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The multi-patch logistic equation with asymmetric migration

Bilel Elbetch Tounsia Benzekri Daniel Massart Tewfik Sari.

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Abstract

This paper considers a multi-patch model, where each patch follows a logistic law, and patches are coupled by asymmetrical migration terms. First, in the case of perfect mixing, i.e when the migration rate tends to infinity, the total population follows a logistic equation with a carrying capacity which in general is different from the sum of the n carrying capacities, and depends on the migration terms. Second, we determine, in some particular cases, the conditions under which fragmentation and asymmetrical migration can lead to a total equilibrium population greater or smaller than the sum of the carrying capacities. Finally, for the three-patch model, we show numerically the existence of at least three critical values of the migration rate for which the total equilibrium population equals the sum of the carrying capacities.

Keywords : Dynamic of population, Asymmetrical migration, Logistic equation, Slow-fast systems, Perfect mixing.

1 Introduction

The study of the dynamics of a fragmented population is fundamental in theoretical ecology, with potentially very important applied aspects: what is the effect of migration on the general population dynamics ? What are the consequences of fragmentation on the persistence or extinction of the population ? When is a single large refuge better or worse than several small ones (this is known as the SLOSS debate; see Hanski [14]) ?

The theoretical paradigm that has been used to treat these questions is that of a single population fragmented into patches coupled by migration, and the sub population in each patch follows a local logistic. This system is modeled by a non linear system of differential equation of the following form:

$$\frac{dx}{dt} = f(x) + \beta \Gamma x, \tag{1.1}$$

where $x = (x_1, \dots, x_n)^T$, with n is the number of patches in the system, x_i represents the population density in the i -th patch, $f(x) = (f_1(x_1), \dots, f_n(x_n))^T$, and $f_i(x_i) =$

$r_i x_i (1 - x_i / K_i)$. The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity of the i -th patch. The term $\beta \Gamma x$ on the right hand side of the system (1.1) describes the effect of the migration between the patches, where β is the migration rate and $\Gamma = (\gamma_{ij})$ is the matrix representing the migrations between the patches. For $i \neq j$, $\gamma_{ij} > 0$ denotes the incoming flux from patch j to patch i . If $\gamma_{ij} = 0$, there is no migration. The diagonal entries of Γ satisfy the following equation

$$\gamma_{ii} = - \sum_{j=1, j \neq i}^n \gamma_{ji}, \quad i = 1, \dots, n, \quad (1.2)$$

which means that what comes out of a patch is distributed between the other $n - 1$ patches.

In the absence of migration, ($\beta = 0$), the system (1.1) admits (K_1, \dots, K_n) as a non trivial equilibrium point. This equilibrium is globally asymptotically stable (GAS) and the total population at equilibrium is equal to the sum of the carrying capacities. The problem is whether or not the equilibrium continues to be positive and GAS, for any $\beta > 0$, and whether or not the total population at equilibrium can be greater than the sum of the carrying capacities. The case $n = 2$ and Γ symmetric

$$\Gamma = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix} \quad (1.3)$$

where $\gamma_{12} = \gamma_{21}$ is normalized to 1 has been considered by Freedman and Waltman [12] and Holt [15]. They analyzed the model in the case of perfect mixing ($\beta \rightarrow +\infty$) and showed that the total equilibrium population can be greater than the sum of the carrying capacities $K_1 + K_2$, so that patchiness has a beneficial effect on the total equilibrium population. More recently, Arditi et al. [1] analyzed the behaviour of the system for all values of β . They showed that only three situations occur: either for any $\beta > 0$, patchiness has a beneficial effect, or this effect is always detrimental, or the effect is beneficial for lower values of the migration coefficient β and detrimental for higher values. Arditi et al. [2] extended these results to the case of two patches coupled by asymmetric migration, corresponding to the matrix

$$\Gamma = \begin{bmatrix} -\gamma_{21} & \gamma_{12} \\ \gamma_{21} & -\gamma_{12} \end{bmatrix}. \quad (1.4)$$

DeAngelis et al. [6,9] considered the case of $n > 2$ patches in a circle, with symmetric migration between any patch and its two neighbours :

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta (x_{i-1} - 2x_i + x_{i+1}), \quad i = 1, \dots, n, \quad (1.5)$$

where we denote $x_0 = x_n$ and $x_{n+1} = x_1$, so that the same relationships hold between x_i , x_{i-1} and x_{i+1} for all values of i . This model corresponds to the matrix Γ whose off-diagonal elements are given by

$$\gamma_{1n} = \gamma_{n1} = \gamma_{i,i-1} = \gamma_{i-1,i} = 1, \quad \text{for } 2 \leq i \leq n \quad \text{and} \quad \gamma_{ij} = 0, \quad \text{otherwise.} \quad (1.6)$$

This system is a one-dimensional discrete-patch version of the standard reaction-diffusion model. In [6, 9] the perfect mixing case is described. The case of the general symmetric migration was considered by the authors in [10]. We studied the system:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j \neq i}^n \gamma_{ij} (x_j - x_i), \quad i = 1, \dots, n, \quad (1.7)$$

where $\beta\gamma_{ij}$ is the rate of migration between patches i and j . This system can be written in the form of System (1.1) with $\Gamma = (\gamma_{ij})$, the symmetric matrix whose diagonal entries are defined by (1.2). We studied the total population at equilibrium, as a function of the migration rate β . We gave conditions on the system parameters that ensure that the migration is beneficial or detrimental, and extended several results of [1, 6, 9].

The aim of this work is to consider the case of n patches connected by asymmetric migration. Thus, we extend [2] by considering the case $n \geq 2$, and we extend [10] by considering the case where Γ is non symmetric.

It is worth noting that an important extension of (1.1) is the so called source-sink model, where the patches are of two types: the source patches, with logistic dynamics $f_i(x_i) = r_i x_i (1 - x_i/K_i)$, as in (1.1), and the sink patches, with exponential decay $f_i(x_i) = -r_i x_i$. The main problem is the number of source patches required for population persistence. For a recent study and bibliographical references the reader can consult Arino et al [4]. For more details and information on the effects patchiness and migration in both continuous and discrete cases, and the results beyond the logistic model, the reader is referred to the work of Levin [17, 18], DeAngelis et al [6–9], Freedman et al [11], Zaker et al [22].

The paper is organized as follows. In Section 2, the mathematical model of n patches, and some preliminaries results, are introduced. In Section 3, the behavior of the model is studied when the migration rate tends to infinity. In Section 4, we compare the total equilibrium population with the sum of the carrying capacities in some particular cases. In Section 5 the three-patch model is considered, and by numerical simulations we show the existence of a new behavior for the dynamics of the total equilibrium population as a function of the migration rate. In Appendix A, we recall some results for the two-patch model with asymmetrical migration. In Appendix B, we prove some useful auxiliary results.

2 The mathematical model and preliminaries results

We consider the model of multi-patch logistic growth, coupled by asymmetric migration terms

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n, \quad (2.1)$$

where $\gamma_{ij} \geq 0$ denotes the incoming flux from patch j to patch i , for $i \neq j$. The system (2.1) can be written in the form (1.1), where f is given by:

$$f(x) = (r_1 x_1 (1 - x_1/K_1), \dots, r_n x_n (1 - x_n/K_n))^T, \quad (2.2)$$

and $\Gamma := (\gamma_{ij})_{n \times n}$ is the matrix whose diagonal entries are given by (1.2). The matrix

$$\Gamma_0 := \Gamma - \text{diag}(\gamma_{11}, \dots, \gamma_{nn}) \quad (2.3)$$

which is the same as Γ , except that the diagonal elements are 0, is called the connectivity matrix. It is the adjacency matrix of the weighted directed graph \mathcal{G} , which has exactly n vertices (the patches), and there is an arrow from patch j to patch i , with weight γ_{ij} , precisely when $\gamma_{ij} > 0$.

As to the non-negativity of the solution, we have the following proposition:

Proposition 2.1. *The domain $\mathbb{R}_+^n = \{(x_1, \dots, x_n) \in \mathbb{R}^n / x_i \geq 0, i = 1, \dots, n\}$ is positively invariant for the system (2.1).*

Proof. The proof is the same as in the symmetrical case [10, Prop 2.1]. □ □

The existence and uniqueness of the positive equilibrium $(x_1^*(\beta), \dots, x_n^*(\beta))$ of System (2.1), and its global asymptotic stability, are proved in [10, Theorem 6.1], when the connectivity matrix Γ_0 is irreducible. In all of this work, we denote by $E^*(\beta)$ the positive equilibrium and by $X_T^*(\beta)$ the total population at equilibrium:

$$E^*(\beta) = (x_1^*(\beta), \dots, x_n^*(\beta)), \quad X_T^*(\beta) = \sum_{i=1}^n x_i^*(\beta). \quad (2.4)$$

Remark 2.2. *The matrix Γ_0 being irreducible means that the weighted directed graph \mathcal{G} is strongly connected, which means that every patch is reachable from every other patch, either directly or through other patches. The matrix Γ is assumed to be irreducible throughout the rest of the paper.*

3 Perfect mixing

In this section our aim is to study the behavior of $E^*(\beta)$ and $X_T^*(\beta)$, defined by (2.4), for large migration rate, i.e when $\beta \rightarrow \infty$.

3.1 The fast dispersal limit

The following lemma was proved in [4, Lemma 2], we include a proof for the ease of the reader.

Lemma 3.1. *Let Γ be the migration matrix. Then, 0 is a single eigenvalue of Γ and all non-zero eigenvalues of Γ have negative real part. Moreover, the kernel of the matrix Γ has dimension one, and is generated by a positive vector. If the matrix Γ is symmetric, then $\ker \Gamma$ is generated by $u = (1, \dots, 1)^T$.*

Proof. Let $s = \max_{i=1, \dots, n} (-\gamma_{ii})$ and let B be the matrix defined by

$$B = \Gamma + sI.$$

First, we note that since the matrix Γ verifies the property (1.2), then Γ is a singular matrix and the vector $u = (1, \dots, 1)^T$ is an eigenvector of Γ^T associated to the eigenvalue 0. Thus u is an eigenvector of B^T , with eigenvalue s .

The matrix B^T is non negative and irreducible, so by the Perron-Frobenius theorem the spectral radius

$$\rho(B^T) = \max \{ |\lambda| : \lambda \text{ is an eigenvalue of } B^T \},$$

is a simple eigenvalue of the matrix B^T and it is the only eigenvalue of B^T which admits a positive eigenvector, so $s = \rho(B^T) = \rho(B)$. Therefore, $\Gamma = B - \rho(B)I$ and $\dim(\ker \Gamma) = \dim(\ker \Gamma^T) = 1$.

All other eigenvalues of B have modulus $< \rho(B)$, so their real parts are $< \rho(B)$. Since each eigenvalue of Γ is $\lambda - \rho(B)$, for some eigenvalue λ of B , all eigenvalues of Γ have negative real part.

Furthermore, according to the Perron-Frobenius theorem, there exists a positive vector δ such that $B\delta = \rho(B)\delta$, that is, $\Gamma\delta = (B - \rho(B)I)\delta = 0$.

In particular, if the matrix Γ is symmetric then $\delta = u$, that is, $\delta_i = 1$, for all i . $\square \quad \square$

In all of this paper, we denote by $\delta = (\delta_1, \dots, \delta_n)$ a positive vector which generates the vector space $\ker \Gamma$.

Remark 3.2. *The existence, uniqueness, and positivity of δ were also proved in Lemma 1 of Cosner et al. [5]. On the other hand, Lemma 2.1 of Guo et al [13] gives explicit formulae for the components of the vector δ , with respect to the coefficients of Γ . For two patches we have $\delta = (\gamma_{12}, \gamma_{21})$, and for three patches we have $\delta = (\delta_1, \delta_2, \delta_3)$, where*

$$\begin{cases} \delta_1 = \gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{32}\gamma_{13}, \\ \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \\ \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32}. \end{cases} \quad (3.1)$$

The following result asserts that $E^*(\infty) \in \ker \Gamma$.

Theorem 3.3. *We consider the system (2.1), then we have*

$$\lim_{\beta \rightarrow +\infty} E^*(\beta) = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} (\delta_1, \dots, \delta_n),$$

where $\alpha_i = r_i/K_i$.

Proof. Denote

$$E^*(\infty) = \left(\delta_1 \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}, \dots, \delta_n \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} \right).$$

The equilibrium point $E^*(\beta)$ is the solution of the algebraic system:

$$r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i) = 0, \quad i = 1, \dots, n. \quad (3.2)$$

The sum of these equations shows that $E^*(\beta)$ satisfies the following equation

$$\sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0. \quad (3.3)$$

Therefore $E^*(\beta)$ belongs to the ellipsoid

$$\mathbb{E}^{n-1} = \left\{ x \in \mathbb{R}^n : \Theta(x) := \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0 \right\}.$$

Note that this ellipsoid is independent of the migration terms β and γ_{ij} .

Therefore the equilibrium point $E^*(\beta)$ is the solution, in the positive cone \mathbb{R}_+^n , of the equation $\Upsilon_\beta = 0$, where

$$\Upsilon_\beta(x_1, \dots, x_n) = \left(\Upsilon_1(x_1, \dots, x_n), \dots, \Upsilon_{n-1}(x_1, \dots, x_n), \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) \right)$$

with

$$\Upsilon_i(x_1, \dots, x_n) = \frac{1}{\beta} r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1 \cdots n-1,$$

obtained from (3.2) by dividing the first $n-1$ equations by β , and replacing the last one by Equation (3.3), which is the sum of the equations. Taking the limit, when $\beta \rightarrow \infty$, of Υ_β , gives

$$\Upsilon_\infty(x) = \left(\sum_{j=1, j \neq 1}^n (\gamma_{1j} x_j - \gamma_{j1} x_1), \dots, \sum_{j=1, j \neq n-1}^n (\gamma_{n-1, j} x_j - \gamma_{j, n-1} x_{n-1}), \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) \right) \quad (3.4)$$

Now, we consider the linear system given by the first $n-1$ equations of (3.4)

$$\sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i) = 0, \quad i = 1 \cdots n-1,$$

which can be rewritten in matricial form:

$$LX = -x_n V, \quad (3.5)$$

where $X = (x_1, \dots, x_{n-1})^T$ is the unknown of the system, $L := (\gamma_{ij})_{n-1 \times n-1}$ is the sub matrix of the matrix Γ , obtained by dropping the last row and the last column of Γ , V is the vector defined by $V := (\gamma_{in})_{n-1 \times 1}$ and x_n is considered as a parameter.

In the next lemma, we show that the solution of the system (3.5) may be expressed as a function of the vector δ . This result can be stated as the following lemma:

Lemma 3.4. *The system (3.5) admits a unique solution given by*

$$\left(\frac{\delta_1}{\delta_n} x_n, \dots, \frac{\delta_{n-1}}{\delta_n} x_n \right)^T.$$

Proof. Since the matrix L is obtained from Γ by dropping the last row, and the rows of Γ sum to zero, the rank of L equals that of Γ , which is $n - 1$, so the sub matrix L is invertible.

Recall that $(\delta_1, \dots, \delta_n)$ is a vector which generates $\ker \Gamma$, so

$$\sum_{j=1, j \neq i}^n (\gamma_{ij} \delta_j - \gamma_{ji} \delta_i) = 0, \quad i = 1, \dots, n.$$

This implies

$$\begin{cases} - \left(\sum_{j=1, j \neq i}^n \gamma_{ji} \right) \frac{\delta_i}{\delta_n} + \sum_{j=1, j \neq i}^{n-1} \gamma_{ij} \frac{\delta_j}{\delta_n} = -\gamma_{in}, & i = 1, \dots, n-1, \\ \gamma_{n1} \frac{\delta_1}{\delta_n} + \dots + \gamma_{nn-1} \frac{\delta_{n-1}}{\delta_n} = \sum_{j=1}^{n-1} \gamma_{jn}. \end{cases} \quad (3.6)$$

The sum of the $n - 1$ first equations of System (3.6) gives the n -th equation, so the system (3.6) is equivalent to

$$- \left(\sum_{j=1, j \neq i}^n \gamma_{ji} \right) \frac{\delta_i}{\delta_n} + \sum_{j=1, j \neq i}^{n-1} \gamma_{ij} \frac{\delta_j}{\delta_n} = -\gamma_{in}, \quad i = 1, \dots, n-1,$$

therefore

$$L \begin{pmatrix} \frac{\delta_1}{\delta_n} & \dots & \frac{\delta_{n-1}}{\delta_n} \end{pmatrix}^T = - \begin{pmatrix} \gamma_{1n} & \dots & \gamma_{n-1n} \end{pmatrix}^T,$$

which completes the proof of lemma. \square

Hence, the solution of the equation $\Upsilon_\infty = 0$ is given by the solution of the following system:

$$\begin{cases} x_i = \frac{\delta_i}{\delta_n} x_n, & i = 1, \dots, n-1. \\ \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) = 0. \end{cases}$$

Replacing x_i in the second equation by $\frac{\delta_i}{\delta_n} x_n$ gives:

$$\frac{1}{\delta_n} x_n \left(\sum_{i=1}^n \delta_i r_i - \frac{1}{\delta_n} x_n \sum_{i=1}^n \delta_i^2 \alpha_i \right) = 0,$$

which admits $x_n = 0$ and $x_n = \delta_n \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}$ as solutions. So, the equation $\Upsilon_\infty = 0$ admits two solutions, 0 and $E^*(\infty)$.

The ellipsoid \mathbb{E}^{n-1} is compact, so the equilibrium $E^*(\beta)$ has at least one limit point in \mathbb{E}^{n-1} , when β goes to infinity. To prove the convergence of $E^*(\beta)$ to $E^*(\infty)$, it suffices to prove that the origin cannot be a limit point of $E^*(\beta)$. We claim that for any β , there exists i such that $x_i^*(\beta) \geq K_i$, which entails that $E^*(\beta)$ is bounded away from the

origin. The coordinates of the vector $\Gamma E^*(\beta)$ sum to zero, hence at least one of them, say, the i -th, is non negative. Then

$$r_i x_i^*(\beta) \left(1 - \frac{x_i^*(\beta)}{K_i}\right) \leq 0,$$

and since $x_i^*(\beta)$ cannot be negative or 0, we have $x_i^*(\beta) \geq K_i$. □ □

As a corollary of the previous theorem, we obtain the following result, which describes the total equilibrium population for perfect mixing:

Corollary 3.5. *We have*

$$X_T^*(+\infty) = \lim_{\beta \rightarrow +\infty} \sum_{i=1}^n x_i^*(\beta) = \left(\sum_{i=1}^n \delta_i \right) \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}. \quad (3.7)$$

Proof. Sum the n components of the point $E^*(\infty)$. □ □

In the case $n = 2$, one has $\delta_1 = \gamma_{12}$ and $\delta_2 = \gamma_{21}$, as shown in Remark 3.2. Therefore (3.7) becomes

$$X_T^*(+\infty) = (\gamma_{12} + \gamma_{21}) \frac{\gamma_{12} r_1 + \gamma_{21} r_2}{\gamma_{12}^2 \alpha_1 + \gamma_{21}^2 \alpha_2},$$

which is the formula [2, Equation 7] given by Arditi et al. If the matrix Γ is symmetric, one has $\delta_i = 1$, for all i , as shown in Lemma 3.1. Therefore (3.7) specializes to the formula given in [10, Equation (24)]:

$$X_T^*(+\infty) = n \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i / K_i}.$$

3.2 Two time scale dynamics

In [10] the authors also obtained the formula (3.7), in the symmetrical n -patch case (i.e the matrix Γ is symmetric), by using singular perturbation theory, see [10, Theorem 4.6]. They showed that, if $(x_1(t, \beta), \dots, x_n(t, \beta))$ is the solution of (1.7), with initial condition (x_1^0, \dots, x_n^0) , then, when $\beta \rightarrow \infty$, the total population $\sum x_i(t, \beta)$ is approximated by $X(t)$, the solution of the logistic equation

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{nK}\right), \quad \text{where } r = \frac{\sum_{i=1}^n r_i}{n}, \quad K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i} \quad \text{and } \alpha_i = \frac{r_i}{K_i} \quad (3.8)$$

with initial condition $X_0 = \sum x_i^0$. Therefore the total population behaves like the solution of the logistic equation given by (3.8). In addition, one obtains the following property: with the exception of a small initial interval, the population densities $x_i(t, \beta)$ are approximated by $X(t)/n$, see [10, Formula (37)]. Therefore, this approximation shows that, when t and β tend to ∞ , the population density $x_i(t, \beta)$ tends toward $\frac{\sum r_i}{\sum \alpha_i}$, and in addition, $x_i(t, \beta)$ quickly jumps from its initial condition x_i^0 to the average X_0/n and then is very close to $X(t)/n$. Our aim is to generalize this result for the asymmetrical n -patch model (2.1) (i.e the matrix Γ is non symmetric). We have the following result

Theorem 3.6. Let $(x_1(t, \beta), \dots, x_n(t, \beta))$ be the solution of the system (2.1) with initial condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1 \dots n$. Let $Y(t)$ be the solution of the logistic equation

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{[\sum_{i=1}^n \delta_i] K} \right), \quad \text{where } r = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i}, \quad K = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} \quad \text{and } \alpha_i = \frac{r_i}{K_i} \quad (3.9)$$

with initial condition $X_0 = \sum_{i=1}^n x_i^0$. Then, when $\beta \rightarrow \infty$, we have

$$\sum_{i=1}^n x_i(t, \beta) = Y(t) + o(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.10)$$

and, for any $t_0 > 0$, we have

$$x_i(t, \beta) = \frac{\delta_i}{\sum_{i=1}^n \delta_i} Y(t) + o(1), \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \quad (3.11)$$

Proof. Let $X(t, \beta) = \sum_{i=1}^n x_i(t, \beta)$. We rewrite the system (2.1) using the variables (X, x_1, \dots, x_{n-1}) , and get:

$$\begin{cases} \frac{dX}{dt} = \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right), \\ \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n-1. \end{cases} \quad (3.12)$$

This system is actually a system in the variables (X, x_1, \dots, x_{n-1}) , since, whenever x_n appears in the right hand side of (3.12), it should be replaced by

$$x_n = X - \sum_{i=1}^{n-1} x_i. \quad (3.13)$$

When $\beta \rightarrow \infty$, (3.12) is a *slow-fast* system, with one *slow variable*, X , and $n-1$ *fast variables*, x_i for $i = 1 \dots n-1$. According to Tikhonov's theorem [16, 19, 20] we consider the dynamics of the fast variables in the time scale $\tau = \beta t$. We get

$$\frac{dx_i}{d\tau} = \frac{1}{\beta} r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n-1.$$

where x_n is given by (3.13). In the limit $\beta \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_i}{d\tau} = \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n-1.$$

This is an $(n-1)$ -dimensional linear differential system in the variable $Z := (x_1, \dots, x_{n-1})$, which can be rewritten in matricial form:

$$\dot{Z} = \mathcal{L}Z + XV, \quad \text{with} \quad \mathcal{L} := L - U, \quad (3.14)$$

where L, V are given by (3.5) and $U = (V; \dots; V)$.

By Lemma B.1, the matrix \mathcal{L} is stable. Therefore, it is invertible and the equilibrium of the system (3.14) is GAS. This equilibrium is given by

$$\left(\frac{\delta_1}{\sum_{i=1}^n \delta_i} X, \dots, \frac{\delta_{n-1}}{\sum_{i=1}^n \delta_i} X \right)^T. \quad (3.15)$$

Indeed, we denote by $L^{(i)}, U^{(i)}$ and $V^{(i)}$ the i -th row of the matrix L, U and the vector V respectively. We have:

$$\begin{aligned} (L^{(i)} - U^{(i)}) \left(\frac{\delta_1}{\sum_{i=1}^n \delta_i} X \quad \dots \quad \frac{\delta_{n-1}}{\sum_{i=1}^n \delta_i} X \right)^T &= \frac{\delta_n}{\sum_{i=1}^n \delta_i} (L^{(i)} - U^{(i)}) \left(\frac{\delta_1}{\delta_n} X \quad \dots \quad \frac{\delta_{n-1}}{\delta_n} X \right)^T \\ &= -\frac{\delta_n}{\sum_{i=1}^n \delta_i} X \gamma_{in} - \frac{\sum_{i=1}^{n-1} \delta_i}{\sum_{i=1}^n \delta_i} X \gamma_{in} \\ &= -X \gamma_{in} = -X V^{(i)}. \end{aligned}$$

Thus, the slow manifold of System (3.12) is given by

$$x_i = \frac{\delta_i}{\sum_{i=1}^n \delta_i} X, \quad i = 1, \dots, n-1. \quad (3.16)$$

As this manifold is GAS, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (3.12) are approximated by the solutions of the *reduced model*, which is obtained by replacing (3.16) into the dynamics of the slow variable, that is:

$$\frac{dX}{dt} = \sum_{i=1}^n r_i \frac{X}{\sum_{i=1}^n \delta_i} \delta_i \left(1 - \frac{X}{(\sum_{i=1}^n \delta_i) K_i} \delta_i \right) = rX \left(1 - \frac{X}{(\sum_{i=1}^n \delta_i) K} \right), \quad (3.17)$$

where r and K are defined in (3.9). Since (3.17) admits

$$X^* = \left(\sum_{i=1}^n \delta_i \right) K = \left(\sum_{i=1}^n \delta_i \right) \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}$$

as a positive equilibrium point, which is GAS in the positive axis, the approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, letting $Y(t)$ be the solution of the reduced model (3.17) with initial condition $Y(0) = X(0, \beta) = \sum_{i=1}^n x_i^0$, then, when $\beta \rightarrow \infty$, we have the approximations (3.10) and (3.11). \square \square

In the case of perfect mixing, the approximation (3.10) shows that the total population behaves like the solution of the single logistic equation (3.9) and then, when t and β tend to ∞ , the total population $\sum x_i(t, \beta)$ tends toward $(\sum_{i=1}^n \delta_i) K = (\sum_{i=1}^n \delta_i) \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}$ as stated in Corollary 3.5. The approximation (3.11) shows that, with the exception of a thin initial boundary layer, where the population density $x_i(t, \beta)$ quickly jumps from

its initial condition x_i^0 to the average $\delta_i X_0 / \sum_{i=1}^n \delta_i$, each patch of the n-patch model behaves like the single logistic equation

$$\frac{du}{dt} = ru \left(1 - \frac{u}{K}\right) \text{ where } r = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i}, \quad K = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} \text{ and } \alpha_i = \frac{r_i}{K_i}. \quad (3.18)$$

Hence, when t and β tend to ∞ , the population density $x_i(t, \beta)$ tends toward $K = \delta_i \sum \frac{\delta_i r_i}{\delta_i^2 \alpha_i}$, as stated in Theorem 3.3.

Remark 3.7. *The single logistic equation (3.18) gives an approximation of the population density in each patch in the case of perfect mixing. The intrinsic growth rate r in (3.18) is the arithmetic mean of the r_1, \dots, r_n , weighted by $\delta_1, \dots, \delta_n$, and the carrying capacity K is the harmonic mean of K_1, \dots, K_n , weighted by $\frac{\delta_i^2 r_i}{\sum_{j=1}^n \delta_j r_j}$, $i = 1, \dots, n$.*

We point out the similarity between our expression for the carrying capacity in the limit $\beta \rightarrow \infty$, and the expression obtained in spatial homogenization, see e.g [21, Formula 81] and also [22, Formula 28].

3.3 Comparison of $X_T^*(+\infty)$ with $\sum_i K_i$.

According to Formula (3.7), it is clear that the total equilibrium population at $\beta = 0$ and at $\beta = +\infty$ are different in general.

In the remainder of this section, we give some conditions, in the space of parameters r_i, K_i, α_i and δ_i , for limit of the total equilibrium population when $\beta \rightarrow \infty$ to be greater or smaller than the sum of the carrying capacities. We show that all three cases are possible, i.e $X_T^*(+\infty)$ can be greater than, smaller than, or equal to $X_T^*(0)$.

First, we start by giving some particular values of the parameters for which $X_T^*(0) = X_T^*(+\infty)$.

Proposition 3.8. *Consider the system (2.1).*

If the vector $\left(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n}\right)$ lies in $\ker \Gamma$, then $X_T^(0) = X_T^*(+\infty)$.*

Proof. Direct consequence of the equation (3.7). □ □

Note that, if the matrix Γ is symmetric, then by Lemma 3.1, $\delta_i = 1$ for all i . Therefore, the hypothesis $\left(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n}\right) \in \ker \Gamma$ becomes $\alpha_1 = \dots = \alpha_n$, which is the same as that of [10, Prop 4.4].

In the next proposition, we give two cases which ensure that $X_T^*(0)$ can be greater or smaller than $X_T^*(+\infty)$. This result can be stated as the following proposition:

Proposition 3.9. *Consider the system (2.1).*

1. *If $\frac{K_1}{\delta_1} \leq \dots \leq \frac{K_n}{\delta_n}$ and $\delta_1 \alpha_1 \leq \dots \leq \delta_n \alpha_n$, or if $\frac{K_1}{\delta_1} \geq \dots \geq \frac{K_n}{\delta_n}$ and $\delta_1 \alpha_1 \geq \dots \geq \delta_n \alpha_n$, then $X_T^*(+\infty) \geq X_T^*(0)$.*

2. If $\frac{K_1}{\delta_1} \geq \dots \geq \frac{K_n}{\delta_n}$ and $\delta_1\alpha_1 \leq \dots \leq \delta_n\alpha_n$, or if $\frac{K_1}{\delta_1} \leq \dots \leq \frac{K_n}{\delta_n}$ and $\delta_1\alpha_1 \geq \dots \geq \delta_n\alpha_n$, then $X_T^*(+\infty) \leq X_T^*(0)$.

In both items, if at least one of the inequalities in $\frac{K_1}{\delta_1} \leq \dots \leq \frac{K_n}{\delta_n}$ or $\frac{K_1}{\delta_1} \geq \dots \geq \frac{K_n}{\delta_n}$ is strict, then the inequality is strict in the conclusion.

Proof. Apply Lemma B.2 with the following choice: $w_i = \delta_i$, $u_i = \frac{K_i}{\delta_i}$, and $v_i = \delta_i\alpha_i$, for all $i = 1, \dots, n$. \square \square

If the matrix Γ is symmetric, one has $\delta_i = 1$, for all i , as shown in Lemma 3.1. Therefore Prop. 3.9 becomes

Corollary 3.10. *Consider the system (2.1). Assume that Γ is symmetric.*

1. If $K_1 \leq \dots \leq K_n$ and $\alpha_1 \leq \dots \leq \alpha_n$, or if $K_1 \geq \dots \geq K_n$ and $\alpha_1 \geq \dots \geq \alpha_n$, then $X_T^*(+\infty) \geq X_T^*(0)$.
2. If $K_1 \geq \dots \geq K_n$ and $\alpha_1 \leq \dots \leq \alpha_n$, or if $K_1 \leq \dots \leq K_n$ and $\alpha_1 \geq \dots \geq \alpha_n$, then $X_T^*(+\infty) \leq X_T^*(0)$.

This result implies Items 1 and 2 of [8, Theorem B.1], which were obtained for the model (1.5) in the particular case $r_i = K_i$.

4 Influence of asymmetric dispersal on total population size

In this section, we will compare, in some particular cases of the system (2.1), the total equilibrium population $X_T^*(\beta) = x_1^*(\beta) + \dots + x_n^*(\beta)$, with the sum of carrying capacities denoted by $X_T^*(0) = K_1 + \dots + K_n$, when the rate of migration β varies from zero to infinity. We show that the total equilibrium population, $X_T^*(\beta)$, is generally different from the sum of the carrying capacities $X_T^*(0)$. Depending on the local parameters of the patches and the kernel of the matrix Γ , $X_T^*(\beta)$ can either be greater than, smaller than, or equal to the sum of the carrying capacities.

4.1 Asymmetric dispersal may be unfavorable to the total equilibrium population

When Γ is symmetric, we have already proved that if all the growth rates are equal then dispersal is always unfavorable to the total equilibrium population, see [10, Proposition 3.1]. We also noticed that the result still holds in the general case when Γ is not necessarily symmetric, see [10, Proposition 6.2]. Hence we have the following

Proposition 4.1. *If $r_1 = \dots = r_n$ then*

$$X_T^*(\beta) = \sum_{i=1}^n x_i^*(\beta) \leq \sum_{i=1}^n K_i, \quad \text{for all } \beta \in [0, \infty[.$$

For a two-patch logistic model, this result has been proved by Arditi et al. [1, Proposition 2, item 3] for symmetric dispersal and for asymmetric dispersal [2, Proposition 1, item 3].

4.2 Asymmetric dispersal may be favorable to the total equilibrium population

In this section, we give a situation where the dispersal is favorable to the total equilibrium population. Mathematically speaking:

Proposition 4.2. *If $\alpha_i/\alpha_j = \gamma_{ji}/\gamma_{ij}$ for all $j < i$, then*

$$X_T^*(\beta) \geq \sum_{i=1}^n K_i \quad \text{for all } \beta \geq 0.$$

Moreover, if there exist i_0 and $j_0 \neq i_0$ such that $r_{i_0} \neq r_{j_0}$, then $X_T^*(\beta) > \sum_{i=1}^n K_i$, for all $\beta > 0$.

Proof. The equilibrium point $E^*(\beta)$ satisfies the system

$$0 = \alpha_i x_i^*(\beta) (K_i - x_i^*(\beta)) + \beta \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta)), \quad i = 1 \cdots n. \quad (4.1)$$

Dividing (4.1) by $\alpha_i x_i^*$, one obtains

$$x_i^*(\beta) = K_i + \beta \sum_{j=1, j \neq i}^n \frac{\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta)}{\alpha_i x_i^*(\beta)}.$$

Taking the sum of these expressions shows that the total equilibrium population X_T^* satisfies the following relation:

$$\begin{aligned} X_T^*(\beta) &= \sum_{i=1}^n K_i + \beta \sum_{i=1}^n \sum_{j=1, j \neq i}^n \frac{\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta)}{\alpha_i x_i^*(\beta)} \\ &= \sum_{i=1}^n K_i + \beta \sum_{j < i} \left(\frac{\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta)}{\alpha_i x_i^*(\beta)} + \frac{\gamma_{ji} x_i^*(\beta) - \gamma_{ij} x_j^*(\beta)}{\alpha_j x_j^*(\beta)} \right) \\ &= \sum_{i=1}^n K_i + \beta \sum_{j < i} \frac{[\sqrt{\alpha_j \gamma_{ij}} x_j^*(\beta) - \sqrt{\alpha_i \gamma_{ji}} x_i^*(\beta)]^2 - [\sqrt{\alpha_i \gamma_{ij}} - \sqrt{\alpha_j \gamma_{ji}}]^2 x_j^*(\beta) x_i^*(\beta)}{\alpha_j \alpha_i x_j^*(\beta) x_i^*(\beta)}. \end{aligned} \quad (4.2)$$

We suppose that

$$\alpha_i/\alpha_j = \gamma_{ji}/\gamma_{ij} \quad \text{for all } i, j \in \{1, \dots, n\} \quad \text{with } j < i, \quad (4.3)$$

then

$$X_T^*(\beta) = \sum_{i=1}^n K_i + \beta \sum_{j < i} \frac{[\sqrt{\alpha_j \gamma_{ij}} x_j^*(\beta) - \sqrt{\alpha_i \gamma_{ji}} x_i^*(\beta)]^2}{\alpha_j \alpha_i x_j^*(\beta) x_i^*(\beta)} \geq \sum_{i=1}^n K_i. \quad (4.4)$$

Equality holds if and only if $\beta = 0$ or $\sqrt{\alpha_j \gamma_{ij}} x_j^*(\beta) - \sqrt{\alpha_i \gamma_{ji}} x_i^*(\beta) = 0$ for all $j < i$. Let us prove that if at least two patches have not the same growth rate then equality cannot hold for $\beta > 0$. Suppose that there exists $\beta^* > 0$ such that the positive equilibrium satisfies $\sqrt{\alpha_j \gamma_{ij}} x_j^*(\beta^*) = \sqrt{\alpha_i \gamma_{ji}} x_i^*(\beta^*)$ for all $j < i$. Then using the equation (4.3), we obtain

$$\gamma_{ij} x_j^*(\beta^*) = \gamma_{ji} x_i^*(\beta^*). \quad (4.5)$$

Replacing the equation (4.5) in the system (3.2), we get that $x_i^*(\beta^*) = K_i$ for all i , which implies that $K_j/K_i = \gamma_{ji}/\gamma_{ij}$. From this equation and the equation (4.3), we get $r_i = r_j$ for $i \neq j$, which gives a contradiction. Hence the equality in (4.4) holds if and only if $\beta = 0$. \square

When the matrix Γ is symmetric, Proposition 4.2 says that if all α_i are equal, dispersal enhances population growth, which is [10, Proposition 3.3].

4.3 Independence of the total equilibrium population with respect to asymmetric dispersal

In the next proposition we give sufficient and necessary conditions for the total equilibrium population not to depend on the migration rate.

Proposition 4.3. *The equilibrium $E^*(\beta)$ does not depend on β if and only if $(K_1, \dots, K_n) \in \ker \Gamma$. In this case we have $E^*(\beta) = (K_1, \dots, K_n) \forall \beta > 0$.*

Proof. The equilibrium $E^*(\beta)$ is the unique positive solution of the equation

$$f(x) + \beta \Gamma x = 0, \quad (4.6)$$

where f is given by (2.2).

Suppose that the equilibrium $E^*(\beta)$ does not depend on β , then we replace in Equation (4.6):

$$f(E^*) + \beta \Gamma E^* = 0. \quad (4.7)$$

The derivative of (4.7) with respect to β gives

$$\Gamma E^* = 0. \quad (4.8)$$

Replacing the equation (4.8) in the equation (4.7), we get $f(E^*) = 0$, so $E^*(\beta) = (K_1, \dots, K_n)$.

From the equation (4.8), we conclude that $(K_1, \dots, K_n) \in \ker \Gamma$.

Now, suppose that $(K_1, \dots, K_n) \in \ker \Gamma$, then (K_1, \dots, K_n) satisfies the equation (4.6). So, $E^* = (K_1, \dots, K_n)$, which proves that the total equilibrium population is independent of the migration rate β . \square

Note that, if the matrix Γ is symmetric, the previous proposition becomes: $K_1 = \dots = K_n := K$ if and only if $E^* = (K, \dots, K)$. In [2], Arditi et al. proved Proposition 4.3 for a two-patch logistic model with migration matrix Γ given by 1.4. Indeed, they proved that, if $\frac{K_1}{\gamma_{12}} = \frac{K_2}{\gamma_{21}}$ (i.e $(K_1, K_2) \in \ker \Gamma$ by Remark 3.2) then, the total equilibrium population satisfies $X_T^*(\beta) = K_1 + K_2$ for all β .

4.4 Two blocks of identical patches

We consider the model (2.1) and we assume that there are two blocks, denoted I and J , of identical patches, such that $I \cup J = \{1, \dots, n\}$. Let p be the number of patches in I and $q = n - p$ be the number of patches in J . Without loss of generality we can take $I = \{1, \dots, p\}$ and $J = \{p + 1, \dots, n\}$. The patches being identical means that they have the same specific growth rate r_i and carrying capacity K_i . Therefore we have

$$\begin{aligned} r_1 = \dots = r_p, & \quad K_1 = \dots = K_p, \\ r_{p+1} = \dots = r_n, & \quad K_{p+1} = \dots = K_n. \end{aligned} \quad (4.9)$$

For each patch $i \in I$ we denote by γ_{iJ} the flux from block J to patch i , and for each patch $j \in J$ we denote by γ_{jI} the flux from block I to patch j , as defined in Table 1. For each patch i we denote by T_i the sum of all migration rates γ_{ji} from patch i to another patch $j \neq i$ (i.e. the outgoing flux of patch i) minus the sum of the migration rates γ_{ik} from patch k to patch i , where k belongs to the same block as i . Hence, we have:

$$\begin{cases} \text{If } i \in I, & \text{then } T_i = \sum_{j \in J} \gamma_{ji} + \sum_{k \in I \setminus \{i\}} (\gamma_{ki} - \gamma_{ik}). \\ \text{If } j \in J, & \text{then } T_j = \sum_{i \in I} \gamma_{ij} + \sum_{k \in J \setminus \{j\}} (\gamma_{kj} - \gamma_{jk}). \end{cases} \quad (4.10)$$

We make the following assumption on the migration rates:

$$\begin{aligned} \gamma_{1J} = \dots = \gamma_{pJ}, & \quad \gamma_{(p+1)I} = \dots = \gamma_{nI} \\ T_1 = \dots = T_p, & \quad T_{p+1} = \dots = T_n \end{aligned} \quad (4.11)$$

where γ_{iJ} , for $i \in I$ and γ_{jI} , for $j \in J$ are defined in Table 1 and T_i are given by (4.10).

Flux	Definition
$\gamma_{iJ} = \sum_{j \in J} \gamma_{ij}$	For $i \in I$, γ_{iJ} is the flux from block J to patch i , i.e. the sum of the migration rates γ_{ij} from patch $j \in J$ to patch i .
$\gamma_{jI} = \sum_{i \in I} \gamma_{ij}$	For $j \in J$, γ_{jI} is the flux from block I to patch j , i.e. the sum of the migration rates γ_{ji} from patch $i \in I$ to patch j .
$\gamma_{IJ} = \sum_{i \in I, j \in J} \gamma_{ij}$	γ_{IJ} is the flux from block J to block I , i.e. the sum of the migration rates γ_{ij} from patch $j \in J$, to patch $i \in I$.
$\gamma_{JI} = \sum_{i \in I, j \in J} \gamma_{ji}$	γ_{JI} is the flux from block I to block J , i.e. the sum of the migration rates γ_{ji} from patch $i \in I$, to patch $j \in J$.

We have the following result

Lemma 4.4. *Assume that the conditions (4.11) are satisfied, then for all $i \in I$ and $j \in I$ one has*

$$\gamma_{iJ} = \gamma_{IJ}/p, \quad \gamma_{jI} = \gamma_{JI}/q, \quad T_i = \gamma_{JI}/p, \quad T_j = \gamma_{IJ}/q. \quad (4.12)$$

where γ_{IJ} and γ_{JI} are defined in Table 1.

Proof. The result follows from $\sum_{i \in I} \gamma_{iJ} = \gamma_{IJ}$, $\sum_{i \in J} \gamma_{jI} = \gamma_{JI}$, $\sum_{i \in I} T_i = \gamma_{JI}$ and $\sum_{i \in J} T_j = \gamma_{IJ}$. \square

In the next theorem, we will show that, at the equilibrium, and under certain conditions relating to the terms of migration, we can consider the n -patch model as a 2-patch model coupled by migration terms, which are not symmetric in general. Mathematically, we can state our main result as follows:

Theorem 4.5. *Assume that the conditions (4.9) and (4.11) are satisfied. Then the equilibrium of (2.1) is of the form*

$$x_1 = x_1^*, \dots, x_p = x_p^*, \quad x_{p+1} = x_n^*, \dots, x_n = x_n^*$$

where (x_1^*, x_n^*) is the solution of the equations

$$\begin{cases} pr_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta (\gamma_{IJ} x_n - \gamma_{JI} x_1) = 0, \\ qr_n x_n \left(1 - \frac{x_n}{K_n}\right) + \beta (\gamma_{JI} x_1 - \gamma_{IJ} x_n) = 0, \end{cases} \quad (4.13)$$

that is to say, (x_1^*, x_n^*) is the equilibrium of a 2-patch model, with specific growth rates pr_1 and qr_n , carrying capacities K_1 and K_n and migration rates γ_{JI} from patch 1 to patch 2 and γ_{IJ} from patch 2 to patch 1.

Proof. Assume that the conditions (4.9) are satisfied. Then the equilibrium of (2.1) is the unique positive solution of the set of algebraic equations

$$\begin{cases} r_1 x_i \left(1 - \frac{x_i}{K_1}\right) + \beta \sum_{k=1, k \neq i}^n (\gamma_{ik} x_k - \gamma_{ki} x_i) = 0, & i = 1, \dots, p, \\ r_n x_j \left(1 - \frac{x_j}{K_n}\right) + \beta \sum_{k=1, k \neq j}^n (\gamma_{jk} x_k - \gamma_{kj} x_j) = 0, & j = p+1, \dots, n. \end{cases} \quad (4.14)$$

We consider the following set of algebraic equations obtained from (4.14) by replacing $x_i = x_1$ for $i = 1 \dots p$ and $x_i = x_n$ for $i = p+1 \dots n$:

$$\begin{cases} r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta (\gamma_{iJ} x_n - T_i x_1) = 0, & i = 1, \dots, p, \\ r_n x_n \left(1 - \frac{x_n}{K_n}\right) + \beta (\gamma_{jI} x_1 - T_j x_n) = 0, & j = p+1, \dots, n. \end{cases} \quad (4.15)$$

Now, using the assumptions (4.11), together with the relations (4.12), we see that the system (4.15) is equivalent to the set of two algebraic equations:

$$\begin{cases} r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta \left(\frac{\gamma_{IJ}}{p} x_n - \frac{\gamma_{JI}}{p} x_1\right) = 0, \\ r_n x_n \left(1 - \frac{x_n}{K_n}\right) + \beta \left(\frac{\gamma_{JI}}{q} x_1 - \frac{\gamma_{IJ}}{q} x_n\right) = 0. \end{cases} \quad (4.16)$$

We first notice that if $x_1 = x_1^*$, $x_n = x_n^*$ is a positive solution of (4.16) then $x_i = x_1^*$ for $i = 1, \dots, p$ and $x_j = x_n^*$ for $j = 1, \dots, n$ is a positive solution of (4.14). Let us prove that (4.16) has a unique solution (x_1^*, x_n^*) . Indeed, multiplying the first equation by p and the second one by q , we deduce that (4.16) can be written in the form (4.13). \square \square

As a corollary of the previous theorem we obtain the following result which describes the total equilibrium population in the two blocks:

Corollary 4.6. *Assume that the conditions (4.9) and (4.11) are satisfied. Then the total equilibrium population $X_T^*(\beta) = px_1^*(\beta) + qx_n^*(\beta)$ of (2.1) behaves like the total equilibrium population of the 2-patch model*

$$\begin{cases} \frac{dy_1}{dt} = r_1 y_1 \left(1 - \frac{y_1}{pK_1}\right) + \beta(\gamma_2 y_n - \gamma_1 y_1), \\ \frac{dy_n}{dt} = r_n y_n \left(1 - \frac{y_n}{qK_n}\right) + \beta(\gamma_1 y_1 - \gamma_2 y_n), \end{cases} \quad (4.17)$$

with specific growth rates r_1 and r_n , carrying capacities pK_1 and qK_n , and migration rates $\gamma_1 = \frac{\gamma_{JI}}{p}$, $\gamma_2 = \frac{\gamma_{IJ}}{q}$.

Proof. From Theorem 4.5, we see that (x_1^*, x_n^*) is the positive solution of (4.13). Hence, $(y_1^* = px_1^*, y_n^* = qx_n^*)$ is the solution of the set of equations

$$\begin{cases} r_1 y_1 \left(1 - \frac{y_1}{pK_1}\right) + \beta \left(\frac{\gamma_{IJ}}{q} y_n - \frac{\gamma_{JI}}{p} y_1\right) = 0, \\ r_n y_n \left(1 - \frac{y_n}{qK_n}\right) + \beta \left(\frac{\gamma_{JI}}{p} y_1 - \frac{\gamma_{IJ}}{q} y_n\right) = 0, \end{cases} \quad (4.18)$$

obtained from (4.13) by using the change of variables $y_1 = px_1$, $y_n = qx_n$. The system (4.18) has a unique positive solution which is the equilibrium point of the 2-patch model (4.17). \square

We can describe the conditions for which, under the conditions (4.9) and (4.11), patchiness is beneficial or detrimental in model (2.1).

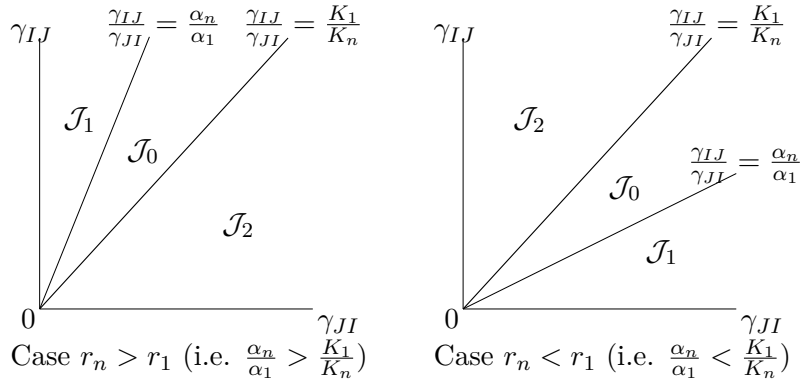


Figure 1: Qualitative properties of model (2.1) under the conditions (4.9) and (4.11). In \mathcal{J}_0 , patchiness has a beneficial effect on the total equilibrium population. This effect is detrimental in \mathcal{J}_2 . In \mathcal{J}_1 , the effect is beneficial for $\beta < \beta_0$ and detrimental for $\beta > \beta_0$.

We consider the regions in the set of parameters γ_{IJ} and γ_{JI} , denoted \mathcal{J}_0 , \mathcal{J}_1 and

\mathcal{J}_2 , depicted in Fig. 1 and defined by:

$$\begin{aligned} \text{If } r_n > r_1 \text{ then } & \begin{cases} \mathcal{J}_1 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{\gamma_{IJ}}{\gamma_{JI}} > \frac{\alpha_n}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{\alpha_n}{\alpha_1} \geq \frac{\gamma_{IJ}}{\gamma_{JI}} > \frac{K_1}{K_n} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{K_1}{K_n} > \frac{\gamma_{IJ}}{\gamma_{JI}} \right\} \end{cases} \\ \text{If } r_n < r_1 \text{ then } & \begin{cases} \mathcal{J}_1 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{\gamma_{IJ}}{\gamma_{JI}} < \frac{\alpha_n}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{\alpha_n}{\alpha_1} \leq \frac{\gamma_{IJ}}{\gamma_{JI}} < \frac{K_1}{K_n} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{JI}, \gamma_{IJ}) : \frac{K_1}{K_n} < \frac{\gamma_{IJ}}{\gamma_{JI}} \right\} \end{cases} \end{aligned} \quad (4.19)$$

where $\alpha_1 = r_1/K_1$ and $\alpha_n = r_n/K_n$.

Proposition 4.7. *Assume that the conditions (4.9) and (4.11) are satisfied. Then the total equilibrium population $X_T^*(\beta) = px_1^*(\beta) + qx_n^*(\beta)$ of (2.1) satisfies the following properties*

1. *If $r_1 = r_n$ then $X_T^*(\beta) < pK_1 + qK_n$ for all $\beta > 0$.*
2. *If $r_n \neq r_1$, let $\mathcal{J}_0, \mathcal{J}_1$ and \mathcal{J}_2 , be defined by (4.19). Then we have:*
 - *if $(\gamma_{JI}, \gamma_{IJ}) \in \mathcal{J}_0$ then $X_T^*(\beta) > pK_1 + qK_n$ for any $\beta > 0$,*
 - *if $(\gamma_{JI}, \gamma_{IJ}) \in \mathcal{J}_1$ then $X_T^*(\beta) > pK_1 + qK_n$ for $0 < \beta < \beta_0$ and $X_T^*(\beta) < pK_1 + qK_n$ for $\beta > \beta_0$, where*

$$\beta_0 = \frac{r_n - r_1}{\frac{\gamma_{IJ}}{\alpha_n} - \frac{\gamma_{JI}}{\alpha_1}} \frac{1}{\frac{\alpha_1}{p} + \frac{\alpha_n}{q}}.$$

- *if $(\gamma_{JI}, \gamma_{IJ}) \in \mathcal{J}_2$ then $X_T^*(\beta) < pK_1 + qK_n$ for any $\beta > 0$.*
- *If $\frac{\gamma_{IJ}}{\gamma_{JI}} = \frac{K_1}{K_n}$, then $X_T^*(\beta) = pK_1 + qK_n$ for all $\beta \geq 0$.*

Proof. This is a consequence of Proposition A.1 and Corollary 4.6. □ □

Let us explain the result of Proposition 4.7 in the particular case where $p = n - 1$. In this case, the condition (4.11) becomes

$$\gamma_{1n} = \dots = \gamma_{n-1,n} \quad \text{and} \quad T_1 = \dots = T_{n-1}, \quad (4.20)$$

where $T_i = \gamma_{ni} + \sum_{k \neq i} (\gamma_{ki} - \gamma_{ik})$.

Therefore, if the matrix Γ is symmetric, the conditions (4.20) are equivalent to the conditions $\gamma_{n1} = \dots = \gamma_{n,n-1}$, which mean that the fluxes of migration between the n -th patch and all $n - 1$ identical patches are equal. Hence, Proposition 4.7, showing that the n -patch model behaves like a 2-patch model, is the same as [10, Prop. 3.4], where the model (2.1) was considered with Γ symmetric, $n - 1$ patches are identical and the fluxes of migration between the n -th patch and all these $n - 1$ identical patches are equal. Thus Proposition 4.7 generalizes Proposition 3.4 of [10], to asymmetric dispersal and for any two identical blocks, provided that the conditions (4.11) are satisfied.

5 Three-patch model

In this section, we consider the model of three patches coupled by asymmetrical terms of migrations. Under the irreducibility hypothesis on the matrix Γ , there are five possible cases, modulo permutation of the three patches, see Figures 2 and 3.

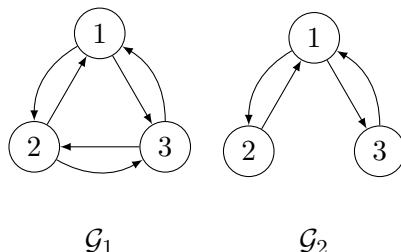


Figure 2: The two graphs \mathcal{G}_1 and \mathcal{G}_2 where we can have the symmetry of migration, if $\gamma_{ij} = \gamma_{ji}$.

The connectivity matrices associated to the graphs \mathcal{G}_1 and \mathcal{G}_2 are given by

$$\Gamma_0^{(1)} = \begin{bmatrix} 0 & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & 0 & \gamma_{23} \\ \gamma_{31} & \gamma_{32} & 0 \end{bmatrix}, \quad \text{and} \quad \Gamma_0^{(2)} = \begin{bmatrix} 0 & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & 0 & 0 \\ \gamma_{31} & 0 & 0 \end{bmatrix}.$$

For the remaining cases, the graphs $\mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 , cannot be symmetrical:

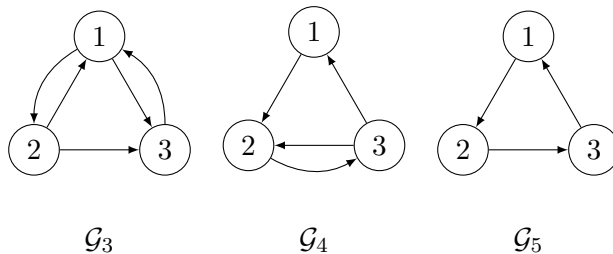


Figure 3: The three graphs $\mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 where we cannot have the symmetry of the migration terms.

The associated connectivity matrices are given by

$$\Gamma_0^{(3)} = \begin{bmatrix} 0 & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & 0 & \gamma_{23} \\ \gamma_{31} & 0 & 0 \end{bmatrix}, \quad \Gamma_0^{(4)} = \begin{bmatrix} 0 & \gamma_{12} & 0 \\ 0 & 0 & \gamma_{23} \\ \gamma_{31} & \gamma_{32} & 0 \end{bmatrix} \quad \text{and} \quad \Gamma_0^{(5)} = \begin{bmatrix} 0 & \gamma_{12} & 0 \\ 0 & 0 & \gamma_{23} \\ \gamma_{31} & 0 & 0 \end{bmatrix}.$$

In Table 2, we give the formula of perfect mixing $X_T^*(+\infty)$ for each of the five cases. In the numerical simulations, we show that we can have new behaviors of $X_T^*(\beta)$. In

Table 2: The perfect mixing abundance $X_T^*(+\infty)$ is computed with Eq. (3.7) for the five cases. The coefficients δ_i are given by the equation (3.1).

Graphs	The formula of perfect mixing $X_T^*(+\infty)$
\mathcal{G}_1	$(\delta_1 + \delta_2 + \delta_3) \frac{\delta_1 r_1 + \delta_2 r_2 + \delta_3 r_3}{\delta_1^2 \alpha_1 + \delta_2^2 \alpha_2 + \delta_3^2 \alpha_3}$
\mathcal{G}_2	$(\gamma_{12}\gamma_{13} + \gamma_{21}\gamma_{13} + \gamma_{12}\gamma_{31}) \frac{\gamma_{12}\gamma_{13}r_1 + \gamma_{21}\gamma_{13}r_2 + \gamma_{12}\gamma_{31}r_3}{(\gamma_{12}\gamma_{13})^2\alpha_1 + (\gamma_{21}\gamma_{13})^2\alpha_2 + (\gamma_{12}\gamma_{31})^2\alpha_3}$
\mathcal{G}_3	$(\gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{12}\gamma_{31} + \delta_2) \frac{(\gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23})r_1 + \delta_2 r_2 + \gamma_{12}\gamma_{31}r_3}{(\gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23})^2\alpha_1 + \delta_2^2\alpha_2 + (\gamma_{12}\gamma_{31})^2\alpha_3}$
\mathcal{G}_4	$(\gamma_{12}\gamma_{23} + \gamma_{23}\gamma_{31} + \gamma_{12}\gamma_{31} + \gamma_{32}\gamma_{31}) \frac{\gamma_{12}\gamma_{23}r_1 + \gamma_{23}\gamma_{31}r_2 + (\gamma_{12}\gamma_{31} + \gamma_{32}\gamma_{31})r_3}{(\gamma_{12}\gamma_{23})^2\alpha_1 + (\gamma_{23}\gamma_{31})^2\alpha_2 + (\gamma_{12}\gamma_{31} + \gamma_{32}\gamma_{31})^2\alpha_3}$
\mathcal{G}_5	$(\gamma_{12}\gamma_{23} + \gamma_{23}\gamma_{31} + \gamma_{12}\gamma_{31}) \frac{\gamma_{12}\gamma_{23}r_1 + \gamma_{23}\gamma_{31}r_2 + \gamma_{12}\gamma_{31}r_3}{(\gamma_{12}\gamma_{23})^2\alpha_1 + (\gamma_{23}\gamma_{31})^2\alpha_2 + (\gamma_{12}\gamma_{31})^2\alpha_3}$

the case $n = 2$, it was shown in [1, 2] that there exists at most one positive value of β such that $X_T^*(\beta) = K_1 + K_2$. In [10], in the case $n = 3$ and Γ is symmetric, we gave numerical values for the parameters such that there exists two positive value of β such that $X_T^*(\beta) = K_1 + K_2 + K_3$, and we were not able to find more than two values. The novelty when Γ is not symmetric is that we can find examples with three positive values. Indeed, we may have the following situation : $\frac{dX_T^*}{d\beta}(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2 + K_3$, and there exist three values $0 < \beta_1 < \beta_2 < \beta_3$ for which we have

$$X_T^*(\beta) \begin{cases} > K_1 + K_2 + K_3 & \text{for } \beta \in]0, \beta_1[\cup]\beta_2, \beta_3[, \\ < K_1 + K_2 + K_3 & \text{for } \beta \in]\beta_1, \beta_2[\cup]\beta_3, +\infty[. \end{cases} \quad (5.1)$$

Note that we obtain the derivative of the total equilibrium population at $\beta = 0$ by differentiating the equation (4.2) at $\beta = 0$, which gives

$$\frac{dX_T^*}{d\beta}(0) = \sum_{i=1}^n \frac{1}{r_i} \sum_{j=1, j \neq i}^n \gamma_{ij} K_j - \gamma_{ji} K_i.$$

The same situation holds for each of the five graphs $\mathcal{G}_1, \mathcal{G}_2, \mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 , i.e, there exist three values $0 < \beta_1 < \beta_2 < \beta_3$ for which (5.1) hold. See Figures 4, (for the graph \mathcal{G}_1), 5, (for the graph \mathcal{G}_2), 6-a, (for the graph \mathcal{G}_3), 6-b, (for the graph \mathcal{G}_4), and 6-c, (for the graph \mathcal{G}_5).

Table 3: The numerical values of the parameters for the logistic growth function and migration coefficients of the model (2.1), with $n = 3$, used in Fig. 4,5,6-a,6-b and Fig 6-c. For all figures we have $(r_1, r_2, r_3, K_1, K_2, K_3) = (4, 0.7, 0.6, 5, 1, 4)$. The perfect mixing abundance $X_T^*(+\infty)$ is computed with Eq. (3.7).

Figure	γ_{21}	γ_{12}	γ_{31}	γ_{13}	γ_{32}	γ_{23}	$\frac{dX_T^*}{d\beta}(0)$	$X_T^*(+\infty)$
4	0.15	3	0.2	0.04	11	0.1	1.06	9.21
5	14.9	10	0.2	0.04	0	0	77.20	9.86
6-a	1.44	0.01	0.2	0.04	1	0	3.11	8.93
6-b	1.52	0	0	1	1	0.002	3.52	8.72
6-c	1.51	0	0	1	1	0	3.46	8.75

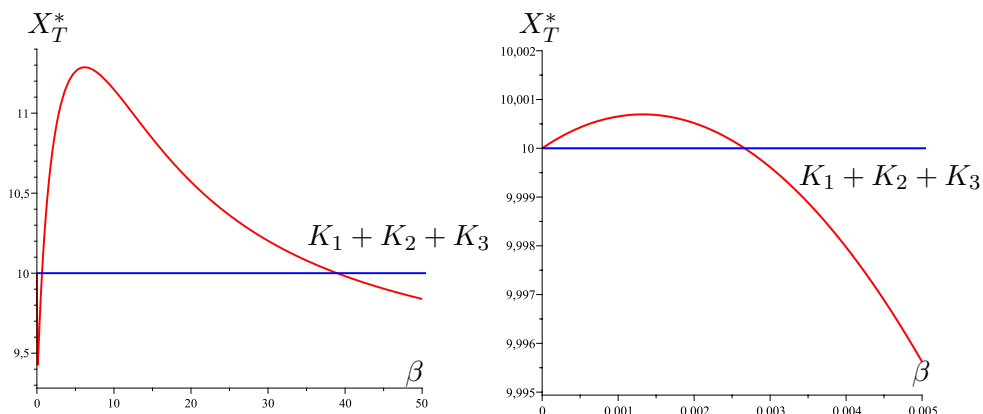


Figure 4: Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of the migration rate β . The figure on the right is a zoom, near the origin, of the figure on the left. The parameter values are given in Table 3.

6 Conclusion

The aim of this paper is to generalize, to a multi-patch model with asymmetric dispersal, the results obtained in [10] for a multi-patch model with symmetric dispersal.

In Section 3 we consider the particular case of perfect mixing, when the migration rate goes to infinity, that is, individuals may travel freely between patches. As in [10], we compute the total equilibrium population in that case, and, by perturbation arguments, we prove that the dynamics in this ideal case provides a good approximation to the case when the migration rate is large. Our results generalize those of [2] (asymmetric migration matrix, only two patches), [8] (arbitrarily many patches, but the migration matrix is symmetric and zero outside the corners and the three main diagonals), and [10] (arbitrarily many patches; arbitrary, but symmetric, migration).

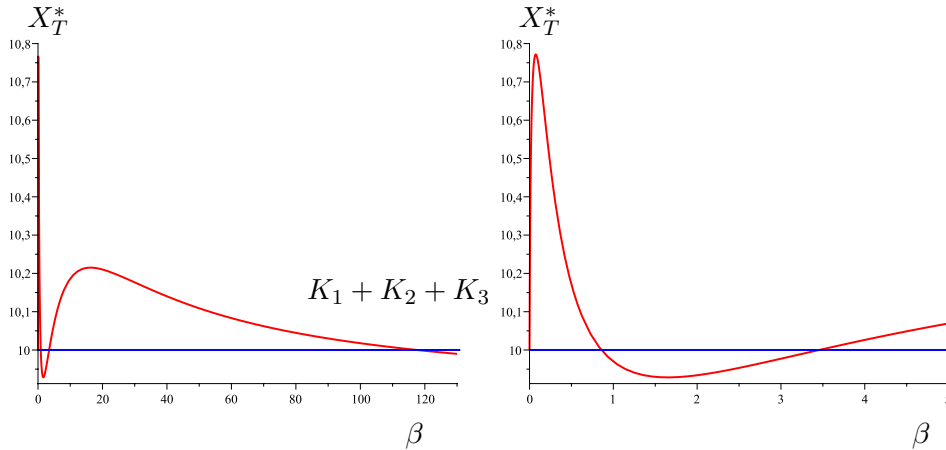


Figure 5: Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of the migration rate β . The figure on the right is a zoom, near the origin, of the figure on the left. The parameter values are given in Table 3.

In Section 4 we consider the equation

$$\text{total equilibrium population} = \text{sum of the carrying capacities of the patches.} \quad (6.1)$$

We give a complete solution in the case when the n patches are partitioned into two blocks of identical patches. Our results mirror those of [2], which deals with the two-patch case. Specifically, Equation (6.1) admits at most one non-trivial solution.

In Section 5 we give numerical values for the dispersion parameters such that Equation (6.1) has at least three non-trivial solutions. In [10] we proved that for three patches and symmetric dispersal, there may be at least two solutions. A mathematical proof that, when $n=3$, Equation (6.1) has at most three solutions, would certainly be desirable, and could spur further work. Upper bounds for arbitrarily many patches would also be interesting.

Appendix

A The 2-patch asymmetric model

We consider the 2-patch logistic equation with asymmetric migrations. For simplicity we denote $\gamma_2 := \gamma_{12}$ the migration rate from patch 2 to patch 1 and $\gamma_1 := \gamma_{21}$ from patch 1 to patch 2. The model is written:

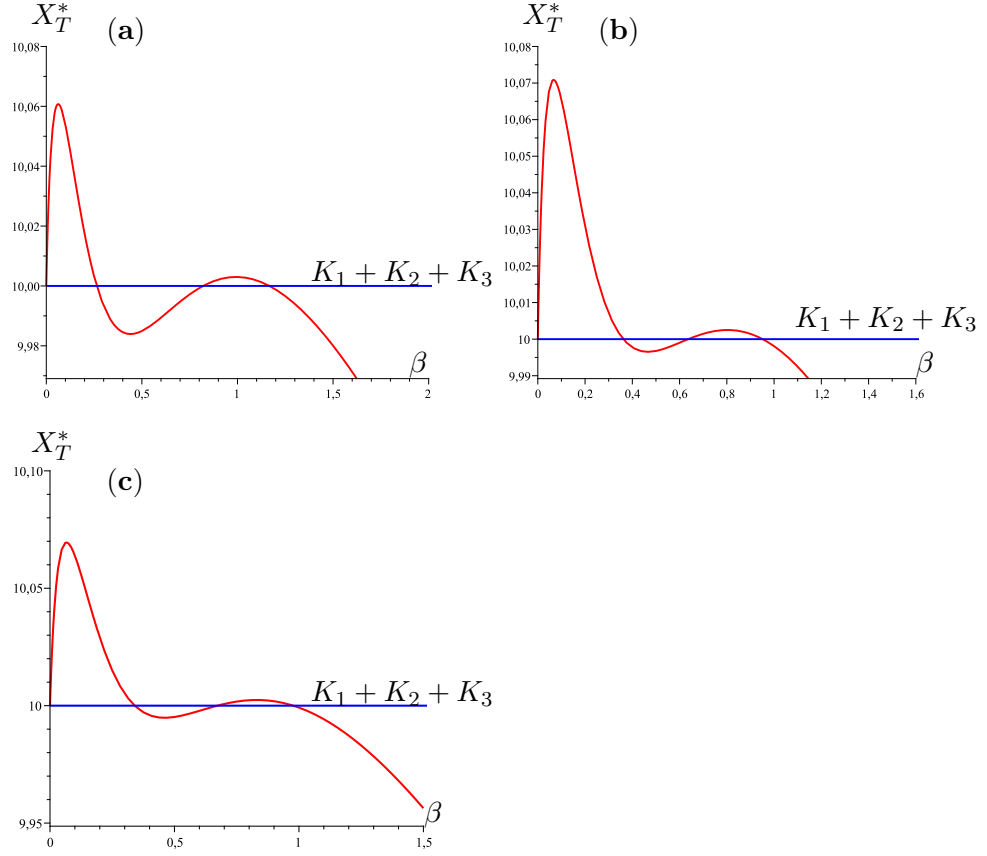


Figure 6: Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of migration rate β . The parameter values are given in Table 3.

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{L_1}\right) + \beta (\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{L_2}\right) + \beta (\gamma_1 x_1 - \gamma_2 x_2). \end{cases} \quad (\text{A.1})$$

Note that the system (A.1) is studied in [1, 6, 11, 12, 15] in the case where the migration rates satisfy $\gamma_1 = \gamma_2$, and in [2] for general migration rates. This system admits a unique equilibrium which is GAS. We denote by $E^*(\beta) = (x_1^*(\beta), x_2^*(\beta))$ this equilibrium and by $X_T^*(\beta)$ the sum of $x_i^*(\beta)$. We consider the regions in the set of the parameters γ_1 and

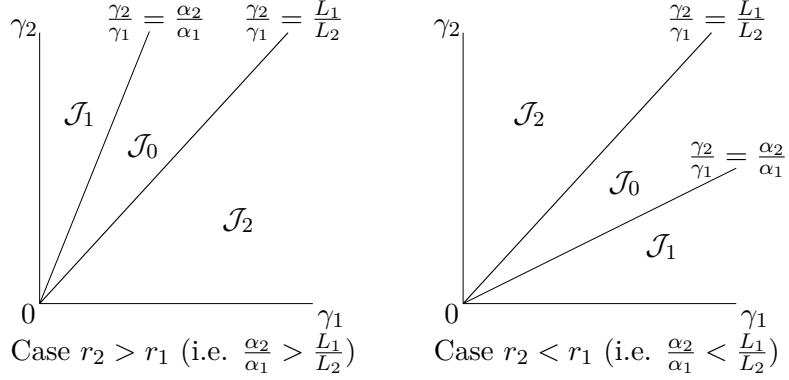


Figure 7: Qualitative properties of model (A.1). In \mathcal{J}_0 , patchiness has a beneficial effect on total equilibrium population. This effect is detrimental in \mathcal{J}_2 . In \mathcal{J}_1 , the effect is beneficial for $\beta < \beta_0$ and detrimental for $\beta > \beta_0$. In the figure $\alpha_1 = r_1/L_1$ and $\alpha_2 = r_2/L_2$.

γ_2 , denoted \mathcal{J}_0 , \mathcal{J}_1 and \mathcal{J}_2 , depicted in Fig. 7 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 > r_1 \text{ then} \\ \text{If } r_2 < r_1 \text{ then} \end{array} \right\} \left\{ \begin{array}{l} \mathcal{J}_1 = \left\{ (\gamma_1, \gamma_2) : \frac{\gamma_2}{\gamma_1} > \frac{\alpha_2}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_1, \gamma_2) : \frac{\alpha_2}{\alpha_1} \geq \frac{\gamma_2}{\gamma_1} > \frac{L_1}{L_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_1, \gamma_2) : \frac{L_1}{L_2} > \frac{\gamma_2}{\gamma_1} \right\} \\ \mathcal{J}_1 = \left\{ (\gamma_1, \gamma_2) : \frac{\gamma_2}{\gamma_1} < \frac{\alpha_2}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_1, \gamma_2) : \frac{\alpha_2}{\alpha_1} \leq \frac{\gamma_2}{\gamma_1} < \frac{L_1}{L_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_1, \gamma_2) : \frac{L_1}{L_2} < \frac{\gamma_2}{\gamma_1} \right\} \end{array} \right. \quad (\text{A.2})$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (A.1).

Proposition A.1. *The total equilibrium population of (A.1) satisfies the following properties*

1. If $r_1 = r_2$ then $X_T^*(\beta) \leq L_1 + L_2$ for all $\beta \geq 0$.
2. If $r_2 \neq r_1$, let \mathcal{J}_0 , \mathcal{J}_1 and \mathcal{J}_2 , be defined by (A.2). Then we have:
 - if $(\gamma_1, \gamma_2) \in \mathcal{J}_0$ then $X_T^*(\beta) > L_1 + L_2$ for any $\beta > 0$
 - if $(\gamma_1, \gamma_2) \in \mathcal{J}_1$ then $X_T^*(\beta) > L_1 + L_2$ for $0 < \beta < \beta_0$ and $X_T^*(\beta) < L_1 + L_2$ for $\beta > \beta_0$, where

$$\beta_0 = \frac{r_2 - r_1}{\frac{\gamma_2}{\alpha_2} - \frac{\gamma_1}{\alpha_1}} \frac{1}{\alpha_1 + \alpha_2}.$$

- if $(\gamma_1, \gamma_2) \in \mathcal{J}_2$ then $X_T^*(\beta) < L_1 + L_2$ for any $\beta > 0$
- If $\frac{\gamma_2}{\gamma_1} = \frac{L_1}{L_2}$, then $x_1^*(\beta) = L_1$ and $x_2^*(\beta) = L_2$ for all $\beta \geq 0$.
Therefore $X_T^*(\beta) = L_1 + L_2$ for all $\beta \geq 0$.

Proof. This result was established by Arditi et al. [2]. Part (1) is Proposition 1 of [2]. The first three items of part (2) are Proposition 2 of [2]. For the last item of part (2), see the last paragraph in page 12 of [2]. The explicit expression of β_0 was not given in [2], however, it is easy to deduce it from the formulas given in [2]. The reader is cautioned that we denote by γ_i the terms γ_i^{-1} of [2]. \square \square

B Some useful results

We begin with a

Lemma B.1. *The matrix \mathcal{L} defined by (3.14) is stable, that is to say, all its eigenvalues have negative real part.*

Proof. We consider the two matrices

$$G := \begin{bmatrix} L - U & V \\ 0 & \dots & 0 & 0 \end{bmatrix}, \quad P := \begin{bmatrix} I & 0 \\ 1 & \dots & 1 & 1 \end{bmatrix},$$

where L and V are the sub-matrices of the matrix Γ given in (3.5) and $U = [V, \dots V]$. We prove that the two matrices Γ and G are conjugate by the matrix P , that is to say $P^{-1}GP = \Gamma$.

The inverse of matrix P is given by

$$P^{-1} = \begin{bmatrix} I & 0 \\ -1 & \dots & -1 & 1 \end{bmatrix}.$$

We have

$$P^{-1}GP = \begin{bmatrix} L & V \\ \gamma_{n1} & \dots & \gamma_{nn-1} & -\sum_{j=1, j \neq 1}^n \gamma_{jn} \end{bmatrix} = \Gamma.$$

Two conjugate matrices have the same eigenvalues. As the matrix G is triangular by block, these eigenvalues are zero and the eigenvalues of the matrix $L - U$. Therefore, since 0 is a simple eigenvalue of the matrix Γ , the eigenvalues of the matrix $L - U$ are the eigenvalues of the matrix Γ except 0. By Lemma 3.1 all non-zero eigenvalues of Γ have negative real part. \square \square

Lemma B.2. *Let $(u_n)_{n \geq 1}$, $(v_n)_{n \geq 1}$ and $(w_n)_{n \geq 1}$ be three real and non-negative sequences. Then,*

1. *if $(u_n)_{n \geq 1}$ and $(v_n)_{n \geq 1}$ are both non-increasing, or both non-decreasing, then we have, for all $N \geq 1$,*

$$\left(\sum_{n=1}^N w_n \right) \left(\sum_{n=1}^N w_n u_n v_n \right) \geq \left(\sum_{n=1}^N w_n u_n \right) \left(\sum_{n=1}^N w_n v_n \right), \quad (\text{B.1})$$

2. if $(u_n)_{n \geq 1}$ is non-decreasing and $(v_n)_{n \geq 1}$ is non-increasing, or if $(u_n)_{n \geq 1}$ is non-increasing and $(v_n)_{n \geq 1}$ is non-decreasing, then, we have, for all $N \geq 1$,

$$\left(\sum_{n=1}^N w_n \right) \left(\sum_{n=1}^N w_n u_n v_n \right) \leq \left(\sum_{n=1}^N w_n u_n \right) \left(\sum_{n=1}^N w_n v_n \right). \quad (\text{B.2})$$

In both items, if $(u_n)_{n \geq 1}$ is not constant, then the inequality in the conclusion is strict.

Proof. We prove Item 1 by induction on N , in the case when $(u_n)_{n \geq 1}$ and $(v_n)_{n \geq 1}$ are both non-decreasing, the other case being identical. Obviously, Equation (B.1) holds for $N = 1$. Now, assume that (B.1) holds for N , then we proceed to show that (B.1) holds for $N + 1$. Since

$u_{N+1} [w_1(v_{N+1} - v_1) + \dots + w_N(v_{N+1} - v_N)] \geq u_1 w_1(v_{N+1} - v_1) + \dots + u_N w_N(v_{N+1} - v_N)$,
the inequality being strict if $(u_n)_{n \geq 1}$ is not constant, we observe that

$$\sum_{n=1}^N w_n u_n v_n + \left(\sum_{n=1}^N w_n \right) u_{N+1} v_{N+1} \geq \left(\sum_{n=1}^N w_n v_n \right) u_{N+1} + \left(\sum_{n=1}^N w_n u_n \right) v_{N+1}. \quad (\text{B.3})$$

From the induction hypothesis and the equation (B.3), it follows that

$$\begin{aligned} \left(\sum_{n=1}^{N+1} w_n \right) \left(\sum_{n=1}^{N+1} w_n u_n v_n \right) &= \left(\sum_{n=1}^N w_n \right) \left(\sum_{n=1}^N w_n u_n v_n \right) + w_{N+1} \left(\sum_{n=1}^N w_n u_n v_n \right) \\ &\quad + w_{N+1}^2 u_{N+1} v_{N+1} + \left(\sum_{n=1}^N w_n \right) w_{N+1} u_{N+1} v_{N+1} \\ &\geq \left(\sum_{n=1}^N w_n \right) \left(\sum_{n=1}^N w_n u_n v_n \right) + w_{N+1}^2 u_{N+1} v_{N+1} \\ &\quad + \left(\sum_{n=1}^N w_n v_n \right) u_{N+1} w_{N+1} + \left(\sum_{n=1}^N w_n u_n \right) v_{N+1} w_{N+1} \\ &\geq \left(\sum_{n=1}^N w_n u_n \right) \left(\sum_{n=1}^N w_n v_n \right) + w_{N+1}^2 u_{N+1} v_{N+1} \\ &\quad + \left(\sum_{n=1}^N w_n v_n \right) u_{N+1} w_{N+1} + \left(\sum_{n=1}^N w_n u_n \right) v_{N+1} w_{N+1} \\ &= \left(\sum_{n=1}^{N+1} w_n u_n \right) \left(\sum_{n=1}^{N+1} w_n v_n \right). \end{aligned}$$

This completes the proof of item 1.

Equation (B.2) can then be proved by reversing all the inequalities in the proof of (B.1) above. \square \square

This result is proved by DeAngelis et al. [7, Lemma 2.6] for Part (2) and in [8, Proposition A.3] for part (1), where $w_n = 1$ for all $n \geq 1$. Here we generalize this result for any positive sequence.

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