



HAL
open science

The multi-patch logistic equation with asymmetric migration

Bilel Elbetch, Tounsia Benzekri, Daniel Massart, Tewfik Sari

► **To cite this version:**

Bilel Elbetch, Tounsia Benzekri, Daniel Massart, Tewfik Sari. The multi-patch logistic equation with asymmetric migration. 2021. hal-03179136v2

HAL Id: hal-03179136

<https://hal.science/hal-03179136v2>

Preprint submitted on 17 May 2021 (v2), last revised 15 Jan 2022 (v4)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

3 **THE MULTI-PATCH LOGISTIC EQUATION WITH**
4 **ASYMMETRIC MIGRATION**

5 ELBETCH BILEL, BENZEKRI TOUNSIA, MASSART DANIEL, SARI TEWFIK

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 law 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.

6 1. INTRODUCTION

7 The study of the dynamics of a fragmented population is fundamental in theo-
8 retical ecology, with potentially very important applied aspects: what is the effect
9 of migration on the general population dynamics ? What are the consequences of
10 fragmentation on the persistence or extinction of the population ? When is a single
11 large refuge better or worse than several small ones (this is known as the SLOSS
12 debate; see Hanski [18]) ?

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

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

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

$$f_i(x_i) = r_i x_i (1 - x_i / K_i), \quad i = 1, \dots, n. \quad (1.2)$$

19 The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying
20 capacity of patch i . The term $\beta\Gamma x$ on the right hand side of the system (1.1)

2010 *Mathematics Subject Classification.* ****,****,****.

Key words and phrases. Population Dynamics; Asymmetrical migration; Logistic equation; Slow-fast systems; Perfect mixing.

Submitted *****, 2021. Published *****, 2021.

21 describes the effect of the migration between the patches, where β is the migration
 22 rate and $\Gamma = (\gamma_{ij})$ is the matrix representing the migrations between the patches.
 23 For $i \neq j$, $\gamma_{ij} > 0$ denotes the incoming flux from patch j to patch i . If $\gamma_{ij} = 0$,
 24 there is no migration. The diagonal entries of Γ satisfy the following equation

$$\gamma_{ii} = - \sum_{j=1, j \neq i}^n \gamma_{ji}, \quad i = 1, \dots, n, \quad (1.3)$$

25 which means that what comes out of a patch is distributed between the other $n - 1$
 26 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

$$\Gamma = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}$$

where $\gamma_{12} = \gamma_{21}$ is normalized to 1 has been considered by Freedman and Waltman
 [14] and Holt [19]. 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

$$\Gamma = \begin{bmatrix} -\gamma_{21} & \gamma_{12} \\ \gamma_{21} & -\gamma_{12} \end{bmatrix}.$$

27 DeAngelis et al. [8, 11] considered the case of $n > 2$ patches in a circle, with
 28 symmetric migration between any patch and its two neighbours :

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta (x_{i-1} - 2x_i + x_{i+1}), \quad i = 1, \dots, n, \quad (1.4)$$

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 non-zero off-diagonal elements are given by

$$\gamma_{1n} = \gamma_{n1} = 1 \quad \text{and} \quad \gamma_{i,i-1} = \gamma_{i-1,i} = 1, \quad \text{for } 2 \leq i \leq n.$$

29 The system (1.4) is a one-dimensional discrete-patch version of the standard reaction-
 30 diffusion model. In [8, 11] the perfect mixing case is described.

31 The case of the general symmetric migration was considered by the authors in
 32 [12]. We studied the system:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n \gamma_{ij} (x_j - x_i), \quad i = 1, \dots, n, \quad (1.5)$$

33 where $\beta\gamma_{ij}$ is the rate of migration between patches i and j . This system can
 34 be written in the form of System (1.1) with $\Gamma = (\gamma_{ij})$, the symmetric matrix
 35 whose diagonal entries are defined by (1.3). We studied the total population at
 36 equilibrium, as a function of the migration rate β . We gave conditions on the
 37 system parameters that ensure that migration is beneficial or detrimental, and
 38 extended several results of [1, 8, 11].

39 The aim of this work is to consider the case of n patches connected by asymmetric
 40 migration. Thus, we extend [2] by considering the case $n \geq 2$, and we extend [12]
 41 by considering the case where Γ is non symmetric.

42 An important extension of (1.1) is the so called source-sink model, where the
 43 patches are of two types: the source patches, $1 \leq i \leq m$, with logistic dynamics,
 44 and the sink patches, $m + 1 \leq i \leq n$, with exponential decay

$$\begin{cases} f_i(x_i) = r_i x_i (1 - x_i/K_i), & i = 1, \dots, m, \\ f_i(x_i) = -r_i x_i, & i = m + 1, \dots, n. \end{cases} \quad (1.6)$$

45 The main problem is the number of source patches required for population per-
 46 sistence. For a recent study and bibliographical references the reader can consult
 47 Arino et al. [4] and Wu et al. [29].

48 There is another important extension of (1.1,1.2), where the dynamics on patch
 49 i is of the form

$$f_i(x_i) = r_i x_i (1 - x_i/K_i) - \gamma_i x_i, \quad i = 1, \dots, n, \quad (1.7)$$

50 with $\gamma_i > 0$. This model is the limit system (when $t \rightarrow +\infty$) of an SIS model
 51 in n patches connected by human migration. For details and further reading, see
 52 Section 5. Note that, when $r_i < \gamma_i$ for some patches, system (1.1,1.7) is a source-
 53 sink model. Contrary to (1.6), the mortality in sink patch is density-dependent.
 54 For more details and bibliographical references the reader is referred to [15].

55 Another example of source-sink model is the system considered by Nagahara et
 56 al. [24], called the ‘‘island chain’’ model, which is of the form:

$$\frac{dx_i}{dt} = x_i (m_i - x_i) + \beta(x_{i-1} - 2x_i + x_{i+1}), \quad i = 1, \dots, n, \quad (1.8)$$

where we denote $x_0 = x_1$ and $x_{n+1} = x_n$. This model is of the form (1.1), Γ being
 the matrix which verifies 1.3, and whose non-zero off-diagonal elements are given
 by

$$\gamma_{i,i-1} = \gamma_{i-1,i} = 1, \quad \text{for } 2 \leq i \leq n.$$

57 In the model (1.8) the ratios $\alpha_i = r_i/K_i$ in (1.2) are equal and are normalized to 1.
 58 The constant m_i represents both the intrinsic growth rate of the species in patch i
 59 and the carrying capacity of the patch. If $m_i > 0$, then patch i is favorable to the
 60 species. It is a source. The case $m_i = 0$ is permitted and corresponds to a sink.
 61 The main purpose is to find the resource allocation (m_1, \dots, m_n) that maximizes
 62 the total population at equilibrium, under the constraint that $\sum_i m_i = m > 0$ is
 63 fixed. For more details and information on the maximization of the total population
 64 with logistic growth in a patchy environment, the reader is referred to [24] and the
 65 references therein.

66 For general information of the effects of patchiness and migration in both con-
 67 tinuous and discrete cases, and the results beyond the logistic model, the reader is
 68 referred to the work of Levin [21, 22], DeAngelis et al. [8, 9, 10, 11], Freedman et
 69 al. [13], Zaker et al. [31].

70 It is worth noting that System (1.1) appears in metapopulation dynamics, in-
 71 volving explicit movements of the individuals between distinct locations. For the
 72 graph theoretic and dynamical system context in which metapopulation models are
 73 formulated, the reader is referred to Arino [3, Section 2].

74 The paper is organized as follows. In Section 2, the mathematical model of n
 75 patches, and some preliminaries results, are introduced. In Section 3, the behavior
 76 of the model is studied when the migration rate tends to infinity. In Section 4, we
 77 compare the total equilibrium population with the sum of the carrying capacities
 78 in some particular cases. In Section 5, the SIS patch model is considered, and the
 79 links with the logistic patch model are investigated. In Section 6 the three-patch
 80 model is considered, and by numerical simulations we show the existence of a new
 81 behavior for the dynamics of the total equilibrium population as a function of the
 82 migration rate. In Appendix A, we recall some results for the two-patch model with
 83 asymmetrical migration. In Appendix B, we prove some useful auxiliary results.

84 2. THE MATHEMATICAL MODEL AND PRELIMINARIES RESULTS

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

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

87 where $\gamma_{ij} \geq 0$ denotes the incoming flux from patch j to patch i , for $i \neq j$. The
 88 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 (1.3). The
 matrix

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

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

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

94 **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*
 95 *positively invariant for the system (2.1).*

96 *Proof.* The proof is the same as in the symmetrical case [12, Prop 2.1]. \square

97 When the connectivity matrix Γ_0 is irreducible, System (2.1) admits a unique
 98 positive equilibrium $(x_1^*(\beta), \dots, x_n^*(\beta))$, which is GAS, see [3, Theorem 2.2], [4,
 99 Theorem 1] or [12, Theorem 6.1]. In all of this work, we denote by $E^*(\beta)$ the
 100 positive equilibrium and by $X_T^*(\beta)$ the total population at equilibrium:

$$E^*(\beta) = (x_1^*(\beta), \dots, x_n^*(\beta)), \quad X_T^*(\beta) = \sum_{i=1}^n x_i^*(\beta). \quad (2.3)$$

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

3. PERFECT MIXING

105

106 In this section our aim is to study the behavior of $E^*(\beta)$ and $X_T^*(\beta)$, defined by
 107 (2.3), for large migration rate, i.e when $\beta \rightarrow \infty$.

108 **3.1. The fast dispersal limit.** The following lemma was proved in [4, Lemma 2],
 109 we include a proof for the ease of the reader.

110 **Lemma 3.1.** *Let Γ be the migration matrix. Then, 0 is a simple eigenvalue of Γ
 111 and all non-zero eigenvalues of Γ have negative real part. Moreover, the kernel of
 112 the matrix Γ is generated by a positive vector.*

113 *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

$$B = \Gamma + sI.$$

114 First, we note that since the matrix Γ verifies the property (1.3), then Γ is a
 115 singular matrix and the vector $u = (1, \dots, 1)^T$ is an eigenvector of Γ^T associated to
 116 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

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

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

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

123 Furthermore, according to the Perron-Frobenius theorem, there exists a positive
 124 vector δ such that $B\delta = \rho(B)\delta$, that is, $\Gamma\delta = (B - \rho(B)I)\delta = 0$. In particular, if
 125 the matrix Γ is symmetric then we may take $\delta = u$, that is, $\delta_i = 1$, for all i . \square

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

128 **Remark 3.2.** *The existence, uniqueness (mod. multiplicative factor), and posi-*
 129 *tivity of δ were also proved in Lemma 1 of Cosner et al. [7]. On the other hand,*
 130 *it is shown in Guo et al. [17, Lemma 2.1] and Gao and Dong [16, Lemma 3.1]*
 131 *that the vector $(\Gamma_{11}^*, \dots, \Gamma_{nn}^*)^T$ is a right eigenvector of Γ associated with the zero*
 132 *eigenvalue. Here, Γ_{ii}^* is the cofactor of the i -th diagonal entry of Γ . Therefore,*
 133 *we have explicite formulae for the components of the vector δ , as functions of the*
 134 *coefficients of Γ , at our disposal. For two patches we have $\delta = (\gamma_{12}, \gamma_{21})^T$, and for*
 135 *three patches we have $\delta = (\delta_1, \delta_2, \delta_3)^T$, where*

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

136 The following result asserts that when $\beta \rightarrow \infty$, the equilibrium $E^*(\beta)$ converges
 137 to an element of $\ker \Gamma$.

Theorem 3.3. *For the system (2.1), we have*

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

138 where $\alpha_i = r_i/K_i$.

Proof. Denote

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

139 Dividing Equation 1.1 at the equilibrium $E^*(\beta)$ by β , for $\beta > 0$, yields

$$\text{for all } \beta > 0, \quad \frac{1}{\beta} f(E^*(\beta)) + \Gamma E^*(\beta) = 0.$$

140 Thus any limit point, when $\beta \rightarrow \infty$, of the set $\{E^*(\beta) : \beta > 0\}$ lies in the kernel of
141 Γ . Now, taking the sum of all equations in

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

we see that $E^*(\beta)$ lies in the ellipsoid

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

142 The ellipsoid \mathbb{E}^{n-1} is compact, so the equilibrium $E^*(\beta)$ has at least one limit point
143 in \mathbb{E}^{n-1} , when β goes to infinity. Since the kernel of Γ has dimension 1, and \mathbb{E}^{n-1}
144 is the boundary of a convex set, $\mathbb{E}^{n-1} \cap \ker \Gamma$ consists of at most two points. Since
145 the origin and $E^*(\infty)$ both lie in $\mathbb{E}^{n-1} \cap \ker \Gamma$, we get that

$$\mathbb{E}^{n-1} \cap \ker \Gamma = \{0, E^*(\infty)\}.$$

Therefore, 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

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

146 and since $x_i^*(\beta)$ cannot be negative or 0, we have $x_i^*(\beta) \geq K_i$.
147 □

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

150 **Proposition 3.4.** *We have*

$$X_T^*(+\infty) = \lim_{\beta \rightarrow +\infty} \sum_{i=1}^n x_i^*(\beta) = \left(\sum_{i=1}^n \delta_i \right) \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}. \quad (3.2)$$

151 Denote $K = (K_1, \dots, K_n)^T$. If $K = \lambda \delta$ with $\lambda > 0$, that is to say $K \in \ker \Gamma$, then
152 $X_T^*(+\infty) = \lambda \sum_{i=1}^n \delta_i = \sum_{i=1}^n K_i$.

153 *Proof.* For the proof of (3.2), it suffices to sum the n components of the point
 154 $E^*(\infty)$. For the case $K \in \ker \Gamma$, it suffices to replace K_i by $\lambda \delta_i$ in (3.2). \square

155 Actually, when $K \in \ker \Gamma$, we have $X_T^*(\beta) = \sum_i K_i$ for all $\beta > 0$, see Prop. 4.6.
 In the case $n = 2$, one has $\delta_1 = \gamma_{12}$ and $\delta_2 = \gamma_{21}$, as shown in Remark 3.2.
 Therefore (3.2) becomes

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

156 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 (3.2) specializes to the formula given in [12, Equation (24)]:

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

157 **3.2. Two time scale dynamics.** In [12] the authors also obtained the formula
 158 (3.2), in the symmetrical n -patch case (i.e the matrix Γ is symmetric), by using
 159 singular perturbation theory, see [12, Theorem 4.6].

160 We showed that, if $(x_1(t, \beta), \dots, x_n(t, \beta))$ is the solution of (1.5), with initial
 161 condition (x_1^0, \dots, x_n^0) , then, when $\beta \rightarrow \infty$, the total population $\sum x_i(t, \beta)$ is ap-
 162 proximated by $X(t)$, the solution of the logistic equation

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{nK} \right), \quad \text{where } r = \frac{\sum_{i=1}^n r_i}{n}, \quad K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i} \quad \text{and } \alpha_i = \frac{r_i}{K_i} \quad (3.3)$$

163 with initial condition $X_0 = \sum x_i^0$. Therefore the total population behaves like
 164 the solution of the logistic equation given by (3.3). In addition, one obtains the
 165 following property: with the exception of a small initial interval, the population
 166 densities $x_i(t, \beta)$ are approximated by $X(t)/n$, see [12, Formula (37)]. Therefore,
 167 this approximation shows that, when t and β tend to ∞ , the population density
 168 $x_i(t, \beta)$ tends toward $\frac{\sum r_i}{\sum \alpha_i}$, and in addition, $x_i(t, \beta)$ quickly jumps from its initial
 169 condition x_i^0 to the average X_0/n and then is very close to $X(t)/n$. Our aim is to
 170 generalize this result for the asymmetrical n -patch model (2.1) (i.e the matrix Γ is
 171 non symmetric). We have the following result

172 **Theorem 3.5.** *Let $(x_1(t, \beta), \dots, x_n(t, \beta))$ be the solution of the system (2.1) with*
 173 *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*
 174 *solution of the logistic equation*

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{[\sum_{i=1}^n \delta_i] K} \right), \quad (3.4)$$

175 where

$$r = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i}, \quad K = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} \quad \text{and } \alpha_i = \frac{r_i}{K_i}, \quad (3.5)$$

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

$$\sum_{i=1}^n x_i(t, \beta) = Y(t) + o(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.6)$$

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

$$x_i(t, \beta) = \frac{\delta_i}{\sum_{i=1}^n \delta_i} Y(t) + o(1), \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \quad (3.7)$$

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

$$\begin{cases} \frac{dX}{dt} = \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right), \\ \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n-1. \end{cases} \quad (3.8)$$

180 This system is actually a system in the variables (X, x_1, \dots, x_{n-1}) , since, whenever
 181 x_n appears in the right hand side of (3.8), it should be replaced by

$$x_n = X - \sum_{i=1}^{n-1} x_i. \quad (3.9)$$

When $\beta \rightarrow \infty$, (3.8) is a *slow-fast* system, with one *slow variable*, X , and $n-1$ *fast variables*, x_i for $i = 1 \dots n-1$. As suggested by Tikhonov's theorem [20, 27, 28], 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 (3.9). In the limit $\beta \rightarrow \infty$, we find the *fast dynamics*

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

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

$$\dot{Z} = \mathcal{L}Z + XV, \quad \text{with} \quad \mathcal{L} := L - U, \quad (3.10)$$

184 where $L := (\gamma_{ij})_{n-1 \times n-1}$ is the sub matrix of the matrix Γ , obtained by dropping
 185 the last row and the last column of Γ , V is the vector defined by $V := (\gamma_{in})_{n-1 \times 1}$
 186 and $U = (V; \dots; V)$.

By Lemma B.1, the matrix \mathcal{L} is stable, that is, all of its eigenvalues have negative real part. Therefore, it is invertible and the equilibrium of the system (3.10) is GAS. This equilibrium is given by

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

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:

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

187 Thus, the slow manifold of System (3.8) is given by

$$x_i = \frac{\delta_i}{\sum_{i=1}^n \delta_i} X, \quad i = 1, \dots, n-1. \quad (3.11)$$

As this manifold is GAS, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (3.8) are approximated by the solutions

of the *reduced model*, which is obtained by replacing (3.11) into the dynamics of the slow variable, that is:

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

where r and K are defined in (3.5). Therefore, the reduced model is (3.4). Since (3.4) admits

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

188 as a positive equilibrium point, which is GAS in the positive axis, the approximation
 189 given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all
 190 $t \geq t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, letting
 191 $Y(t)$ be the solution of the reduced model (3.4) with initial condition $Y(0) =$
 192 $X(0, \beta) = \sum_{i=1}^n x_i^0$, then, when $\beta \rightarrow \infty$, we have the approximations (3.6) and
 193 (3.7). \square

194 In the case of perfect mixing, the approximation (3.6) shows that the total popu-
 195 lation behaves like the solution of the single logistic equation (3.5) and then, when
 196 t and β tend to ∞ , the total population $\sum x_i(t, \beta)$ tends toward $(\sum_{i=1}^n \delta_i) K =$
 197 $(\sum_{i=1}^n \delta_i) \frac{\sum \delta_i r_i}{\sum \delta_i^2 \alpha_i}$ as stated in Prop. 3.4. The approximation (3.7) shows that, with
 198 the exception of a thin initial boundary layer, where the population density $x_i(t, \beta)$
 199 quickly jumps from its initial condition x_i^0 to $\delta_i X_0 / \sum_{i=1}^n \delta_i$, each patch of the
 200 n-patch model behaves like the logistic equation

$$\frac{du}{dt} = ru \left(1 - \frac{u}{\delta_i K} \right) \text{ where } r = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i}, \quad K = \frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i}, \quad \alpha_i = \frac{r_i}{K_i}. \tag{3.12}$$

201 Hence, when t and β tend to ∞ , the population density $x_i(t, \beta)$ tends toward
 202 $\delta_i \frac{\sum \delta_i r_i}{\sum \delta_i^2 \alpha_i}$, as stated in Theorem 3.3.

203 **Remark 3.6.** *The single logistic equation (3.12) gives an approximation of the pop-*
 204 *ulation density in each patch in the case of perfect mixing. The intrinsic growth rate*
 205 *r in (3.12) is the arithmetic mean of the r_1, \dots, r_n , weighted by $\delta_1, \dots, \delta_n$, and the*
 206 *carrying capacity K is the harmonic mean of K_i/δ_i , weighted by $\delta_i r_i, i = 1, \dots, n$.*
 207 *We point out the similarity between our expression for the carrying capacity in the*
 208 *limit $\beta \rightarrow \infty$, and the expression obtained in spatial homogenization, see e.g [30,*
 209 *Formula 81] and also [31, Formula 28].*

210 **3.3. Comparison of $X_T^*(+\infty)$ with $\sum_i K_i$.** According to Formula (3.2), it is
 211 clear that the total equilibrium population at $\beta = 0$ and at $\beta = +\infty$ are different
 212 in general.

213 In the remainder of this section, we give some conditions, in the space of param-
 214 eters r_i, K_i, α_i and δ_i , for limit of the total equilibrium population when $\beta \rightarrow \infty$
 215 to be greater or smaller than the sum of the carrying capacities. We show that all
 216 three cases are possible, i.e $X_T^*(+\infty)$ can be greater than, smaller than, or equal
 217 to $X_T^*(0)$. First, we start by giving some particular values of the parameters for
 218 which equality holds.

219 **Proposition 3.7.** Consider the system (2.1). If the vector $\left(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n}\right)^T$ lies in
 220 $\ker \Gamma$, then $X_T^*(+\infty) = \sum_i K_i$.

221 *Proof.* Direct consequence of the equation (3.2). \square

222 Note that, if the matrix Γ is symmetric, then by Lemma 3.1, Prop. 3.7 says that
 223 if all α_i are equal, then $X_T^*(\infty) = \sum_i K_i$, which is [12, Prop 4.4].

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

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

227 (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
 228 $\delta_1 \alpha_1 \geq \dots \geq \delta_n \alpha_n$, then $X_T^*(+\infty) \geq X_T^*(0)$.

229 (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
 230 $\delta_1 \alpha_1 \geq \dots \geq \delta_n \alpha_n$, then $X_T^*(+\infty) \leq X_T^*(0)$.

231 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 $\frac{K_1}{\delta_1} \geq \dots \geq$
 232 $\frac{K_n}{\delta_n}$ is strict, then the inequality is strict in the conclusion.

233 *Proof.* Apply Lemma B.2 with the following choice: $w_i = \delta_i$, $u_i = \frac{K_i}{\delta_i}$, and $v_i =$
 234 $\delta_i \alpha_i$, for all $i = 1, \dots, n$. \square

235 If the matrix Γ is symmetric, one has $\delta_i = 1$, for all i , as shown in Lemma 3.1.
 236 Therefore Prop. 3.8 becomes

237 **Corollary 3.9.** Consider the system (2.1). Assume that Γ is symmetric.

238 (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 $\alpha_1 \geq \dots \geq$
 239 α_n , then $X_T^*(+\infty) \geq X_T^*(0)$.

240 (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 $\alpha_1 \geq \dots \geq$
 241 α_n , then $X_T^*(+\infty) \leq X_T^*(0)$.

242 This result implies Items 1 and 2 of [10, Theorem B.1], which were obtained for
 243 the model (1.4) in the particular case $r_i = K_i$.

244 4. INFLUENCE OF ASYMMETRIC DISPERSAL ON TOTAL POPULATION SIZE

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

252 **4.1. Asymmetric dispersal may be unfavorable to the total equilibrium**
 253 **population.** When Γ is symmetric, we have already proved that if all the growth
 254 rates are equal then dispersal is always unfavorable to the total equilibrium popu-
 255 lation, see [12, Prop. 3.1]. We also noticed that the result still holds in the general
 256 case when Γ is not necessarily symmetric, see [12, Prop. 6.2]. Hence we have the
 257 following

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

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

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

262 **4.2. Asymmetric dispersal may be favorable to the total equilibrium pop-**
263 **ulation.** In this section, we give a situation where the dispersal is favorable to the
264 total equilibrium population. Mathematically speaking:

Proposition 4.2. *Assume that for all $j < i$, $\alpha_i \gamma_{ij} = \alpha_j \gamma_{ji}$. Then*

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

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

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

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

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:

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

The conditions $\alpha_i \gamma_{ij} = \alpha_j \gamma_{ji}$ can be written $\kappa_{ij} := \alpha_i / \gamma_{ji} = \alpha_j / \gamma_{ij}$ for all $j < i$, such that $\gamma_{ij} \neq 0$ and $\gamma_{ji} \neq 0$. Therefore, there exists $\kappa_{ij} > 0$ such that

$$\alpha_j = \kappa_{ij} \gamma_{ij} \quad \text{and} \quad \alpha_i = \kappa_{ij} \gamma_{ji} \quad \text{for all } i, j \text{ with } \gamma_{ij} \neq 0 \text{ and } \gamma_{ji} \neq 0.$$

268 Replacing α_i and α_j in (4.2), one obtains

$$X_T^*(\beta) = \sum_{i=1}^n K_i + \beta \sum_{j < i} \frac{\kappa_{ij} (\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta))^2}{\alpha_j \alpha_i x_j^*(\beta) x_i^*(\beta)} \geq \sum_{i=1}^n K_i. \quad (4.3)$$

269 Equality holds if and only if $\beta = 0$ or $\gamma_{ij} x_j^*(\beta) - \gamma_{ji} x_i^*(\beta) = 0$, for all i and j . Let us
270 prove that if at least two patches have different growth rates, then equality cannot

271 hold for $\beta > 0$. Suppose that there exists $\beta^* > 0$ such that the positive equilibrium
272 satisfies

$$\forall i, j, \quad \gamma_{ij}x_j^*(\beta^*) = \gamma_{ji}x_i^*(\beta^*). \quad (4.4)$$

273 Replacing the equation (4.4) in the system (4.1), we get that $x_i^*(\beta^*) = K_i$, for all
274 i . Therefore, from (4.4), it is seen that, for all i and j , $K_j\gamma_{ij} = K_i\gamma_{ji}$. From these
275 equations and the conditions $\alpha_i\gamma_{ij} = \alpha_j\gamma_{ji}$, we get $r_i = r_j$, for all i and j . This
276 is a contradiction with the hypothesis that there exists two patches with different
277 growth rates. Hence the equality in (4.3) holds if and only if $\beta = 0$. \square

278 When the matrix Γ is irreducible and symmetric, the hypothesis of Prop. 4.2
279 implies that $\alpha_i = \alpha_j$ for all i and j . Indeed if two patches i and j are connected
280 (i.e $\gamma_{ij} = \gamma_{ji} \neq 0$), then we have $\alpha_i = \alpha_j$. As the matrix Γ is irreducible, for
281 two arbitrary patches, there exists a finite sequence (i, \dots, j) which begins in i and
282 ends in j , such that $\gamma_{ab} \neq 0$ for all successive patches a and b in (i, \dots, j) . Hence
283 $\alpha_a = \alpha_b$ for all a and b in (i, \dots, j) . Hence, $\alpha_i = \alpha_j$. So, when the matrix Γ is
284 symmetric, Prop. 4.2 says that if all α_i are equal, dispersal enhances population
285 growth, which is [12, Prop. 3.3].

286 Note that, when $n = 2$, Prop 4.2 asserts that if $\alpha_2/\alpha_1 = \gamma_{12}/\gamma_{21}$, then $X_T^*(\beta) >$
287 $K_1 + K_2$, which is a result of Arditi et al. [2, Prop. 2, item b]. See also Prop. A.1,
288 and note that the condition $\alpha_2/\alpha_1 = \gamma_{12}/\gamma_{21}$ implies that $(\gamma_{12}, \gamma_{21}) \in \mathcal{J}_0$.

For three patches or more, if the matrix Γ does not verify the condition $(\forall i, j, \gamma_{ij} =$
 $0 \iff \gamma_{ji} = 0)$, then the hypothesis of Prop. 4.2, that for all $j < i$, $\alpha_i\gamma_{ij} = \alpha_j\gamma_{ji}$
cannot be satisfied. Note that the hypothesis $\alpha_i\gamma_{ij} = \alpha_j\gamma_{ji}$ implies that, for all
 $i = 1, \dots, n$, one has

$$\sum_{j=1}^n \frac{\gamma_{ij}}{\alpha_j} = \sum_{j=1, j \neq i}^n \frac{\gamma_{ij}}{\alpha_j} - \sum_{j=1, j \neq i}^n \frac{\gamma_{ji}}{\alpha_i} = \sum_{j=1, j \neq i}^n \frac{\alpha_i\gamma_{ij} - \alpha_j\gamma_{ji}}{\alpha_i\alpha_j} = 0.$$

289 Therefore we can make the following remark:

290 **Remark 4.3.** *The hypothesis of Prop. 4.2 implies that $(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n})^T \in \ker \Gamma$.*

291 We make the following conjecture:

Conjecture 4.4. *If $(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n})^T \in \ker \Gamma$ then*

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

292 This conjecture is true for the particular case of Prop. 4.2. It is also true for
293 two-patch models and for n -patch models with symmetric dispersal. It agrees with
294 Prop. 3.7.

295 **Proposition 4.5.** *The derivative of the total equilibrium population $X_T^*(\beta)$ at $\beta =$
296 0 is given by:*

$$\frac{dX_T^*}{d\beta}(0) = \sum_{i=1}^n \left(\frac{1}{r_i} \sum_{j=1}^n \gamma_{ij} K_j \right). \quad (4.5)$$

297 *In particular, if $K \in \ker \Gamma$, where $K = (K_1, \dots, K_n)^T$, then $\frac{dX_T^*}{d\beta}(0) = 0$.*

Proof. By differentiating the equation (4.2) at $\beta = 0$, we get:

$$\frac{dX_T^*}{d\beta}(0) = \sum_{i=1}^n \sum_{j=1, j \neq i}^n \frac{\gamma_{ij}x_j^*(0) - \gamma_{ji}x_i^*(0)}{\alpha_i x_i^*(0)},$$

298 which gives (4.5), since $x_i^*(0) = K_i$ for all $i = 1, \dots, n$.

299 If $K \in \ker \Gamma$, then $\sum_{j=1}^n \gamma_{ij}K_j = 0$ for all i , so that $\frac{dX_T^*}{d\beta}(0) = 0$. \square

300 Actually, when $K \in \ker \Gamma$, we prove that $X_T^*(\beta)$ is constant, so that $\frac{dX_T^*}{d\beta}(\beta) = 0$
 301 for all $\beta \geq 0$, not only for $\beta = 0$, see Proposition 4.6.

302 **4.3. Independence of the total equilibrium population with respect to**
 303 **asymmetric dispersal.** In the next proposition we give sufficient and necessary
 304 conditions for the total equilibrium population not to depend on the migration rate.

305 **Proposition 4.6.** *The equilibrium $E^*(\beta)$ does not depend on β if and only if*
 306 *$(K_1, \dots, K_n)^T \in \ker \Gamma$. In this case we have $E^*(\beta) = (K_1, \dots, K_n)$ for all $\beta > 0$.*

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

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

308 where f is given by (2.2). Suppose that the equilibrium $E^*(\beta)$ does not depend on
 309 β , then we replace in Equation (4.6):

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

310 The derivative of (4.7) with respect to β gives

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

311 Replacing the equation (4.8) in the equation (4.7), we get $f(E^*(\beta)) = 0$, so $E^*(\beta) =$
 312 (K_1, \dots, K_n) . From the equation (4.8), we conclude that $(K_1, \dots, K_n)^T \in \ker \Gamma$.

313 Now, suppose that $(K_1, \dots, K_n)^T \in \ker \Gamma$, then (K_1, \dots, K_n) satisfies the equa-
 314 tion (4.6), for all $\beta \geq 0$. So, $E^*(\beta) = (K_1, \dots, K_n)$, for all $\beta \geq 0$, which proves
 315 that the total equilibrium population is independent of the migration rate β . \square

316 If the matrix Γ is symmetric, the previous proposition asserts that the K_i , for
 317 $i = 1, \dots, n$, are equal if and only if $E^* = (K, \dots, K)$, where K is the common
 318 value of the K_i . This is [12, Proposition 3.2]. For $n = 2$, Prop. 4.6 asserts that if
 319 $K_1/K_2 = \gamma_{12}/\gamma_{21}$ then $X_T^*(\beta) = K_1 + K_2$ for all β , which is [2, Proposition 2, item
 320 c]. See also the last item of Prop. A.1.

321 **4.4. Two blocks of identical patches.** We consider the model (2.1) and we
 322 assume that there are two blocks, denoted I and J , of identical patches, such that
 323 $I \cup J = \{1, \dots, n\}$. Let p be the number of patches in I and $q = n - p$ be the
 324 number of patches in J . Without loss of generality we can take $I = \{1, \dots, p\}$ and
 325 $J = \{p + 1, \dots, n\}$. The patches being identical means that they have the same
 326 specific growth rate r_i and carrying capacity K_i . Therefore we have

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

327 For each patch $i \in I$ we denote by γ_{iJ} the flux from block J to patch i , and for
 328 each patch $j \in J$ we denote by γ_{jI} the flux from block I to patch j , as defined in
 329 Table 1. For each patch i we denote by T_i the sum of all migration rates γ_{ji} from
 330 patch i to another patch $j \neq i$ (i.e. the outgoing flux of patch i) minus the sum of

331 the migration rates γ_{ik} from patch k to patch i , where k belongs to the same block
 332 as i . Hence, we have:

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

333 We make the following assumption on the migration rates:

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

334 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).

TABLE 1. Definitions and notations of fluxes

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 $j \in J$.

335

336

We have the following result:

337 **Lemma 4.7.** *Assume that the conditions (4.11) are satisfied, then for all $i \in I$ and*
 338 *$j \in J$ one has*

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

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

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

342

343

344

345

In the next theorem, we will show that, at the equilibrium, and under certain conditions relating to the migration rates, 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 4.8. *Assume that the conditions (4.9) and (4.11) are satisfied. Then the equilibrium of (2.1) is of the form*

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

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

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

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

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

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

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

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

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

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

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

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

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

$$\begin{cases} \frac{dy_1}{dt} = r_1 y_1 \left(1 - \frac{y_1}{pK_1}\right) + \beta (\gamma_2 y_n - \gamma_{21} y_1), \\ \frac{dy_n}{dt} = r_n y_n \left(1 - \frac{y_n}{qK_n}\right) + \beta (\gamma_{21} y_1 - \gamma_2 y_n), \end{cases} \quad (4.17)$$

366 with specific growth rates r_1 and r_n , carrying capacities pK_1 and qK_n , and migra-
 367 tion rates $\gamma_{21} = \frac{\gamma_{JI}}{p}$, $\gamma_2 = \frac{\gamma_{IJ}}{q}$.

368 *Proof.* From Theorem 4.8, we see that (x_1^*, x_n^*) is the positive solution of (4.13).
 369 Hence, $(y_1^* = px_1^*, y_n^* = qx_n^*)$ is the solution of the set of equations

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

370 obtained from (4.13) by changing variables to $y_1 = px_1$, $y_n = qx_n$. The system
 371 (4.18) has a unique positive solution which is the equilibrium point of the 2-patch
 372 model (4.17). \square

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

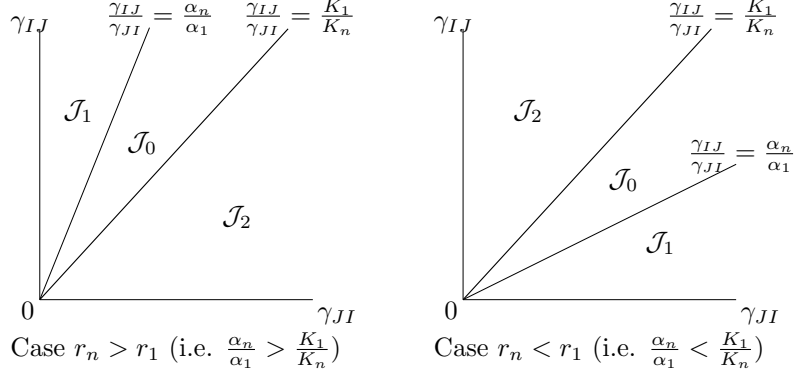


FIGURE 1. Qualitative properties of Model (2.1) under the conditions (4.9) and (4.11). In \mathcal{J}_0 , patchiness has a beneficial effect on the total equilibrium population. This effect is detrimental in \mathcal{J}_2 . In \mathcal{J}_1 , the effect is beneficial for $\beta < \beta_0$ and detrimental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

375 We consider the regions in the set of parameters γ_{IJ} and γ_{JI} , denoted \mathcal{J}_0 , \mathcal{J}_1
 376 and \mathcal{J}_2 , depicted in Fig. 1 and defined by:

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

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

378 **Proposition 4.10.** Assume that the conditions (4.9) and (4.11) are satisfied. Then
 379 the total equilibrium population $X_T^*(\beta) = px_1^*(\beta) + qx_n^*(\beta)$ of (2.1) satisfies the
 380 following properties

- 381 (1) If $r_1 = r_n$ then $X_T^*(\beta) < pK_1 + qK_n$ for all $\beta > 0$.
 382 (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:
 383 • 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

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

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

386 *Proof.* This is a consequence of Proposition A.1 and Corollary 4.9. □

387 Let us explain the result of Proposition 4.10 in the particular case where $p = n - 1$.
 388 In this case, the condition (4.11) becomes

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

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

390 Therefore, if the matrix Γ is symmetric, the conditions (4.20) are equivalent to the
 391 conditions $\gamma_{n1} = \dots = \gamma_{n,n-1}$, which mean that the fluxes of migration between
 392 the n -th patch and all $n - 1$ identical patches are equal. Hence, Proposition 4.10,
 393 showing that the n -patch model behaves like a 2-patch model, is the same as [12,
 394 Prop. 3.4], where the model (2.1) was considered with Γ symmetric, $n - 1$ patches
 395 are identical and the fluxes of migration between the n -th patch and all these $n - 1$
 396 identical patches are equal. Thus Proposition 4.10 generalizes Proposition 3.4 of
 397 [12], to asymmetric dispersal and for any two identical blocks, provided that the
 398 conditions (4.11) are satisfied.

399 5. LINKS BETWEEN SIS AND LOGISTIC PATCH MODELS

400 **5.1. The SIS patch model.** In [15], Gao studied the following SIS patch model
 401 in an environment of n patches connected by human migration:

$$\begin{cases} \frac{dS_i}{dt} = -\beta_i \frac{S_i I_i}{N_i} + \gamma_i I_i + \varepsilon \sum_{j=1}^n \gamma_{ij} S_j, & i = 1, \dots, n, \\ \frac{dI_i}{dt} = \beta_i \frac{S_i I_i}{N_i} - \gamma_i I_i + \varepsilon \sum_{j=1}^n \gamma_{ij} I_j, & i = 1, \dots, n, \end{cases} \quad (5.1)$$

402 where S_i and I_i are the number of susceptible and infected, in patch i , respectively;
 403 $N_i = S_i + I_i$ denotes the total population in patch i . The parameters β_i and γ_i are
 404 positive transmission and recovery rates, respectively. The matrix $\Gamma = (\gamma_{ij})$ satisfies
 405 (1.3) and describes the movement between patches. The coefficient ε quantifies the
 406 diffusion, as our β in (2.1).

Using the variables $N_i, I_i, i = 1, \dots, n$, the system (5.1) has a cascade structure

$$\frac{dN_i}{dt} = \varepsilon \sum_{j=1}^n \gamma_{ij} N_j, \quad i = 1, \dots, n, \quad (5.2)$$

$$\frac{dI_i}{dt} = \beta_i \frac{(N_i - I_i) I_i}{N_i} - \gamma_i I_i + \varepsilon \sum_{j=1}^n \gamma_{ij} I_j, \quad i = 1, \dots, n, \quad (5.3)$$

407 Therefore the infected populations I_i are the solutions of the non-autonomous sys-
 408 tem of differential equations

$$\frac{dI_i}{dt} = \beta_i I_i \left(1 - \frac{I_i}{N_i(t)} \right) - \gamma_i I_i + \varepsilon \sum_{j=1}^n \gamma_{ij} I_j, \quad i = 1, \dots, n, \quad (5.4)$$

409 where the total populations $N_i(t)$ are the solutions of the system (5.2). Hence,
 410 the autonomous $2n$ -dimensional system (5.1), is equivalent to the family of n -
 411 dimensional non-autonomous systems (5.4), indexed by the solutions $N_i(t)$ of (5.2).
 412 Note that since the γ_{ij} verify the property (1.3), the total population is constant:

413 $\sum_{i=1}^n N_i(t) = N$, where $N := \sum_{i=1}^n (S_i(0) + I_i(0))$. If the matrix $\Gamma = (\gamma_{ij})$ is
 414 irreducible, then $N_i(t)$, the total population in patch i , converges towards the limit

$$\lim_{t \rightarrow +\infty} N_i(t) = N_i^* \quad \text{where } N_i^* := \frac{N}{\sum_i \delta_i} \delta_i, \quad i = 1, \dots, n, \quad (5.5)$$

415 where $\delta = (\delta_1, \dots, \delta_n)^T$ is a positive vector which generates the vector space $\ker \Gamma$.
 416 Therefore (5.4) is an asymptotically autonomous system, whose limit system is
 417 obtained by replacing $N_i(t)$ in (5.4), by their limits N_i^* , given by (5.5):

$$\frac{dI_i}{dt} = \beta_i I_i \left(1 - \frac{I_i}{N_i^*}\right) - \gamma_i I_i + \varepsilon \sum_{j=1}^n \gamma_{ij} I_j, \quad i = 1, \dots, n. \quad (5.6)$$

The main problem for (5.1) is to determine the condition under which the disease free equilibrium, corresponding to the equilibrium $I = 0$ of (5.6), is GAS, or the endemic equilibrium, corresponding to the positive equilibrium of (5.6), is GAS. It is known, see [15, Theorem 2.1], that the disease free equilibrium is GAS if $\mathcal{R}_0 \leq 1$, and there exists a unique endemic equilibrium, which is GAS, if $\mathcal{R}_0 > 1$. Here \mathcal{R}_0 is the basic reproduction number of the model (5.1), defined as:

$$\mathcal{R}_0 = \rho(FV^{-1}) \quad \text{where } F = \text{diag}(\beta_1, \dots, \beta_n) \text{ and } V = \text{diag}(\gamma_1, \dots, \gamma_n) - \varepsilon \Gamma.$$

418 A reference work on the basic reproduction number for metapopulations is Arino
 419 [4], whereas Castillo-Garsow and Castillo-Chavez [6] give a more general account
 420 of the subject.

421 **5.2. Comparisons between the results on (2.1) and the results on (5.6).**
 422 Gao [15] gave many interesting results on the effect of population dispersal on total
 423 infection size. Our aim is to discuss some of the links between his results and the
 424 results of the present paper. We focus on two results on the total infection size
 425 $T_n(\varepsilon) = \sum_{i=1}^n I_i^*(\varepsilon)$, where $(I_1^*(\varepsilon), \dots, I_n^*(\varepsilon))$ is the positive equilibrium of (5.6).
 426 We consider the results of Gao [15] on $T_n(+\infty)$ and $T_n'(0)$.

427 **Proposition 5.1.** [15, Theorem 3.3], [15, Theorem 3.5]. *If $\mathcal{R}_0(+\infty) > 1$, then*

$$T_n(+\infty) = \left(1 - \frac{1}{\mathcal{R}_0(+\infty)}\right) N, \quad \text{with } \mathcal{R}_0(+\infty) = \frac{\sum_i \beta_i \delta_i}{\sum_i \gamma_i \delta_i}. \quad (5.7)$$

428 *If $\beta_i \neq \gamma_i$ for all i , then*

$$T_n'(0) = \sum_i \left(\frac{1}{|\beta_i - \gamma_i|} \sum_j \gamma_{ij} I_j^*(0) \right), \quad \text{with } I_j^*(0) = \frac{\beta_j - \gamma_j}{\beta_j} N_j^*. \quad (5.8)$$

429 It is worth noting that the formulas (5.7) and (5.8) involve the system (5.6). An
 430 important property of this system is given in the following remark.

431 **Remark 5.2.** *Let $N^* = (N_1^*, \dots, N_n^*)^T$ be the vector of the carrying capacities in
 432 the system (5.6). One has $N^* \in \ker \Gamma$, as shown by (5.5).*

433 Our aim is to compare the results given by the formulas (5.7) and (5.8) when
 434 $\gamma_i \rightarrow 0$, to our results, for the system

$$\frac{dx_i}{dt} = \beta_i x_i \left(1 - \frac{x_i}{N_i^*}\right) + \varepsilon \sum_{j=1}^n \gamma_{ij} x_j, \quad i = 1, \dots, n. \quad (5.9)$$

435 Note that the system (5.6) reduces to (5.9) when $\gamma_i = 0$ for all i . More precisely
 436 we show that, as $\gamma_i \rightarrow 0$, the formulas (5.7) and (5.8) are the same as the results
 437 predicted by Prop. 3.4 and Prop.4.5.

438 **Proposition 5.3.** *Let $T_n(\varepsilon)$ be the total infection size of (5.6). Let $X_T^*(\varepsilon)$ be the*
 439 *total population size of (5.9). One has*

$$\lim_{\max_i \{\gamma_i\} \rightarrow 0} T_n(+\infty) = X_T^*(+\infty) = N, \quad \lim_{\max_i \{\gamma_i\} \rightarrow 0} T_n'(0) = \frac{dX_T^*}{d\varepsilon}(0) = 0. \quad (5.10)$$

440 *Proof.* When $\gamma_i \rightarrow 0$ for all i , one has $\mathcal{R}_0(+\infty) \rightarrow +\infty$ and $I_i^*(0) \rightarrow N_i^*$. Therefore,
 441 from (5.7) and (5.8) it is deduced that

$$T_n(+\infty) \rightarrow N, \quad T_n'(0) \rightarrow \sum_i \frac{1}{\beta_i} \sum_j \gamma_{ij} N_j^* = 0. \quad (5.11)$$

442 Using the property $N^* \in \ker \Gamma$, from Prop. 3.4 and Prop.4.5, it is deduced that:

$$X_T^*(+\infty) = N, \quad \frac{dX_T^*}{d\varepsilon}(0) = 0. \quad (5.12)$$

443 From (5.11) and (5.12) we deduce (5.10). □

444 Actually as shown in Prop.4.6, we have the stronger result $X_T^*(\beta) = N$ for all
 445 $\beta \geq 0$. But our aim here was only the comparison between (5.11) and (5.12).

446 As shown in Prop.5.2, the results of Gao [15] on the logistic patch model (5.6)
 447 yield results on the logistic patch model (5.9) by taking the limit $\gamma_i \rightarrow 0$. However,
 448 the scope of this approach is weakened by the fact that it only applies to the
 449 logistic model (5.9), for which the vector of carrying capacities satisfies $N^* \in \ker \Gamma$,
 450 see Remark 5.2. But this property is not true in general for our system (2.1), where
 451 the condition $K \in \ker \Gamma$ does not hold in general.

452 Our aim in this section is to show that any logistic patch model (2.1), without
 453 the condition $K \in \ker \Gamma$, can be written in the form (5.6), with the condition
 454 $N^* \in \ker \Gamma$. Indeed we have the following result:

455 **Lemma 5.4.** *Consider $r_i > 0$, $K_i > 0$ and Γ as in the system (2.1). Let $\delta_i > 0$*
 456 *be such that $(\delta_1, \dots, \delta_n)^T \in \ker \Gamma$. Let N be such that $N > \frac{\sum_i \delta_i}{\delta_i} K_i$ for $i = 1, \dots, n$.*
 457 *Let N_i^* defined by (5.5). Let $\beta_i = \frac{r_i}{K_i} N_i^*$ and $\gamma_i = \beta_i - r_i$. Then one has*

$$r_i x_i (1 - x_i / K_i) = \beta_i x_i (1 - x_i / N_i^*) - \gamma_i x_i, \quad \text{for } i = 1, \dots, n \quad (5.13)$$

458 *Proof.* The conditions (5.13) are satisfied if and only if $r_i = \beta_i - \gamma_i$ and $r_i / K_i =$
 459 β_i / N_i^* . Therefore

$$\begin{cases} \beta_i = N_i^* \frac{r_i}{K_i} = N_i^* \alpha_i, \\ \gamma_i = \beta_i - r_i = (N_i^* - K_i) \alpha_i. \end{cases} \quad (5.14)$$

460 To ensure that $\gamma_i > 0$ for all i , just choose N in (5.5) such that $N_i^* > K_i$ for
 461 $i = 1, \dots, n$, that is to say, $N > \frac{\sum_i \delta_i}{\delta_i} K_i$. □

Remark 5.5. *According to the change of parameters (5.14), the logistic patch model*
 (2.1) *can be written in the form of Gao (5.6), i.e. with the property that $N^* \in \ker \Gamma$.*

For the perfect mixing case, the formula (5.7) and our formula (3.2) are the same. Indeed replacing β_i and γ_i by (5.14) in (5.7), and using (5.5), we get:

$$\left(1 - \frac{1}{\mathcal{R}_0(+\infty)}\right) N = \left(1 - \frac{\sum_i (N_i^* - K_i) \alpha_i}{\sum_i N_i^* \alpha_i}\right) N = \sum_i \delta_i \frac{\sum_i r_i \delta_i}{\sum_i \alpha_i \delta_i^2}.$$

For the derivative, the formula (5.8) and our formula (4.5) are the same. Indeed, if we replace β_i and γ_i by (5.14), in (5.8), we get:

$$I_j^*(0) = \frac{\beta_j - \gamma_j}{\beta_j} N_j^* = \frac{r_j}{N_j^* \alpha_j} N_j^* = K_j.$$

Therefore

$$\sum_i \left(\frac{1}{|\beta_i - \gamma_i|} \sum_j \gamma_{ij} I_j^*(0) \right) = \sum_i \left(\frac{1}{r_i} \sum_j \gamma_{ij} K_j \right).$$

462 The theory of asymptotically autonomous systems answers the question “under
463 which conditions do the solutions of the original $2n$ -dimensional system (5.1) have
464 the same asymptotic behavior as those of the n -dimensional limit system (5.6) ?”.
465 For details and further reading on the theory of asymptotically autonomous systems
466 the reader is referred to Markus [23] and Thieme [25, 26]. For applications of this
467 theory to epidemic models, see Castillo-Chavez and Thieme [5].

468 Hence, it is important to know whether or not some of the results of Gao [15]
469 on the SIS model (5.1) can be deduced from our results on the logistic model (2.1).
470 It is worth noting that the discussion in this section shows that our results on the
471 logistic patch model imply results on the model (5.6) and hence, results on the
472 original model $2n$ -dimensional system (5.1). However, it is needed that $\beta_i > \gamma_i$
473 for $i = 1, \dots, n$. Indeed, according to (5.14), one has $r_i = \beta_i - \gamma_i > 0$. On the
474 other hand, the condition $\beta_i > \gamma_i$ is not required in all patches of the system (5.1).
475 Another challenging problem is the study of the model (5.6), in the general case
476 where $N^* = (N_1^*, \dots, N_n^*)^T$ is not necessarily in the kernel of Γ .

477

6. THREE-PATCH MODEL

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

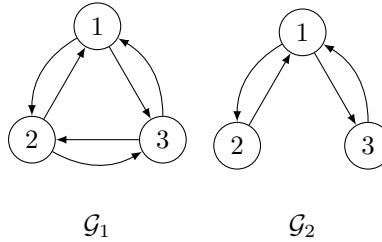


FIGURE 2. The two graphs \mathcal{G}_1 and \mathcal{G}_2 for which the migration matrix may be symmetric, if $\gamma_{ij} = \gamma_{ji}$.

481 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:

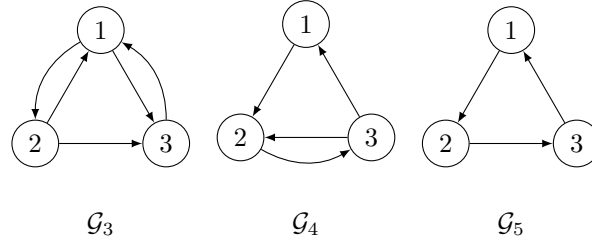


FIGURE 3. The three graphs $\mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 for which the migration matrix cannot be symmetric.

482 The associated connectivity matrices are given by
483

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

484 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

TABLE 2. The generator δ of $\ker \Gamma$, for the five cases. The perfect mixing abundance $X_T^*(+\infty)$ is computed with Eq. (3.2).

Graphs	The formula of perfect mixing $X_T^*(+\infty)$
\mathcal{G}_1	The coefficients δ_i are given by the equation (3.1)
\mathcal{G}_2	$\delta_1 = \gamma_{12}\gamma_{13}, \delta_2 = \gamma_{21}\gamma_{13}, \delta_3 = \gamma_{12}\gamma_{31},$
\mathcal{G}_3	$\delta_1 = \gamma_{12}\gamma_{13} + \gamma_{32}\gamma_{13}, \delta_2 = \gamma_{21}\gamma_{13}, \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32},$
\mathcal{G}_4	$\delta_1 = \gamma_{32}\gamma_{13}, \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \delta_3 = \gamma_{21}\gamma_{32}.$
\mathcal{G}_5	$\delta_1 = \gamma_{32}\gamma_{13}, \delta_2 = \gamma_{21}\gamma_{13}, \delta_3 = \gamma_{21}\gamma_{32}.$

485 of $X_T^*(\beta)$. In the case $n = 2$, it was shown in [1, 2] that there exists at most one
486 positive value of β such that $X_T^*(\beta) = K_1 + K_2$. In [12], in the case $n = 3$ and Γ
487 is symmetric, we gave numerical values for the parameters such that there exists
488 two positive values of β such that $X_T^*(\beta) = K_1 + K_2 + K_3$, and we were not able
489 to find more than two values. The novelty when Γ is not symmetric is that we
490 can find examples with three positive values. Indeed, we may have the following
491

492 situation : $\frac{dX_T^*}{d\beta}(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2 + K_3$, and there exist three values
 493 $0 < \beta_1 < \beta_2 < \beta_3$ for which we have

$$X_T^*(\beta) \begin{cases} > K_1 + K_2 + K_3 & \text{for } \beta \in]0, \beta_1[\cup]\beta_2, \beta_3[, \\ < K_1 + K_2 + K_3 & \text{for } \beta \in]\beta_1, \beta_2[\cup]\beta_3, +\infty[. \end{cases} \quad (6.1)$$

494 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
 495 exist three values $0 < \beta_1 < \beta_2 < \beta_3$ for which (6.1) hold. See Figures 4, (for the
 496 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),
 497 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. (3.2) and the derivative of the total equilibrium population at $\beta = 0$ is computed with Eq. (4.5).

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

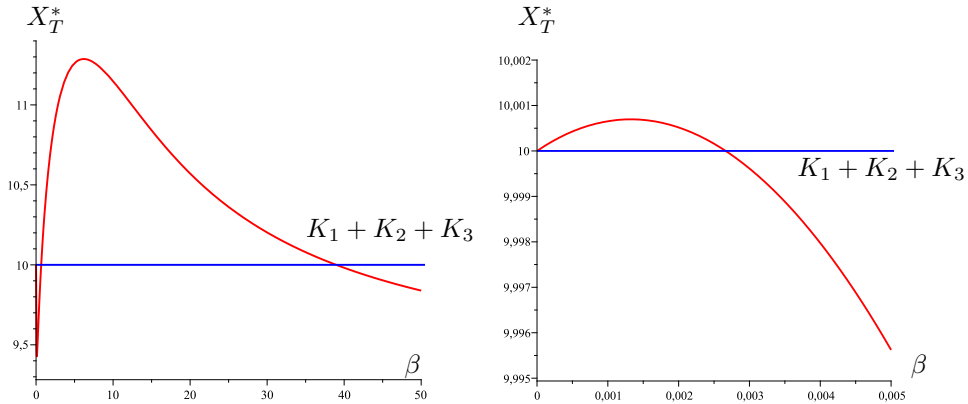


FIGURE 4. Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of the migration rate β . The figure on the right is a zoom, near the origin, of the figure on the left. The parameter values are given in Table 3.

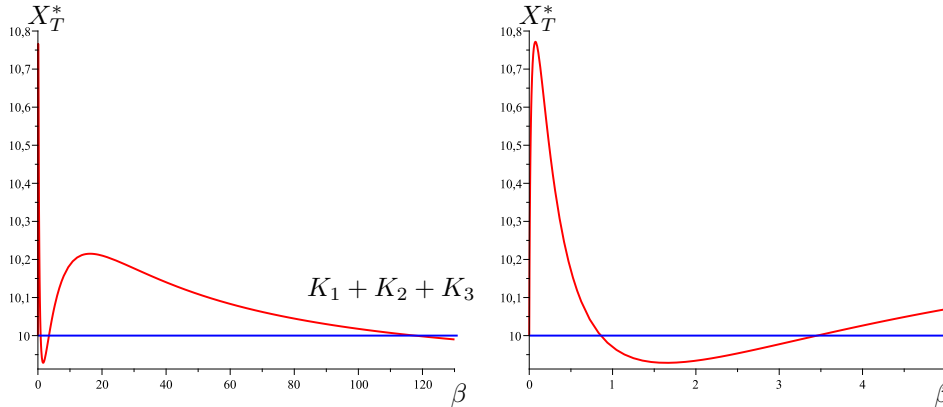


FIGURE 5. Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of the migration rate β . The figure on the right is a zoom, near the origin, of the figure on the left. The parameter values are given in Table 3.

498

7. CONCLUSION

499 The aim of this paper is to generalize, to a multi-patch model with asymmet-
 500 ric dispersal, the results obtained in [12] for a multi-patch model with symmetric
 501 dispersal.

502 In Section 3 we consider the particular case of perfect mixing, when the migra-
 503 tion rate goes to infinity, that is, individuals may travel freely between patches. As
 504 in [12], we compute the total equilibrium population in that case, and, by pertur-
 505 bation arguments, we prove that the dynamics in this ideal case provides a good
 506 approximation to the case when the migration rate is large. Our results general-
 507 ize those of [2] (asymmetric migration matrix, only two patches), [10] (arbitrarily
 508 many patches, but the migration matrix is symmetric and zero outside the corners
 509 and the three main diagonals), and [12] (arbitrarily many patches; arbitrary, but
 510 symmetric, migration).

511 In Section 4 we consider the equation

$$\text{total equilibrium population} = \text{sum of the carrying capacities of the patches.} \tag{7.1}$$

512 We give a complete solution in the case when the n patches are partitioned into two
 513 blocks of identical patches. Our results mirror those of [2], which deals with the
 514 two-patch case. Specifically, Equation (7.1) admits at most one non-trivial solution.

515 In Section 5, we consider a SIS patch model and we give the links with the
 516 logistic model.

517 In Section 6 we give numerical values for the dispersion parameters such that
 518 Equation (7.1) has at least three non-trivial solutions. In [12] we proved that for
 519 three patches and symmetric dispersal, there may be at least two solutions. A math-
 520 ematical proof that, when $n=3$, Equation (7.1) has at most three solutions, would

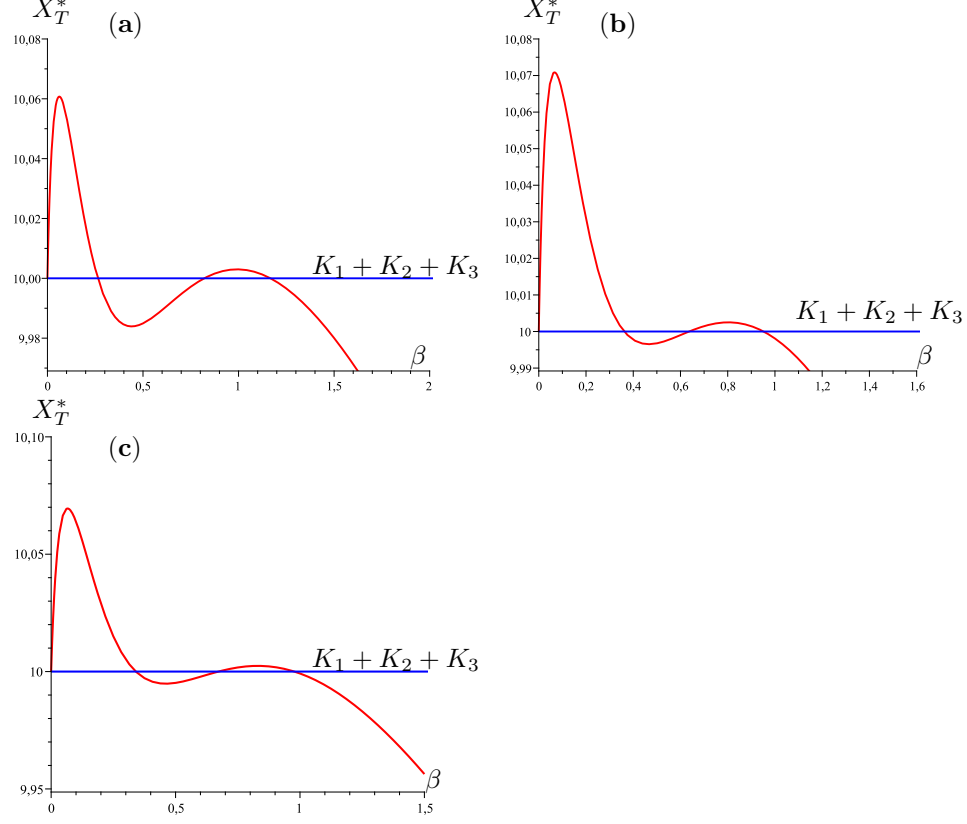


FIGURE 6. Total equilibrium population X_T^* of the system (2.1) ($n = 3$) as a function of the migration rate β . The parameter values are given in Table 3.

521 certainly be desirable, and could spur further work. Upper bounds for arbitrarily
 522 many patches would also be interesting.

523

APPENDIX

524

APPENDIX A. THE 2-PATCH ASYMMETRIC MODEL

525 We consider the 2-patch logistic equation with asymmetric migrations. We de-
 526 note by γ_{12} the migration rate from patch 2 to patch 1 and γ_{21} from patch 1 to
 527 patch 2. The model is written:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{L_1}\right) + \beta (\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{L_2}\right) + \beta (\gamma_{21} x_1 - \gamma_{12} x_2). \end{cases} \quad (\text{A.1})$$

528 Note that the system (A.1) is studied in [1, 8, 13, 14, 19] in the case where the
 529 migration rates satisfy $\gamma_{21} = \gamma_{12}$, and in [2] for general migration rates. This system
 530 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

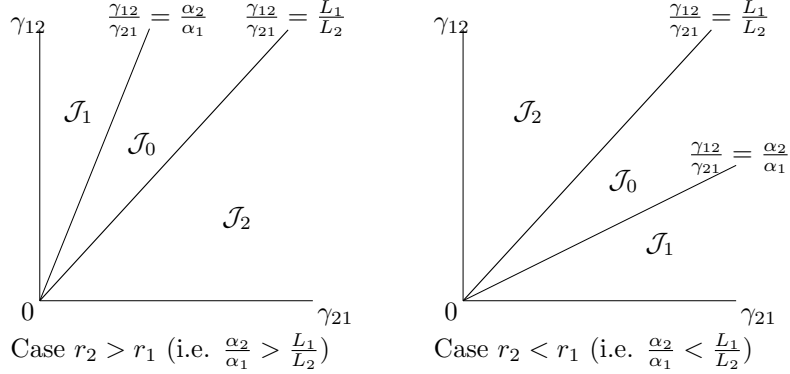


FIGURE 7. Qualitative properties of model (A.1). In \mathcal{J}_0 , patchiness has a beneficial effect on total equilibrium population. This effect is detrimental in \mathcal{J}_2 . In \mathcal{J}_1 , the effect is beneficial for $\beta < \beta_0$ and detrimental for $\beta > \beta_0$. In the figure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

531
532 set of the parameters γ_{21} and γ_{12} , denoted \mathcal{J}_0 , \mathcal{J}_1 and \mathcal{J}_2 , depicted in Fig. 7 and
533 defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 > r_1 \text{ then} \\ \text{If } r_2 < r_1 \text{ then} \end{array} \right\} \left\{ \begin{array}{l} \mathcal{J}_1 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} > \frac{\alpha_2}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\alpha_2}{\alpha_1} \geq \frac{\gamma_{12}}{\gamma_{21}} > \frac{L_1}{L_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{L_1}{L_2} > \frac{\gamma_{12}}{\gamma_{21}} \right\} \\ \mathcal{J}_1 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} < \frac{\alpha_2}{\alpha_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\alpha_2}{\alpha_1} \leq \frac{\gamma_{12}}{\gamma_{21}} < \frac{L_1}{L_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{L_1}{L_2} < \frac{\gamma_{12}}{\gamma_{21}} \right\} \end{array} \right. \quad (\text{A.2})$$

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

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

- 538 (1) *If $r_1 = r_2$ then $X_T^*(\beta) \leq L_1 + L_2$ for all $\beta \geq 0$.*
539 (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:*
540
 - *if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_0$ then $X_T^*(\beta) > L_1 + L_2$ for any $\beta > 0$*
 - *if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_1$ 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*

$$\beta_0 = \frac{r_2 - r_1}{\frac{\gamma_{12}}{\alpha_2} - \frac{\gamma_{21}}{\alpha_1}} \frac{1}{\alpha_1 + \alpha_2}.$$

- 541
 - *if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_2$ then $X_T^*(\beta) < L_1 + L_2$ for any $\beta > 0$*

- 542 • If $\frac{\gamma_{12}}{\gamma_{21}} = \frac{L_1}{L_2}$, then $x_1^*(\beta) = L_1$ and $x_2^*(\beta) = L_2$ for all $\beta \geq 0$.
 543 Therefore $X_T^*(\beta) = L_1 + L_2$ for all $\beta \geq 0$.

544 *Proof.* This result was established by Arditì et al. [2]. Part (1) is Proposition 1 of
 545 [2]. The first three items of part (2) are Proposition 2 of [2]. For the last item of
 546 part (2), see the last paragraph in page 12 of [2]. The explicit expression of β_0 was
 547 not given in [2], however, it is easy to deduce it from the formulas given in [2]. \square

548

APPENDIX B. SOME USEFUL RESULTS

549 We begin with a

550 **Lemma B.1.** *The matrix \mathcal{L} defined by (3.10) is stable, that is to say, all its eigen-*
 551 *values 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 , V , and U are defined right after (3.10). 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

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

552 Two conjugate matrices have the same eigenvalues. As the matrix G is block-
 553 triangular, its eigenvalues are zero and the eigenvalues of the matrix $L - U$. There-
 554 fore, since 0 is an simple eigenvalue of the matrix Γ , the eigenvalues of the matrix
 555 $L - U$ are the eigenvalues of the matrix Γ except 0. By Lemma 3.1 all non-zero
 556 eigenvalues of Γ have negative real part. \square

557 **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*
 558 *sequences. Then,*

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

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

- 561 (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*
 562 *non-increasing and $(v_n)_{n \geq 1}$ is non-decreasing, then, we have, for all $N \geq 1$,*

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

563 *In both items, if $(u_n)_{n \geq 1}$ is not constant, then the inequality in the conclusion is*
 564 *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

$$u_{n+1} [w_1(v_{n+1} - v_1) + \dots + w_n(v_{n+1} - v_n)] \geq u_1 w_1(v_{n+1} - v_1) + \dots + u_n w_n(v_{n+1} - v_n),$$

565 the inequality being strict if $(u_n)_{n \geq 1}$ is not constant, we observe that

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

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

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

566 This completes the proof of item 1.

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

569 This result is proved by DeAngelis et al. [9, Lemma 2.6] for Part (2) and in [10,
570 Proposition A.3] for part (1), where $w_n = 1$ for all $n \geq 1$. Here we generalize this
571 result to any positive sequence.

572 REFERENCES

573 [1] R. Arditi, C. Lobry and T. Sari, Is dispersal always beneficial to carrying capacity? New
574 insights from the multi-patch logistic equation, *Theoretical Population Biology* 106 (2015),
575 45-59. <http://doi:10.1016/j.tpb.2015.10.001>
576 [2] R. Arditi, C. Lobry and T. Sari, Asymmetric dispersal in the multi-patch logistic equation,
577 *Theoretical Population Biology* 120 (2018), 11-15. <http://doi:10.1016/j.tpb.2015.10.001>
578 [3] J. Arino, Diseases in metapopulations, in *Modeling and Dynamics of Infectious Diseases*, Z.
579 Ma, Y. Zhou, J. Wu (eds.), Series in Contemporary Applied Mathematics, World Scientific
580 Press, Vol. 11 (2009), 64-122.

- 581 [4] J. Arino, N. Bajeux and S. Kirkland, Number of Source Patches Required for Population Per-
582 sistence in a Source–Sink Metapopulation with Explicit Movement, *Bulletin of Mathematical*
583 *Biology* 81 (2019), 1916-1942. <https://doi.org/10.1007/s11538-019-00593-1>
- 584 [5] C. Castillo-Chavez and H.R. Thieme, Asymptotically autonomous epidemic models, in *Math-*
585 *ematical Population Dynamics: Analysis of Heterogeneity*, Vol. 1, Theory of Epidemics, O.
586 Arino, D. Axelrod, M. Kimmel, and M. Langlais, eds., Wuerz, Winnipeg, 1995, pp. 33-50.
- 587 [6] C.W. Castillo-Garsow, and C. Castillo-Chavez, A Tour of the Basic Reproductive Number
588 and the Next Generation of Researchers, in H. Callender Highlander et al. (eds.), *An In-*
589 *troduction to Undergraduate Research in Computational and Mathematical Biology*, (2020),
590 87-124, Foundations for Undergraduate Research in Mathematics, Springer Nature Switzer-
591 land. https://doi.org/10.1007/978-3-030-33645-5_2
- 592 [7] C. Cosner, J. C. Beier, R.S. Cantrell, D. Impoinvil , L. Kapitanski, M. D. Potts, A. Troyo
593 and S.Ruan, The effects of human movement on the persistence of vector-borne diseases,
594 *Theoretical Biology* 258 (2009), 550-560.
- 595 [8] D. L. DeAngelis, C. C. Travis and W. M. Post, Persistence and stability of seed-dispersel
596 species in a patchy environment, *Theoretical Population Biology* 16 (1979), 107-125. [http://dx.doi.org/10.1016/0040-5809\(79\)90008-X](http://dx.doi.org/10.1016/0040-5809(79)90008-X)
- 597 [9] D. L. DeAngelis, W. Ni and B. Zhang, Dispersal and heterogeneity: single species, *Mathe-*
598 *matical Biology* 72 (2015), 239-254. <http://doi:10.1007/s00285-015-0879-y>
- 600 [10] D. L. DeAngelis, W. Ni and B. Zhang, Effects of diffusion on total biomass in heterogeneous
601 continuous and discrete-patch systems, *Theoretical Ecology* 9 (2016). <http://doi10.1007/s12080-016-0302-3>
- 602 [11] D. L. DeAngelis and B. Zhang, Effects of dispersal in a non-uniform environment on popula-
603 tion dynamics and competition: a patch model approach, *Discrete and Continuous Dynamical*
604 *System series B* 19 (2014), 3087-3104. <http://dx.doi.org/10.3934/dcdsb.2014.19.3087>
- 605 [12] B. Elbetch, T. Benzekri , D. Massart and T. Sari, The multi-patch logistic equation, *Discrete*
606 *and Continuous Dynamical System series B* 22 (2020). [http://dx.doi.org/10.3934/dcdsb.](http://dx.doi.org/10.3934/dcdsb.2021025)
607 [2021025](http://dx.doi.org/10.3934/dcdsb.2021025)
- 608 [13] H. I. Freedman, B. Rai and P. Waltman, Mathematical Models of Population Interactions with
609 Dispersal II: Differential Survival in a Change of Habitat, *Journal of Mathematical Analysis*
610 *and Applications* 115 (1986), 140-154. [https://doi.org/10.1016/0022-247X\(86\)90029-6](https://doi.org/10.1016/0022-247X(86)90029-6)
- 611 [14] H. I. Freedman and P. Waltman, Mathematical Models of Population Interactions with Dis-
612 persal I: Stability of two habitats with and without a predator, *SIAM Journal on Applied*
613 *Mathematics* 32 (1977), 631-648. <http://dx.doi.org/10.1137/0132052>
- 614 [15] D. Gao, How does dispersal affect the infection size?, *SIAM Journal on Applied Mathematics*
615 Vol. 80, No. 5, (2020), pp. 2144-2169. <http://doi.10.1137/19M130652X>
- 616 [16] D. Gao and C.-P. Dong Fast diffusion inhibits disease outbreaks, *Proceedings of the American*
617 *Mathematical Society*, 148 (2020), pp. 1709-1722. <http://doi.10.1090/proc/14868>
- 618 [17] H. Guo, M. Y. Li and Z. Shuai, Global stability of the endemic equilibrium of multigroup
619 SIR epidemic models, *Canadian Applied Mathematical Quarterly* 14 (2006), 259-284.
- 620 [18] I. Hanski, *Metapopulation Ecology*, Oxford University Press, 1999.
- 621 [19] R. D. Holt, Population dynamics in two patch environments: some anomalous consequences
622 of an optimal habitat distribution, *Theoretical Population Biology* 28 (1985), 181-201. [http://dx.doi.org/10.1016/0040-5809\(85\)90027-9](http://dx.doi.org/10.1016/0040-5809(85)90027-9)
- 623 [20] C. Lobry, T. Sari and S. Touhami, On Tykhonov's theorem for convergence of solutions of
624 slow and fast systems, *Electronic Journal of Differential Equations* 19 (1998), 1-22. [http://refhub.elsevier.com/S0040-5809\(15\)00102-1/sbref11](http://refhub.elsevier.com/S0040-5809(15)00102-1/sbref11)
- 625 [21] S. A. Levin, Dispersion and population interactions, *American Naturalist* 108 (1974), 207-228.
626 <https://doi.org/10.1086/282900>
- 627 [22] S. A. Levin, Spatial patterning and the structure of ecological communities, in *Some Mathe-*
628 *matical Questions in Biology*, VII, Lectures on Math. in the Life Sciences, American Mathe-
629 *matical Society*, Providence, R.I., 8 (1976), 1-35.
- 630 [23] L. Markus, Asymptotically autonomous differential systems, *Contributions to the Theory of*
631 *Nonlinear Oscillations III* (S. Lefschetz, ed.) (1956), 17-29. *Annals of Mathematics Studies*
632 *36*, Princeton Univ. Press.
- 633 [24] K. Nagahara, Y. Lou and E. Yanagida, Maximizing the total population with logistic growth
634 in a patchy environment, *Journal of Mathematical Biology* 82, 2 (2021). [https://doi:10.](https://doi:10.1007/s00285-021-01565-7)
635 [1007/s00285-021-01565-7](https://doi:10.1007/s00285-021-01565-7)

- 639 [25] H. R. Thieme, Convergence results and a Poincaré-Bendixson trichotomy for asymptoti-
640 cally autonomous differential equations, *Journal of Mathematical Biology* 30 (1992), 755-763.
641 <https://doi.org/10.1007/BF00173267>
- 642 [26] H. R. Thieme. Asymptotically Autonomous Differential Equations in the Plane, *Rocky Moun-
643 tain Journal of Mathematics*, 24 (1), 351-380 Winter 1993. [https://doi.org/10.1216/rmj/
644 1181072470](https://doi.org/10.1216/rmj/1181072470)
- 645 [27] A. N. Tikhonov, Systems of differential equations containing small parameters in the deriva-
646 tives, *Matematicheskii Sbornik (N.S.)* 31 (1952), 575-586. [http://refhub.elsevier.com/
647 S0040-5809\(15\)00102-1/sbref18](http://refhub.elsevier.com/S0040-5809(15)00102-1/sbref18)
- 648 [28] W. R. Wasow, *Asymptotic Expansions for Ordinary Differential Equations*, Robert E. Krieger
649 Publishing Company, Huntington, NY, 1976.
- 650 [29] H. Wu, Y. Wang, Y. Li and D. L. DeAngelis, Dispersal asymmetry in a two-patch system
651 with source-sink populations, *Theoretical Population Biology* 131 (2020), 54-65. [https://
652 doi.org/10.1016/j.tpb.2019.11.004](https://doi.org/10.1016/j.tpb.2019.11.004)
- 653 [30] B. P. Yurk and C. A. Cobbold, Homogenization techniques for population dynamics in
654 strongly heterogeneous landscapes, *Journal of Biological Dynamics* 12 (1) (2018), 171-193.
655 <https://425doi.org/10.1080/17513758.2017.1410238>
- 656 [31] N. Zaker, L. Ketchemen and F. Lutscher, The Effect of Movement Behavior on Population
657 Density in Patchy Landscapes. *Bulletin of Mathematical Biology* 82 (1) (2020), 1-24. [https://
658 //doi.473org/10.1007/s11538-019-00680-3](https://doi.473org/10.1007/s11538-019-00680-3)

659 ELBETCH BILEL
660 DEPARTMENT OF MATHEMATICS, UNIVERSITY DR. MOULAY TAHAR OF SAIDA, ALGERIA.
661 *Email address:* bilel.elbetch@univ-saida.dz

662 BENZEKRI TOUNSIA
663 DEPARTMENT OF MATHEMATICS, USTHB, BAB EZZOUAR, ALGIERS, ALGERIA.
664 *Email address:* tbenzekri@usthb.dz

665 MASSART DANIEL
666 IMAG, UNIV MONTPELLIER, CNRS, MONTPELLIER, FRANCE.
667 *Email address:* daniel.massart@umontpellier.fr

668 SARI TEWFIK,
669 ITAP, UNIV MONTPELLIER, INRAE, MONTPELLIER SUPAGRO, MONTPELLIER, FRANCE.
670 *Email address:* tewfik.sari@irstea.fr