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## Stability in an age-structured metapopulation model

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**Abstract.** We present a discrete model for a metapopulation of a single species with overlapping generations. Based on the dynamical behavior of the system in absence of dispersal, we have shown that a migration mechanism which depends only on age can not stabilize a previously unstable homogeneous equilibrium, but can drive a stable uncoupled system to instability if the migration rules are strongly related to age structure.

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### 1. Introduction

In a great variety of species reproduction, survival and movement can be strongly correlated with age. Discrete time age structured models have received much attention since the pioneering work of Leslie. An useful review of these models is presented in Caswell [4] while some fundamental questions such as stability, bifurcations, oscillations and other dynamic features were investigated by Cushing [5], Levin and Goodyear [18], Silva and Hallam [24, 25], Wilkan and Mjøllhas [26]. But despite the inclusion of reproduction and survival depending on age and density-dependent mechanisms of regulation these models lack an essential feature: dispersal.

During the past few years there has been a growing interest in studies of population models that include spatial movement. An interesting overview of the subject was presented in Hanski and Gilpin [8]. A spatially explicit metapopulation model or simply metapopulation model consists of a model where space and time are discrete and the whole population is divided in isolated patches where reproduction and survival takes place. These patches are surrounded by a hostile environment. Migration between nearby patches may occur either before or after the reproduction. The role of migration in metapopulation dynamics have been extensively studied, e.g., Hastings [14], Lloyd [19], and Doebeli [7] who argued that dispersal can simplify the ensemble dynamics. Dispersal was shown to be correlated with persistence in linked host-parasitoid models [11], persistence in single species metapopulation models [1], and co-existence in linked systems of competing species [12]. Rohani et al. [21]

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have shown that migration plays no role in the stability of the homogeneous state in single species metapopulation models provided it is density-independent. The irrelevance of dispersal in metapopulation stability has to be interpreted with care since the result is no longer true in multiple species systems as shown in [22] where migration induced instability was shown to be responsible for pattern formation in a host-parasitoid linked population systems. Pattern formation can also appear in single-species metapopulations when migration is density-dependent [23].

Although the models mentioned in the last paragraph address an important issue which is the role dispersion in population dynamics they still may receive criticism for they do not allow age to be responsible for triggering the migratory movements. An exception was the model presented by Hastings [13] where a single species model with age structure is studied. In a simple 2-patch model with density-dependent fertilities he assumed that dispersal is age-dependent to show that spatial heterogeneities can arise if the dispersal rates vary significantly among the age classes, for example, if juveniles have low dispersal rates in comparison with the adults or vice-versa.

In this paper we present a general setting for a single species, age-structured metapopulation model; by first presenting a general setting for an age-structured single patch model. In section 4 we show how the classic Leslie model fits in our setting, and we study the stability properties of such linear model; since much of it is used later, in section 5, when we present a nonlinear model, by adding density-dependent recruitment. On both linear and nonlinear examples, some common features are observed between the single patch model and the global model. In section 6 we show how the instability caused by dispersal can arise. Comments and discussion are presented in section 7.

## 2. Single Patch model

We start by presenting the general single patch model setting used in this paper. For the sake of simplicity, we consider age and time intervals to be equal in length, using  $t = 1, 2, 3, \dots$  for time and  $i = 1, 2, \dots, N$  for marking the age classes. Let  $F : \mathbb{R}^N \rightarrow \mathbb{R}^N$  be a function describing the local population dynamics. Next time step population vector at site  $j$  is

$$\mathbf{x}_{t+1} = F(\mathbf{x}_t) \quad (1)$$

where  $\mathbf{x}_t = (x_t^1, \dots, x_t^N)^T$ , with  $x_t^k$  representing the population in age class  $k$  during time  $t$ .

## 3. Metapopulation model

For the general metapopulation model, we consider a landscape composed of  $n$  identical patches, labeled as  $1, 2, \dots, n$ , connected by migratory movements. Each site is the habitat for an age-structured population, with dynamics described by equation (1) in absence of dispersal, which will be sometimes referred as local population. We consider that, in each time step, after the local dynamics, modeled by a function  $F$  as in the single patch model, takes place; a migration process starts in each site.

Such migration process is modeled as follows: a fraction  $\mu_k$  of the individuals of age class  $k$  from a given site  $i$  emigrates to other sites. The percent of these individuals that emigrate from this site  $i$  to a given site  $j$  is  $a_{ij}$ ; in other words, a fraction  $a_{ij}\mu_k$  of the individuals of age class  $k$  from a given site  $i$  migrates from site  $i$  to site  $j$ . The matrix  $A$  defined this way is called the connectivity matrix. Clearly,  $a_{jj} = 0$  and  $\sum_{j=1}^n a_{ij} = 1$  for all  $i = 1, 2, \dots, n$ . If we denote the population vector at the site  $j$  by  $\mathbf{x}_t^j = (x^{1j}, \dots, x^{Nj})^T$ , with  $x_t^{kj}$  representing the population in age class  $k$  at site  $j$  during time  $t$ , the metapopulation model can be written as

$$\mathbf{x}_{t+1}^j = (\mathbf{I} - \mathbf{M})F(\mathbf{x}_t^j) + \sum_{i=1}^n a_{ij}MF(\mathbf{x}_t^i) \quad (2)$$

where  $\mathbf{M} = \text{diag}(\mu_1, \mu_2, \dots, \mu_N)$ ;  $0 \leq \mu_k \leq 1, k = 1, 2, \dots, N$ .

Defining  $\mathbf{B} = \mathbf{A} - \mathbf{I}$ , equation (2) can be rewritten as

$$\mathbf{x}_{t+1}^j = F(\mathbf{x}_t^j) + \sum_{i=1}^n b_{ij}MF(\mathbf{x}_t^i). \quad (3)$$

Observe that  $\sum_{j=1}^n b_{ij} = 0$  for all  $i = 1, 2, \dots, n$ . Therefore  $\lambda = 0$  is an eigenvalue of the matrix  $\mathbf{B}$  associated with the eigenvector  $[1, 1, \dots, 1]^T$ . Let  $\lambda_1, \lambda_2, \dots, \lambda_n$  be the eigenvalues of  $\mathbf{B}$ , with  $\lambda_1 = 0$  being the eigenvalue mentioned above. By a straightforward application of Gershgorin's Theorem [17], we have that all eigenvalues of  $\mathbf{B}$  are in the disk centered at  $z = -1$  with radius 1 in the complex plane, i.e.,  $\lambda_j \in \{\lambda \in \mathbb{C} : |\lambda + 1| \leq 1\}$ . If we further assume that  $\mathbf{B}$  is symmetric, this reads as  $-2 \leq \lambda_j \leq 0$ .

Equation (3) can be rewritten in matrix form as

$$\mathbf{X}_{t+1} = \Phi(\mathbf{X}_t) + \mathbf{M}\Phi(\mathbf{X}_t)\mathbf{B}, \quad (4)$$

where  $\mathbf{X}_t = [\mathbf{x}_t^1, \dots, \mathbf{x}_t^j, \dots, \mathbf{x}_t^n]$  is the now the population matrix and  $\Phi(\mathbf{X}_t) = [F(\mathbf{x}_t^1), \dots, F(\mathbf{x}_t^j), \dots, F(\mathbf{x}_t^n)]$  is the operator responsible for the local dynamics.

#### 4. A Linear Model

As an example of a linear model within the general setting presented, consider a female dominant species, such that the males density does not need to be taken into consideration. This model will consider two basic processes: survival and reproduction. Survival consists in the passage of an individual for the next age class, and it is characterized by the survival probability  $p_i$ ,  $0 < p_i \leq 1, i = 1, 2, \dots, N$ , which represent the probability of a female in age class  $i$  reach the age class  $i + 1$ . Such survival probability can depend on a variety of factors, but here we consider them as constants. Hence,

$$x_{t+1}^{i+1} = p_i x_t^i, \quad i = 1, \dots, N - 1; \quad (5)$$

where  $x_t^i$  represents the number of females in age class  $i$  at time  $t$ . In order to estimate the density in the first age class, we shall consider the reproduction process.

Representing by  $f_i$  the fertility rate in the age class  $i$ , i.e., the number of daughters generated by each female in age class  $i$ , it follows that

$$x_{t+1}^1 = \sum_{i=1}^N f_i x_t^i, \quad i = 1, \dots, N-1. \quad (6)$$

Again, for simplicity, we consider that the fertility rates  $f_i$  are constants. Equations (5) and (6) can be written in matrix form as

$$\mathbf{x}_{t+1} = L\mathbf{x}_t \quad (7)$$

where  $\mathbf{x} = (x^1, \dots, x^N)^T$  and  $L$  is the Leslie  $N \times N$  matrix in the form

$$L = \begin{bmatrix} f_1 & f_2 & \cdots & f_{N-1} & f_N \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{N-1} & \end{bmatrix}. \quad (8)$$

In the above matrix, the empty spaces must be considered as zeros:  $L$  contains non zero elements only in its first line and in its sub-diagonal. For simplicity, consider that  $f_N \neq 0$ . This local model and its metapopulation version fit in our general setting presented in the previous sections by taking

$$F(\mathbf{x}) = L\mathbf{x}.$$

Some important parameters associated with the Leslie matrix above shall be defined. We denote by  $l_i$  the chance of a just born individual reach the age class  $i$ , which is computed by

$$l_i = \prod_{j=1}^{i-1} p_j, \quad i = 2, \dots, N. \quad (9)$$

By definition, it follows that  $l_1 = 1$ . Now we can express mathematically the basic reproductive number  $R_0$  as

$$R_0 = \sum_{i=1}^N f_i l_i. \quad (10)$$

The net reproductive number represents the just born future contribution for the species persistence, i.e., it is an estimate to the number of individuals that a just born will generate during its entire life. It will be shown that  $R_0$  plays a decisive role in the stability of the system (7) and its metapopulation version.

Using the parameters  $l_i$ ,  $i = 1, 2, \dots, N$  and  $R_0$  we can obtain the fertility age distribution, characterized by the constants

$$m_i = \frac{f_i l_i}{R_0}, \quad i = 1, \dots, N. \quad (11)$$

One can easily check that  $\sum_{i=1}^N m_i = 1$ , since  $m_i$  represents the percentual contribution of the age class  $i$  in the net reproductive number  $R_0$ .

#### 4.1. The single patch linear model: equilibrium points and their stability

Here we state the stability properties of the single patch linear model. One can easily check that the trivial equilibria  $(0, \dots, 0)$  is the only equilibrium point of such system.

The relation

$$L\mathbf{v} = \sigma\mathbf{v}, \quad (12)$$

where  $\mathbf{v} = (v_1, v_2, \dots, v_N)^T$  is the eigenvector related to the eigenvalue  $\sigma$  of  $L = J(\mathbf{x}^*)$ , leads to the following characteristic equation for the eigenvalues of  $L$

$$\sum_{k=1}^N \frac{l_k f_k}{\sigma^k} = 1. \quad (13)$$

Using the above equation, we state the condition for the stability of the trivial equilibria in the following result.

**Theorem 1.** *The trivial equilibria  $\mathbf{x}^* = (0, 0, \dots, 0)^T$  of the linear single patch model  $\mathbf{x}_{t+1} = L\mathbf{x}_t$  is asymptotically stable if and only if  $R_0 < 1$ .*

*Proof.* Consider the auxiliar function

$$f(\sigma) = \sum_{k=1}^N \frac{l_k f_k}{\sigma^k}, \quad 0 < \sigma < \infty. \quad (14)$$

It is straightforward that  $f$  is a continuous function, monotonic decreasing in  $(0, \infty)$  with  $\lim_{\sigma \rightarrow 0} f(\sigma) = \infty$  and  $\lim_{\sigma \rightarrow \infty} f(\sigma) = 0$ . Thus exists a real and positive  $\sigma_1$  such that  $f(\sigma_1) = 1$ . Since  $\sigma_1$  is an eigenvalue of  $J(\mathbf{x}^*)$ , the system is stable only if  $\sigma_1 < 1$ . If this condition is satisfied we have

$$1 = f(\sigma_1) > f(1) = R_0,$$

since  $f(1) = R_0$  and  $f$  is a decreasing function. On the other hand, let  $R_0 < 1$  and  $e^{\alpha+i\beta}$ , where  $\beta > 0$ , be any eigenvalue of  $L$ . Then

$$\left| \sum_{k=1}^N l_k f_k e^{-k\alpha - ik\beta} \right| = 1.$$

However

$$\left| \sum_{k=1}^N l_k f_k e^{-k\alpha - ik\beta} \right| \leq \left| \sum_{k=1}^N l_k f_k e^{-k\alpha} \right|.$$

Thus

$$\left| \sum_{k=1}^N l_k f_k e^{-k\alpha} \right| \geq 1.$$

Dividing the above expression by  $R_0$  we have

$$\left| \sum_{k=1}^N m_k e^{-k\alpha} \right| \geq \frac{1}{R_0} > 1.$$

Since  $\sum_{k=1}^N m_k = 1$ , it is necessary that  $e^{-\alpha} > 1$  and it follows that  $|e^{\alpha+i\beta}| = |e^{\alpha}| < 1$ , completing the proof.  $\square$

#### 4.2. The multipatch linear model: equilibrium points and their stability

For this case, equation (3) becomes

$$X_{t+1} = LX_t + MLX_t B \quad (15)$$

Assuming that  $B$  is nondefective, there is a nonsingular matrix  $P$  such that  $B = P\Lambda P^{-1}$ , where  $\Lambda = \text{diag}(\lambda_1, \dots, \lambda_n)$  is the eigenvalue matrix of  $B$ . Notice that  $\lambda_1, \dots, \lambda_n$  are all real, by the symmetry of  $B$ . Making the change of variables

$$Y_t = X_t P, \quad (16)$$

we have the uncoupled system

$$Y_{t+1} = LY_t + MLY_t \Lambda \quad (17)$$

or, in vector form,

$$\mathbf{y}_{t+1}^j = (I + \lambda_j M) L \mathbf{y}_t^j \quad (18)$$

where  $\mathbf{y}_t^j$  is the population vector of site  $j$  in the new coordinates.

Clearly the zero  $N \times n$  matrix is an equilibrium solution for both equations (15) and (17). Moreover the stability analysis is equivalent for these systems. Therefore, we can assume that  $B$  is a diagonal matrix, without any loss of generality. Also, a renumbering of the sites is enough to assume that the very first entry in this diagonal  $B$  is zero. In this way, the dynamics of the Leslie model in its metapopulation version is given by

$$\mathbf{x}_{t+1}^j = (I + \lambda_j M) L \mathbf{x}_t^j \quad j = 1, \dots, n \quad (19)$$

where  $\mathbf{x}_t^j$  is the population vector at site  $j$ , as defined in section 3. Notice that, since  $I + \lambda_j M = \text{diag}(1 + \lambda_j \mu_1, \dots, 1 + \lambda_j \mu_N)$ , we have that  $I + \lambda_j M$  is a Leslie type matrix. Define

$$f_k^j = (1 + \lambda_j \mu_k) f_k; \quad k = 1, \dots, N;$$

and

$$\begin{cases} l_1^j = l_1; \\ l_k^j = l_k \prod_{i=2}^k (1 + \lambda_j \mu_i) \quad k = 2, \dots, N. \end{cases} \quad (20)$$

Also define

$$R_0^j = \sum_{k=1}^N f_k^j l_k^j; \quad j = 1, \dots, n. \quad (21)$$

Notice that the above quantities can be negative or even complex without further assumptions on B. By an straightforward calculation, one can check that the eigenvalues of the  $j^{th}$  system in (19) are given by

$$\sum_{k=1}^N \frac{l_k^j f_k^j}{\sigma^k} = 1. \quad (22)$$

By noticing that  $|f_k^j| \leq f_k$ ,  $|l_k^j| \leq l_k$ ,  $|R_0^j| \leq R_0$ , with equality when  $j = 1$ , we can state the following result.

**Theorem 2.** *The stability of the trivial homogeneous equilibrium of the Leslie metapopulation model (15) depends only on the stability of the single patch model. In other words, the trivial homogeneous equilibrium of (15) is asymptotically stable if and only if  $R_0 < 1$ .*

*Proof.* As observed, the stability analysis of the equilibrium points of (15) and (19) is equivalent since we assumed B is diagonalizable. Suppose the homogeneous equilibria is asymptotically stable. This can only happens if the  $N$  sized zero vector is a stable equilibrium for each of the systems in (19). But for  $j = 1$ , this only happens if  $R_0 < 1$ . Therefore  $R_0 < 1$  is a necessary condition for the asymptotical stability of the trivial equilibria.

On the other hand, let  $R_0 < 1$  and  $e^{\alpha+i\beta}$ , where  $\beta > 0$ , be any eigenvalue of the  $j^{th}$  system in (19). Then

$$\left| \sum_{k=1}^N l_k^j f_k^j e^{-k\alpha - ik\beta} \right| = 1.$$

However

$$1 = \left| \sum_{k=1}^N l_k^j f_k^j e^{-k\alpha - ik\beta} \right| \leq \sum_{k=1}^N l_k f_k e^{-k\alpha}.$$

Thus

$$\sum_{k=1}^N l_k f_k e^{-k\alpha} \geq 1.$$

Dividing the above expression by  $R_0$  we have

$$\sum_{k=1}^N m_k e^{-k\alpha} \geq \frac{1}{R_0} > 1.$$

Since  $\sum_{k=1}^N m_k = 1$ , it is necessary that  $e^{-\alpha} > 1$  and it follows that  $|e^{\alpha+i\beta}| = |e^\alpha| < 1$ , completing the proof.  $\square$

## 5. A Nonlinear model - Density dependent recruitment

Here, our model consider the existence of an inferior class for the just-generated individuals. Depending on the species considered, this class can be entitled as the eggs class or larvae class. This separation is done because the growth during this period is different, and its length also differs from other classes. We suppose that the individuals of this stage are subject to a density dependent recruitment, i.e., that the survival rate on this period is density dependent, represented by a certain function  $g$ . The local dynamics of such system is given by

$$\mathbf{x}_{t+1} = F(\mathbf{x}_t) \quad (23)$$

where  $F$  is defined by

$$\begin{cases} F : \mathbb{R}^N \rightarrow \mathbb{R}^N \\ \mathbf{x} = (x^1, \dots, x^N)^T \rightarrow (F_1(\mathbf{x}), \dots, F_N(\mathbf{x}))^T \end{cases} \quad (24)$$

where

$$\begin{cases} F_1(\mathbf{x}) = wg(w) \\ F_k(\mathbf{x}) = p_{k-1}x^k; \quad k = 2, \dots, N \end{cases} \quad (25)$$

with  $w$  representing the density in the inferior class, which is given by

$$w = \sum_{k=1}^N f_k x^k.$$

We assume that  $g$  satisfies the following properties:

- (1)  $g(0) = 1$ ;
- (2)  $\lim_{x \rightarrow \infty} g(x) = 0$ ;
- (3)  $g'(x) < 0$ ;
- (4)  $\left(-\frac{xg'(x)}{g(x)}\right)' > 0$ .

The first three items just tell us that the probability of an individual to be recruited is a decreasing function of the number of individuals in the inferior class. The fourth item will ease the stability analysis, and does not impose serious restrictions to the model. Various examples match such restrictions, as the Ricker recruitment [20],

$$g(x) = e^{-\alpha x}, \quad \alpha > 0;$$

the Beverton-Holt recruitment [2],

$$g(x) = \frac{1}{1 + \alpha x}, \quad \alpha > 0;$$

and the Hassell recruitment [10],

$$g(x) = \frac{1}{(1 + \alpha x)^\beta}, \quad \alpha, \beta > 0.$$

For a better understanding of the dispersal effects in the metapopulation model, we shall first study the stability of the equilibria in the single patch model (23).



### 5.1. The single patch nonlinear model: equilibrium points and their stability

One can easily check that the system (23) has two equilibrium points [24]: the trivial one, with  $w^* = 0$  and  $\mathbf{x}^* = (0, 0, \dots, 0)^T$ , and a non-trivial one, given by  $\mathbf{x}^* = w^* g(w^*) (l_1, l_2, \dots, l_N)^T$ , where  $w^*$  satisfies

$$g(w^*) = \frac{1}{R_0}. \quad (26)$$

Since  $g(x) \leq 1$ , it is necessary that  $R_0 \geq 1$  to (26) be satisfied, and given that  $R_0 = 1$  implies  $g(w^*) = 1 \Rightarrow w^* = 0$ , it follows that the system (23) has a nontrivial equilibrium point if and only if the condition

$$R_0 > 1. \quad (27)$$

is satisfied.

By direct computation, it follows that the jacobian matrix of (23) has the form

$$J(\mathbf{x}) = \begin{bmatrix} f_1 h'(w) & f_2 h'(w) & \cdots & f_{N-1} h'(w) & f_N h'(w) \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{N-1} & \end{bmatrix}, \quad (28)$$

where  $h(x) = g(x)x$ .

#### 5.1.1. The trivial equilibria stability

For the trivial equilibria, it can be easily checked that the jacobian matrix takes the form of a Leslie matrix (8). Therefore the stability properties of the trivial equilibria for this nonlinear model are the same as the stability properties of the linear model presented before, which are resumed in the next theorem.

**Theorem 3.** *The trivial equilibria  $\mathbf{x}^* = (0, 0, \dots, 0)^T$  of the nonlinear model (23) is asymptotically stable if and only if  $R_0 < 1$ .*

#### 5.1.2. The nontrivial equilibria stability

For the nontrivial equilibria  $\mathbf{x}^* = w^* g(w^*) (l_0, l_1, \dots, l_{N-1})^T$ , using the relation (12), the characteristic equation becomes

$$h'(w^*) \sum_{k=1}^N \frac{l_k f_k}{\sigma^k} = 1.$$

Dividing the above equation by  $R_0 h'(w^*)$  we obtain

$$\frac{1}{R_0} \sum_{k=1}^N \frac{l_k f_k}{\sigma^k} = \frac{1}{R_0 h'(w^*)}.$$

Recalling that

$$m_k = \frac{l_k f_k}{R_0},$$

we have

$$\sum_{k=1}^N \frac{m_k}{\sigma^k} = \frac{1}{R_0 h'(w^*)}. \quad (29)$$

Multiplying the above equation by  $-R_0 h'(w^*) \sigma^N$ , we obtain the following characteristic polynomial for

$$p(\sigma) = \sigma^N - \sum_{k=1}^N m_k R_0 h'(w^*) \sigma^{N-k}. \quad (30)$$

We can already predict that the stability properties of (23) equilibrium points depend on  $R_0 h'(w^*) = R_0 g'(w^*) w^* + 1$ , since  $R_0 h'(w^*)$  appears in almost all terms of the characteristic polynomial. However, given a recruitment function  $h$ , the parameter which defines the stability region is  $R_0$ . For this reason, the use of  $R_0 h'(w^*)$  does not suit the problem, since  $R_0 h'(w^*)$  is a decreasing function of  $R_0$  with range  $(-\infty, 1]$  while  $R_0$  is a parameter ranging in  $(0, \infty)$ . It is convenient to describe the stability properties using a parameter  $H = H(R_0)$ , a increasing function with range in  $(0, \infty)$ . Our choice is the use of

$$H = -R_0 g'(w^*) w^*, \quad (31)$$

because

- $H > 0$  since  $g'(x) < 0$  by hypothesis;
- $H = H(R_0)$ ;
- $H$  is a increasing function, since we assumed  $H'(w^*) = \left(-\frac{w^* g'(w^*)}{g(w^*)}\right)' > 0$  what implies that  $H$  is a increasing function in  $w^*$  which, by turn, is a increasing function in  $R_0$ . For example, one can easily check that in the case of the Ricker recruitment ( $g(x) = e^{-\alpha x}$ ,  $\alpha > 0$ )  $H = \ln R_0$ .

In this way we have  $R_0 h'(w^*) = 1 - H$  and it will be possible establish the stability condition for  $\mathbf{x}^* = w^* g(w^*) (l_1, l_2, \dots, l_N)^T$  using the parameter  $H$ , as shown in the result below.

**Theorem 4.** *Let  $R_0 > 1$ . If  $0 < H < 2$  the nontrivial equilibria  $\mathbf{x}^* = w^* g(w^*) (l_1, l_2, \dots, l_N)^T$  of the nonlinear model (23) is asymptotically stable. Besides, if  $0 < H < 1$  and  $m_k \neq 0$  for two consecutive classes, the approach to the equilibrium is monotonic, while if  $1 < H < 2$  the approach to the equilibrium is oscillatory.*

*Proof.* Suppose that  $0 < H < 2$ . Using (29) and representing an arbitrary eigenvalue of  $J(\mathbf{x}^*)$  by  $e^{\alpha+i\beta}$ , it follows that

$$\left| \sum_{k=1}^N m_k e^{-k\alpha - ik\beta} \right| = \left| \frac{1}{1-H} \right| > 1.$$

But

$$\left| \sum_{k=1}^N m_k e^{-k\alpha - ik\beta} \right| \leq \left| \sum_{k=1}^N m_k e^{-k\alpha} \right|.$$

Thus

$$\left| \sum_{k=1}^N m_k e^{-k\alpha} \right| > 1.$$

Recalling that  $\sum_{k=1}^N m_k = 1$ , it is necessary that  $e^{-\alpha} > 1$  and so  $|e^{\alpha+i\beta}| = |e^{\alpha}| < 1$ , what guarantees the stability of the nontrivial equilibria. In relation to the asymptotical behavior, we have:

– Suppose that  $0 < H < 1$  and define the auxiliar function  $f$  by

$$f(\sigma) = \sum_{k=1}^N \frac{m_k}{\sigma^k}.$$

Thus  $\sigma_1$  is a real eigenvalue of  $J(\mathbf{x}^*)$  if and only if  $f(\sigma_1) = \frac{1}{1-H}$ . In this case we have  $\frac{1}{1-H} > 0$ . Since  $f(\sigma)$  is continuous and monotonic decreasing in  $(0, \infty)$  with  $\lim_{\sigma \rightarrow 0} f(\sigma) = \infty$  e  $\lim_{\sigma \rightarrow \infty} f(\sigma) = 0$ , there are a unique real positive  $\sigma_1$  such that  $f(\sigma_1) = \frac{1}{1-H}$ . Besides that,  $\sigma_1$  is the dominant eigenvalue of  $J(\mathbf{x}^*)$ : denoting  $\sigma_1$  by  $e^\gamma$  and  $e^{\alpha+i\beta}$  any other eigenvalue of  $J(\mathbf{x}^*)$ , where  $\beta > 0$  and  $\beta \neq 2\pi, 4\pi, \dots$ . The real part of  $f(e^{\alpha+i\beta})$  must satisfy

$$\sum_{k=1}^N m_k e^{-k\alpha} \cos k\beta = \frac{1}{1-H}.$$

Similarly,

$$\sum_{k=1}^N m_k e^{-k\gamma} = \frac{1}{1-H}.$$

Thus

$$\left| \sum_{k=1}^N m_k e^{-k\alpha} \cos k\beta \right| = \left| \frac{1}{1-H} \right| = \left| \sum_{k=1}^N m_k e^{-k\gamma} \right|.$$

But

$$\left| \sum_{k=1}^N m_k e^{-k\alpha} \cos k\beta \right| \leq \sum_{k=1}^N m_k e^{-k\alpha} |\cos k\beta| \leq \sum_{k=1}^N m_k e^{-k\alpha},$$

So

$$\sum_{k=1}^N m_k e^{-k\gamma} \leq \sum_{k=1}^N m_k e^{-k\alpha} \implies e^\alpha \leq e^\gamma.$$

A last detail has to be observed: equality does not happen in the above expression. In fact, it would be possible only if  $\alpha = \gamma$  and  $\beta = \pi, 3\pi, \dots$ . In such case,  $e^{\gamma+i\beta}$  would represent a real negative eigenvalue of  $J(\mathbf{x}^*)$  with absolute value equal to  $\sigma_1$ . But, since we have  $m_k, m_{k+1} > 0$  for some  $k$ , the absolute value of  $\sum_{k=1}^N m_k e^{-k\gamma} \cos k\beta$  is different from  $\sum_{k=1}^N m_k e^{-k\gamma}$  and thus different from  $\frac{1}{1-H}$ .

- Now suppose that  $1 < H < 2$ . In this case  $\frac{1}{1-H} < -1$ . Given that  $f$  is strictly positive for  $\sigma > 0$ , the eigenvalues of  $J(\mathbf{x}^*)$  are complex or negative, what implies that the approach to the equilibria is oscillatory.  $\square$

Notice that if we are dealing with a species such that the females reproduce only once in life, we have  $m_k = 1$  for a given  $k$  and  $m_i = 0, i \neq k$ , and the characteristic equation (29) becomes

$$\frac{1}{\sigma^k} = \frac{1}{1-H},$$

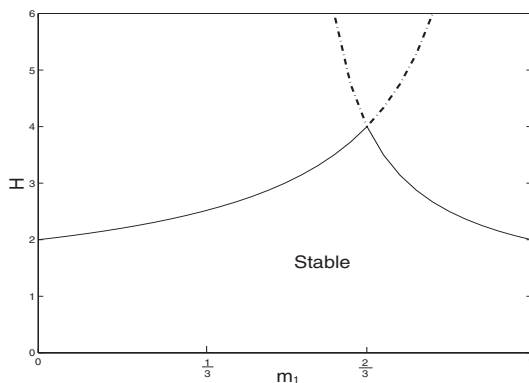
what implies that  $|\sigma| < 1 \Leftrightarrow 0 < H < 2$ . This shows that Theorem 2 can not be improved with no further information on the parameters  $m_1, m_2, \dots, m_N$ .

It is interesting to notice that in the case of Beverton-Holt recruitment ( $g(x) = \frac{1}{1+\alpha x}$ ,  $\alpha > 0$ ) an easy calculation can show that  $0 < H < 1$ , which ensures the stability of the nontrivial equilibrium no matter how the reproductive effort is distributed through age.

If we consider few age classes, the calculation of the nontrivial equilibrium stability region is a direct task. For two age classes, one can easily check [3] that the region where

$$H < 1 + \frac{1}{1-m_1} \text{ and } H < 1 + \frac{1}{2m_1-1} \quad (32)$$

is the stability region of the nontrivial equilibria  $w^*g(w^*)(l_1, l_2)^T$ , depicted in Figure 1. One can also check that as  $H$  crosses the curve  $H = 1 + \frac{1}{1-m_1}$  a flip bifurcation occurs while a Hopf bifurcation occurs as  $H$  crosses the curve  $H = 1 + \frac{1}{2m_1-1}$ . At the point of intersection of these two curves, a codimension 2 bifurcation takes place and more complicated dynamics can be expected.



**Fig. 1.** Stability region of the nontrivial equilibria of the system with two age classes, limited by the curves  $H = 0$ ,  $H = 1 + \frac{1}{1-m_1}$  e  $H = 1 + \frac{1}{2m_1-1}$

### 5.2. The metapopulation homogeneous equilibrium states and their stability

Here we are interested in how a migration mechanism can affect the stability of the local equilibria states. For, we linearize the metapopulation model, given by the local dynamics operator described above and (4), about its homogeneous equilibrium points of the form

$$X^* = (\mathbf{x}^*, \dots, \mathbf{x}^*),$$

where  $\mathbf{x}^* \in \mathbb{R}^N$  is a local equilibrium state, i.e.,  $F(\mathbf{x}^*) = \mathbf{x}^*$ . Assuming that  $B$  is symmetric, such points are equilibrium points of (4) since  $\Phi(X^*) = X^*$  and  $\sum_{j=1}^n b_{ij} = \sum_{i=1}^n b_{ij} = 0$ . Recall that for the local model we have two fixed points, namely the trivial equilibria

$$\mathbf{x}^* = (0, \dots, 0)^T, \quad (33)$$

and, for  $R_0 > 1$ , there is a nontrivial equilibria,

$$\mathbf{x}^* = w^* g(w^*) (l_1, \dots, l_N)^T, \quad (34)$$

where  $g(w^*) = \frac{1}{R_0}$ .

Linearization of equation (4) about the equilibrium  $X^*$  results yields the  $n$  uncoupled vector systems (See Jansen and Lloyd [15])

$$\delta_{t+1}^j = (1 + \lambda_j M) D F(x^*) \delta_t^j, \quad j = 1, \dots, n \quad (35)$$

where  $\delta_t^j \in \mathbb{R}^N$  is a perturbation for the equilibrium position  $\mathbf{x}^*$  at time step  $t$ . We now analyze the stability of  $X^*$  for (33) and (34).

### 5.2.1. The trivial equilibria $X^* = (\mathbf{0}, \dots, \mathbf{0})$ stability

By direct computation, one can easily check that  $DF(\mathbf{0}) = L$ ,

$$DF(\mathbf{0}) = L = \begin{bmatrix} f_1 & f_2 & \cdots & f_{N-1} & f_N \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{N-1} & \end{bmatrix}. \quad (36)$$

Thus the results obtained from the linear model in section 3 give us

$$\begin{aligned} R_0 < 1 &\Rightarrow X^* = (\mathbf{0}, \dots, \mathbf{0}) \text{ stable} \\ R_0 > 1 &\Rightarrow X^* = (\mathbf{0}, \dots, \mathbf{0}) \text{ unstable.} \end{aligned} \quad (37)$$

### 5.2.2. The nontrivial equilibria stability

For the equilibria  $X^* = (\mathbf{x}^*, \dots, \mathbf{x}^*)$ , where  $\mathbf{x}^* = w^*g(w^*)(l_1, \dots, l_N)^T$ , with  $g(w^*) = \frac{1}{R_0}$  and  $R_0 > 1$ ,  $DF(\mathbf{x}^*)$  takes the form

$$DF(\mathbf{x}) = \begin{bmatrix} f_1 h'(w) & f_2 h'(w) & \cdots & f_{N-1} h'(w) & f_N h'(w) \\ p_1 & & & & \\ & p_2 & & & \\ & & \ddots & & \\ & & & p_{N-1} & \end{bmatrix}, \quad (38)$$

where  $h(w) = wg(w)$ . Thus the matrix  $J = (I + \lambda_j M)DF(\mathbf{x}^*)$  takes the form of a Leslie matrix,

$$J = \begin{bmatrix} f_1^j h'(w^*) & f_2^j h'(w^*) & \cdots & f_{N-1}^j h'(w^*) & f_N^j h'(w^*) \\ (1 + \lambda_j \mu_2) p_1 & & & & \\ & (1 + \lambda_j \mu_3) p_2 & & & \\ & & \ddots & & \\ & & & (1 + \lambda_j \mu_N) p_{N-1} & \end{bmatrix}, \quad (39)$$

and therefore the eigenvalues of the  $j^{th}$  system in (35) are given by the characteristic equation

$$h'(w^*) \sum_{k=1}^N \frac{l_k^j f_k^j}{\sigma^k} = 1, \quad j = 1, 2, \dots, n. \quad (40)$$

Defining

$$m_k^j = \frac{f_k^j l_k^j}{R_0} \quad (41)$$

and recalling that  $H = -R_0 g'(w^*) w^*$ , the characteristic equation (40) can be rewritten as

$$\sum_{k=1}^N \frac{m_k^j}{\sigma^k} = \frac{1}{1 - H}, \quad j = 1, 2, \dots, n. \quad (42)$$

Under certain restrictions on the migration parameter  $\mu_k$ , we can state an analog of Theorem 4.

**Theorem 5.** *Let  $R_0 > 1$ . If  $0 < H < 2$  the nontrivial equilibria  $\mathbf{X}^* = (\mathbf{x}^*, \dots, \mathbf{x}^*)$ , where  $\mathbf{x}^* = w^*g(w^*)(l_1, l_2, \dots, l_N)^T$  of the nonlinear metapopulation model is asymptotically stable. Besides, assuming that the migration fractions satisfy  $0 \leq \mu_k \leq \frac{1}{2}$  for all  $k = 1, \dots, N$ ; we have that if  $0 < H < 1$  and  $m_k^j \neq 0$  for two consecutive classes for all  $j = 1, \dots, n$ , the approach to the equilibrium is monotonic, while if  $1 < H < 2$  the approach to the equilibrium is oscillatory.*

*Proof.* Suppose that  $0 < H < 2$ . Using (42) and representing an arbitrary eigenvalue of  $J$  for the  $j^{\text{th}}$  equation in (35) by  $e^{\alpha+i\beta}$ , it follows that

$$\left| \sum_{k=1}^N m_k^j e^{-k\alpha - ik\beta} \right| = \left| \frac{1}{1-H} \right| > 1.$$

But

$$\left| \sum_{k=1}^N m_k^j e^{-k\alpha - ik\beta} \right| \leq \sum_{k=1}^N m_k e^{-k\alpha},$$

since  $|m_k^j| \leq m_k$ . Thus

$$\left| \sum_{k=1}^N m_k e^{-k\alpha} \right| > 1.$$

Recalling that  $\sum_{k=1}^N m_k = 1$ , it is necessary that  $e^{-\alpha} > 1$  and so  $|e^{\alpha+i\beta}| = |e^{\alpha}| < 1$ , what guarantees the stability of the nontrivial equilibria.

Now assume that  $0 \leq \mu_k \leq \frac{1}{2}$ . This, together with the symmetry of  $B$ , implies that  $m_k^j \geq 0$ , with  $\sum_{k=1}^N m_k \leq 1$ . Therefore the arguments used in second part of the Theorem 4 proof can be applied for this case, and the result on the asymptotical behavior follows.  $\square$

Next, by observing that  $\lambda_1 = 0$  is an eigenvalue of  $B$ , we show that migration cannot stabilize a unstable uncoupled system, since the stability region of  $\mathbf{X}^*$  is contained in the stability region of the uncoupled system at  $\mathbf{x}^*$ . This is a well known result ([21], [15]) for non age-structured metapopulation models.

**Theorem 6.** *All eigenvalues of the one patch nonlinear system (23) at the nontrivial equilibria  $\mathbf{x}^*$  are eigenvalues of the nonlinear coupled system at its nontrivial equilibria  $\mathbf{X}^* = (\mathbf{x}^*, \dots, \mathbf{x}^*)$ . Besides, if  $0 < H < 1$  the dominant eigenvalue is the same for both systems.*

*Proof.* Taking  $j = 1$  in (42), and recalling that  $f_k^1 = f_k$ ,  $l_k^1 = l_k$  and therefore  $m_k^1 = m_k$  we obtain the same characteristic equation for the local system at the

nontrivial equilibria  $\mathbf{x}^*$ . For the dominant eigenvalue, consider let  $\sigma = \rho e^{i\theta}$  be an eigenvalue of the metapopulation system at the site  $j$ . Thus  $\sigma$  satisfies

$$1 = (1 - H) \sum_{k=1}^N \frac{m_k^j}{\rho^k e^{ik\theta}} \leq (1 - H) \sum_{k=1}^N \frac{m_k}{\rho^k}. \quad (43)$$

Let  $\sigma$  be the dominant eigenvalue for the local (one-patch) system. From Section 2 we have that  $\sigma$  is real and positive and satisfies

$$1 = (1 - H) \sum_{k=1}^N \frac{m_k}{\sigma^k}.$$

Therefore,

$$(1 - H) \sum_{k=1}^N \frac{m_k}{\sigma^k} \leq (1 - H) \sum_{k=1}^N \frac{m_k}{\rho^k} \xrightarrow{H \leq 1} \sum_{k=1}^N \frac{m_k}{\rho^k} \leq \sum_{k=1}^N \frac{m_k}{\sigma^k}.$$

Since  $\sum_{k=1}^N m_k = 1$  it follows that  $\rho \leq \sigma$ .  $\square$

An immediate conclusion from the above theorem is that, under the hypothesis on the fertility age distribution of Theorems 4 and 5, the approach to the homogeneous equilibria is monotonic, as occur with the one-patch system, independently of the migration parameters, therefore improving Theorem 5. There are other cases where migration causes no effect on the stability of  $\mathbf{X}^*$ . Among them, we have the age independent migration, as shown in Theorem 7.

**Theorem 7.** *If  $\mu_k = \mu$ ,  $k = 1, 2, \dots, N$ , the dominant eigenvalue of the coupled nonlinear metapopulation system at  $\mathbf{X}^*$  is the dominant eigenvalue of the local system (23) at  $\mathbf{x}^*$ .*

*Proof.* In such case,

$$f_k^j = (1 + \lambda_j \mu) f_k, \text{ and } l_k^j = (1 + \lambda_j \mu)^{k-1} l_k.$$

Thus

$$m_k^j = (1 + \lambda_j \mu)^k m_k$$

and (42) can be rewritten as

$$\sum_{k=1}^N \frac{m_k}{\left(\frac{\sigma}{(1 + \lambda_j \mu)}\right)^k} = \frac{1}{1 - H}. \quad (44)$$

Comparing with the characteristic equation for the uncoupled system we have that the eigenvalues  $\sigma$  of coupled system are given by

$$\frac{\sigma}{(1 + \lambda_j \mu)} = \rho_i; \quad i = 1, \dots, N \text{ and } j = 1, \dots, n$$



where  $\rho_i, i = 1, \dots, N$  are the eigenvalues of the single patch system. Let  $|\rho| = \max_{1 \leq i \leq N} \{|\rho_i|\}$ . Since  $|1 + \lambda_j \mu| \leq 1$ , it follows that

$$|\sigma| \leq |1 + \lambda_j \mu| |\rho| \Rightarrow |\sigma| \leq |\rho|.$$

□

Theorem 7 tell us that if there is no age structure in the migration process, then dispersal is not able to produce instabilities. This fact confirms the results of Rohani et al. [21]. The absence of structure of species interaction in population models makes impossible for movement alone generate instability in homogeneous states [15]. A word of caution should be added when interpreting these results. It is assumed that migration is density independent. Allowing a density dependent migration mechanism can lead to dispersal driven instabilities and therefore pattern formation even in a single species with no age or size structure [23].

## 6. The instability caused by dispersal

Despite the results of the previous section, in a large variety of cases migration can reduce the stability region. Such cases occur when migration is strongly related to age. As an example, consider the case with the sites arranged in a ring and connected only to its nearest neighbors, with B given by

$$B = \begin{bmatrix} -1 & \frac{1}{2} & & & \frac{1}{2} \\ \frac{1}{2} & -1 & \frac{1}{2} & & \\ & & \ddots & \ddots & \ddots \\ & & & \frac{1}{2} & -1 & \frac{1}{2} \\ \frac{1}{2} & & & & \frac{1}{2} & -1 \end{bmatrix}. \quad (45)$$

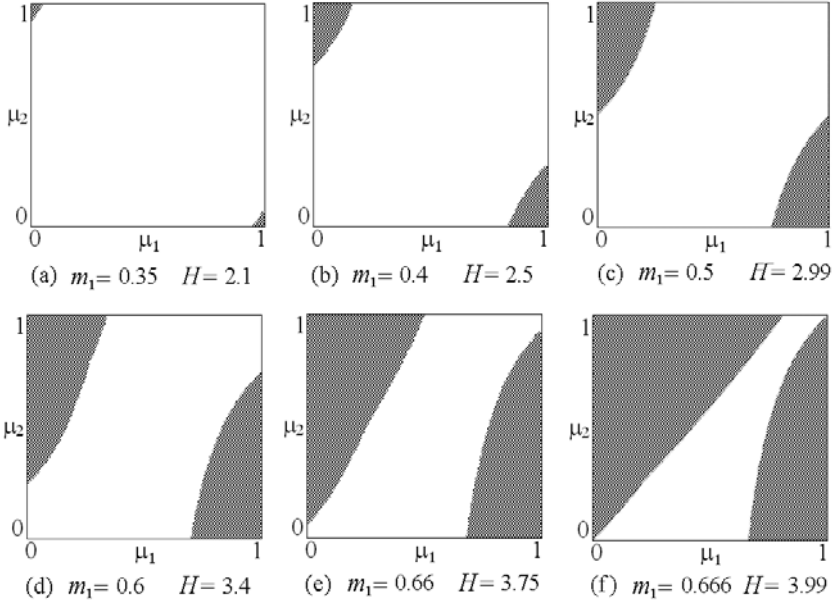
One can easily check [6] that the eigenvalues of B are

$$\lambda_j = 1 - \cos \frac{2\pi(j-1)}{n}, \quad j = 1, \dots, n. \quad (46)$$

Also notice that, by multiplying (42) by  $(1-H)\sigma^N$ , we get that the eigenvalues of the coupled system are the roots of

$$p_j(\sigma) = \sigma^N - (1-H) \sum_{k=1}^N m_k^j \sigma^{N-k}, \quad j = 1, \dots, n;$$

and so an easy way for analyzing the stability of the coupled system is by determining conditions such that the roots of each of the polynomials  $p_j$  be all inside the unit disc. Our tools in the determining of such conditions are based in very simple polynomial principles. As widely known, it is necessary that  $p(1) > 0$  and  $(-1)^n p(-1) > 0$  for having all the roots of a certain polynomial  $p$  with modulus



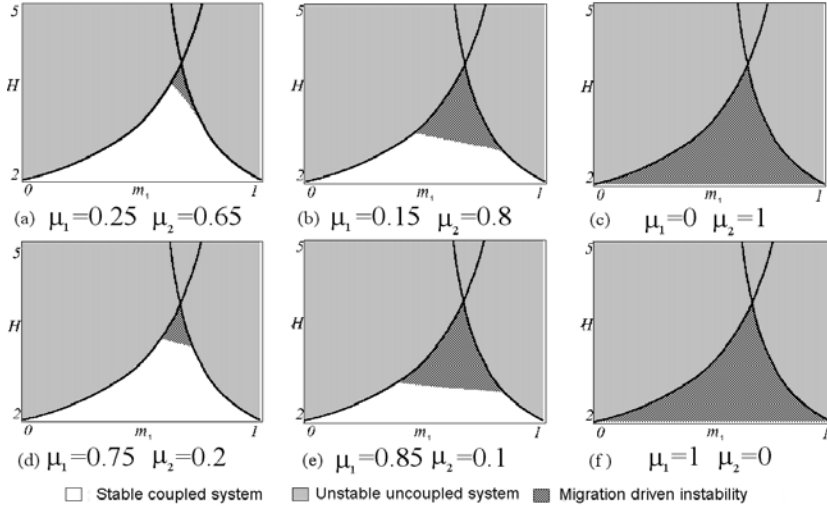
**Fig. 2.** Stability test result for each pair  $(\mu_1, \mu_2)$  in a 20 sites ring, with two age classes structured local populations, for fixed values of  $m_1$  and  $H$  (the black region represents instability)

less than one. If these conditions fail, the polynomial has a real root greater than one (if  $p(1) \leq 0$ ) or the system has a real root less than  $-1$  (if  $(-1)^n p(-1) \leq 0$ ).<sup>1</sup>

Figure 1 shows the stability region for the uncoupled system with two age classes, which is bounded by the curves  $H = 0$ ,  $H = 1 + \frac{1}{1-m_1}$  and  $H = 1 + \frac{1}{2m_1-1}$ . We have evaluated the characteristic polynomial roots for the coupled case, for all migration configurations in an array of 20 sites; using local parameters values ( $m_1$  and  $H$ ) such that the uncoupled system would present a stable nontrivial equilibria. The results are plotted in Figure 2, where each point  $(\mu_1, \mu_2)$  of the unit square has been painted of black, if the homogeneous equilibrium is unstable, or white, in case of a stable homogeneous equilibrium. In all tests performed, we noticed that the larger is  $H$ , the greater is the instability region. For  $H \approx 4$  and  $m_1 \approx \frac{2}{3}$ , where the two stability region boundary curves in Figure 1 intersect, we have the greatest migration driven instability region.

In Figure 3, we have evaluated the characteristic polynomial roots for fixed values of  $\mu_1$  and  $\mu_2$ , letting  $m_1$  and  $H$  free to vary. One can notice that the migration driven instability region grows as  $\mu_1$  and  $\mu_2$  go farther apart: in Figures 3(a), 3(b) and 3(c) show that as  $(\mu_1, \mu_2)$  get close to  $(0, 1)$  the stability region is reduced to  $0 < H < 2$ ; and the same occurs if  $(\mu_1, \mu_2)$  approaches to  $(1, 0)$ , as shown in Figures 3(d), 3(e) and 3(f). In fact, this occurs for any number of age classes in

<sup>1</sup> A more complicated version for the complex roots is provided in the Jury test [16].



**Fig. 3.** Stability test result for various configurations of a 20 sites ring, with two age classes structured local populations. The black curves define the uncoupled case stability region, bounded by  $H = 0$ ,  $H = 1 + \frac{1}{1-m_1}$  and  $H = 1 + \frac{1}{2m_1-1}$ , while the white region represents the coupled system stability region

arrays with a even number of patches. If  $\mu_1 = 1$  and  $\mu_i = 0, i = 2, \dots, n-1$ , we have

$$p_j(\sigma) = \sigma^N - \left( m_1 \sigma^{N-1} + \dots + m_{N-1} \sigma + m_N \right) \cos \frac{2\pi(j-1)}{n} (1-H), \quad (47)$$

thus

$$p_j(1) = 1 - \cos \frac{2\pi(j-1)}{n} (1-H) > 0, \quad j = 1, \dots, n \quad (48)$$

is satisfied for  $H \geq 2$ , since  $p_{\frac{n}{2}+1}(1) > 0 \Leftrightarrow H < 2$ . Similarly, if  $\mu_1 = 0$  and  $\mu_i = 1, i = 2, \dots, n-1$ , we have

$$\begin{aligned} (-1)^N p_j(-1) &= \\ 1 - (-1)^N (1-H) \left( m_1 (-1)^{N-1} + \sum_{i=2}^N m_i (-1)^{N-i} \left( \cos \frac{2\pi(j-1)}{n} \right)^{i-1} \right), \end{aligned} \quad (49)$$

and the condition  $(-1)^N p_j(-1) > 0 \quad j = 1, \dots, n$  is satisfied only if  $0 < H < 2$ , since

$$\begin{aligned} (-1)^N p_{\frac{n}{2}+1}(-1) &= 1 - (-1)^N (1-H) \left( m_1 (-1)^{N-1} + \sum_{i=2}^N m_i (-1)^{N-i} \right) \\ &= 1 - (-1)^{2N-1} (1-H) \left( \sum_{i=1}^N m_i \right) = 2 - H. \end{aligned} \quad (50)$$

The above result can be generalized for other choices of  $M$ , if we impose conditions on the fertility parameters  $m_i, i = 1, \dots, n$ , as shown in Theorems 8 and 9.

**Theorem 8.** *Consider the nonlinear metapopulation model presented in section 5 with  $B$  given by (45). If*

- (i)  $n$  is even;
- (ii)  $\mu_s = 1$  for some  $s$  and  $\mu_i = 0, i \neq s$ ;
- (iii)  $m_1 = m_2 = \dots = m_{s-1} = 0$ ;

*then the nontrivial equilibria  $X^*$  is stable if and only if  $0 < H < 2$ .*

*Proof.* Under the above restrictions, we have

$$p_j(\sigma) = \sigma_N - (1 - H) \cos \frac{2\pi(j-1)}{n} \left[ m_s \sigma^{N-s} + \dots + m_{N-1} \sigma + m_N \right] \quad (51)$$

Thus the condition

$$p_j(1) = 1 - (1 - H) \cos \frac{2\pi(j-1)}{n} > 0 \quad j = 1, \dots, n \quad (52)$$

cannot be satisfied, since  $p_{\frac{n}{2}+1}(1) = 2 - H > 0 \Leftrightarrow H < 2$ . Recalling Theorem 5, it follows that  $X^*$  is stable if and only if  $0 < H < 2$ .  $\square$

Notice that the conditions (ii) and (iii) of Theorem 8 mean that there is a certain age,  $s$ , when the individuals become reproductive and are obligated to emigrate to their neighbor patches. In Theorem 9 we show that if the individuals do not reproduce every year up to reach a certain age  $s$ , when they migrate, the stability region is also reduced to  $0 < H < 2$ .

**Theorem 9.** *Consider the nonlinear metapopulation model presented in section 5 with  $B$  given by (45). If*

- (i)  $n$  is even;
- (ii)  $\mu_1 = \mu_2 = \dots = \mu_{s-1} = 0$  and  $\mu_s = \mu_{s+1} = \dots = \mu_N = 1$ ;
- (iii)  $s - 1$  is odd;
- (iv)  $m_2 = m_4 = \dots = m_{2k} = \dots = m_{s-2} = 0$ ;

*then the nontrivial equilibria  $X^*$  is stable if and only if  $0 < H < 2$ .*

*Proof.* Under the above assumptions, we have

$$p_j(\sigma) = \sigma^N - (1 - H) \left[ \sum_{i=1}^{s-1} m_i \sigma^{N-i} + \sum_{i=s}^N m_i \sigma^{N-i} \cos^{i-(s-1)} \frac{2\pi(j-1)}{n} \right].$$

Therefore,

$$p_{\frac{n}{2}+1}(-1) = (-1)^N - (1 - H) \left[ \sum_{i=1}^{s-1} m_i (-1)^{N-i} + \sum_{i=s}^N m_i (-1)^{N-i} (-1)^{i-(s-1)} \right].$$

Multiplying the above expression by  $(-1)^N$  and recalling that, by hypothesis,  $s - 1$  is odd we have

$$(-1)^N p_{\frac{n}{2}+1}(-1) = (-1)^N - (1 - H) \left[ \sum_{i=1}^{s-1} m_i (-1)^i - \sum_{i=s}^N m_i \right];$$

and by hypothesis (iii) and (iv)

$$\sum_{i=1}^{s-1} m_i (-1)^i - \sum_{i=s}^N m_i = - \sum_{i=1}^N m_i = -1$$

so it follows that

$$(-1)^N p_{\frac{n}{2}+1}(-1) = 2 - H.$$

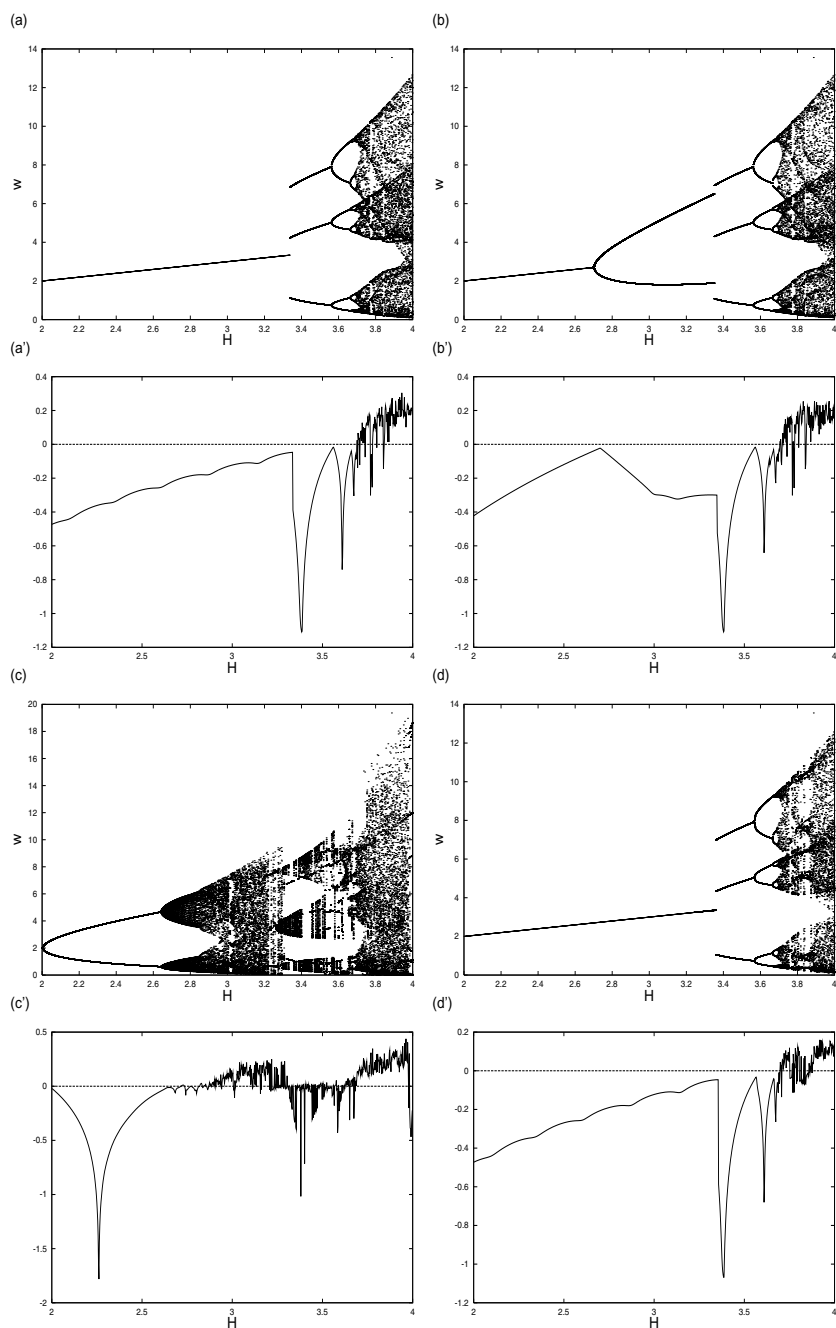
Therefore,

$$(-1)^N p_{\frac{n}{2}+1}(-1) > 0 \Leftrightarrow H < 2,$$

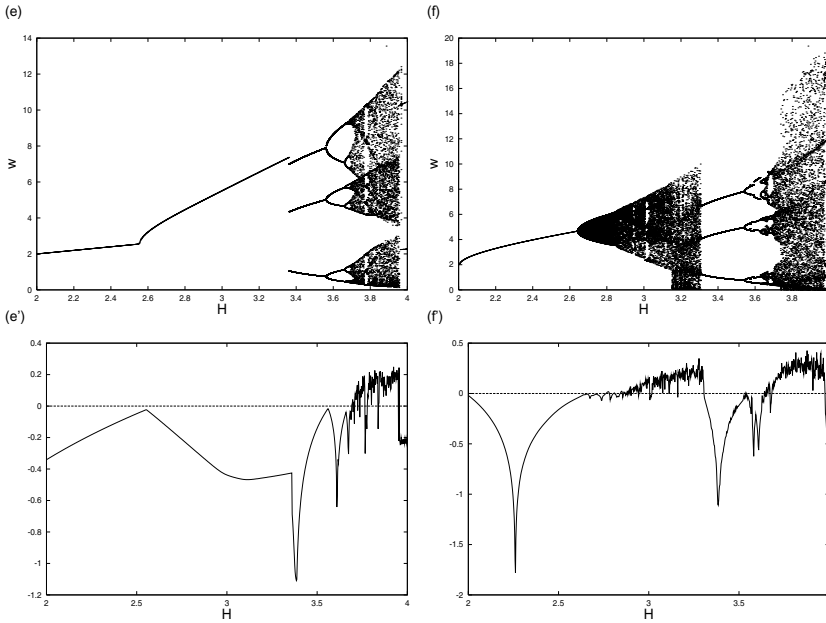
what implies that  $H < 2$  is a necessary condition for the stability of  $W^*$ . Since Theorem 3 shows its sufficiency, it follows that  $W^*$  is a stable equilibrium if and only if  $H < 2$ .  $\square$

The dynamics within the region of instability caused by dispersal can be rather complex. The stability loss of the homogeneous state can occur through different bifurcation types. In Figure 4 we plotted bifurcation diagrams along with the corresponding Lyapunov exponent diagrams for the inferior class  $w$  of site 1 using the reproductive effort as the varying parameter. The simulations were made using a Ricker recruitment ( $g(x) = e^{-x}$ ) in a ring of 6 equal patches where each subpopulation were structured as juveniles and adults ( $N = 2$ ). In the bifurcation diagrams, for each value of  $H$ , the system was iterated 10000 times, always following the attractor (by using the result of the last iteration as the initial condition for the next iteration); and the last 200 iterations were plotted. Negative Lyapunov exponent indicates stable or periodic motion, zero Lyapunov exponent indicates quasiperiodic motion, while a positive exponent indicates chaotic behavior. We performed more simulations with different number of patches and different parameters. We observed that when homogeneity is lost (first bifurcation) the stable motion is replaced by a simple periodic motion in most of the cases (see Figures 4(a), 4(b), 4(c), 4(d)) although there are values of the migration fraction that lead to quasiperiodic oscillations (Figure 5(f)) or to other stable nonhomogeneous attractors (Figure 5(e)). This appears to happen only when juvenile and adult dispersal abilities are significantly different. When such asymmetry is extreme we able to observe chaotic behavior in the metapopulation while the 1-patch system would be stable. This can be seen in Figure 5(f) where we have positive Lyapunov exponents for the coupled system while the local system would present stability, since  $m_1 = 0.6$  and  $H < 3.5$  is inside the uncoupled system stability region depict in Figure 1.

We performed simulations on  $n$ -patch systems with two age classes determining the stability boundary. Given the reproductive effort and its age distribution ( $H$



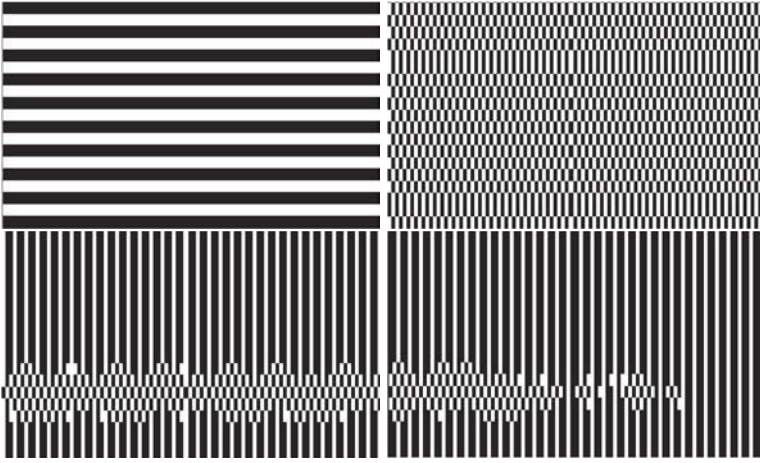
**Fig. 4.** Bifurcation (and correspondent Lyapunov exponent) diagram for the inferior class population versus  $H$ , in a 6 sites two-age structured metapopulation, with  $m_1 = 0.6$ . (a)  $\mu_1 = 0.25$  and  $\mu_2 = 0.65$ , (b)  $\mu_1 = 0.15$  and  $\mu_2 = 0.8$ , (c)  $\mu_1 = 0.001$  and  $\mu_2 = 0.999$ , (d) 1-patch local model



**Fig. 5.** (e)  $\mu_1 = 0.85$  and  $\mu_2 = 0.1$ , (f)  $\mu_1 = 0.999$  and  $\mu_2 = 0.001$

and  $m_1$ ) we numerically obtained the values of the dispersal fraction of each age class ( $\mu_1$  and  $\mu_2$ ) that drives the homogeneous equilibrium unstable. Examining Figure 2 one may suggest that the homogeneous state will be more subjected to instability caused by dispersal if the values of  $H$  and  $m_1$  are close to the stability boundary of the 1-patch model (see Figure 1). In other words, the closest the point  $(m_1, H)$  is from the curve determining the stability boundary in the local model (see Figure 1) the largest will be the set of values  $(\mu_1, \mu_2)$  that makes the homogeneous equilibrium unstable. Therefore, if the local model is “almost” unstable, then it more likely that age-dependent dispersal will induce heterogeneities. On the other hand, if the local model is “very” stable, then only very different values for the dispersal fractions can drive the system unstable. The later situation appears to be very common in natural populations (Hastings [13]), for one can easily imagine examples of natural populations that only the juveniles migrate while the adults are static and vice versa.

Dispersal induced instabilities lead to pattern formation as shown in Figure 6, where we have space-time plots. In a space-time plot the patches are along the vertical axis while 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 a pixel at position  $(t; i)$  is painted black, else it is painted white. As a general rule the striped pattern depicted in Figure 6(a) appears when juveniles have low value for migration fraction compared with adults. The “chess board” pattern appears resulting from a loss of stability of the homogeneous state due to age-dependent dispersal when adults disperse much more than juveniles. Another interesting



**Fig. 6.** Space-time plots for (a)  $H = 3.4$ ,  $m_1 = 0.6$ ,  $\mu_1 = 0.75$ ,  $\mu_2 = 0.1$ , (b)  $H = 3.4$ ,  $m_1 = 0.6$ ,  $\mu_1 = 0.75$ ,  $\mu_2 = 0.1$ . (c)–(d)  $H = 3.94$ ,  $m_1 = 0.6666$ ,  $\mu_1 = 0.0$ ,  $\mu_2 = 0.4$

phenomenon is shown in Figure 6(c) and (d). There we depict the phenomenon of chaotic transients. Some patches oscillate in regular motion while other patches form connected a region where chaotic motion prevails for a long period of time. But these bursts of chaotic oscillations suddenly disappear and the regular periodic motion is established in the whole ensemble. The size of the chaotic regions and the duration of the chaotic transient appear to be strongly dependent on the number of sites (large number of patches make easier to chaotic regions to rise) and on the initial configuration. Certainly such issue deserves more investigation.

## 7. Discussion

In this paper we presented a general model framework for studying the stability of the homogeneous state in age-structured metapopulations. We proposed two versions: a linear model which is a coupled Leslie type system and a nonlinear model which is a coupled version of a density-dependent recruitment age-structured system used by Levin and Goodyear [18] and Silva and Hallam [24, 25]. The interaction among patches was assumed to occur in a linear fashion, which means that migration is density independent as often assumed in the literature [9, 12–15, 21, 22].

The linear metapopulation model behaves essentially like the uncoupled Leslie matrix model as far as the stability of the trivial homogeneous equilibrium (metapopulation extinction) is concerned. We were able to define quantities  $R_0^j$  for each patch  $j = 1, 2, \dots, n$ , which, in some sense, represent the classic net reproductive rate  $R_0$  taking into account the interaction among patches. The reason why density independent migration does not affect the stability of the homogenous state relies on the fact that  $R_0^j \leq R_0^1 = R_0$ , that is, there exists a patch, for simplicity labeled as  $j = 1$ , which has the maximum net reproductive rate among all patches and which coincides with the net reproductive rate of the isolated patch system.



The nonlinear model have two homogeneous equilibria, the trivial equilibrium (metapopulation extinction) and a positive one for which all subpopulation equilibrium densities coincide with the positive equilibrium density for the isolated patch system. The stability properties of the trivial equilibrium is immediately reduced to the study of the linear model and the conclusion that density independent migration does not interfere in the stability of the homogeneous state follows as a corollary.

The stability properties of the positive homogeneous state are much more complex. We were able to define a positive parameter  $H$  which measures the reproductive effort of the isolated patch (for example, in the case of the Ricker recruitment  $H = \ln R_0$ ) and we found a threshold value,  $H = 2$ , below which density independent migration does not interfere in the stability properties of the homogeneous equilibrium. Moreover, below this threshold value, not even the distribution of the reproductive effort through age plays any role in the stability of the homogeneous equilibrium. But when  $H > 2$ , the stability of the homogeneous state depends on the magnitude of the reproductive effort, how it is distributed on the age axis, how migration is related to age, and how these distributions are correlated. In particular, for  $H > 2$ , there is room for a simple age-dependent-migration mechanism to create instabilities leading to pattern formation when there is a significant difference in the migration capabilities among age classes. When such a difference is somehow extreme, we were able to detect even chaotic dynamics in a system that without coupling would present stable dynamics.

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