

## DENSITY-DEPENDENT DISPERSAL IN MULTIPLE SPECIES METAPOPOPULATIONS

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**ABSTRACT.** A multiple species metapopulations model with density-dependent dispersal is presented. Assuming the network configuration matrix to be diagonalizable we obtain a decoupling of the associated perturbed system from the homogeneous state. It was possible to analyze in detail the instability induced by the density-dependent dispersal in two classes of  $k$ -species interaction models: a hierarchically organized competitive system and an age-structured model.

**1. Introduction.** Seeking explanations for the observed heterogeneous density distributions of species on natural habitats is a central problem in ecology. There are many well documented studies of problems related to patchiness and pattern formation e.g., [13], [18], [17], [19]. The classical mathematical approaches to this problem were based on continuous spatial state variable and continuous time models (partial differential equations and integro-differential equations) (see [18] and references therein). When the habitat is naturally fragmented, the continuous spatial variable is no longer required, and it is better replaced by a discrete description of the spatial variable. The Coupled Map Lattice (CML) framework described in [12] seems to be a quite useful mathematical formulation. In fact, this modeling approach was employed to study the role of dispersal in a discrete system of linked populations (Hassell et al. [5], Commins et al. [2], Ruxton & Doebeli [23], Ruxton & Rohani [24]). The complexity of the density patterns encountered in these studies follows in the class of spatial patterns described in Kaneko [11]. The explanations for the spatial pattern formation in these studies were based on the highly nonlinear local dynamics rather than the complexity of the dispersal mechanism. Even very simple dispersal mechanisms such as density-independent or passive dispersal can lead to pattern formation in CML models. The instability of the homogeneous state is caused by a Turing mechanism (see [29], [17]) when the local patch model contains more than one species and dispersal is species dependent ([21]). In fact, what is necessary is not exactly more than one species in the strict biological sense, but a dynamical system with more than one state variable with connection between

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patches to be state variable specific. For example, the complex dynamics found in [6] and the spatial patterns encountered in [3] in an age-structured single species metapopulation model were induced by an uneven dispersal age distribution. When the local patch model has only one state variable (unstructured single species model) the result of [20] states that is impossible for dispersal alone to induce an instability in the homogeneous state of a metapopulation formed by  $n$  equal patches. The first attempt to consider density-dependent dispersal in CML models was done in [22], assuming a very particular functional form of density-dependence in the movement of individual between patches. His conclusions suggest that density-dependence has little effect on the stability of the homogeneous state, although it was shown, at least for a narrow parameter range, that the density-dependent dispersal could drive the system to the instability of the homogeneous equilibrium. The idea of a density-dependent dispersal process leading to pattern formation in a single species model was further explored in [9], [25]. Unstable homogeneous equilibrium can be the result of an intense nonlinear coupling. More precisely, if the rate of change in the number of migrants with respect to the local patch density at equilibrium state is large enough (larger than one), then there is a possibility of observing heterogeneous spatial patterns caused by movement of individual between patches ([25]). Density-dependent dispersal in multi species metapopulations were introduced in [7] in their study of the effects of cross-dispersal (the dispersal of one species depends on the density of the other species coexisting in the patch) in the instability of the homogeneous state. Their findings indicate that the type of interaction (competition, mutualism, predator-prey) can be decisive for the instability induced by dispersal. In this paper we consider a general multi species metapopulation model with density-dependent dispersal and study the effects of the density-dependent dispersal in the process of spatial pattern generation. We first introduce a decoupling technique similar to the one introduced in [10] that works in any reasonable network of  $n$  patches with  $k$  species coupled with density-dependent dispersal at the emigration stage (when individuals leave the patch). Then we apply the technique to two different local models. First we consider a system of  $k$  species to satisfy a certain hierarchy as in [1]. Then we consider the local model to be of a single species with an age structured ( $k$  age classes). The last section of the article is left for the final remarks and discussion.

**2. The metapopulation model.** Our metapopulation model consists of  $n$  equal patches. In each patch there are  $k$  species that interact with each other. We model the time evolution of the ensemble as a discrete dynamical system of  $nk$  equations. In each time step two major processes are considered: the local dynamics (within patch dynamics) and dispersal (transfer of individuals to others patches). The local dynamics consist of survival, reproduction, and interaction with the other species in the patch. Let  $x_{\ell j}^t$  be the number of individuals of species  $\ell$  living at patch  $j$  at time  $t$ ,  $\ell = 1, 2, \dots, k$ ,  $j = 1, 2, \dots, n$ , and  $t = 0, 1, 2, \dots$ . The vector  $\mathbf{x}_j^t = (x_{1j}^t, x_{2j}^t, \dots, x_{kj}^t) \in \mathbb{R}^k$  is the population vector of patch  $j$  and accounts for the number of each species inhabiting patch  $j$  at time  $t$ . Assume the local dynamics to be described by a  $C^1$  function  $\mathbf{f} : \mathbb{R}^k \rightarrow \mathbb{R}^k$ . Thus, without considering dispersal, the dynamics of an isolated patch  $j$  is given by

$$\mathbf{x}_j^{t+1} = \mathbf{f}(\mathbf{x}_j^t). \quad (1)$$

According to Ims and Yoccoz [8], the transfer of individuals between patches consists of three steps: emigration, migration, and immigration. In the emigration

stage the individual leaves the patch. It is followed by the migration stage, which involves displacements in nonhabitat. Immigration consists of settlement in the new patch. We assume that the migration step is very short and that no individuals are lost during this process. Therefore, only the emigration and immigration stages will be considered in the model.

The emigration process is basically described by the dispersal fraction of each species. Let  $\mu_\ell$  be the proportion of individuals of species  $\ell$  leaving its patch. We assume  $\mu_\ell$  to be independent of the patch location but density-dependent, thus  $\mu_\ell : \mathbb{R}^k \rightarrow \mathbb{R}$  is a  $C^1$  function and  $\mu_\ell(x_{1j}^t, x_{2j}^t, \dots, x_{kj}^t)$  accounts for the proportion of individuals from species  $\ell$  leaving patch  $j$  at time  $t$ . Notice that  $\mu_\ell$  is a  $k$  variable real function which allows the inclusion of the influence of the other species in the dispersal fraction of species  $\ell$ . Of course, we must have  $0 \leq \mu_\ell \leq 1$  for all  $\ell = 1, 2, \dots, k$ .

The immigration (arrival at a new patch) process is assumed to be density-independent and species independent. It is described by the form in which each node in the network is connected with the other nodes, or the so-called network topology. This will entirely describe the network configuration matrix  $C$ , with coefficients  $c_{ij}$ ,  $0 \leq c_{ij} \leq 1$ ,  $i, j = 1, 2, \dots, n$  reflecting the preference of individuals that leave patch  $j$  and establish in patch  $i$ . That is,  $c_{ij}x_{\ell j}^t\mu_\ell(x_{1j}^t, x_{2j}^t, \dots, x_{kj}^t)$  is the number of individuals from species  $\ell$  at time  $t$  opting for leaving patch  $j$  and moving to patch  $i$ . Of course  $c_{ii} = 0$  for all  $i = 1, 2, \dots, n$ . Moreover, assumption on the conservation during dispersal implies that  $\sum_{i=1}^n c_{ij} = 1$  for all  $j = 1, 2, \dots, n$ .

Assuming that local dynamics precedes dispersal, we can write the  $nk$  equations describing the dynamics of the whole system in the vector form as

$$\mathbf{x}_i^{t+1} = (I_k - M(\mathbf{f}(\mathbf{x}_i^t)))\mathbf{f}(\mathbf{x}_i^t) + \sum_{j=1}^n c_{ij}M(\mathbf{f}(\mathbf{x}_j^t))\mathbf{f}(\mathbf{x}_j^t), \quad t = 0, 1, 2, \dots, \quad (2)$$

for all  $i = 1, 2, \dots, n$ , where  $M(\mathbf{x}) = \text{diag}(\mu_1(\mathbf{x}), \mu_2(\mathbf{x}), \dots, \mu_k(\mathbf{x}))$   $\mathbf{x} \in \mathbb{R}^k$  is a  $k \times k$  diagonal matrix with entries  $\mu_1, \mu_2, \dots, \mu_k$  along the main diagonal, and  $I_k$  is the  $k \times k$  identity matrix. The first term in the above equation represents the individuals that did not disperse while the second term stands for the contribution of the migrants arriving in the patch.

Let  $\Phi : \mathbb{R}^k \rightarrow \mathbb{R}^k$  defined by  $\Phi(\mathbf{x}) = M(\mathbf{x})\mathbf{x}$ ,  $\mathbf{x} \in \mathbb{R}^k$ . Thus,  $\Phi(\mathbf{x}_j^t)$  is the vector with the number of migrants of each species leaving patch  $j$  at time  $t$  as components. We can write (2) in the form

$$\mathbf{x}_i^{t+1} = \mathbf{f}(\mathbf{x}_i^t) - \sum_{j=1}^n b_{ij}\Phi(\mathbf{f}(\mathbf{x}_j^t)), \quad \forall i = 1, 2, \dots, n, \quad t = 0, 1, 2, \dots, \quad (3)$$

where  $b_{ij}$  are the entries of the matrix  $B = I_n - C$ . Let  $\phi_i : \mathbb{R}^k \rightarrow \mathbb{R}$  be such that  $\Phi(\mathbf{x}) = (\phi_1(\mathbf{x}), \phi_2(\mathbf{x}), \dots, \phi_k(\mathbf{x}))$ ,  $\mathbf{x} \in \mathbb{R}^k$ . The partial derivatives  $\frac{\partial \phi_i}{\partial x_j}$  measure the impact of species  $j$  on the dispersal of species  $i$ , and of course it is a function of the population vector  $\mathbf{x} = (x_1, x_2, \dots, x_n)$ . We say that species  $i$  has a positive (negative) density dependence dispersal with respect to species  $j$  if  $\frac{\partial \phi_i}{\partial x_j} > 0$  ( $\frac{\partial \phi_i}{\partial x_j} < 0$ ) for all  $\mathbf{x} \in \mathbb{R}^k$ . The case  $i \neq j$  refers to the cross-migration response, extensively studied in [7]. The case  $i = j$  refers to a self-regulated dispersal process which is well documented in [30]. The increase of dispersal activity as a response to an increase in local density ( $\frac{\partial \phi_i}{\partial x_j} > 0$ ) may occur because of loss of environmental conditions

due to crowding ([4]). Negative density dependence  $\frac{\partial \phi_i}{\partial x_j} < 0$  corresponds to the opposite situation, where individuals are more apt to leave patches of low density, perhaps in search of sexual partners or to aggregate to increase protection against predators ([16]).

**3. The stability of the homogeneous state.** Let  $\mathbf{x}^* \in \mathbb{R}^k$ ,  $\mathbf{x}^* = (x_1^*, x_2^*, \dots, x_k^*)$  an equilibrium point of the isolated patch model. Let  $\mathbf{X}^* \in \mathbb{R}^{k \times n}$  be the vector composed by  $n$  copies of  $(x_1^*, x_2^*, \dots, x_k^*)$ , thus  $\mathbf{X}^* = (\mathbf{x}^*, \dots, \mathbf{x}^*) \in \mathbb{R}^{k \times n}$ . The vector  $\mathbf{X}^*$  represents the complete homogeneous state in the network of patches, meaning all patches at the same state  $\mathbf{x}^*$ . A simple substitution of  $\mathbf{x}_j^t$  for  $\mathbf{x}^*$  in (2) (or in (3)) leads to  $\mathbf{x}^* = \mathbf{f}(\mathbf{x}^*)$ ,  $i = 1, 2, \dots, n$ , provided  $\sum_{j=1}^n c_{ij} = 1$  ( $\sum_{j=1}^n b_{ij} = 0$ ) for all  $i = 1, 2, \dots, n$ . Therefore, if all lines of  $C$  have the same sum, one, then the homogeneous equilibrium  $\mathbf{X}^*$  is a solution of the metapopulation model (2). From this point on we will assume that condition on matrix  $C$  in order to ensure the existence of the homogeneous equilibrium. In fact,  $C$  is a doubly stochastic matrix with entries not larger than one and zero diagonal. Doubly stochasticity is not a very strong requirement since it is satisfied by any symmetric coupling system with conservation during dispersal.

Once the existence of the homogeneous equilibrium  $\mathbf{X}^*$  is guaranteed, we can study its stability. Standard linearization around  $\mathbf{X}^*$  yields

$$\Delta^{t+1} = J(\mathbf{X}^*)\Delta^t, \quad t \geq 0, \tag{4}$$

where  $\Delta^t \in \mathbb{R}^{kn}$  is the perturbation from the equilibrium  $\mathbf{X}^*$ , and  $J(\mathbf{X}^*)$  is the  $nk \times nk$  Jacobian matrix of system (3) evaluated at  $\mathbf{X}^*$ . Simple calculations allow us to write

$$J(\mathbf{X}^*) = I_n \otimes D\mathbf{f}(\mathbf{x}^*) - B \otimes (D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*)), \tag{5}$$

where  $\otimes$  is the Kronecker product <sup>1</sup>.

We now proceed with a decoupling of the system (4). Assume the configuration matrix  $C$  is diagonalizable. Since  $B = I_n - C$ ,  $B$  is also a diagonalizable  $n \times n$  matrix. Let  $\lambda_1, \lambda_2, \dots, \lambda_n$  be the eigenvalues of  $B$  and let  $\Lambda = \text{diag}(\lambda_1, \lambda_2, \dots, \lambda_n)$ . Therefore, there is an invertible  $n \times n$  matrix  $P$  such that  $\Lambda = PBP^{-1}$ . Making the change of variables  $Y^t = (P \otimes I_k)\Delta^t$  in the system (4), we have

$$\begin{aligned} Y^{t+1} &= (P \otimes I_k)\Delta^{t+1} \\ &= (P \otimes I_n)[I_n \otimes D\mathbf{f}(\mathbf{x}^*) - B \otimes (D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*))]\Delta^t \\ &= [(PI_n) \otimes (I_k D\mathbf{f}(\mathbf{x}^*)) - (PB) \otimes I_k(D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*))]\Delta^t \\ &= [(P \otimes D\mathbf{f}(\mathbf{x}^*)) - (PB) \otimes (D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*))]\Delta^t. \end{aligned} \tag{6}$$

But  $\Delta^t = (P \otimes I_k)^{-1}Y^t = (P^{-1} \otimes I_k)Y^t$ , thus

$$\begin{aligned} Y^{t+1} &= [(PP^{-1}) \otimes (D\mathbf{f}(\mathbf{x}^*)I_k) - (PBP^{-1}) \otimes (D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*)I_k)]Y^t \\ &= [I_n \otimes D\mathbf{f}(\mathbf{x}^*) - \Lambda \otimes (D\Phi(\mathbf{x}^*)D\mathbf{f}(\mathbf{x}^*))]Y^t. \end{aligned} \tag{7}$$

But  $\Lambda = \text{diag}(\lambda_1, \lambda_2, \dots, \lambda_n)$ , therefore

$$Y^{t+1} = \bigoplus_{j=1}^n [I_k - \lambda_j D\Phi(\mathbf{x}^*)]D\mathbf{f}(\mathbf{x}^*)Y^t, \tag{8}$$

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<sup>1</sup>Let  $A = [a_{ij}]_{i,j=1}^m \in \mathbb{R}^{m \times m}$  and  $B = [b_{ij}]_{i,j=1}^n \in \mathbb{R}^{n \times n}$ , the Kronecker product is defined by  $A \otimes B = [a_{ij}B]_{i,j=1}^m \in \mathbb{R}^{mn \times mn}$ .

where  $\bigoplus$  denotes the direct sum or block decomposition of matrices, that is

$$\bigoplus_{i=1}^n A_i = \begin{bmatrix} A_1 & & & \\ & A_2 & & \\ & & \ddots & \\ & & & A_n \end{bmatrix}.$$

A different decoupling technique was employed in [10] in the case of density-independent dispersal (in such case  $D\Phi(\mathbf{x}^*) = M$ ). Their approach groups the states variable as  $n \times k$  matrices instead of using  $nk$  component vectors to store the species numbers in each patch as we do. In essence both approaches are equivalent.

The advantage of the decoupling procedure is clear. Instead of considering the eigenvalues of the  $nk \times nk$  of  $J(\mathbf{X}^*)$  given by the cumbersome expression in (5), we can consider the  $n$  simples  $k \times k$  matrices  $[I_k - \lambda_j D\Phi(\mathbf{x}^*)]D\mathbf{f}(\mathbf{x}^*)$ ,  $j = 1, 2, \dots, n$ .

Notice that 1 is an eigenvalue of the configuration matrix  $C$  and thus,  $\lambda_1 = 0$  is an eigenvalue of  $B$ . Consequently, one of the blocks in the decomposition of  $J(\mathbf{X}^*)$  is necessarily  $D\mathbf{f}(\mathbf{x}^*)$ , which implies the well-known result ([20]) saying that dispersal alone cannot stabilize a system of  $n$  equal patches that would display unstable behavior in the absence of movement between patches. On the other hand, dispersal can lead to loss of stability of the homogeneous state thereby leading to spatial patterns. Pattern formation can arise in two different ways. When dispersal is density-independent it requires more than one species interacting ([20]). The heterogeneous patterns observed ([20], [21]) arise through a mechanism first described by Turing [29]. When dispersal is density-dependent, pattern formation generated by dispersal can appear even in an unstructured single species metapopulation model ([25]). The mechanism that gives rise to the loss of stability of the homogeneous state is quite different than the one proposed by [29]. In this case, the stability of the homogeneous equilibrium is lost because of overshooting caused by excessive rate of change in migrants when the patch density is near the equilibrium ([25]).

The decoupling result states in (8) can be applied to a variety of situations. We have used the term species so far simply for the clarity of the argument. In fact, what is needed is a local autonomous dynamical system with  $k$  state variables. These  $k$  state variables can represent real species density or age class density. In the next sections we will present two different examples of such models.

**4. Hierarchical local model.** Assume the local dynamics in each patch is given by an hierarchical model satisfying the following property. There is a ranking scheme in the set of  $k$  species organizing the species from the most dominant (rank 1) to the least dominant (rank  $k$ ) in such way that, given a certain species (rank  $\ell$ ), its local dynamics depend only on its own density and on the densities of the species that are more dominant in the ranking scheme  $(1, 2, \dots, \ell - 1)$ . In this way species one depends only on species one, species two depends only on species two and species one, and so forth. Such models have been considered in [1]. Recall that  $\mathbf{f} : \mathbb{R}^k \rightarrow \mathbb{R}^k$  describes the local dynamics in each patch. Let  $f_i : \mathbb{R}^k \rightarrow \mathbb{R}$ ,  $i = 1, 2, \dots, k$ , be such that  $\mathbf{f}(\mathbf{x}) = (f_1(\mathbf{x}), f_2(\mathbf{x}), \dots, f_k(\mathbf{x}))$ ,  $\forall \mathbf{x} \in \mathbb{R}^k$ . The hierarchical organization implies that  $f_1$  depends only on  $x_1$ ,  $f_2$  depends only on  $x_1$  and  $x_2$ , and so forth. Thus the Jacobian matrix  $D\mathbf{f}(\mathbf{x}^*)$  is a lower triangular  $k \times k$  matrix.

We will assume that the same hierarchical organization holds with respect to dispersal. Therefore the  $k \times k$  matrix  $D\Phi(\mathbf{x}^*)$  is lower triangular. The simplicity of

the matrices  $[I_k - \lambda_j D\Phi(\mathbf{x}^*)]Df(\mathbf{x}^*)$ ,  $j = 1, 2, \dots, n$ , allows the easy calculation of its eigenvalues  $\xi_{ij}$ ,  $i = 1, \dots, k$ ,  $j = 1, 2, \dots, n$  given by

$$\xi_{ij} = \left(1 - \lambda_j \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)\right) \frac{\partial f_i}{\partial x_i}(\mathbf{x}^*). \tag{9}$$

The stability region of the homogeneous equilibrium is determined by the condition  $|\xi_{ij}| < 1$  for all  $i = 1, \dots, k$ ,  $j = 1, 2, \dots, n$ . Assume that in the absence of density-dependent effects the emigration is symmetric. This means that the net configuration matrix  $C$  is symmetric and so is  $B = I_n - C$ . Thus,  $B$  has real eigenvalues. Moreover, a simple application of the Gershgorin theorem allows us to say that the spectrum of  $B$  is contained in the interval  $[0, 2]$ . Let  $\gamma$  be the largest eigenvalue of  $B$ , that is  $\gamma = \max_{\{i=1,2,\dots,n\}} \lambda_i$ . It is not difficult to see that

$$\max_{\{j=1,\dots,n\}} \left|1 - \lambda_j \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)\right| = \begin{cases} \left(1 - \gamma \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)\right), & \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) < 0, \\ 1, & 0 \leq \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) \leq \frac{2}{\gamma}, \\ \left(\gamma \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) - 1\right), & \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) > \frac{2}{\gamma}. \end{cases} \tag{10}$$

Thus (9) and (10) imply that

$$|\xi_{ij}| < 1 \text{ for all } \begin{matrix} i = 1, \dots, k, \\ j = 1, \dots, n \end{matrix} \Leftrightarrow \begin{cases} \left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| \left(1 - \gamma \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)\right) < 1, & \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) < 0, \\ \left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| < 1, & 0 \leq \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) \leq \frac{2}{\gamma}, \\ \left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| \left(\gamma \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) - 1\right) < 1, & \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) > \frac{2}{\gamma}. \end{cases} \tag{11}$$

In this way we obtained the stability region of the homogeneous equilibrium in terms of  $\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)$  and  $\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)$ ,  $i = 1, 2, \dots, k$ .

In order to detect instabilities induced by dispersal we assume the local equilibrium  $\mathbf{x}^*$  to be stable, that is, all the eigenvalues of  $Df(\mathbf{x}^*)$  have modulus less than one. But since  $Df(\mathbf{x}^*)$  is lower triangular it is equivalent to say  $\max_{\{i=1,\dots,k\}} \left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| < 1$ . Figure 1 shows the projection of the stability region for species  $i$  given by (11)

with the imposition of the condition  $\left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| < 1$ . The internal region (white) corresponds to the stability of the homogeneous state while the external region (gray) corresponds to instability caused by dispersal. Notice that in order to have dispersal driven instability it is sufficient to have the system parameters controlling  $\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)$ , and  $\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)$  be such that the ordered pair  $\left(\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*), \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)\right)$  is in the gray region for some  $i$ . In order to have instabilities caused by dispersal we need at least one of the two processes (local dynamics and dispersal) to have a severe nonlinearity in at least one of the species. Since we impose  $\max_{\{i=1,\dots,k\}} \left|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)\right| < 1$ ,

a sufficiently large value of  $\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)$  will drive the system in to the homogeneously unstable dynamics. Notice that there are bounds for  $\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*)$  that can guarantee the stability of the homogeneous stable. It is clear that if  $0 < \frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) < \frac{2}{\gamma}$  for each species  $i = 1, 2, \dots, k$ , then  $\mathbf{X}^*$  is stable. The constant  $\frac{2}{\gamma}$  depends only on the net configuration matrix and clearly satisfies  $\frac{2}{\gamma} > 1$ . It is interesting to notice that if

$\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) > \frac{2}{\gamma}$  or  $\frac{\partial \phi_i}{\partial x_i}(\mathbf{x}^*) < 0$  for some  $i$ , its is possible to adjust the value of  $\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)$  (keeping the restriction  $|\frac{\partial f_i}{\partial x_i}(\mathbf{x}^*)| < 1$ ) to drive the system in the gray region of Figure 1.

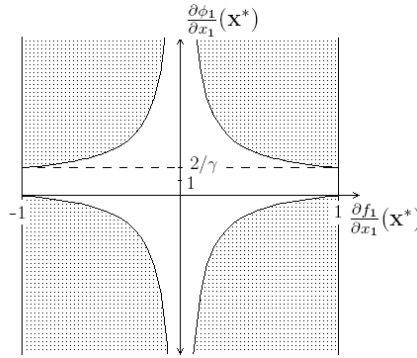


FIGURE 1. Instability region driven by density-dependent dispersal (gray region). The white region corresponds to the stability region for the equilibrium point  $\mathbf{x}^*$ .

Inside the region of instability driven by dispersal, the dynamics can be very rich, including other stable equilibrium, periodic points, and even chaotic oscillations. We have performed some simulations with a two species patch model coupled with the two nearest neighbors in a ring of  $n$  patches. We have considered the local dynamics to be given by

$$\begin{cases} x_1^{t+1} = x_1^t e^{r_1(1-x_1^t)} \\ x_2^{t+1} = x_2^t e^{r_2(1-\alpha x_1^t-x_2^t)}, \end{cases} \tag{12}$$

where  $r_1, r_2 > 0$  are the intrinsic rate of increase of species one and two respectively, and  $0 < \alpha < 1$  measures the impact of species one on species two. It is easy to see that the above competing system has four points of equilibrium:  $(0, 0), (0, 1), (1, 0)$ , and  $(1, 1 - \alpha)$ . The first three are unstable, while coexistence equilibrium point  $(1, 1 - \alpha)$  is linearly stable if and only if  $0 < r_1 < 2$ , and  $0 < r_2 < \frac{2}{1-\alpha}$ . Assume  $r_1, r_2$  and  $\alpha$  satisfy the last condition, which ensures the stability of the local model. Assume no cross-dispersal effects. The only density-dependent in the dispersal process is expressed by

$$\mu_i(x_i) = \frac{\bar{\mu}}{1 + e^{\beta(1-x_i)}}, \tag{13}$$

where  $0 \leq \bar{\mu} \leq 1$  is the maximum dispersal fraction, and  $\beta$  is a parameter regulating shape of the curve (see Figure 2), which also measures the strength of the density-dependent effects. Notice that  $\beta = 0$  corresponds to the case of density-independent dispersal. This functional formulation is adapted from [30]. The limit cases  $\beta \rightarrow +\infty$  and  $\beta \rightarrow -\infty$  describe the case studied in [26] where dispersal is triggered by a critical density.

In Figure 3 we illustrate the instability driven by dispersal by showing the time series of species two after disregarding some transients. In Figure 3 (a), we show a stable period four solution. In Figure 3 (b) we see a chaotic oscillation. Chaotic solutions are detected by computing the largest Liapunov number of the system (3). This was done for a ring with three patches, and the results are shown in Figure 4.

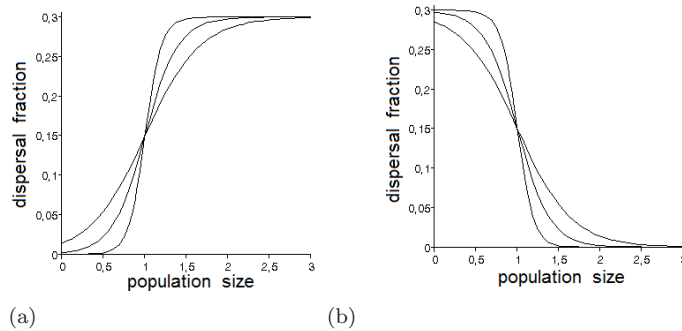


FIGURE 2. (a)  $\beta > 0$ , (b)  $\beta < 0$ .

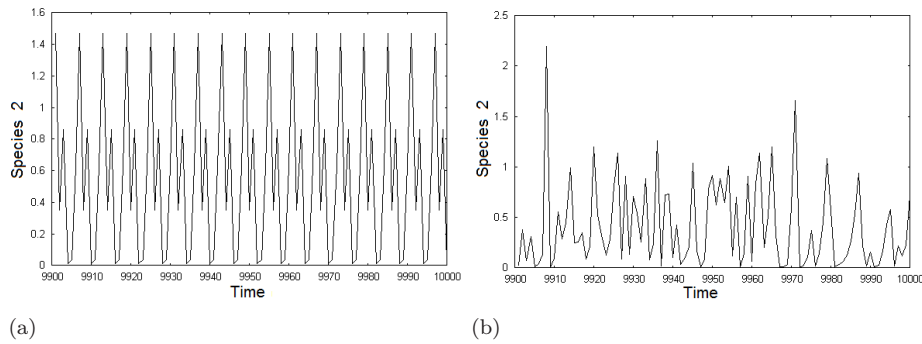


FIGURE 3. Time series of species versus time. Ring with five patches. (a)  $r_1 = 0.05, r_2 = 3.0095, \alpha = 0.6, \beta = 100$  and  $\bar{\mu} = 0.99$ ; (b)  $r_1 = 1.25, r_2 = 3.95, \alpha = 0.6, \beta = 75$  and  $\bar{\mu} = 0.99$ .

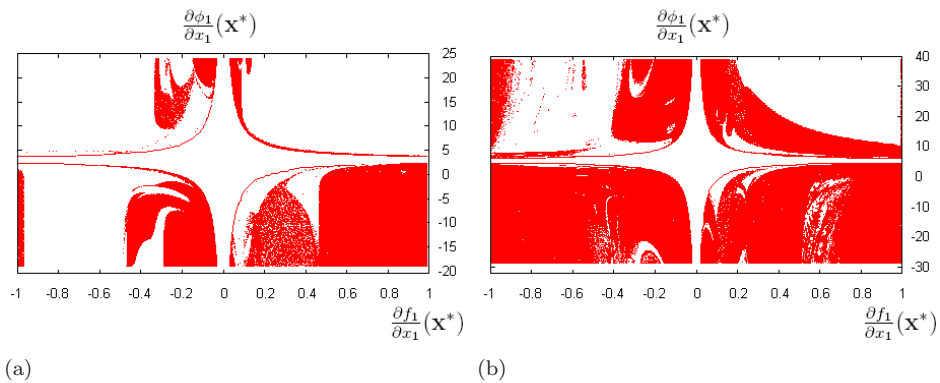


FIGURE 4. Chaotic region. Ring with three patches,  $r_2 = 3.0095$ . (a)  $\bar{\mu} = 0.43$ , (b)  $\bar{\mu} = 0.9$ .

There we plot the projection of the stability region (internal white) for species one exactly as in Figure 1. The difference is that now the region outside (corresponding



to the stability driven by dispersal) the white region is shaded if for that corresponding values of  $\frac{\partial f_1}{\partial x_1}(\mathbf{x}^*)$ , and  $\frac{\partial \phi_1}{\partial x_1}(\mathbf{x}^*)$  the metapopulation system given in (3) has a Liapunov number larger than one. Thus, that region represents the chaotic dynamics induced by dispersal. The strength of coupling (usually measured by the dispersal fraction  $\mu$  in density-independent dispersal models) is usually associated with a more stable and homogeneous dynamics. In our case, the parameter  $\bar{\mu}$  can be a measure of coupling. Strength in coupling acts in favor of spatial heterogeneities. But in this case (see Figs. 4(a) and 4(b)), the amount of coupling acts in favor of spatial heterogeneities.

Dispersal induced instabilities lead to pattern formations as shown in Figure 5, where we have space-time plots. The patches are along the vertical axis (in the following order:  $x_{11}^t, x_{21}^t, x_{12}^t, x_{22}^t, \dots, x_{1n}^t, x_{2n}^t$ ), while the time is along the horizontal axis. The evolution of the system is followed, transients are thrown away, and if the local density is above the local equilibrium the position  $(t, \ell)$  is painted black, otherwise it is painted white.

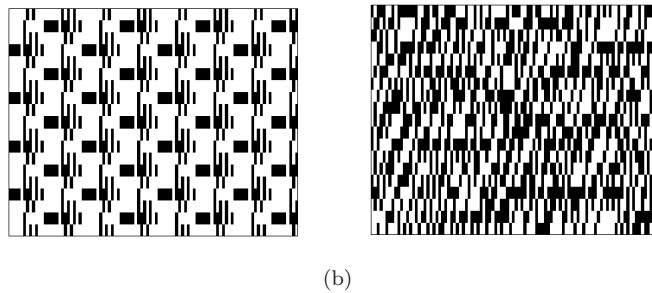


FIGURE 5. Space-time plots for a ring with ten patches,  $\alpha = 0.6$ . (a)  $r_1 = 0.5$ ,  $r_2 = 3.95$ ,  $\bar{\mu} = 0.99$  and  $\beta = 100$ , (b)  $r_1 = 1.05$ ,  $r_2 = 3.0095$ ,  $\bar{\mu} = 0.99$  and  $\beta = -100$ .

**5. An age-structured metapopulation.** In this section we study a single species age-structured metapopulation model. We assume the isolated patch model to be a special case of the class of nonlinear Leslie type models studied in [27] and [28]. The local population is divided into  $k$  age classes of same duration, precisely, one time step. Let  $p_i$ ,  $i = 1, 2, \dots, k - 1$  be the density-independent transition probability of age class  $i$  at time  $t$ . Thus,

$$x_i^{t+1} = p_{i-1}x_{i-1}^t, \quad i = 2, \dots, k. \tag{14}$$

The nonlinearity is present only in an inferior class (eggs and/or larvae) whose population at time  $t$  is denoted by  $w^t$ . The precise mathematical formulation of  $w^t$  depends on the age-specific fertilities  $g_i$ ,  $i = 1, \dots, k$ , and it is expressed as

$$w^t = \sum_{i=1}^k g_i x_i^t. \tag{15}$$

The nonlinearity reflects a density-dependent recruitment process in the inferior class. The individuals of the first age class (new recruits) are expressed as

$$x_1^{t+1} = q(w^t)w^t, \tag{16}$$

where  $q(w^t)$  is the probability of surviving this stage. The recruitment survival probability is modeled by a  $C^1$  function  $q : \mathbb{R} \rightarrow [0, 1]$  satisfying the following properties

- (i)  $q(0) = 1$ ;
- (ii)  $\lim_{x \rightarrow \infty} q(x) = 0$ ;
- (iii)  $q'(x) < 0, \forall x > 0$ .

A popular example is to take  $q(x) = e^{-\alpha x}$ ,  $\alpha > 0$  obtaining the celebrated Ricker recruitment (see [14]). The above properties of the function  $q$  reflect the effect of the intra-specific competition during the egg-larvae stage. Equations (14)-(16) completely describe the local dynamical system.

The elasticity of the recruitment survival probability  $E(w)$  is defined by

$$E(w) = \frac{-wq'(w)}{q(w)}. \quad (17)$$

It expresses the ratio of relative (or percent) change in the recruitment survival probability to the relative change in population density. Notice that, writing the number of recruits  $R$  when the population of individuals in the egg-larvae stage is  $w$  by  $R(w)$ , we can write

$$R(w) = wq(w). \quad (18)$$

Thus

$$\frac{R'(w)}{q(w)} = 1 - E(w). \quad (19)$$

Therefore

$$R'(w) > 0 \Leftrightarrow E(w) < 1. \quad (20)$$

That is, the number of recruits increases if and only if the elasticity of the recruitment survival is less than one. It is important to define  $l_i = \prod_{j=1}^{i-1} p_j$ ,  $i = 2, \dots, k$  as the density-independent probability of an individual to reach age class  $i$ . Of course  $l_1 = 1$ . As usual  $R_0 = \sum_{i=1}^k g_i l_i$  is the basic reproductive number, that is, the number of new individuals generated by an average individual during its entire life. The age-specific fertility distribution is defined by  $m_i = \frac{g_i l_i}{R_0}$ ,  $i = 1, 2, \dots, k$ .

In the absence of dispersal, the dynamical system described above has two equilibria ([27]). The trivial equilibrium  $\mathbf{0} = (0, 0, \dots, 0)$  and the positive equilibrium  $\mathbf{x}^* = w^* q(w^*) (l_1, l_2, \dots, l_k)$ , where  $w^* > 0$  is the unique solution of the equation  $q(w^*) = \frac{1}{R_0}$ . Notice that the  $i^{\text{th}}$  component  $\mathbf{x}^*$  is precisely  $R(w^*) l_i$ , that is the number of recruits at equilibrium multiplied by the probability of arriving alive at age class  $i$ . Clearly, if  $R_0 < 1$ , only the trivial equilibrium exists. When  $R_0 > 1$  the unique positive equilibrium is well defined. The critical value  $R_0 = 1$  is a bifurcation point ([27]). A simple argument can be used (see [3]) to show that if  $H = E(w^*) < 2$ , then  $\mathbf{x}^*$  is stable, for any choice of  $m_i = 1, 2, \dots, k$ . The elasticity at equilibrium  $H = E(w^*)$  can be thought of as a measure of the reproductive power of the population; in fact, choosing  $q(x) = e^{-\alpha x}$ ,  $\alpha > 0$  (Ricker recruitment) allows us to say that  $H = \ln R_0$ .

Now we consider a network of  $n$  patches with an age structured population model discussed above. As in the previous section, we will assume symmetric interactions, thus the network configuration matrix  $C$  is supposed to be symmetric. We will also suppose no cross-emigration responses, that is, the dispersal fraction of age  $i$ ,  $\mu_i$ , depends only on the density of species  $i$ . Taking this in consideration, then  $k \times k$

matrix  $D\Phi(\mathbf{x}^*)$  is a diagonal matrix. Simple calculations lead to the expression for the  $k \times k$  blocks  $(I_k - \lambda_j D\Phi(\mathbf{x}^*))Df(\mathbf{x}^*) =$

$$\begin{bmatrix} \left(1 - \lambda_j \frac{\partial \phi_1}{\partial x_1}\right) g_1 R'(w^*) & \left(1 - \lambda_j \frac{\partial \phi_1}{\partial x_1}\right) g_2 R'(w^*) & \cdots & \cdots & \left(1 - \lambda_j \frac{\partial \phi_1}{\partial x_1}\right) g_k R'(w^*) \\ \left(1 - \lambda_j \frac{\partial \phi_2}{\partial x_2}\right) p_1 & & & & \\ & \left(1 - \lambda_j \frac{\partial \phi_3}{\partial x_3}\right) p_2 & & & \\ & & \ddots & & \\ & & & & \left(1 - \lambda_j \frac{\partial \phi_k}{\partial x_k}\right) p_{k-1} \end{bmatrix}.$$

The above matrix is of Leslie type, therefore it is easy to get the characteristic equation satisfied by its eigenvalues  $\sigma_1, \sigma_2, \dots, \sigma_k$  ([27])

$$R'(w^*) \sum_{i=1}^k \frac{\tilde{l}_{ij} \tilde{g}_{ij}}{\sigma^i} = 1, j = 1, \dots, n, \tag{21}$$

where

$$\tilde{g}_{ij} = \left(1 - \lambda_j \frac{\partial \phi_1}{\partial x_1}(x_1^*)\right) g_i, i = 1, 2, \dots, k, \tag{22}$$

$$\begin{cases} \tilde{l}_{1j} = 1, \\ \tilde{l}_{\ell j} = \prod_{i=2}^{\ell} \left(1 - \lambda_j \frac{\partial \phi_i}{\partial x_i}(x_1^*)\right) l_i, \quad \ell = 2, \dots, k, j = 1, \dots, n. \end{cases} \tag{23}$$

Dividing (21) by  $\frac{R'(w^*)}{g(w^*)}$  and writing  $\tilde{m}_{ij} = \frac{\tilde{l}_{ij} \tilde{g}_{ij}}{R_0}$ , the characteristic equation of the  $j$ -block takes the form

$$\sum_{i=1}^k \frac{\tilde{m}_{ij}}{\sigma^i} = \frac{1}{1 - H}, j = 1, \dots, n, \tag{24}$$

where  $H = E(w^*)$  is the elasticity at the equilibrium.

Suppose  $0 \leq \frac{\partial \phi_i}{\partial x_i}(x_1^*) \leq \frac{2}{\gamma}$ , for all  $i = 1, 2, \dots, k$ , where  $\gamma$  is as in the previous section. It follows that  $\left|1 - \lambda_j \frac{\partial \phi_i}{\partial x_i}(x_1^*)\right| \leq 1$ . Thus

$$|\tilde{m}_{ij}| = \left|\frac{\tilde{g}_{ij} \tilde{l}_{ij}}{R_0}\right| = \frac{1}{R_0} \left[\prod_{\ell=1}^i \left|1 - \lambda_j \frac{\partial \phi_\ell}{\partial x_\ell}(x_1^*)\right|\right] g_i l_i \leq \frac{g_i l_i}{R_0} = m_i, \tag{25}$$

$i = 1, \dots, k, j = 1, \dots, n$ . Let  $e^{a+ib}$  be an arbitrary eigenvalue of the  $j$ -block in the decomposition (8), then if  $H < 2$  (notice that by definition  $H > 0$ ) the equation (24) allows us to write

$$\left|\sum_{\ell=1}^k \tilde{m}_{\ell j} e^{-\ell a - i \ell b}\right| = \left|\frac{1}{1 - H}\right| > 1. \tag{26}$$

Now (25) and (26) imply

$$\left|\sum_{\ell=1}^k \tilde{m}_{\ell j} e^{-\ell a - i \ell b}\right| \leq \sum_{\ell=1}^k m_\ell e^{-\ell a}. \tag{27}$$

Thus  $\left|\sum_{\ell=1}^k m_\ell e^{-\ell a}\right| > 1$ . But  $\sum_{\ell=1}^k m_\ell = 1$ , then we must have  $e^{-a} > 1$ , which implies  $|e^{a+ib}| = e^a < 1$ . Summarizing, if  $H < 2$  and  $0 \leq \frac{\partial \phi_i}{\partial x_i}(x_1^*) \leq \frac{2}{\gamma}, i = 1, 2, \dots, k$ , then

the homogeneous equilibrium  $\mathbf{X}^*$  is stable for any choice of age-specific fertility distribution  $m_i$ ,  $i = 1, 2, \dots, k$ . This extends the results obtained in [3] for the case of density-dependent dispersal.

In the case when  $0 < H < 2$  and the above restrictions for  $\frac{\partial \phi_i}{\partial x_i}(x_i^*)$  are not valid, the density-dependent migration can induce instabilities. In fact, if we consider only two age classes, variations of the parameter  $\beta$  induce the existence of periodic attractors lead to quasi-periodic attractors. This phenomenon is illustrated in Figures 6(a) and 6(b) for  $\beta = -22.05$  and  $\beta = -23$ , respectively. It is important to recall that the negative values for  $\beta$  correspond to the density-dependent migration function illustrated in Figure 2(b). The transition point between the stable equilibrium point and the periodic cycle occurs for some value  $\beta^* \in (-20, -19.9)$ .

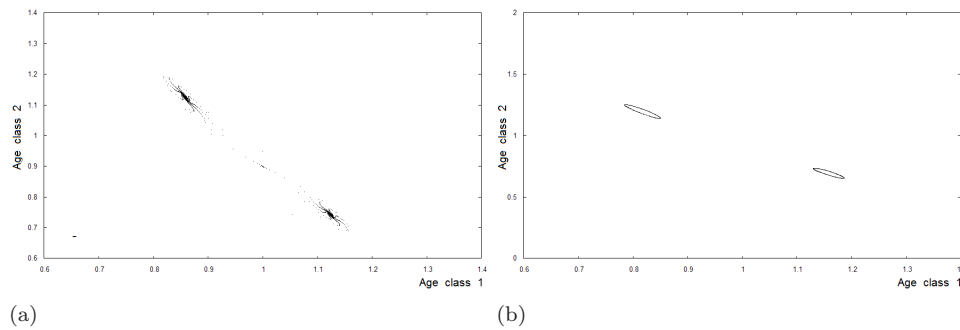


FIGURE 6. Phase portrait for a ring with three patches. Parameters:  $g_1 = 3$ ,  $g_2 = 1$ ,  $\bar{\mu}_1 = 0.8$ ,  $\bar{\mu}_2 = 0.3$  and with (a)  $\beta = -22.05$ , (b)  $\beta = -23$ .

In Figure 7 we show space-time plots illustrating the pattern formation in the case of quasi-periodic attractors (Fig. 7(a)); chaotic behavior is shown in Figure 7(b).

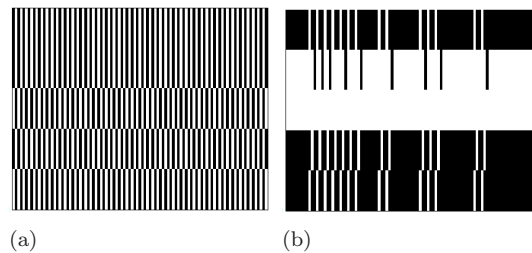


FIGURE 7. Space-time plots for a ring with three patches. Parameters:  $g_1 = 3$ ,  $g_2 = 1$ ,  $\bar{\mu}_1 = 0.8$ ,  $\bar{\mu}_2 = 0.3$  and with (a)  $\beta = -23$ , (b)  $\beta = 47$ .

Considering the case of only two age classes, say juveniles and adults, we will be able to obtain the exact stability region of the homogeneous equilibrium and imposing the stability of the isolated age class model we will be able to obtain the region of instability caused by the dispersal. In addition, we will assume that only

the juveniles can disperse, that is,  $\mu_2 = 0$ . The characteristic polynomial  $p_j(\sigma)$  of the  $j$ -block decomposition is calculated using (24) is

$$p^j(\sigma) = \sigma^2 - \frac{(1-H)}{R_0} \left( 1 - \lambda_j \frac{\partial \phi_1}{\partial x_1}(x_1^*) \right) (g_1 \sigma + g_2 p_1). \tag{28}$$

We consider three interesting cases. Routine calculations using the polynomials given in (28) allow us to obtain the stability boundary curves in each case. In Figure 8(a) we consider the case  $0 < m_1 \leq \frac{2}{3}$  and the boundary stability curves are given by  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 - \frac{1}{1-H} \right)$ ,  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 + \frac{1}{(1-m_1)(1-H)} \right)$ ,  $H = 0$  and  $H = 1 + \frac{1}{1-m_1}$ . In the case of  $\frac{2}{3} < m_1 < 1$  the stability region is delimited

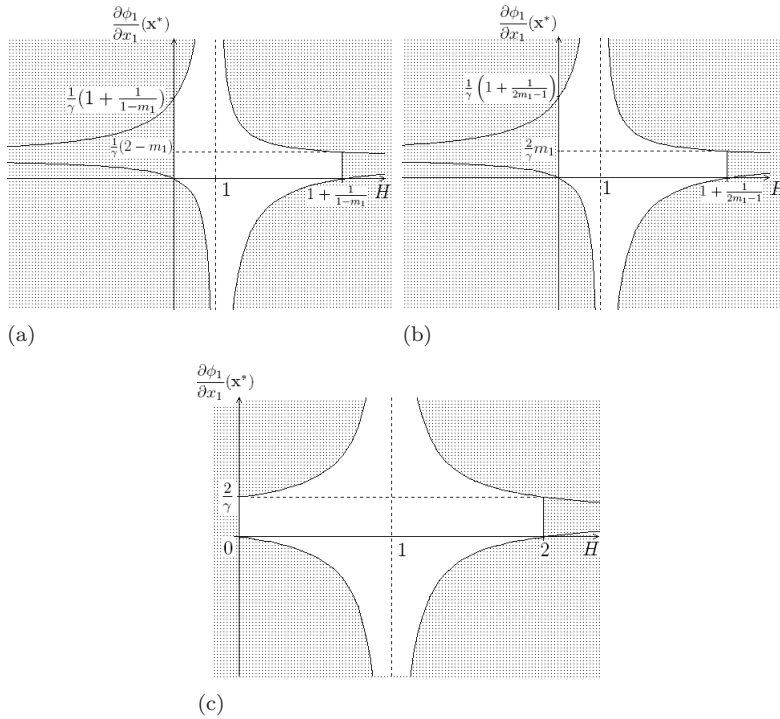


FIGURE 8. Stability region (white region) for the equilibrium point in the case of a age structured model. The gray region corresponds to the instability region, driven by density-dependent dispersal. (a)  $0 < m_1 \leq \frac{2}{3}$ ; (b)  $\frac{2}{3} < m_1 < 1$  and (c)  $m_1 = 1$ .

by the curves  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 - \frac{1}{1-H} \right)$ ,  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 - \frac{1}{(1-2m_1)(1-H)} \right)$ ,  $H = 0$  and  $H = 1 - \frac{1}{1-2m_1}$  (see Figure 8(b)). Figure 8(c) shows the stability region in the case of  $m_1 = 1$ , the boundary curves are given by  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 - \frac{1}{1-H} \right)$  and  $\frac{\partial \phi_1}{\partial x_1}(x_1^*) = \frac{1}{\gamma} \left( 1 + \frac{1}{1-H} \right)$ .

**6. Discussion.** Analytic treatment of multiple-species metapopulation with non-linear coupling can be a very difficult task. Even under some simplifying assumptions such as the lack environmental heterogeneity, that is, all patches have the

same quality with respect to local dynamics and dispersal (local dynamics is given by the function  $\mathbf{f}$  and the dispersal fraction of species is given by the function  $\mu_i$ , independently of the patch location), the mathematical treatment can be difficult. The decomposition of the Jacobian matrix associated with the homogeneous equilibrium is an essential tool allowing the study of the instabilities induced by density-dependent dispersal leading to pattern formation. This technique can also be useful in the study of synchronization in multiple species metapopulations (e.g., [15]). We studied two types of local  $k$ -species system, a hierarchically organized community (after Best et al. [1]) and a single species age structured population with  $k$  age classes and nonlinear recruitment (proposed in Silva & Hallam [27], [28]). In both cases self-dispersal response was shown to act in favor of pattern formation. In the hierarchically organized community we allow cross-dispersal effects according to the hierarchy. It was shown that the cross-dispersal effects have no influence in the process behind the loss of stability of the homogeneous state. It is interesting to observe that if the hierarchy is not present in the  $k$ -species community, then cross-dispersal effects are very important in the process of pattern formation (Huang and Diekmann [7]). In the case of the age-structured local model, we assumed no cross-dispersal effects in order to allow the analytic treatment in full generality. With this assumption the  $k \times k$  matrices appearing in the decomposition of the Jacobian matrix of the metapopulation system evaluated at the homogeneous equilibrium are of Leslie type. This allows the ideas developed in Silva & Hallam [27] and further explored in De Castro et al. [3] to be applied. It is important to make a distinction between instability induced by density-independent dispersal in multiple species metapopulation (as in Rohani & Ruxton [21], or Hastings [6]) and the heterogeneities induced by a density-dependent process. In the first case the nonlinearities in the local model are averaged over all species producing a stable dynamics. But there are localized stronger nonlinear effects that are hidden when dispersal is not considered. When there is an uneven distribution of dispersal effectiveness among the species, these hidden nonlinearities can lead the system to instability through a mechanism first explained in Turing [29] (see also [17]). In the second case the mechanism is relatively simpler. It is not necessary to have more than one species in each patch ([25]). The loss of stability of the previously stable local system happens through a mechanism of overshooting the equilibrium caused by excessive number of migrants when the local population is near the equilibrium.

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