

Synchrony in tritrophic food chain metacommunities

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The synchronous behaviour of interacting communities is studied in this paper. Each community is described by a tritrophic food chain model, and the communities interact through a network with arbitrary topology, composed of patches and migration corridors. The analysis of the local synchronization properties (via the master stability function approach) shows that, if only one species can migrate, the dispersal of the consumer (i.e., the intermediate trophic level) is the most effective mechanism for promoting synchronization. When analysing the effects of the variations of demographic parameters, it is found that factors that stabilize the single community also tend to favour synchronization. Global synchronization is finally analysed by means of the connection graph method, yielding a lower bound on the value of the dispersion rate that guarantees the synchronization of the metacommunity for a given network topology.

Keywords: food chain; metacommunity; network; synchronization

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1. Introduction

In the last decades, many plant and animal populations have been shown to synchronize (i.e., to behave in unison) over large areas. Examples are aphids and butterflies [24,33,59], moths [30,36,41], fish [47], crabs [27], birds [13,49], voles and mice [9,28], hares [47], squirrels [47,50], sheep [23], arctic herbivores [45], early blooming forest floor species [44], as well as many others [32,37]. Synchrony is the consequence of two independent factors: the dispersal of populations among patches and the existence of common meteorological driving forces (Moran effect). The theory is well established; see [10,29,42] for dispersal, [54] for the Moran effect, and [16] for the mixed case.

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 [20]. Since then, a great effort has been devoted to this case study (see [12,21,40,50,57,58], just to mention a few), with some of these contributions supporting the idea that the synchronization of Canadian lynx is primarily due to global environmental fluctuations. However, some recent results [10,38,39] have

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shown that networks of tritrophic food chain models can easily give rise to synchronization in the absence of a common meteorological driving force, provided there is a sufficiently high dispersal. This result and the discovery of a high gene flow of the Canadian lynx over distances of 3000 km [56] suggest that, most likely, migration is a key factor for the spatial synchronization of the lynx population.

This is why we concentrate in this paper on the case in which dispersal is the only cause of synchrony. Thus, our metacommunity is characterized by three basic elements: a graph in which nodes i and arcs (i, j) represent patches and dispersal flows between patches; a model describing the dynamics of the population vector $n^{(i)}$ in patch i when isolated from the other patches; the dispersal rates of each component of the population vector.

Depending upon the metacommunity model, various forms of synchronization are possible. The strongest one is *complete synchronization*, which occurs when a synchronous solution $n^{(i)}(t) = n^{(j)}(t)$ 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 is small. Much weaker but quite interesting forms of synchronization are *phase synchronization* [11,14,38], *out-of-phase synchronization* [18,55], and *intermittent synchronization* [15,25]. In general, when the parameters of a metacommunity are not too far from the values giving rise to complete synchronization, i.e., when the parameters are in the so-called pre-synchronization region, some weak form of synchronization is present and is revealed by various spatio-temporal patterns.

In this paper, we first show how the available general theory of local synchronization [1,29,42] can be used to discuss networks of food chains composed of resource, consumer, and predator populations. The patch model we use is a standard tritrophic food chain model and the main result is that the dispersal of the consumer population is much more effective than those of the other populations in promoting synchronous behaviours. Then, we show how factors like competition, interference, and cooperation among consumers or predators can be taken into account in order to detect if they promote synchronization or if they oppose it. The results are consistent with a general principle that stabilizing factors promote synchronization. Finally, the analysis is extended to the study of global synchronization through the use of the general available theory [4–7] and the role of stabilizing factors is assessed.

2. The metacommunity model

The metacommunity we consider in this paper is composed of N identical patches connected through corridors, along which migration occurs in both directions. Each patch i ($i = 1, 2, \dots, N$) is occupied by p populations whose abundances are the components of a p -dimensional vector $n^{(i)}$. The metacommunity is described by

$$\dot{n}^{(i)}(t) = f(n^{(i)}(t)) + d \sum_{j \in S_i} H(n^{(j)}(t) - n^{(i)}(t)), \quad i = 1, 2, \dots, N, \quad (1)$$

where $\dot{n}^{(i)}(t) = f(n^{(i)}(t))$ is the *patch model*, namely the equation governing the dynamics of an isolated patch; S_i is the set of patches directly connected to patch i (i.e., the neighbourhood of i); d is dispersal; and $H = \text{diag}[h_1, h_2, \dots, h_p]$ (with $h_l \geq 0$ for all l , and, without loss of generality, $\max_l h_l = 1$) is the *dispersion profile*, i.e., a constant diagonal matrix specifying the propensity of dispersing of all components of the population vector.

A particular solution of Equation (1), called *synchronous solution*, is characterized by

$$n^{(1)}(t) = n^{(2)}(t) = \dots = n^{(N)}(t) \quad \forall t. \quad (2)$$

As a matter of fact, when Equation (2) holds, all the dispersal flows $dH(n^{(j)}(t) - n^{(i)}(t))$ in Equation (1) vanish for all t , and the dynamics of each patch is simply governed by $\dot{n}(t) = f(n(t))$. Notice that this is possible thanks to the assumption that all patches are identical. When Equation (2) holds, the trajectory of system (1) is confined to a p -dimensional linear manifold Σ called *synchronization manifold*. It is of utmost importance to assess whether the synchronous solution (2) is stable, i.e., whether system (1) converges to (2) from any nearby initial state (in which case we say that the metapopulation displays *local synchronization*) or from any state (*global synchronization*). In the following two sections, we study these two problems with reference to thitrophic food chain metacommunities, where the components x , y , and z of the three-dimensional population vector n are the abundances of resource, consumers, and predators in the patch. The dynamics of the three populations in an isolated patch are described by

$$\begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{a_1xy}{1 + a_1b_1x}, \\ \dot{y} &= e_1 \frac{a_1xy}{1 + a_1b_1x} - m_1y - \frac{a_2yz}{1 + a_2b_2y}, \\ \dot{z} &= e_2 \frac{a_2yz}{1 + a_2b_2y} - m_2z, \end{aligned} \tag{3}$$

where r and K are the net growth rate and carrying capacity of the resource, and (a_i, b_i, m_i, e_i) , $i = 1, 2$, are the attack rate, handling time, mortality rate, and efficiency of consumers ($i = 1$) and predators ($i = 2$). Model (3) is known as the Rosenzweig–MacArthur model since it is the natural extension to three trophic levels of the model proposed long ago by Rosenzweig and MacArthur [53] for ditrophic food chains. Model (3) resembles some of the models proposed for the study of the Canadian boreal forest [10,31] but is slightly simpler than them and has been deeply studied. In particular, it can have a chaotic behaviour [26,34], but in relatively narrow ranges of its parameter space [35]. Here the parameters are fixed at the following values (already used in the literature as reference values):

$$\begin{aligned} r &= 1.15, & K &= 1.07, \\ a_1 &= 5, & b_1 &= 0.6, & m_1 &= 0.4, & e_1 &= 1, \\ a_2 &= 0.1, & b_2 &= 20, & m_2 &= 0.0037, & e_2 &= 1, \end{aligned} \tag{4}$$

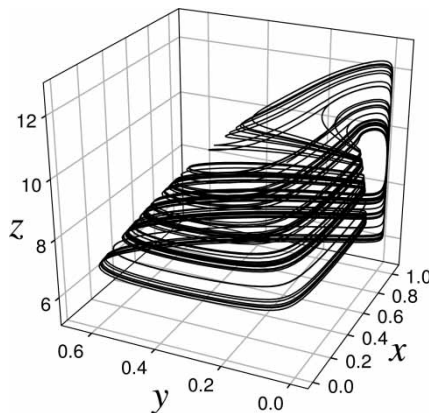


Figure 1. The tea-cup chaotic attractor of the Rosenzweig–MacArthur model (3), (4).

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because for these values the model has a chaotic attractor (Figure 1) and the discussion of the possibility of synchronizing the metapopulation by suitably selecting the dispersal d is particularly interesting.

3. Local synchronization

Through straightforward manipulations, Equation (1) can be rewritten as

$$\dot{n}^{(i)}(t) = f(n^{(i)}(t)) - d \sum_{j=1}^N g_{ij} H n^{(j)}(t), \quad i = 1, 2, \dots, N,$$

where the $N \times N$ connectivity matrix $G = [g_{ij}]$ describes the topology of the network composed of patches and corridors. More precisely, for $i \neq j$, $g_{ij} = g_{ji} = -1$ if patches i, j are directly connected and $g_{ij} = g_{ji} = 0$ otherwise, whereas $g_{ii} = -\sum_{j \neq i} g_{ij}$ is the degree of patch i , i.e., the number of corridors incident with i . To avoid degeneracies, we assume that any pair of patches is connected either directly or through a chain of corridors. Thus G is a real, symmetric, irreducible matrix. In addition, all off-diagonal elements are non-positive, and each row has a zero sum. As a consequence, the eigenvalues λ_i of G are real and

$$0 = \lambda_1 < \lambda_2 \leq \lambda_3 \leq \dots \leq \lambda_N.$$

Given a network, i.e., a connectivity matrix G , the local stability of the synchronization manifold Σ can be ascertained by looking at the evolution of the differences $(n^{(i)}(t) - n^{(1)}(t))$, $i = 2, 3, \dots, N$, which are described, after neglecting the higher-order terms in the Taylor expansion, by a $p \times (N - 1)$ -dimensional linear system with a time-varying Jacobian matrix given by

$$J = \begin{bmatrix} \frac{\partial f}{\partial n} - d(g_{22} - g_{12})H & \cdots & -d(g_{2N} - g_{1N})H \\ \vdots & \ddots & \vdots \\ -d(g_{N2} - g_{12})H & \cdots & \frac{\partial f}{\partial n} - d(g_{NN} - g_{1N})H \end{bmatrix}.$$

Through a suitable change of coordinates based on the eigenvectors of the matrix G , it can be shown [29,42] that this Jacobian matrix is equivalent to a block-diagonal matrix with matrices $[\partial f / \partial n - d\lambda_i H]$, $i = 2, 3, \dots, N$, on the diagonal. Such matrices describe the dynamics of the metapopulation close to the synchrony manifold. Thus, if the largest Liapunov exponents of these matrices, denoted by $L_{[\partial f / \partial n - d\lambda_i H]}$, are negative, i.e.,

$$L_{[\partial f / \partial n - d\lambda_i H]} < 0, \quad i = 2, 3, \dots, N, \tag{5}$$

then the synchronous solution (2) is locally stable, i.e., the metapopulation synchronizes.

Equation (5) is a condition for local synchronization and, as such, it only guarantees the synchronization of the metacommunity for initial conditions close to the synchronous solution (2). This implies that, in principle, the existence of unstable invariant sets on the synchronization manifold Σ could give rise to trajectories diverging from Σ , even if Equation (5) is met. Moreover, parts of the synchronous solution (2) which are locally repelling (remember that the Liapunov exponents are asymptotic averages) could give rise to bursting phenomena, which vanish in nominal conditions but could persist indefinitely otherwise (e.g., when noise is acting on the system

or a slight parameter mismatch among patches exists) [22] (see also [11] for a general discussion). Having pointed out these criticalities, in the following we will consider Equation (5) as the condition for local stability.

Given a metacommunity, conditions (5) can be easily checked by using any standard algorithm (e.g. [46]) for the computation of the largest Liapunov exponent of each time-varying matrix

$$\frac{\partial f}{\partial n} - \lambda_i d H, \quad i = 2, 3, \dots, N,$$

where $\partial f/\partial n$ is evaluated along a solution of $\dot{n} = f(n)$. These matrices depend upon the patch characteristics (patch model f and dispersion profile H) and upon the product $\lambda_i d$. Given f and H , one can therefore consider the family of matrices

$$\frac{\partial f}{\partial n} - \varepsilon H,$$

with $\varepsilon > 0$ and denote by $L(\varepsilon)$ the largest Liapunov exponent of each element of the family. The function $L(\varepsilon)$ is known as *master stability function* (MSF) [42], and is very useful for discussing the impact of patch characteristics on the synchronization of the metapopulation.

In fact, if the isolated patch is chaotic, as model (3)–(4) is, then $L(0) = \bar{L} > 0$ (where \bar{L} is the largest Liapunov exponent of the matrix $\partial f/\partial n$), so that the only three types of MSFs that can be found are the following:

- (i) $L(\varepsilon) > 0$ for all $\varepsilon > 0$;
- (ii) there exists an $\underline{\varepsilon} > 0$ such that $L(\underline{\varepsilon}) = 0$ and $L(\varepsilon) < 0$ for all $\varepsilon > \underline{\varepsilon}$;
- (iii) all other cases.

Type i MSFs guarantee that condition (5) cannot be satisfied, i.e., no metapopulation can synchronize even for high dispersal. In contrast, type ii MSFs guarantee that all metapopulations can synchronize provided the dispersal is sufficiently high, i.e.,

$$d > \frac{1}{\lambda_2} \underline{\varepsilon}. \tag{6}$$

The threshold value $\underline{\varepsilon}/\lambda_2$ depends upon the network G through the eigenvalue λ_2 , which is very high ($\lambda_2 = N$) in fully connected networks and very small in weakly connected ones (e.g., $\lambda_2 \simeq 1/N^2$ in a circular lattice), but the threshold also depends upon the patch characteristics (f, H) through $\underline{\varepsilon}$. Finally, for a type iii MSF, some (but not all) metapopulations can synchronize if dispersal can be suitably selected. Generally speaking, there will be one or more intervals where $L(\varepsilon)$ is negative, i.e., intervals

$$(\varepsilon'_1, \varepsilon''_1), (\varepsilon'_2, \varepsilon''_2), \dots, \quad \text{with} \quad \varepsilon'_1 < \varepsilon''_1 \leq \varepsilon'_2 < \varepsilon''_2 \leq \dots, \tag{7}$$

such that $L(\varepsilon'_i) = L(\varepsilon''_i) = 0$ and $L(\varepsilon) < 0$ for all $\varepsilon'_i < \varepsilon < \varepsilon''_i, i = 1, 2, \dots$. Then in all networks with

$$\frac{\lambda_N}{\lambda_2} < \frac{\varepsilon''_i}{\varepsilon'_i}, \tag{8}$$

for some i , the synchronous solution is stable for

$$\frac{1}{\lambda_2} \varepsilon'_i < d < \frac{1}{\lambda_N} \varepsilon''_i, \tag{9}$$

i.e., synchrony can be lost if dispersal is increased. It is worth noticing that Equation (8) is always satisfied in fully connected networks, because in that case all positive eigenvalues of G coincide.

The MSF of model (3)–(4) has been computed for the three dispersion profiles

$$\begin{aligned} H^I &= \text{diag}[1, 0, 0], \\ H^{II} &= \text{diag}[0, 1, 0], \\ H^{III} &= \text{diag}[0, 0, 1], \end{aligned}$$

corresponding to the extreme cases in which only one of the three populations disperses, and the result, shown in Figure 2, is quite interesting since the MSF is of type i, ii, and iii in cases I, II, and III, respectively. This means that no metacommunity can synchronize if dispersal involves only the resource, while any metacommunity can synchronize if only consumers disperse. No counterexamples have been found to these rules, which, however, should not be taken as theorems. In contrast, the fact that the MSF is of type iii when only predators disperse is not robust because type ii MSFs have also been obtained for $H = H^{III}$ by varying the parameters of the patch model. However, the result shown in Figure 2 is of interest because until now type iii MSFs have been detected in very few chaotic oscillators [1].

Let us now show how one can detect the impact of a demographic parameter on synchronization. For this, once the MSF $L(\varepsilon)$ has been computed for a reference model (like model (3) with the reference parameter values (4)), let us indicate with δ a positive variation of a parameter and recompute the MSF $L(\varepsilon, \delta)$ for the perturbed model. Thus, $L(\varepsilon, 0)$ is the MSF of the reference model, i.e., one of the three functions described in Figure 2, and $L(0, 0) = \bar{L}$.

If the reference MSF, $L(\varepsilon, 0)$ is of type ii, then, by continuity, the MSF $L(\varepsilon, \delta)$ will also be of type ii, provided δ is not too large. In other words, for sufficiently small parameter perturbations, there exists a function $\underline{\varepsilon}(\delta)$ such that $L(\underline{\varepsilon}(\delta), \delta) = 0$. The functions $L(\varepsilon, \delta)$ and $\underline{\varepsilon}(\delta)$ are sketched in Figure 3 under the naive assumption that the MSF depends linearly upon ε and δ . Figure 3(a) depicts the case of a so-called stabilizing parameter [52] (i.e., a parameter that reduces the Liapunov exponent $L(0, \delta)$ of a single isolated patch), while Figure 3(b) depicts the opposite case of a destabilizing parameter ($L(0, \delta)$ increasing with δ). Figure 3(a) shows that $\underline{\varepsilon}(\delta)$ decreases with δ , so that the synchronization condition (6) can be satisfied with lower dispersal when δ increases. For this reason, in the case of Figure 3(a), if the dispersal is fixed, then high values of δ promote synchronization, i.e., δ is synchronizing. Conversely, in Figure 3(b), the function $\underline{\varepsilon}(\delta)$ is increasing and δ is desynchronizing. The conclusion is that in the case of type ii MSFs, the synchronizing factors are nothing but the stabilizing factors.

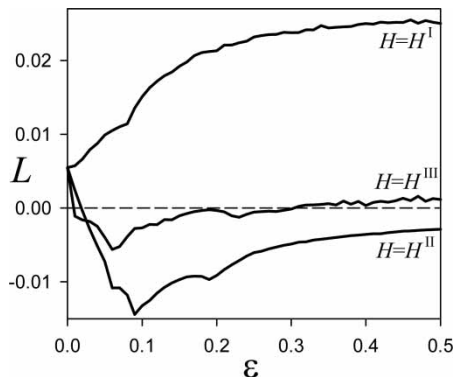


Figure 2. The MSFs of the Rosenzweig–McArthur model (3)–(4) when the only dispersing species is the resource ($H = H^I$, type i), consumers ($H = H^{II}$, type ii), or predators ($H = H^{III}$, type iii).

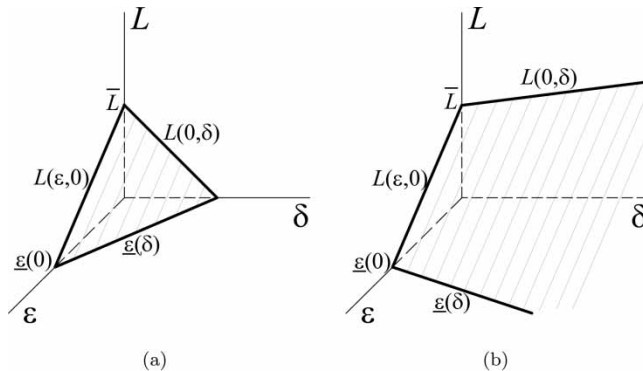


Figure 3. The sketch of a type ii MSF $L(\epsilon, \delta)$ and of the function $\underline{\epsilon}(\delta)$: (a) δ is stabilizing; (b) δ is destabilizing.

The same conclusion does not hold for MSFs of types i and iii. In fact, if the reference MSF is of type i, then it remains such for small parameter perturbations δ , so that the synchronization of the metacommunity is not possible no matter if δ is stabilizing or destabilizing. In the case of type iii MSFs, let us consider the first interval $(\epsilon'_1, \epsilon''_1)$ defined in Equation (7) and, to simplify the notation, let $\underline{\epsilon} = \epsilon'_1$ and $\bar{\epsilon} = \epsilon''_1$. Then Figure 3 still makes sense for small values of ϵ and δ , so that the minimum dispersal needed for synchronization, namely $\underline{\epsilon}(\delta)/\lambda_2$, decreases (increases) with δ if δ is stabilizing (destabilizing). In contrast, no relationship can reasonably be established between stabilizing factors and the loss of synchronization at high dispersal rates, because nothing can be inferred on $\bar{\epsilon}(\delta)$. However, understanding what happens at high dispersal rates is not particularly relevant in the context of metacommunities because it is known that many (if not all) populations are characterized by very low dispersal rates.

The results we have just pointed out are very important for various reasons. First, because they allow one to infer a property of a metacommunity (synchronization) from a property of a single community (stabilizing or destabilizing demographic parameter). This implies that the impact of a demographic factor on the emergence of collective dynamics (like synchronization) can reasonably be conjectured on the basis of observations or experiments performed on a single patch. Second, the results reinforce a recent analogous conclusion [16], namely that biological chaos is an obstacle for the synchronization of metacommunities through the Moran effect. In other words, the idea that stabilizing (destabilizing) factors are synchronizing (desynchronizing) seems to be valid in general and not only for the case examined in this paper dealing with synchronization due exclusively to dispersal. Finally, the bridge we have established between local (i.e., patch) chaos and global (i.e., network) synchronization reinforces an important evolutionary conjecture [17], namely that biological evolution drives local dynamics towards the edge of chaos and global dynamics towards weak forms of synchronization.

Obviously, the conclusions drawn from Figure 3, which depicts a naive and simplified interpretation of an MSF, cannot be argued to hold in general, even if the same conclusions can obviously be obtained (through the implicit function theorem) under a slightly more general assumption, namely that $L(\epsilon, \delta)$ is decreasing with respect to ϵ and decreasing (increasing) with respect to δ when δ is stabilizing (destabilizing). Thus, it makes sense to check whether the results derived from Figure 3 hold for particular classes of metacommunities, and this is, indeed, what we do in the following for our class of tritrophic food chains.

Instead of studying the effects on synchronization of the parameters appearing in the patch model (3), we now try to see if some demographic phenomena that are not taken into account in the Rosenzweig–MacArthur model (3) are synchronizing or desynchronizing. More precisely, we consider six phenomena, namely competition, interference, and cooperation among consumers

or predators, and we measure with a small positive parameter δ the relevance of the phenomena. Obviously, for $\delta = 0$, we obtain model (3) where, indeed, the six phenomena are neglected. For $\delta \neq 0$, one or two equations of model (3) must be modified as specified below.

- (1) Intraspecific competition among consumers. In agreement with the derivation of the classical logistic equation $\dot{x} = rx(1 - x/K)$ (see resource equation in the absence of consumers), the intraspecific competition among consumers can be dealt with by introducing an extra-mortality proportional to y^2 in the consumer equation, which becomes

$$\dot{y} = e_1 \frac{a_1xy}{1 + a_1b_1x} - m_1y - \frac{a_2yz}{1 + a_2b_2y} - \delta y^2.$$

- (2) Intraspecific competition among predators. Consistently with the previous case, we perturb only the predator equation, which becomes

$$\dot{z} = e_2 \frac{a_2yz}{1 + a_2b_2y} - m_2z - \delta z^2.$$

- (3) Interference among consumers. Interference among individuals feeding on a common resource is usually taken into account by lowering the functional response of the individuals, as proposed in [2]. Thus, interference among consumers requires to modify the first two equations of model (3) as follows:

$$\begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{a_1xy}{1 + a_1b_1x + \delta y}, \\ \dot{y} &= e_1 \frac{a_1xy}{1 + a_1b_1x + \delta y} - m_1y - \frac{a_2yz}{1 + a_2b_2y}. \end{aligned}$$

- (4) Interference among predators. Consistently with the previous case, we modify the last two equations of model (3) in the following way:

$$\begin{aligned} \dot{y} &= e_1 \frac{a_1xy}{1 + a_1b_1x} - m_1y - \frac{a_2yz}{1 + a_2b_2y + \delta z}, \\ \dot{z} &= e_2 \frac{a_2yz}{1 + a_2b_2y + \delta z} - m_2z. \end{aligned}$$

- (5) Cooperation among consumers. If cooperation enhances predation, we can simply multiply the consumer functional response by a factor greater than 1, which is here written as $(1 + \delta y/(y + y_0))$, where the parameter y_0 is fixed ($y_0 = 0.3$ in our numerical analysis). This means that abundant consumers predate $(1 + \delta)$ times more than scarce consumers. Thus, the first two equations of model (3) must be modified as follows:

$$\begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{a_1xy}{1 + a_1b_1x} \left(1 + \delta \frac{y}{y + y_0}\right), \\ \dot{y} &= e_1 \frac{a_1xy}{1 + a_1b_1x} \left(1 + \delta \frac{y}{y + y_0}\right) - m_1y - \frac{a_2yz}{1 + a_2b_2y}. \end{aligned}$$

(6) Cooperation among predators. Similarly to the previous case, the modified consumer and predator equations are ($z_0 = 9$ in our numerical analysis):

$$\begin{aligned} \dot{y} &= e_1 \frac{a_1xy}{1 + a_1b_1x} - m_1y - \frac{a_2yz}{1 + a_2b_2y} \left(1 + \delta \frac{z}{z + z_0} \right), \\ \dot{z} &= e_2 \frac{a_2yz}{1 + a_2b_2y} \left(1 + \delta \frac{z}{z + z_0} \right) - m_2z. \end{aligned}$$

In order to make the remaining part of this section more attractive, this is a good point for conjecturing, on a purely intuitive background, which factors are synchronizing and which are desynchronizing. For doing this, one can use the idea previously pointed out, i.e., stabilizing (destabilizing) factors are synchronizing (desynchronizing). Thus, for example, one might imagine that stronger predators can be more effective in keeping their prey under control, thus avoiding large fluctuations of the consumer population. This means that one should be inclined to imagine that factor 6 (i.e., cooperation among predators) should be a stabilizing factor and, hence, also a synchronizing factor. Before proceeding, the reader is invited to make his/her own guess for each of the six above factors.

In order to detect the impact of all factors on synchronization, we have systematically computed the largest Liapunov exponent $L(\varepsilon, \delta)$ on a 25×25 grid for each one of the six factors and for $H = H^{II}$ (dispersing consumer) as well as for $H = H^{III}$ (dispersing predator). Thus, our analysis has required the computation of $2 \times 6 \times 25 \times 25 = 7500$ largest Liapunov exponents of a 3×3 time-varying Jacobian matrix, which have been computed with a standard algorithm [46]. Obviously, in none of the examined cases the MSF $L(\varepsilon, \delta)$ is linear in ε and δ (as in Figure 3), neither it is monotone (recall that, in chaotic regions, there are always thin subregions of regular behaviour where the largest Liapunov exponent drops to zero). However, the statement stabilizing (destabilizing) factors are synchronizing (desynchronizing) factors turns out to be true in all cases. The result of the analysis is that four factors, namely 1, 3, 4, and 6 (i.e., intraspecific competition and interference among consumers; interference and cooperation among predators), are stabilizing and hence synchronizing, while the remaining two, namely 2 and 5 (i.e., intraspecific competition among predators; cooperation among consumers), are destabilizing and hence desynchronizing, no matter which is the dispersing population. Figure 4 shows one example of the first class, namely the case of interference among dispersing consumers: the MSF is of type ii and the two functions $L(0, \delta)$ and $\underline{\varepsilon}(\delta)$ qualitatively recall those reported in Figure 3(a) even if they are not monotonically decreasing. However, it is fully justified to summarize Figure 4 by saying that consumer interference is a synchronizing factor. Similarly, Figure 5 shows the case of intraspecific

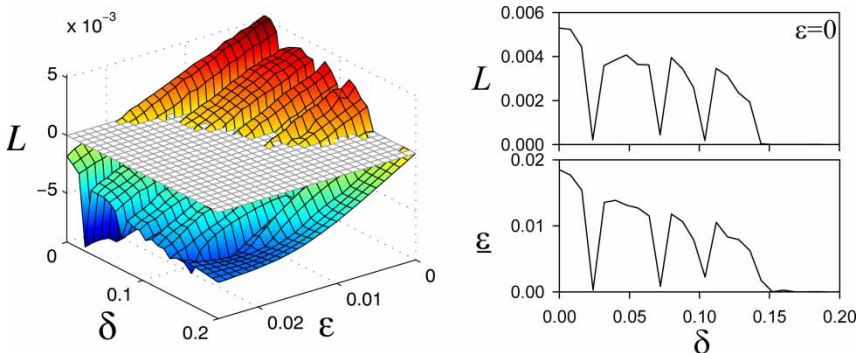


Figure 4. The MSF for the case of interference among dispersing consumers ($H = H^{II}$, factor 3: interference among consumers).

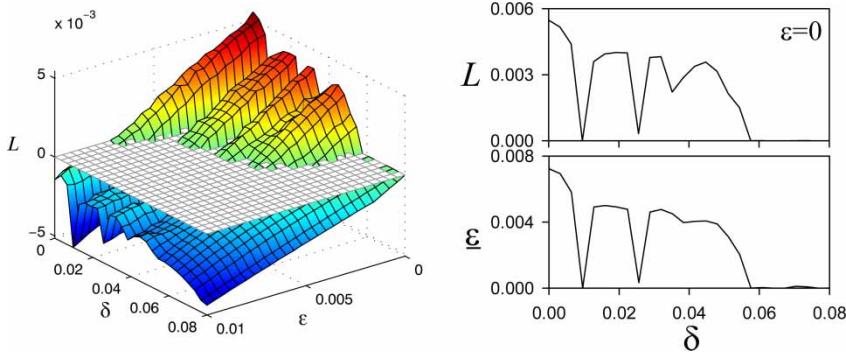


Figure 5. The MSF, for low values of ϵ and δ , for the case of intraspecific competition among consumers when predators disperse ($H = H^{III}$, factor 1: Intraspecific competition among consumers).

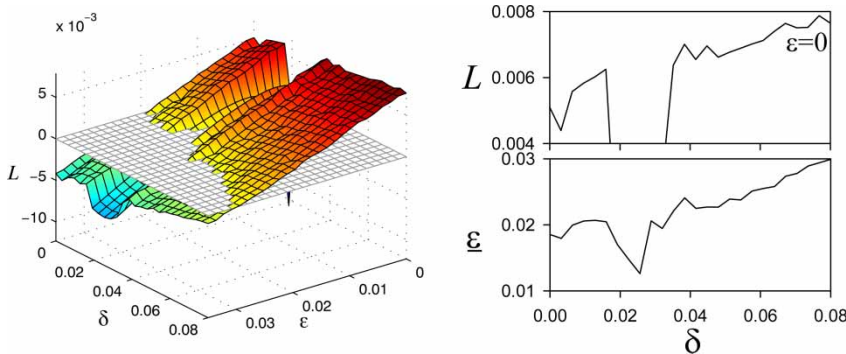


Figure 6. The MSF for the case of cooperation among dispersing consumers ($H = H^{II}$, factor 5: cooperation among consumers).

competition among consumers with dispersing predators. Again the functions $L(0, \delta)$ and $\underline{\epsilon}(\delta)$ resemble only vaguely to those of Figure 3(a) but still the result is that intraspecific competition among consumers is a synchronizing factor. Finally, an example of a desynchronizing factor is shown in Figure 6.

4. Global synchronization

In this section, we show how general results on global synchronization can be applied to the meta-community (1). Most methods for global synchronization of periodic and chaotic oscillators are based on the eigenvalues of the connectivity matrix and on the dynamics of the single oscillator [3,8,19,43,62,63]. An alternative approach, called *connection graph method* (CGM) [4], combines the Liapunov function approach with graph theoretical arguments. The method guarantees synchronization from arbitrary initial conditions and not just local stability of the synchronous solution (2).

It is worth noting that if global synchronization is guaranteed for a value of the dispersal d , it is also guaranteed for all higher values (the proof follows from the Liapunov function argument discussed in the Appendix; further details can be found in [4]). This is in contrast with local synchronization which can be lost by increasing dispersal, as shown in case iii of Figure 2. The CGM states that a value of the dispersal that guarantees global synchronization in a network

can be predicted from the threshold for global synchronization in the simple two-patch network. More precisely, the main theorem of the CGM [4] can be formulated for the metacommunity (1) as follows.

The global synchronization of the metacommunity (1) is guaranteed if the dispersal d exceeds the value

$$d^* = \frac{2d^{(2)}}{N} \max_{1 \leq k \leq m} z_k, \tag{10}$$

where $d^{(2)}$ is a dispersal that guarantees global synchronization of two coupled patches with the same dispersal profile H , N is the number of patches, and m is the number of corridors in the network. Given one path P_{ij} from each patch i to each patch j (with $i < j$), the quantity z_k associated to each corridor $k = 1, 2, \dots, m$ is the sum of the lengths of all the paths P_{ij} containing corridor k .

The first step is to find the dispersal $d^{(2)}$ that guarantees the global synchronization of two coupled patches. An analytical derivation of $d^{(2)}$ for the patch model (3)–(4) is given in Appendix.

The second step is to calculate the quantities z_k , which only depend upon the network topology. This calculation is straightforward and can be performed as follows. We first choose one path P_{ij} from each patch i to each patch j with $i < j$ (typically, the shortest path) and determine the length $|P_{ij}|$ of the path, i.e., the number of corridors in P_{ij} . Then, for each corridor k of the network, we calculate the sum z_k of the lengths of all P_{ij} 's containing k . Finally, in accordance with Equation (10), we determine the corridor with the maximum z_k .

For example, for the metapopulation network depicted in Figure 7, assuming $d^{(2)}$ has already been computed (see Appendix), we only need to calculate z_k for the seven corridors $k = a, b, \dots, g$ in order to obtain the bound (10). For that, let us first choose the paths between the nodes. Our choice is $P_{12} = a, P_{13} = ab, P_{14} = f, P_{15} = ag, P_{16} = fed, P_{23} = b, P_{24} = af, P_{25} = g, P_{26} = bc, P_{34} = cde, P_{35} = bg, P_{36} = c, P_{45} = e, P_{46} = ed, P_{56} = d$. Thus, the sum of lengths of all the paths containing corridor k is

$$\begin{aligned} k = a : \quad z_a &= |P_{12}| + |P_{13}| + |P_{15}| + |P_{24}| = 1 + 2 + 2 + 2 = 7, \\ k = b : \quad z_b &= |P_{13}| + |P_{23}| + |P_{26}| + |P_{35}| = 2 + 1 + 2 + 2 = 7, \\ k = c : \quad z_c &= |P_{26}| + |P_{34}| + |P_{36}| = 2 + 3 + 1 = 6, \\ k = d : \quad z_d &= |P_{16}| + |P_{34}| + |P_{46}| + |P_{56}| = 3 + 3 + 2 + 1 = 9, \\ k = e : \quad z_e &= |P_{16}| + |P_{34}| + |P_{45}| + |P_{46}| = 3 + 3 + 1 + 2 = 9, \\ k = f : \quad z_f &= |P_{14}| + |P_{16}| + |P_{24}| = 1 + 3 + 2 = 6, \\ k = g : \quad z_g &= |P_{15}| + |P_{25}| + |P_{35}| = 2 + 1 + 2 = 5, \end{aligned}$$

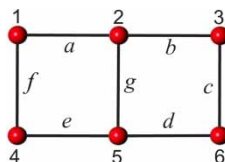


Figure 7. Example of a network configuration. A set of paths connecting each pair of nodes is the following: $P_{12} = a, P_{13} = ab, P_{14} = f, P_{15} = ag, P_{16} = fed, P_{23} = b, P_{24} = af, P_{25} = g, P_{26} = bc, P_{34} = cde, P_{35} = bg, P_{36} = c, P_{45} = e, P_{46} = ed, P_{56} = d$.

so that the maximum of z_k is $z_d = z_e = 9$. Hence, according to Equation (10), the global synchronization of the network is guaranteed if d is larger than

$$d^* = \frac{2d^{(2)}}{6}9 = 3d^{(2)}.$$

The computation of $\max_k z_k$ for various network topologies can be found in [4–7].

Let us now discuss the connections between local and global synchronization. Since the latter implies the former, it is obvious that, when searching for global synchronization, one can *a priori* exclude case i of Section 3 (see Figure 2). But also case iii can be excluded: as a matter of fact, even if condition (9) can be met for a given network, the resulting local synchrony is certainly not global since it is lost by increasing the dispersal d , thus violating the main result of the CGM (see above).

Therefore, for the metacommunity (1) to be globally synchronizable, it is necessary that the MSF is of type ii, i.e., $L(\varepsilon) < 0$ for all $\varepsilon > \underline{\varepsilon} > 0$. For the food chain model (3)–(4), we have seen that this happens when $H = H^{\text{II}} = \text{diag}[0, 1, 0]$, i.e., when the consumer is the only dispersing species. But the MSF turns out to be of type ii also when $H = H^0 = \text{diag}[1, 1, 1]$, i.e., when the three populations disperse equally, since it can be shown that in this case $L(\varepsilon) = \bar{L} - \varepsilon$. The analysis presented in the Appendix actually relates to this latter situation, but can easily be extended to the case $H = H^{\text{II}}$.

From the above discussion, it is also clear that no relationship exists between $\underline{\varepsilon}$ and d^* , the lower bounds of the dispersal d guaranteeing local and global synchronization, respectively, except the obvious condition $\underline{\varepsilon} \leq d^*$ (actually, in most cases the value of d^* resulting from the Liapunov function approach – see Appendix – is very conservative and thus it is much larger than $\underline{\varepsilon}$). As a consequence, when one considers the effects on global synchronization of the parameter variations ($\delta \neq 0$) analysed in Section 3, no conclusions can be *a priori* drawn just on the basis of the results obtained for local synchronization. It is certainly reasonable to expect that what favours the local synchronization should also favour the global one. This is true for factors 1, 3, 4, and 6 (i.e., intraspecific competition and interference among consumers; interference and cooperation among predators – see also Section 3 and the Appendix), which make both $\underline{\varepsilon}$ and d^* decrease when δ increases from 0. But the opposite happens for the destabilizing factor 2 (i.e., intraspecific competition among predators), which also makes d^* decrease, whereas $\underline{\varepsilon}$ increases with δ . This factor, therefore, makes local synchronization more difficult to achieve but enhances the global one.

5. Concluding remarks

Synchronous behaviour of plant and animal populations over large areas is a well-documented phenomenon, while the role of all factors involved in it is not fully understood yet. In this paper, we have studied the problem assuming that each community is composed of three populations (resource, consumer, and predator) whose dynamics are governed by a standard Rosenzweig–MacArthur model with parameters in the region of chaotic behaviour. The communities interact through a network with arbitrary topology, composed of patches – where the communities live – and corridors – along which migration occurs.

The local and global stability of the synchronous state have been studied. As far as the former is concerned, the MSF approach [1,29,42] has shown that, under the assumption that only one species migrates, the dispersal of the consumer is the most effective mechanism for promoting synchrony. Several factors not included in the Rosenzweig–MacArthur model have also been considered, such as competition, interference, and cooperation among consumers and predators,

in order to assess their role in synchronization. The results, generally speaking, say that the factors stabilizing the single community also tend to favour synchronization. This allows one to infer a property of the metacommunity (i.e., the effect of a demographic parameter on synchronization) from a property of the single community (i.e., the effect of the same parameter on the single patch community).

Global synchronization has been analysed by means of the CGM [4–7], which, given the network topology, allows one to derive a lower bound for the dispersal rate along corridors that guarantees synchronization. It is worth noticing that both the MSF approach and the CGM can be extended to directed networks [7,42], where migration along corridors is possible only in one direction, thus allowing one to study important problems like those related with seed dispersal due to wind.

Perhaps more promising, however, is the particularization to the case of slow–fast metacommunities where special forms of synchrony can be studied through the singular perturbation approach [51]. This would allow, for example, the study of synchronization of insect-pest outbreaks in forest [30].

Finally, it should be emphasized that our study has not exploited particular properties of specific network topologies, so that our findings are valid in general. Special attention could be deserved to networks which are of particular interest. An important example are small-world networks [61] where the introduction of a few long-range connections (in addition to the corridors connecting nearby patches) is generally believed to enhance synchronization [1,11,60], although this has been questioned recently in some specific ecological contexts [48].

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Appendix A. Global synchronization of the two-patch network

In this appendix, we discuss the global synchronization of the metapopulation (1), (3) in the special case $N = 2$, i.e., when there are only two coupled patches. For the sake of clarity, we choose the dispersion profile $H^0 = \text{diag}[1, 1, 1]$, i.e., we assume that the three populations disperse equally, but the extension of the analysis to the case of generic dispersal profiles is straightforward. We first need to check the boundedness of the solutions, namely that no trajectories of the system go to infinity.

A.1 Boundedness of the solutions of model (3)

We show that the analysis of the asymptotic behaviour of model (1), (3) for $N = 2$ can be restricted to a bounded region of the positive orthant of the state space because such a region is an absorbing domain, in the sense that all trajectories enter the domain in finite time and remain in it forever. Two connected patches of the kind (3) are described by:

$$\begin{aligned}
 \dot{x}^{(1)} &= rx^{(1)} \left(1 - \frac{x^{(1)}}{K} \right) - \frac{a_1 x^{(1)} y^{(1)}}{1 + a_1 b_1 x^{(1)}} + d(x^{(2)} - x^{(1)}), \\
 \dot{y}^{(1)} &= \frac{a_1 x^{(1)} y^{(1)}}{1 + a_1 b_1 x^{(1)}} - m_1 y^{(1)} - \frac{a_2 y^{(1)} z^{(1)}}{1 + a_2 b_2 y^{(1)}} + d(y^{(2)} - y^{(1)}), \\
 \dot{z}^{(1)} &= \frac{a_2 y^{(1)} z^{(1)}}{1 + a_2 b_2 y^{(1)}} - m_2 z^{(1)} + d(z^{(2)} - z^{(1)}), \\
 \dot{x}^{(2)} &= rx^{(2)} \left(1 - \frac{x^{(2)}}{K} \right) - \frac{a_1 x^{(2)} y^{(2)}}{1 + a_1 b_1 x^{(2)}} + d(x^{(1)} - x^{(2)}), \\
 \dot{y}^{(2)} &= \frac{a_1 x^{(2)} y^{(2)}}{1 + a_1 b_1 x^{(2)}} - m_1 y^{(2)} - \frac{a_2 y^{(2)} z^{(2)}}{1 + a_2 b_2 y^{(2)}} + d(y^{(1)} - y^{(2)}), \\
 \dot{z}^{(2)} &= \frac{a_2 y^{(2)} z^{(2)}}{1 + a_2 b_2 y^{(2)}} - m_2 z^{(2)} + d(z^{(1)} - z^{(2)}),
 \end{aligned} \tag{A1}$$

where $e_1 = e_2 = 1$ (see Equation (4)) in order to simplify the notation. Model (A1) is positive, in the sense that $x^{(i)}(0), y^{(i)}(0), z^{(i)}(0) \geq 0, i = 1, 2$, implies $x^{(i)}(t), y^{(i)}(t), z^{(i)}(t) \geq 0$ for all $t \geq 0$. This can be checked by noting, for example, that $\dot{x}^{(1)} \geq 0$ when $x^{(1)} = 0$ and all other variables are nonnegative (the same reasoning can be repeated for all the other state variables).

Consider the parameterized function

$$V_c = x^{(1)} + y^{(1)} + z^{(1)} + x^{(2)} + y^{(2)} + z^{(2)} - 2c,$$

where c is a constant parameter, and notice that the plane $V_c = 0$ is partly contained in the positive orthant if $c > 0$. The time derivative of V_c along the trajectories of system (A1) is given by

$$\begin{aligned} \dot{V}_c &= \dot{x}^{(1)} + \dot{y}^{(1)} + \dot{z}^{(1)} + \dot{x}^{(2)} + \dot{y}^{(2)} + \dot{z}^{(2)} \\ &= rx^{(1)} \left(1 - \frac{x^{(1)}}{K} \right) - m_1 y^{(1)} - m_2 z^{(1)} + rx^{(2)} \left(1 - \frac{x^{(2)}}{K} \right) - m_1 y^{(2)} - m_2 z^{(2)}, \end{aligned}$$

so that, if $m_1 > m_2$ (as in Equation (4)), we can bound \dot{V}_c in the positive orthant as follows:

$$\dot{V}_c < rx^{(1)} \left(1 - \frac{x^{(1)}}{K} \right) - m_2 (y^{(1)} + z^{(1)}) + rx^{(2)} \left(1 - \frac{x^{(2)}}{K} \right) - m_2 (y^{(2)} + z^{(2)}).$$

Hence, if we fix c at a positive value, i.e., if we take a plane $V_c = 0$ intersecting the positive orthant, we can conclude that, on the positive part of the plane where $y^{(1)} + z^{(1)} + y^{(2)} + z^{(2)} = 2c - x^{(1)} - x^{(2)}$, \dot{V}_c satisfies the inequality

$$\dot{V}_c < rx^{(1)} \left(1 - \frac{x^{(1)}}{K} \right) - m_2 (c - x^{(1)}) + rx^{(2)} \left(1 - \frac{x^{(2)}}{K} \right) - m_2 (c - x^{(2)}).$$

Trivial computations show that \dot{V}_c is negative if $c > c^*$, with

$$c^* = \frac{K}{4rm_2} (r + m_2)^2$$

since, under the above condition, both polynomials $rx^{(i)}(1 - x^{(i)}/K) - m_2(c - x^{(i)})$ ($i = 1, 2$) are negative for all $x^{(i)} \geq 0$. Thus, the conclusion is that the region in the positive orthant containing the origin and bounded by $V_{c^*} = 0$ is an absorbing domain, so that the analysis of the asymptotic behaviour of model (A1) can be restricted to the bounded region

$$0 \leq x^{(i)} \leq c^*, \quad 0 \leq y^{(i)} \leq c^*, \quad 0 \leq z^{(i)} \leq c^*, \quad i = 1, 2. \tag{A2}$$

A.2 Global synchronization

System (A1) can be rewritten as

$$\begin{aligned} \dot{x}^{(1)} &= f(x^{(1)}) - g(x^{(1)})y^{(1)} + d(x^{(2)} - x^{(1)}), \\ \dot{y}^{(1)} &= g(x^{(1)})y^{(1)} - m_1 y^{(1)} - \tilde{g}(y^{(1)})z^{(1)} + d(y^{(2)} - y^{(1)}), \\ \dot{z}^{(1)} &= \tilde{g}(y^{(1)})z^{(1)} - m_2 z^{(1)} + d(z^{(2)} - z^{(1)}), \\ \dot{x}^{(2)} &= f(x^{(2)}) - g(x^{(2)})y^{(2)} + d(x^{(1)} - x^{(2)}), \\ \dot{y}^{(2)} &= g(x^{(2)})y^{(2)} - m_1 y^{(2)} - \tilde{g}(y^{(2)})z^{(2)} + d(y^{(1)} - y^{(2)}), \\ \dot{z}^{(2)} &= \tilde{g}(y^{(2)})z^{(2)} - m_2 z^{(2)} + d(z^{(1)} - z^{(2)}), \end{aligned} \tag{A3}$$

where $f(x^{(i)}) = rx^{(i)}(1 - x^{(i)}/K)$, $g(x^{(i)}) = a_1 x^{(i)}/(1 + a_1 b_1 x^{(i)})$, and $\tilde{g}(y^{(i)}) = a_2 y^{(i)}/(1 + a_2 b_2 y^{(i)})$ for $i = 1, 2$. Letting

$$\begin{aligned} X &= \frac{x^{(2)} - x^{(1)}}{2}, & u &= \frac{x^{(1)} + x^{(2)}}{2}, \\ Y &= \frac{y^{(2)} - y^{(1)}}{2}, & v &= \frac{y^{(1)} + y^{(2)}}{2}, \\ Z &= \frac{z^{(2)} - z^{(1)}}{2}, & w &= \frac{z^{(1)} + z^{(2)}}{2}, \end{aligned} \tag{A4}$$

we obtain the so-called difference system

$$\begin{aligned} \dot{X} &= \frac{1}{2} \{ [f(x^{(2)}) - f(x^{(1)})] - [g(x^{(2)})y^{(2)} - g(x^{(1)})y^{(1)}] \} - 2dX, \\ \dot{Y} &= \frac{1}{2} \{ [g(x^{(2)})y^{(2)} - g(x^{(1)})y^{(1)}] - [\tilde{g}(y^{(2)})z^{(2)} - \tilde{g}(y^{(1)})z^{(1)}] \} - (m_1 + 2d)Y, \\ \dot{Z} &= \frac{1}{2} \{ [\tilde{g}(y^{(2)})z^{(2)} - \tilde{g}(y^{(1)})z^{(1)}] \} - (m_2 + 2d)Z. \end{aligned} \tag{A5}$$

To get rid of the variables $x^{(i)}, y^{(i)}, z^{(i)}$, $i = 1, 2$, we apply the mean value theorem, i.e., $f(x^{(2)}) - f(x^{(1)}) = f_x(\xi_1)(x^{(2)} - x^{(1)}) = 2f_x(\xi_1)X$, and $g(x^{(2)}) - g(x^{(1)}) = g_x(\xi_2)(x^{(2)} - x^{(1)}) = 2g_x(\xi_2)X$, where $x^{(1)} \leq \xi_i \leq x^{(2)}$, $i =$

1, 2. At the same time, it follows from Equation (A4) that

$$\begin{aligned} x^{(1)} &= u - X, & x^{(2)} &= u + X, \\ y^{(1)} &= v - Y, & y^{(2)} &= v + Y, \\ z^{(1)} &= w - Z, & z^{(2)} &= w + Z, \end{aligned}$$

such that in Equation (A5)

$$\begin{aligned} [g(x^{(2)})y^{(2)} - g(x^{(1)})y^{(1)}] &= [g(x^{(2)})(v + Y) - g(x^{(1)})(v - Y)] \\ &= [g(x^{(2)}) - g(x^{(1)})]v + [g(u + X) + g(u - X)]Y \\ &= 2g_x(\xi_2)Xv + [g(u + X) + g(u - X)]Y, \end{aligned}$$

and analogously

$$[\tilde{g}(y^{(2)})z^{(2)} - \tilde{g}(y^{(1)})z^{(1)}] = 2\tilde{g}_y(\eta)Yw + [\tilde{g}(v + Y) + \tilde{g}(v - Y)]Z,$$

where $y^{(1)} \leq \eta \leq y^{(2)}$. Thus, system (A5) simplifies to

$$\begin{aligned} \dot{X} &= [f_x(\xi_1) - g_x(\xi_2)v - 2d]X - \frac{1}{2}[g(u + X) + g(u - X)]Y, \\ \dot{Y} &= g_x(\xi_2)vX + \left\{ \frac{1}{2}[g(u + X) + g(u - X)] - \tilde{g}_y(\eta)w - (m_1 + 2d) \right\}Y \\ &\quad - \frac{1}{2}[\tilde{g}(v + Y) + \tilde{g}(v - Y)]Z, \\ \dot{Z} &= \tilde{g}_y(\eta)wY + \left\{ \frac{1}{2}[\tilde{g}(v + Y) + \tilde{g}(v - Y)] - (m_2 + 2d) \right\}Z. \end{aligned} \tag{A6}$$

Our goal is to obtain conditions under which the trivial equilibrium $X = Y = Z = 0$ (corresponding to the synchronous solution $x^{(1)} = x^{(2)}, y^{(1)} = y^{(2)}, z^{(1)} = z^{(2)}$) is globally stable. This can be done by constructing a Liapunov function, i.e., a smooth, positive definite function that decreases along trajectories of system (A6). Consider the Liapunov function

$$\Phi = \frac{1}{2}(X^2 + Y^2 + Z^2).$$

The time derivative of Φ along the trajectories of system (A6) is given by

$$\dot{\Phi} = -[A_{11}X^2 + 2A_{12}XY + A_{22}Y^2 + 2A_{23}YZ + A_{33}Z^2],$$

where

$$\begin{aligned} A_{11} &= 2d - f_x(\xi_1) + g_x(\xi_2)v, \\ A_{12} &= \frac{1}{4}[g(u + X) + g(u - X)] - \frac{1}{2}g_x(\xi_2)v, \\ A_{22} &= 2d + m_1 + \tilde{g}_y(\eta)w - \frac{1}{2}[g(u + X) + g(u - X)], \\ A_{23} &= \frac{1}{4}[\tilde{g}(v + Y) + \tilde{g}(v - Y)] - \frac{1}{2}\tilde{g}_y(\eta)w, \\ A_{33} &= 2d + m_2 - \frac{1}{2}[\tilde{g}(v + Y) + \tilde{g}(v - Y)]. \end{aligned}$$

Thus $\dot{\Phi}$ is negative along trajectories of system (A6) if the quadratic form $S = A_{11}X^2 + 2A_{12}XY + A_{22}Y^2 + 2A_{23}YZ + A_{33}Z^2$ is positive definite. To simplify the analysis, we split S as $S = S_1 + S_2$, where $S_1 = A_{11}X^2 + 2A_{12}XY + A_{22}Y^2/2$ and $S_2 = A_{22}Y^2/2 + 2A_{23}YZ + A_{33}Z^2$. Here, the coefficients A_{11} , A_{22} , and A_{33} depend on the dispersal d and favour positiveness of the two quadratic forms S_1 and S_2 . For S_1 and S_2 to be positive, A_{11} , A_{22} , and A_{33} must overcome the contributions associated to the coefficients A_{12} and A_{23} . This is achieved when the dispersal d exceeds a critical value.

Applying the Sylvester criterion for positive definiteness of the two quadratic forms, we obtain the conditions

$$A_{11} > 0, \quad A_{22} > 0, \quad A_{33} > 0, \quad \frac{1}{2} A_{11} A_{22} > A_{12}^2, \quad \frac{1}{2} A_{22} A_{33} > A_{23}^2. \tag{A7}$$

The functions that are present in the A_{ij} 's coefficients can be bounded as follows:

$$\begin{aligned} f_x(\xi_1) \leq f_x(0) = r, \quad g_x(\xi_2)v \geq 0, \quad \tilde{g}_y(\eta)w \geq 0, \\ g(u + X) + g(u - X) \leq 2g(c^*) < \frac{2}{b_1}, \\ \tilde{g}(v + Y) + \tilde{g}(v - Y) \leq 2\tilde{g}(c^*) < \frac{2}{b_2}, \end{aligned} \tag{A8}$$

where we have exploited the bounds given in Equation (A2).

Using Equation (A8), we can replace Equation (A7) with more conservative conditions, setting A_{11} , A_{22} , A_{33} to their lower bounds and A_{12} , A_{23} to their upper bounds. We obtain

$$\begin{aligned} d > \frac{r}{2}, \quad d > \frac{1}{2} \left[\frac{1}{b_1} - m_1 \right], \quad d > \frac{1}{2} \left[\frac{1}{b_2} - m_2 \right], \\ (2d - r) \left(2d + m_1 - \frac{1}{b_1} \right) > \frac{1}{2b_1^2}, \\ \left(2d + m_1 - \frac{1}{b_1} \right) \left(2d + m_2 - \frac{1}{b_2} \right) > \frac{1}{2b_2^2}. \end{aligned} \tag{A9}$$

For the given set of parameters (4), it turns out that $(2d - r) > (2d + m_1 - 1/b_1)$ and $(2d + m_1 - 1/b_1) < (2d + m_2 - 1/b_2)$, so that the last two inequalities in Equation (A9) are met if

$$\left(2d + m_1 - \frac{1}{b_1} \right)^2 > \frac{1}{2b_1^2}, \quad \left(2d + m_1 - \frac{1}{b_1} \right)^2 > \frac{1}{2b_2^2}.$$

Since $1/b_1^2 > 1/b_2^2$ (see Equation (4)), we finally obtain the condition

$$d > d^{(2)} = \frac{1}{2} \left(\frac{\sqrt{2}}{2b_1} - m_1 + \frac{1}{b_1} \right).$$

This inequality gives a bound for the dispersal d sufficient to make the quadratic form $\dot{\Phi}$ negative definite. This, in turn, guarantees the global stability of the synchronous state in the coupled system (A3) with parameters (4).

The same Liapunov approach can be extended to two coupled patches when the single patch is a Rosenzweig–MacArthur model modified in order to include factors like intraspecific competition, interference, or cooperation, as done in Section 3. In such a case, the difference system (A5) contains extra terms depending upon a parameter δ measuring the intensity of the factor. It can be checked that the extra terms related to factors 1, 3, 4, and 6 (i.e., intraspecific competition and interference among consumers; interference and cooperation among predators), which were shown to be stabilizing, but also factor 2 (i.e., intraspecific competition among predators), which is destabilizing, contribute to the stability of the origin of system (A5), thus favouring global synchronization. For example, factor 1 yields an extra term $-2\delta v Y$ to the second equation of the difference system (A5). Since $v = (y^{(1)} + y^{(2)})/2$ is always nonnegative, the term $-2\delta v Y$ makes the trivial equilibrium of system (A5) more stable and therefore lowers the critical value of the dispersal required for global synchronization.