, the proportionality factor depends solely on the to-
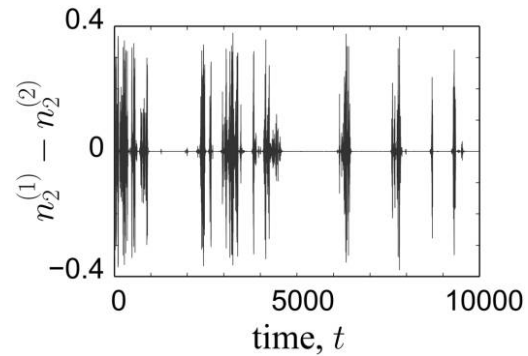

Figure 6: Intermittent synchronization for $\varepsilon = 0.53$ and $d_1 = d_2 = 0.025$ in a two-patch metacommunity. The values on the vertical axis represent the difference between the two predator abundances.

pology of the plot describing the dispersal flows; this could help predict the impact of structural changes associated with industrial development and land use. In particular, the analysis confirms the common belief that the establishment of new migration corridors makes synchronization easier, while the suppression of existing connections is a desynchronizing factor.

Our metacommunity model admits a synchronous solution (stable or unstable), that is, a solution with identical populations in all patches, for all parameter values. This structural property, which is strictly needed for deriving the above theoretical results, is satisfied only if the metacommunity has a number of specific properties, for example, that all patches be identical. Because our metacommunity model is not the most general model in which such properties hold, it would be interesting to extend the analysis to other metacommunities. One could, for example, consider the case in which some of the populations present in each patch (e.g., trees and insect pests and predators) disperse through different paths. This would require modifying equation (3) by inserting a matrix $\mathbf{C}$ for each component of the population vector. Another interesting extension would be to relax the assumption that $\mathbf{D}$ is constant because, in many cases of interest, dispersal is controlled by environmental conditions or by population densities (active dispersal).

In the second part of the article, we applied our method of analysis to the case of prey-predator communities. Part of the analysis is related to the study of the behavior of a single isolated patch, and, as such, it can be viewed as the natural follow-up of earlier studies on periodically forced prey-predator systems (Kuznetsov et al. 1992; Rinaldi et al. 1993; King and Schaffer 1999). On the other hand, the study can also be viewed as the extension of the analysis

concerning prey-predator metacommunities carried out by Jansen (2001; see also Hillary and Bees 2004) for the special case of a constant environment. The model used for describing the prey-predator interactions is the standard Rosenzweig-MacArthur model, with demographic parameters depending on environmental noise. As for the environmental model, we have used one of the most popular chaotic models, namely, the Rössler system, which can easily mimic the apparently random deviations of many meteorological variables from a standard seasonal pattern. One can then use these deviations to determine the current value of the demographic parameters, through a weighting coefficient called environmental variability.

The analysis has been carried out by computing the conditional biological Lyapunov exponents for (almost 1 million) different values of the parameters of the two submodels. The results emerging from this systematic analysis are as follows. (1) Biological chaos is present, provided that the environmental variability is sufficiently high (see fig. 2). Thus, the Moran effect is more likely to occur in metacommunities with low environmental variability. (2) If the frequency of the environmental noise is comparable with that of the unperturbed prey-predator oscillations, then biochaos is more likely (see fig. 3). In other words, when the environmental clock is tuned to the biological clock, the Moran effect is less likely. Equivalently, red and blue noise do not prevent synchronization. (3) If the environment is coherent, that is, if the spectrum of the environmental noise is narrow, then biochaos is more likely, and therefore the Moran effect is less likely. (4) Synchronization is favored by high dispersal rates (see fig. 4), in particular by high dispersal rates of the population with faster dynamics (see fig. 5).

Because the above conclusions have been proved to hold only for the metacommunity model (eqq. [10]–[12]), it would be of interest to extend the analysis under different assumptions to check whether the conclusions remain valid. In particular, one could consider other prey-predator models, including, for example, various chemostat models that are particularly suited for studying aquatic ecosystems (Hillary and Bees 2004). On the basis of a similar extension concerning the case of periodic environment (Gragnani and Rinaldi 1995), we believe that the results should remain valid. More intriguing is the extension to the case in which the demographic parameters depend on many environmental variables. For periodically varying environments, Rinaldi and Muratori (1993) have shown that, in this case, the regions in parameter space where biochaos is produced become much more irregular. Finally, still remaining in the simple case of a single environmental variable, one could consider environmental noises, such as that of figure 1*B*, that can be interpreted as random shocks, such as fires, earthquakes, hurricanes, and epidemics, which might synchronize geographically disjoint populations even in the absence of relevant dispersal rates.

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