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Abstract. The paper considers a n-patch model with migration terms, where each patch follows a logistic law. First, we give some properties of the total equilibrium population. In some particular cases, we determine the conditions under which fragmentation and migration can lead to a total equilibrium population which might be greater or smaller than the sum of the n carrying capacities. Second, 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. Finally, for the three-patch model we show numerically that the increase in number of patches from two to three gives a new behavior for the dynamics of the total equilibrium population as a function of the migration rate.

1. **Introduction.** Population dynamics is a wide field of mathematics, which contains many problems, for example fragmentation of population and the effect of migration in the general dynamics of population. Bibliographies can be found in the work of Levin [12, 13] and Holt [10]. There are ecological situations that motivate the representation of space as a finite set of patches connected by migrations, for instance an archipelago with bird population and predators. It is an example of insular bio-geography. The standard question in this type of biomathematical problems, is to study the effect of migration on the general population dynamics, and the consequences of fragmentation on the persistence or extinction of the population.

Freedman and Waltman [8] were among the first to consider the case of two patches

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta(x_2 - x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta(x_1 - x_2), \end{cases} \tag{1}$$

2010 *Mathematics Subject Classification.* Primary: 37N25, 92D25; Secondary: 34D23, 34D15.

Key words and phrases. Fragmented habitat, Migration rate, Logistic growth, Carrying capacity, Perfect mixing.

This work was supported by CNRS-PICS project CODYSYS 278552.

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where x_i is the population in patch i, the parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity patch i, and β is the migration rate assumed to be symmetric in both directions. They analyzed the model in the case of perfect mixing ($\beta \to +\infty$) and showed that the total equilibrium population $x_1^*(\beta) + x_2^*(\beta)$ can be greater than the sum of the carrying capacities $K_1 + K_2$.

The 2-patch model (1) was extensively studied by many authors, among them DeAngelis et al. [4], Holt [10], Freedman et al. [7]. It is worth noting that the two-patch model (1) had never been completely analysed until the work of Arditi et al. [1] which gave the complete study of the model (1), i.e the comparison of X_T^* with K_1+K_2 for all values of β. One distinguishing characteristic is the depiction of three situations for the position of $x_1^*(\beta)+x_2^*(\beta)$ compared to K_1+K_2. Under some conditions, fragmentation leads to a total equilibrium population strictly greater or smaller than the sum of the carrying capacities, see Fig. 1 in [1].

DeAngelis and Zhang [5], DeAngelis et al. [6] and Zhang et al. [19] have considered the model

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

where we denote $x_0 = x_n$ and $x_{n+1} = x_1$, allowing the patches to join in a circle so that the same relationships hold between x_i, x_{i-1} and x_{i+1} for all values of i. An interesting result of (2) is that in the case $r_i = K_i$, for $i = 1, \cdots, n$, for any $\beta > 0$, the total population at steady state satisfies

$$\sum_{i=1}^{n} x_i^*(\beta) > \sum_{i=1}^{n} K_i. \tag{3}$$

Our aim is to extend some of the results in [1, 2, 5, 6] to the more general case of the n-patch model:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j\neq i}^{n} \gamma_{ij} \left(x_j - x_i\right), \qquad i = 1, \cdots, n. \tag{4}$$

where n is the number of the patches in the system. The parameter β represents the dispersal rate of the population; $\gamma_{ij} = \gamma_{ji} \geq 0$ denotes the flux between patches j and i, for $j \neq i$. Note that if $\gamma_{ij} > 0$ there is a flux of migration between patches i and j and if $\gamma_{ij} = 0$ there is no migration. In the case where $\beta = 0$, there is no migration , and the system (4) admits $(K_1, \cdots, K_n)$ as a non trivial equilibrium point, which furthermore is globally asymptotically stable (GAS). 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 is greater than the sum of the carrying capacities.

The paper is organized as follows. In Section 2, the mathematical model of n patches, and some notation, are introduced. In Section3, we give some results on the comparison of the total equilibrium population with the sum of the carrying capacities. In Section 4, the behavior of the model is studied when the migration rate tends to infinity. In Section 5, we consider the three-patch model and by numerical simulations we prove the existence of a new behavior of the total equilibrium population. In section 6, we consider the multi-patch logistic growth, coupled by asymmetric migration terms. In Appendix A, we give some properties of the total equilibrium population. In Appendix B, we recall some results which are used in our proofs.

In all the paper, we denote by: $\mathbb{R}_+$ the non negative real numbers. Given a vector $u \in \mathbb{R}^n$ let u^T denotes its transpose. We denote by Re and $|.|$ the real part and the module of a complex number respectively.

2. **Mathematical model.** We consider the model of multi-patch logistic growth, coupled by symmetric migration terms (4). This system of differential equations can be written:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1}^{n} \gamma_{ij} x_j, \qquad i = 1, \cdots, n \tag{5}$$

where

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ij}, \qquad i = 1, \cdots, n \tag{6}$$

denotes the outgoing flux of patch i. The matrix

$$\Gamma := (\gamma_{ij})_{n\times n} \tag{7}$$

is called the connectivity matrix. Its columns sum to 0 since the matrix Γ is symmetric and the diagonal elements γ_{ii}, defined by (6), assert that each row of γ sums to 0. The model of (1) studied in [1, 4, 7, 8, 10] corresponds to the case where the migration rate $\gamma_{12} = \gamma_{21} > 0$ can be normalized to 1, by replacing β by β/γ_{12}. The model (2) studied in [5, 6, 19] corresponds to the case where

$$\gamma_{1n} = \gamma_{n1} = \gamma_{i,i-1} = \gamma_{i-1,i} = 1 \text{ for } 2 \leq i \leq n \text{ and } \gamma_{ij} = 0 \text{ otherwise.} \tag{8}$$

We have the following result:

Proposition 2.1. *The domain* $\Omega = \{(x_1, \ldots, x_n) \in \mathbb{R}^n / x_i \geq 0, i = 1, \ldots, n.\}$ *is positively invariant for the system* (4).

Proof. If $x_i = 0$, and $x_j \geq 0$, for all $j \neq i$, then we have

$$\frac{dx_i}{dt} = \sum_{j=1, j\neq i} \gamma_{ij} x_j \geq 0, \qquad i = 1, \cdots, n.$$

Therefore, $x_i(t)$ cannot become negative, which shows that Ω is positively invariant for the system (4). □

Proposition 2.2. *Assume that the connectivity matrix* $\Gamma := (\gamma_{ij})_{n\times n}$ *is irreducible. The model* (4) *has a unique positive equilibrium point which is GAS in the positive cone* $\mathbb{R}^n_+ \setminus \{0\}$.

Proof. The result follows from [16]. □

Remark 2.3. The matrix Γ being irreducible means that the set of patches cannot be partitioned into two nonempty disjoint subsets, I and J, such that there is no migrations between a patch in subset I and a patch in subset J. The matrix Γ is assumed to be irreducible throughout the rest of the paper. Therefore species can reach any patch from any patch either directly or through other patches.

3. **Comparison of the total equilibrium population with the sum of carrying capacities.** In all of this work, the GAS equilibrium of the system (4), whose existence is shown in Proposition 2.2, is denoted by $E^*(\beta) = (x_1^*(\beta), \dots, x_n^*(\beta))$. The equilibrium point $E^*(\beta)$ is the solution of the algebraic system:

$$r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j\neq i}^{n} \gamma_{ij} (x_j - x_i) = 0, \qquad i = 1, \cdots, n. \tag{9}$$

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

$$\sum_{i=1}^{n} r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0. \tag{10}$$

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

$$\mathbb{E}^{n-1} = \left\{ x \in \mathbb{R}^n : \Theta(x) := \sum_{i=1}^{n} r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0 \right\}. \tag{11}$$

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

Our aim is to compare the total equilibrium population

$$X_T^*(\beta) = x_1^*(\beta) + \cdots + x_n^*(\beta), \tag{12}$$

with the sum of carrying capacities $K_1 + \ldots + K_n$, when the rate of migration β varies from zero to infinity. Let us begin with some interesting particular cases of the system (4).

3.1. **Equal growth rates.** In the next proposition, we show that if the growth rates are equal in all patches, then the total equilibrium population is always smaller than the sum of the carrying capacities:

Proposition 3.1. *If $r_1 = \cdots = r_n$, then the total equilibrium population, defined by (12) satisfies $X_T^*(\beta) \leq \sum_{i=1}^n K_i$, for all $\beta \in [0, \infty[$.*

Proof. The equation of the tangent space to the ellipsoid $\mathbb{E}^{n-1}$, defined by (11), at point $\mathcal{A} = (K_1, \dots, K_n)$ is given by

$$\sum_{i=1}^{n} (x_i - K_i) \frac{\partial \Theta}{\partial x_i}(\mathcal{A}) = 0, \tag{13}$$

where Θ is given by (11). Since $\frac{\partial \Theta}{\partial x_i}(\mathcal{A}) = -r_i$, (13) can be written as follows:

$$\sum_{i=1}^{n} r_i (x_i - K_i) = 0. \tag{14}$$

If we take $r_1 = \cdots = r_n$ in (14), we get that the equation of the tangent plane to $\mathbb{E}^{n-1}$ at the point $\mathcal{A}$ is

$$\sum_{i=1}^{n} x_i = \sum_{i=1}^{n} K_i.$$

By the convexity of $\mathbb{E}^{n-1}$, any point of $\mathbb{E}^{n-1}$ lies in the half-space defined by the inequation $\sum_{i=1}^n x_i \leq \sum_{i=1}^n K_i$. Therefore $E^*(\beta)$ satisfies

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

Which completes the proof of the proposition. □

3.2. **Equal carrying capacities.** In the next proposition, we show that if the carrying capacities are equal in all patches, then the total equilibrium population does not depend on the migration rate and is always equal to the sum of the carrying capacities:

Proposition 3.2. *If $K_1 = \cdots = K_n =: K$, then $X_T^*(\beta) = nK$ for all $\beta \geq 0$.*

Proof. As shown in item 1 of the proposition A.3, we have $x_i^*(\beta) = K$ for all $\beta \geq 0$ and all $i = 1 \cdots n$. Therefore $X_T^*(\beta) = nK$. □

3.3. **Equal ratios r_i/K_i.** In the next proposition, we show that if the ratios $\alpha_i = \frac{r_i}{K_i}$ are equal in all patches, then the total equilibrium is always larger than the sum of the carrying capacities:

Proposition 3.3. *If $\alpha_1 = \ldots = \alpha_n =: \alpha$, then*

$$X_T^*(\beta) \geq \sum_{i=1}^{n} K_i, \qquad \text{for all } \beta \geq 0. \tag{15}$$

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

Proof. From Lemma A.2 we deduce that for all $\beta \geq 0$ we have

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

Equality can hold if and only if $\beta = 0$ or $x_j^*(\beta) = x_i^*(\beta)$ for all $j < i$. Let us prove that if at least two patches have not the same carrying capacity then equality cannot hold for $\beta > 0$. Suppose that there exists $\beta > 0$ such that the positive equilibrium satisfies $x_j^*(\beta) = x_i^*(\beta)$ for all $j < i$, then $x_1^*(\beta) = \ldots = x_n^*(\beta)$. Denote by $x^* > 0$ their common value. Then all terms $\gamma_{ij}\,(x_j - x_i)$ in (9) vanish, so that these equations become

$$r_i x^* \left(1 - \frac{x^*}{K_i}\right) = 0, \qquad i = 1, \cdots, n.$$

Therefore $K_i = x^*$ for all i, which gives a contradiction. Hence the equality (15) can hold if and only if $\beta = 0$. □

In [5, page 3092], DeAngelis et al. have shown this result in the particular case of the model (2), and $r_i = K_i$, $i = 1 \cdots n$, see (3).

3.4. **All patches but one are identical.** We assume now that $n-1$ patches are identical, that is to say, they have the same carrying capacities and the growth rates. We assume also that the flux of migration between the n-th patch and all these $n-1$ identical patches are equal. Hence we have the following conditions

$$K_1 = \cdots = K_{n-1} =: K, \quad r_1 = \ldots = r_{n-1} =: r \text{ and } \gamma_{n1} = \ldots = \gamma_{nn-1} =: \gamma \tag{16}$$

Under conditions (16), we show that the n-patch model behaves like a 2-patch model, that is, there are only three situations as depicted in Fig. 1. This figure is similar to Figure 2 of [1]. This property holds regardless of the flux of migration

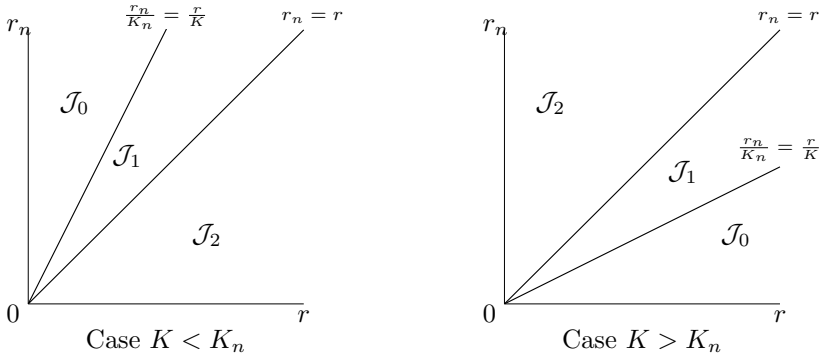


FIGURE 1. Qualitative properties of model (4) when (16) holds. In $\mathcal{J}_0$, patchiness has a beneficial effect on total carrying capacity. This effect is detrimental in $\mathcal{J}_2$. In $\mathcal{J}_1$, the effect is beneficial for $\beta < \beta_0$ and detrimental for $\beta > \beta_0$.

between the identical $n-1$ patches, provided that the connectivity matrix Γ, defined by (7), is irreducible. More precisely, define regions $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$ by:

$$\text{If } K < K_n \text{ then } \begin{cases} \mathcal{J}_0 = \left\{(r, r_n) : r_n \geq \frac{K_n}{K} r\right\} \\ \mathcal{J}_1 = \left\{(r, r_n) : \frac{K_n}{K} r > r_n > r\right\} \\ \mathcal{J}_2 = \{(r, r_n) : r \geq r_n\} \end{cases} \tag{17}$$

$$\text{If } K_n < K \text{ then } \begin{cases} \mathcal{J}_0 = \left\{(r, r_n) : r_n \leq \frac{K_n}{K} r\right\} \\ \mathcal{J}_1 = \left\{(r, r_n) : \frac{K_n}{K} r < r_n < r\right\} \\ \mathcal{J}_2 = \{(r, r_n) : r \leq r_n\} \end{cases} \tag{18}$$

We have the following proposition:

Proposition 3.4. *Assume that the conditions (16) hold in the system (4). We consider the regions, denoted $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$, depicted in Fig. 1, and defined by (17) when $K < K_n$ and by (18) when $K > K_n$. Let $\alpha_n = r_n/K_n$ and $\alpha = r/K$.*

1. *If $(r, r_n) \in \mathcal{J}_0$ then $X_T^*(\beta) > (n-1)K + K_n$ for all $\beta > 0$.*
2. *If $(r, r_n) \in \mathcal{J}_1$ then $X_T^*(\beta) > (n-1)K + K_n$ for $0 < \beta < \beta_0$ and $X_T^*(\beta) < (n-1)K + K_n$ for $\beta > \beta_0$ where β_0 is given by*

$$\beta_0 = \frac{r_n - r}{\gamma(\alpha - \alpha_n)} \frac{1}{1/\alpha_n + (n-1)/\alpha}. \tag{19}$$

3. *If $(r, r_n) \in \mathcal{J}_2$ then $X_T^*(\beta) < (n-1)K + K_n$ for all $\beta > 0$.*

Proof. Assume that the conditions (16) hold and $K < K_n$. From item (2) in Proposition A.3 we deduce that

$$x_1^*(\beta) = \cdots = x_{n-1}^*(\beta) =: x^*(\beta) < x_n^*(\beta). \tag{20}$$

Now, using Lemma A.1, the total equilibrium population becomes

$$X_T^*(\beta) = (n-1)K + K_n + \beta \left(\sum_{j=1}^{n-1} \frac{\gamma\left(x^*(\beta) - x_n^*(\beta)\right)}{\alpha_n x_n^*} + \sum_{i=1}^{n-1} \frac{\gamma\left(x_n^*(\beta) - x^*(\beta)\right)}{\alpha x^*} \right).$$

Therefore

$$X_T^*(\beta) = (n-1)K + K_n + (n-1)\beta\gamma \frac{(x^*(\beta) - x_n^*(\beta))(\alpha x^*(\beta) - \alpha_n x_n^*(\beta))}{\alpha\alpha_n x^*(\beta) x_n^*(\beta)}. \quad (21)$$

1. If $(r, r_n) \in \mathcal{J}_0$, then $\alpha_n \geq \alpha$. Hence $(\alpha x^* - \alpha_n x_n^*) < \alpha(x^* - x_n^*) < 0$, which implies that $(x^* - x_n^*)(\alpha x^* - \alpha_n x_n^*) > 0$, and then $X_T^*(\beta) > (n-1)K + K_n$ for $\beta > 0$.

2. If $(r, r_n) \in \mathcal{J}_1$, then $r_n > r$ and $\alpha > \alpha_n$. According to Equation (21), the equality

$$X_T^*(\beta) := (n-1)x^*(\beta) + x_n^*(\beta) = (n-1)K + K_n,$$

is equivalent to $\beta = 0$ or $\alpha x^*(\beta) - \alpha_n x_n^*(\beta) = 0$. Thus $x^*(\beta)$ and $x_n^*(\beta)$ are the solutions of the linear system

$$\begin{cases} \alpha x^*(\beta) - \alpha_n x_n^*(\beta) = 0, \\ (n-1)x^*(\beta) + x_n^*(\beta) = (n-1)K + K_n, \end{cases}$$

which admits a unique solution

$$x^*(\beta) = \frac{1}{\alpha} \frac{(n-1)K + K_n}{(n-1)/\alpha + 1/\alpha_n}, \quad x_n^*(\beta) = \frac{1}{\alpha_n} \frac{(n-1)K + K_n}{(n-1)/\alpha + 1/\alpha_n}. \quad (22)$$

As $(x_1^*(\beta), \cdots, x_n^*(\beta))$ is an equilibrium point of the system (4), it satisfies the following system

$$\begin{cases} 0 = r x^*(\beta) \left(1 - \dfrac{x^*(\beta)}{K}\right) + \beta\gamma \left(x_n^*(\beta) - x^*(\beta)\right), \\ 0 = r_n x_n^*(\beta) \left(1 - \dfrac{x_n^*(\beta)}{K_n}\right) + (n-1)\beta\gamma \left(x^*(\beta) - x_n^*(\beta)\right), \end{cases} \quad (23)$$

obtained from (9) by replacing $x_i = x_i^*(\beta)$ and using (16) and (20). Using the formulas (22), the system (23) has a unique solution β_0 given by

$$\beta_0 = \frac{r_n - r}{\gamma(\alpha - \alpha_n)} \frac{1}{1/\alpha_n + (n-1)/\alpha}, \quad (24)$$

which is positive since $r_n > r$ and $\alpha > \alpha_n$. According to Lemma A.4 we have:

$$\frac{dX_T^*}{d\beta}(0) = (n-1)\gamma(K - K_n)\left(\frac{1}{r_n} - \frac{1}{r}\right),$$

which is positive since $r < r_n$ and $K < K_n$. So:

- If $\beta \in (0, \beta_0]$, then $X_T^*(\beta) > (n-1)K + K_n$.
- If $\beta \in (\beta_0, \infty[$, then $X_T^*(\beta) < (n-1)K + K_n$.

3. If $(r, r_n) \in \mathcal{J}_2$ then $r \geq r_n$. We have:

$$\alpha x^*(\beta) - \alpha_n x_n^*(\beta) = \frac{r}{K} x^*(\beta) - \frac{r_n}{K_n} x_n^*(\beta)$$

From item (2) in Proposition A.3 we deduce that $x^*(\beta)/K > 1$ and $x_n^*(\beta)/K_n < 1$. Therefore

$$\alpha x^*(\beta) - \alpha_n x_n^*(\beta) > r - r_n \geq 0,$$

which gives $X_T^*(\beta) < (n-1)K + K_n$ for $\beta > 0$.

We use item 2- (b) of Proposition A.3 and the same procedures to study the case where $K > K_n$. □

Remark 3.5. This proof is adapted from [1]. Actually, if we take $n = 2$ and $\gamma = 1$ in Proposition 3.4, we find the results given by Arditi et al in [1, Proposition 2, page 54].

4. **Perfect mixing.** In this section our aim is to study the behavior of the system (4) for large migration rate, i.e when $\beta \to \infty$. We need the following result:

Lemma 4.1. The connectivity matrix Γ has rank $n-1$. Except 0 which is a simple eigenvalue of Γ, whose eigenvector is $u = (1, \dots, 1)^T$, all other eigenvalues of Γ are negative.

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

$$B = \Gamma + sI,$$

is non-negative and irreducible. Then by the Perron-Frobenius theorem [9, Theorem 2, page 53], the spectral radius of B is a simple eigenvalue, and it is the only eigenvalue of B which admits a positive eigenvector. Now observe that $(1, \dots, 1)^T$ is an eigenvector of B, and the corresponding eigenvalue is s. This proves that $s = \rho(B)$ is a simple eigenvalue of B, and since $s = \rho(B)$ any other eigenvalue λ of B satisfies $\lambda < s$. Therefore 0 is a simple eigenvalue of $\Gamma = -sI + B$, that is, the rank of Γ is $n-1$, and all other eigenvalues of Γ are negative. □

We have the following result :

Theorem 4.2. *We have*

$$\lim_{\beta \to +\infty} E^*(\beta) = \left(\frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i}, \dots, \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i} \right). \tag{25}$$

where $\alpha_i = r_i/K_i$.

Proof. Denote

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

Recall that the equilibrium point $E^*(\beta)$ is the unique positive solution of the algebraic system (9). Therefore it is defined, in the positive cone, by the fact that it belongs to the ellipsoid $\mathbb{E}^{n-1}$ defined by (11), and the equation $F_\beta(E^*(\beta)) = 0$, where

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

The ellipsoid $\mathbb{E}^{n-1}$ is compact, so $E^*(\beta)$ has at least one limit point in $\mathbb{E}^{n-1}$, when β goes to infinity. Besides, F_β converges, uniformly on compact sets, to the linear map

$$\mathbb{R}^n \longrightarrow \mathbb{R}^{n-1}$$
$$(x_1, \dots, x_n)^T \longmapsto \Lambda(x_1, \dots, x_n)^T$$

where Λ is the sub matrix of the connectivity matrix Γ defined by (7), obtained by dropping the last row of Γ. Hence any limit point $(x_1, \dots, x_n)$ of $E^*(\beta)$ satisfies $\Lambda(x_1, \dots, x_n)^T = 0$.

Since Λ is obtained from Γ by dropping the last row, and the rows of Γ sum to zero, the rank of Λ equals that of Γ, which is $n-1$ by Lemma 4.1.

Therefore, by the convexity of $\mathbb{E}^{n-1}$, $\Lambda(x_1, \dots, x_n)^T = 0$ has exactly two solutions in $\mathbb{E}^{n-1}$, which are the origin and $E^*(\infty)$. To prove the convergence of $E^*(\beta)$ to $E^*(\infty)$, it suffices to prove that the origin cannot be a limit point of $E^*(\beta)$.

Write $E^*(\beta) = (x_1(\beta), \dots, x_n(\beta))$. 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.

Let $x_i(\beta) = \min\{x_1(\beta), \cdots, x_n(\beta)\}$. We have

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

whence

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

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 4.1. *We have*

$$X_T^*(+\infty) = \lim_{\beta\to+\infty} \sum_{i=1}^{n} x_i^*(\beta) = n \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i}. \tag{26}$$

Remark 4.3. Notice that the formula (26) shows that the total equilibrium population does not depend on the flux of migration γ_{ij}. This formula was obtained for the 2-patch case by Freedman and Waltman [8, Theorem 1]. It was also obtained in [6, Theorem B.1] for the model (2) corresponding to the particular case (8) of the migration flux.

Proposition 4.4. *If $\alpha_1 = \cdots = \alpha_n =: \alpha$, then $X_T^*(+\infty) = \sum_{i=1}^n K_i$.*

Proof. We use Equation (26) for $\alpha_1 = \cdots = \alpha_n =: \alpha$. □

Arditi et al. [1] also obtained the formula (26), in the 2-patch case, by using singular perturbation theory, see [1, Formula (A.13)]. They showed that, if $(x_1(t,\beta), x_2(t,\beta))$ is the solution of (1), with initial condition (x_{10}, x_{20}), then, when $\beta \to \infty$, the total population $x_1(t,\beta)+x_2(t,\beta)$ is approximated by $Y(t)$, the solution of the logistic equation

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{2K}\right), \text{ where } r = \frac{r_1 + r_2}{2} \text{ and } K = \frac{r_1 + r_2}{r_1/K_1 + r_2/K_2}, \tag{27}$$

with initial condition $Y(0) = x_{10} + x_{20}$. Therefore the total population behaves like the unique logistic equation given by (27). In addition, one obtains the following property: with the exception of a small initial interval, the population densities $x_1(t,\beta)$ and $x_2(t,\beta)$ are both approximated by $Y(t)/2$, see [1, Proposition 3]. Therefore, this approximation shows that, when t and β tend to ∞, the population density $x_i(t,\beta)$ tends toward $\frac{r_1+r_2}{\alpha_1+\alpha 2}$, as stated in Theorem 4.2 and in addition, $x_i(t,\beta)$ quickly jumps from its initial condition x_{i0} to the average $(x_{10}+x_{20})/2$ and then is very close to $Y(t)/2$. Our aim is to show that this result is true for the n-patch model (4).

Theorem 4.5. *Let $(x_1(t,\beta), \ldots, x_n(t,\beta))$ be the solution of the system (4) with initial condition $(x_{10}, \cdots, x_{n0})$ satisfying $x_{i0} \geq 0$ for $i = 1 \cdots n$. Let $Y(t)$ be the solution of the logistic equation*

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{nK}\right), \text{ where } r = \frac{\sum_{i=1}^n r_i}{n} \text{ and } K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i/K_i}, \tag{28}$$

with initial condition $Y(0) = \sum_{i=1}^{n} x_{i0}$. *Then, when* $\beta \to \infty$, *we have*

$$\sum_{i=1}^{n} x_i(t,\beta) = Y(t) + o(1), \qquad \textit{uniformly for } t \in [0,+\infty) \tag{29}$$

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

$$x_i(t,\beta) = \frac{Y(t)}{n} + o(1), \quad i = 1,\dots,n, \qquad \textit{uniformly for } t \in [t_0,+\infty). \tag{30}$$

Proof. Since Γ is symmetric with real coefficients, there exists an orthogonal matrix P such that

$$P^{-1}\Gamma P = D$$

where D is the diagonal matrix whose diagonal elements are the eigenvalues

$$\lambda_1 \leq \cdots \leq \lambda_{n-1} < \lambda_n = 0$$

of Γ, see Lemma 4.1. We rewrite the system (5) in vector form:

$$\frac{dx}{dt} = f(x) + \beta\Gamma x, \tag{31}$$

where $x = (x_1, \cdots, x_n)^T$ and

$$f(x) = \left(r_1 x_1(1 - x_1/K_1), \cdots, r_n x_n(1 - x_n/K_n)\right)^T. \tag{32}$$

Using the variables $y = P^{-1}x$, the system (31) becomes:

$$\frac{dy}{dt} = P^{-1}f(Py) + \beta D y. \tag{33}$$

This system of n differential equations can be written

$$\begin{cases} \dfrac{dy_i}{dt} = g_i(y) + \beta\lambda_i y_i, \quad i = 1, \cdots, n-1 \\ \dfrac{dy_n}{dt} = g_n(y), \end{cases} \tag{34}$$

where the components g_i, for $i = 1, \cdots, n$, are defined by

$$P^{-1}f(Py) = \left(g_1(y), \cdots, g_n(y)\right)^T. \tag{35}$$

When $\beta \to \infty$, (34) is a *slow-fast* system, with one *slow variable*, y_n, and $n-1$ *fast variables*, y_i for $i = 1 \cdots n-1$. According to Tikhonov's theorem [11, 17, 18] we consider the dynamics of the fast variables in the time scale $\tau = \beta t$. One obtains

$$\frac{dy_i}{d\tau} = \frac{1}{\beta} g_i(y) + \lambda_i y_i \quad i = 1, \cdots, n-1. \tag{36}$$

In the limit $\beta = \infty$, we find the *fast dynamics*

$$\frac{dy_i}{d\tau} = \lambda_i y_i, \quad i = 1, \cdots, n-1. \tag{37}$$

The *slow manifold*, which is the equilibrium point of the fast dynamics (37), is unique and is given by:

$$y_i = 0 \text{ for } i = 1 \cdots n-1. \tag{38}$$

Since $\lambda_i < 0$ for $i = 1, \dots, n-1$, the slow manifold is GAS for (37). So, the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (34) are approximated by the solutions of the *reduced model* which

is obtained by replacing y_i, $i = 1, \cdots, n-1$, by (38) into the dynamics of the slow variable y_n, given by the last equation in (34). One obtains:

$$\frac{dy_n}{dt} = g_n((0, \cdots, 0, y_n)^T). \tag{39}$$

Let us compute $g_n((0, \cdots, 0, y_n)^T)$ which is the last component of the vector (35), given by $P^{-1} f\left(P(0, \cdots, 0, y_n)^T\right)$. We first notice that

$$P(0, \cdots, 0, y_n)^T = \frac{1}{\sqrt{n}}(y_n, \cdots, y_n)^T,$$

since it is obtained by multiplying by y_n the last column of P, which is simply the normalized eigenvector $u/\sqrt{n}$ of Γ, corresponding to the eigenvalue $\lambda_n = 0$, see Lemma 4.1. On the other hand, since P is orthogonal, the last row of $P^{-1} = P^T$ is equal to $u^T/\sqrt{n}$. Therefore, using the definition (32) of the vector f, one has

$$g_n((0, \cdots, 0, y_n)^T) = \frac{1}{\sqrt{n}} \sum_{i=1}^{n} r_i \frac{y_n}{\sqrt{n}} \left(1 - \frac{y_n}{\sqrt{n} K_i}\right) = r y_n \left(1 - \frac{y_n}{\sqrt{n} K}\right),$$

where r and K are defined in (28). Hence the reduced equation (39) is

$$\frac{dy_n}{dt} = r y_n \left(1 - \frac{y_n}{\sqrt{n} K}\right). \tag{40}$$

Since (40) admits $\sqrt{n}K$ 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 y_n and for all $t \geq t_0 > 0$ for the fast variables y_i, $i = 1, \cdots, n-1$, where t_0 is as small as we want.

Using $y_n = X/\sqrt{n}$, where $X = \sum_{i=1}^{n} x_i$, one obtains that $\sum_{i=1}^{n} x_i(t, \beta)$ is approximated by a solution of the equation

$$\frac{dX}{dt} = r X \left(1 - \frac{X}{nK}\right). \tag{41}$$

Therefore, let $Y(t)$ be the solution of (41) of initial condition $Y(0) = \sum_{i=1}^{n} x_{i0}$, then, when $\beta \to \infty$, we have the approximation (29). To prove (30), we observe that the last column of P is $u/\sqrt{n}$, so for all i, $x_i(t, \beta)$ is $y_n(t, \beta)/\sqrt{n}$, plus some linear combination of the $y_i(t, \beta)$ for $i < n$, all of which converge to zero, uniformly in t. □

In the case of perfect mixing, the approximation (29) shows that the total population behaves like the unique logistic equation (28) and then, when t and β tend to ∞, the total population $\sum x_i(t, \beta)$ tends toward $nK = n\frac{\sum r_i}{\sum \alpha_i}$, where $\alpha_i = r_i/K_i$, as stated in Corollary 4.1. The approximation (30) 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_{i0} to the average $Y(0)/n$, each patch of the n-patch model behaves like the single logistic equation

$$\frac{dx}{dt} = r x \left(1 - \frac{x}{K}\right), \tag{42}$$

where r and K are defined in (28). Hence, when t and β tend to ∞, the population density $x_i(t, \beta)$ tends toward $K = \frac{\sum r_i}{\sum \alpha_i}$, as stated in Theorem 4.2.

5. **Three-patch model.** Our aim in this section is to show that when $n \geq 3$ the behavior of the n-patch logistic equation is richer and more intricate than in the case $n = 2$, where only three situations can occur: the case where the total equilibrium population is always greater than the sum of carrying capacities, the case where it is always smaller, and a third case, where the effect of migration is beneficial for lower values of the migration coefficient β and detrimental for the higher values. More precisely, it was shown in [1] that, if $n = 2$, the following trichotomy holds

- If $X_T^*(+\infty) > K_1 + K_2$ then $X_T^*(\beta) > K_1 + K_2$ for all $\beta > 0$.
- If $\frac{d}{d\beta} X_T^*(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$, then there exists $\beta_0 > 0$ such that $X_T^*(\beta) > K_1 + K_2$ for $0 < \beta < \beta_0$, $X_T^*(\beta) < K_1 + K_2$ for $\beta > \beta_0$ and $X_T^*(\beta_0) = K_1 + K_2$.
- If $\frac{d}{d\beta} X_T^*(0) < 0$, then $X_T^*(\beta) < K_1 + K_2$ for all $\beta > 0$.

Therefore, the condition $X_T^*(\beta) = K_1 + K_2$ holds only for $\beta = 0$ and at most for one positive value $\beta = \beta_0$. The value β_0 exists if and only if $\frac{d}{d\beta} X_T^*(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$.

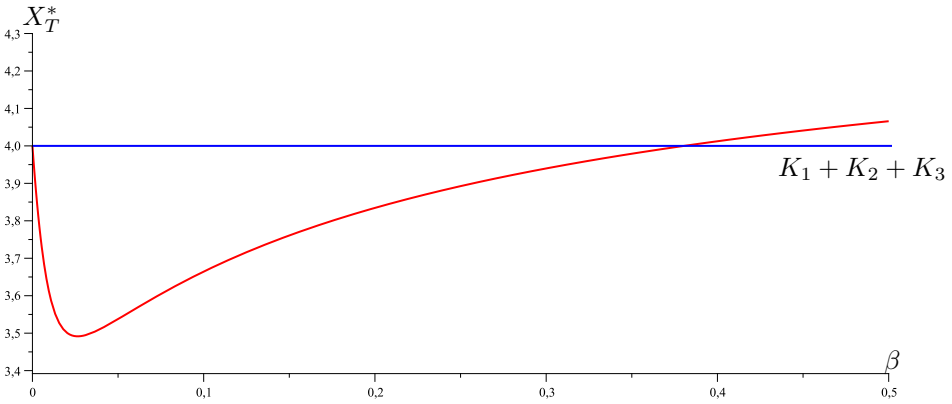


FIGURE 2. Total equilibrium population X_T^* of the system (4) ($n = 3$) as a function of migration rate β. The parameter values are given in Table 5.

In the numerical simulations we take $n = 3$ and $\gamma_{ij} = 1$ for all $i, j = 1, 2, 3$. We show that we can have new behaviors of $X_T^*(\beta)$ due to the addition of the third patch. We show that we can have the following situations, which do not exist in the two-patch model:

- We can have simultaneously $\frac{dX_T^*}{d\beta}(0) < 0$ and $X_T^*(+\infty) > K_1 + K_2 + K_3$, as shown in Fig. 2.
- We can have $\frac{dX_T^*}{d\beta}(0) > 0$ and $X_T^*(+\infty) > K_1 + K_2 + K_3$ and there exist values of β for which we have $X_T^*(\beta) < K_1 + K_2 + K_3$, as shown in Fig. 3.
- We can have $\frac{dX_T^*}{d\beta}(0) < 0$ and $X_T^*(+\infty) < K_1 + K_2 + K_3$ and there exist values of β for which we have $X_T^*(\beta) > K_1 + K_2 + K_3$, as shown in Fig. 4.

Therefore the equality $X_T^*(\beta) = K_1 + K_2 + K_3$ can occur for two positive values of β, not only for a unique positive value as in the two-patch case.

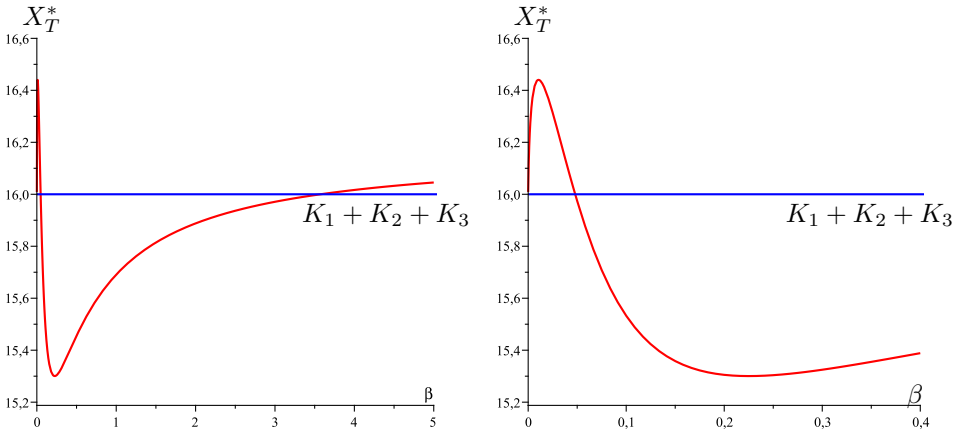


FIGURE 3. Total equilibrium population X_T^* of the system (4) ($n = 3$) as a function of migration rate β. The figure on the right is a zoom, near the origin, of the figure on the left. The parameter values are given in Table 5.

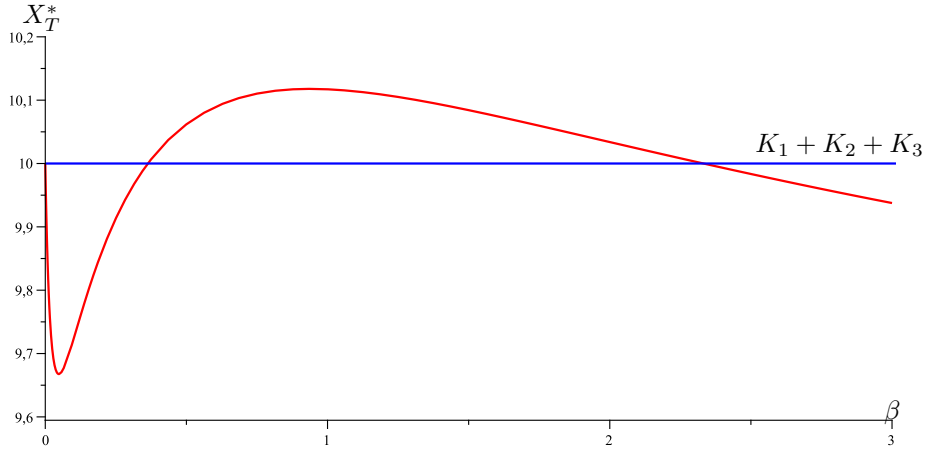


FIGURE 4. Total equilibrium population X_T^* of the system (4) ($n = 3$) as a function of migration rate β. The parameter values are given in Table 5.

6. **Asymmetric dispersal.** Arditi et al. [2] generalized the mathematical analysis of the two-patch model (1) to the asymmetric case

$$\begin{cases} \dfrac{dx_1}{dt} = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right) + \beta(\gamma_{12} x_2 - \gamma_{21} x_1), \\ \dfrac{dx_2}{dt} = r_2 x_2 \left(1 - \dfrac{x_2}{K_2}\right) + \beta(\gamma_{21} x_1 - \gamma_{12} x_2), \end{cases} \tag{43}$$

where $\gamma_{12} \neq \gamma_{21}$. They showed that there are only three cases as in the symmetric dispersal case. In this section we give some results on the general multi-patch

TABLE 1. The numerical values of the parameters for the logistic growth function of the model (4), with $n = 3$, used in Fig. 2, 3, 4. All migration coefficients satisfy $\gamma_{ij} = 1$. The derivative of the total equilibrium population at $\beta = 0$ is computed with Eq. (58), and the perfect mixing abundance $X_T^*(+\infty)$ is computed with Eq. (26).

Figure	r_1	r_2	r_3	K_1	K_2	K_3	$\frac{dX_T^*(0)}{d\beta}$	$X_T^*(+\infty)$
2	0.12	18	0.02	0.5	1.5	2	-79.19	$4.44 > \sum K_i = 4$
3	0.04	3	0.2	0.5	6	9.5	299.33	$16.17 > \sum K_i = 16$
4	4	0.7	0.06	5	1	4	-24.58	$9.42 < \sum K_i = 10$

logistic growth, coupled with asymmetric migration terms :

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j\neq i}^{n} \left(\gamma_{ij} x_j - \gamma_{ji} x_i\right), \qquad i = 1, \cdots, n. \tag{44}$$

where $\gamma_{ij} \geq 0$ denotes the incoming flux from patch j to patch i, for $i \neq j$. As in the symmetric dispersal case (4), the system (44) can be written in the form (5) where

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ji}, \qquad i = 1, \cdots, n \tag{45}$$

denotes the outgoing flux of patch i. The connectivity matrix is defined by (7). Its columns sum to 0 since the diagonal elements γ_{ii}, defined by (45), assert that what comes out of a patch is distributed between the other $n - 1$ patches. As in the symmetric dispersal case, the positive cone $\mathbb{R}_+^n$ is positively invariant for the system (44). We have the following result, whose proof needs the Lemma B.2, which is recalled in Appendix B.

Theorem 6.1. *Assume that the connectivity matrix $\Gamma := (\gamma_{ij})_{n\times n}$ is irreducible. The model (44) has a unique positive equilibrium point which is GAS in the positive cone $\mathbb{R}_+^n \setminus \{0\}$.*

Proof. Consider the system (44). We define the following matrix

$$A = \beta\Gamma + \mathrm{diag}(r_1, \cdots, r_n), \tag{46}$$

where Γ is the connectivity matrix defined by (7). Therefore $A = (a_{ij})$ where

$$a_{ij} = \begin{cases} \beta\gamma_{ij} & \text{if } i \neq j \\ r_i - \beta \sum_{k\neq i} \gamma_{ik} & \text{if } i = j \end{cases} \tag{47}$$

Note that, the matrix (47) is the Jacobian matrix of the system (44) evaluated at $x = 0$. According to a result of Lu and Takeuchi [14, Corollary 1], the system (44) possesses a globally stable positive equilibrium if $s(A) > 0$ where $s(A)$ is the stability modulus of the matrix A. Let us prove that $s(A) > 0$. Let $u = (1, \cdots, 1)^T$. We have

$$A^T u = (r_1, \cdots, r_n)^T \geq \lambda u, \quad \text{where} \quad \lambda = \min\{r_1, \cdots, r_n\} > 0.$$

Therefore, since A is a Metzler matrix, according to Lemma B.2, we have

$$s(A) = s(A^T) \geq \lambda > 0.$$

□

Some of the results obtained in the symmetrical case can be easily extended to the asymmetric case. For instance we have the following result:

Proposition 6.2. *If $r_1 = \cdots = r_n$, then the total equilibrium population, defined by (12) satisfies $X_T^*(\beta) \leq \sum_{i=1}^n K_i$, for all $\beta \in [0, \infty[$.*

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

$$r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j\neq i}^{n} (\gamma_{ij} x_j - \gamma_{ji} x_i) = 0, \qquad i = 1, \cdots, n. \tag{48}$$

As in the symmetric dispersal case, the sum of these equations shows that $E^*(\beta)$ satisfies the equation (10). Therefore $E^*(\beta)$ belongs to the ellipsoid defined by (11). The rest of the proof is the same as the proof of Prop. 3.1 and simply consists in noticing that the interior of the ellipsoid is strictly convex. □

7. **Conclusion.** The goal of this paper was to generalize to a multi-patch model the results obtained in [1] for a two-patch model. The migration between patches is modeled by a symmetric Metzler matrix, called the connectivity matrix. When the connectivity matrix is irreducible, the system is shown (Prop. 2.2) to have a unique non-trivial equilibrium, which furthermore is globally asymptotically stable. One of the questions we have looked at is

Question 7.1. *Is it possible, depending on the migration rate, that the total population be larger than the sum of the capacities of each patch ?*

We have answered this question (Prop. 3.4- Sec.3) in the particular case when all patches, but one, are identical in carrying capacity growth rate, and migration rate to and from the "central" patch. The results are similar to those of [1], in that there exists a critical value of the migration rate where the answer to Question 7.1 changes.

In Section 4 we looked at another particular case, that of perfect mixing, when the migration rate goes to infinity, in other words, when there is no restriction whatsoever on travel. We computed the equilibrium in this situation, and by perturbation arguments (see [17]), we proved that the dynamics in this ideal case provide a good approximation to the case when the migration rate is large.

In Section 5 we considered the case when there are only three patches. We provided numerical evidence to the fact that the answer to Question 7.1 is more subtle than in the two-patch case, in particular there may be at least two critical values where the answer changes.

In Section 6 we considered the asymmetrical dispersal case, that is, the connectivity matrix is no longer assumed to be symmetric. We proved that the globally asymptotically stable equilibrium still exists in this case (see Theorem 6.1).

Some questions remain open : what are the exact conditions on the model under which there might be several critical values where the answer to Question 7.1 changes ? is it possible to give a general classification of all possible cases ? To what extend would the classification of all possible cases characterize the model ? We think this problem is very difficult and warrants further work.

Appendix A. **Some properties of the total equilibrium population.** In this section, we give some properties of the total equilibrium population $X_T^*(\beta) = \sum_{i=1}^n x_i^*(\beta)$.

Lemma A.1. The total equilibrium population X_T^* satisfies the following relation:

$$X_T^*(\beta) = \sum_{i=1}^{n} K_i + \beta \sum_{i=1}^{n} \sum_{j=1, j\neq i}^{n} \frac{\gamma_{ij}(x_j^*(\beta) - x_i^*(\beta))}{\alpha_i x_i^*(\beta)}. \tag{49}$$

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

$$0 = \alpha_i x_i^*(\beta)\left(K_i - x_i^*(\beta)\right) + \beta \sum_{j=1, j\neq i}^{n} \gamma_{ij}\left(x_j^*(\beta) - x_i^*(\beta)\right), \quad i = 1 \cdots n. \tag{50}$$

Dividing (50) by $\alpha_i x_i^*$, one obtains

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

Taking the sum of these expressions gives (49). □

Lemma A.2. We suppose that $\alpha_1 = \ldots = \alpha_n =: \alpha$, then

$$X_T^*(\beta) = \sum_{i=1}^{n} K_i + \frac{\beta}{\alpha} \sum_{j<i} \frac{\gamma_{ij}(x_j^*(\beta) - x_i^*(\beta))^2}{x_j^*(\beta) x_i^*(\beta)}. \tag{51}$$

Proof. We have

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

which gives (51), since $\gamma_{ij} = \gamma_{ji}$. □

Proposition A.3. *Consider the system* (4).

1. *If* $K_1 = \cdots = K_n =: K$, *then* $x_1^* = \ldots = x_n^* = K$.
2. *If* (16) *hold then* $x_1^* = \ldots = x_{n-1}^* =: x^*$ *and*
   (a) *If* $K < K_n$ *then* $K < x^* < x_n^* < K_n$.
   (b) *If* $K > K_n$ *then* $K > x^* > x_n^* > K_n$.

Proof. Suppose that $K_1 = \cdots = K_n =: K$ then the equations (9) giving the equilibrium point are satisfied for $x_i = K$. Therefore $E^*(\beta) = (K, \ldots, K)$ does not depend on β. This proves the first item of the proposition.

Now, for the proof of the second item, suppose that (16) hold, that is to say $K_1 = \cdots = K_{n-1} =: K$, $r_1 = \cdots = r_{n-1} =: r$ and $\gamma_{n1} = \cdots = \gamma_{nn-1} =: \gamma$. Then the equations (9) are written

$$\begin{cases} r x_i \left(1 - \dfrac{x_i}{K}\right) + \beta \displaystyle\sum_{j=1, j\neq i}^{n} \gamma_{ij}(x_j - x_i) = 0, \quad i = 1 \cdots n-1, \\ r_n x_n \left(1 - \dfrac{x_n}{K_n}\right) + \beta\gamma \displaystyle\sum_{j=1}^{n-1} (x_j - x_n) = 0. \end{cases} \tag{52}$$

Now, consider the following system of algebraic equations

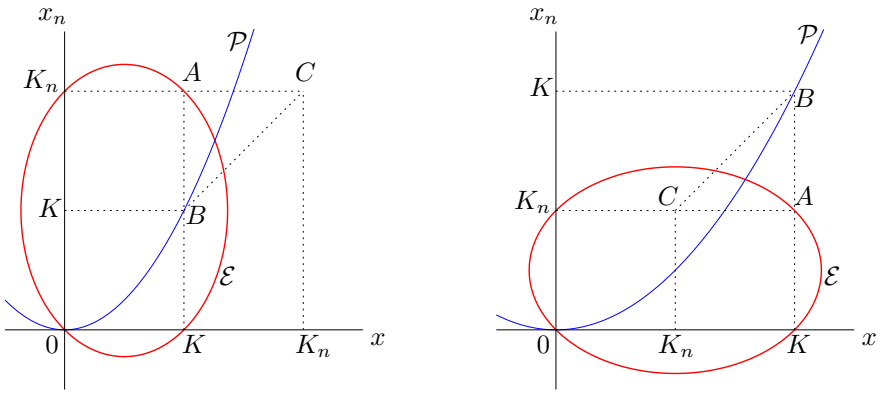
$$\begin{cases} rx\left(1-\dfrac{x}{K}\right)+\beta\gamma(x_n-x)=0, \\ r_nx_n\left(1-\dfrac{x_n}{K_n}\right)+(n-1)\beta\gamma(x-x_n)=0. \end{cases} \tag{53}$$

obtained from (52) by replacing $x_i = x$, for $i = 1 \cdots n-1$ and using the conditions $\gamma_{in} = \gamma$, for $i = 1 \cdots n-1$. We first notice that if $(x = x^*, x_n = x_n^*)$ is a positive solution of (53) then $(x_1 = x^*, \cdots, x_{n-1} = x^*, x_n = x_n^*)$ is a positive solution of system (52). Let us prove that System (53) has a unique solution (x^*, x_n^*). Indeed, multiplying the first equation of (53) by $n-1$ gives the following system

$$\begin{cases} (n-1)rx\left(1-\dfrac{x}{K}\right)+(n-1)\beta\gamma(x_n-x)=0, \\ r_nx_n\left(1-\dfrac{x_n}{K_n}\right)+(n-1)\beta\gamma(x-x_n)=0. \end{cases} \tag{54}$$

The system (54) represents the equilibrium point of a two-patch model. It is known, see [1, Prop. 1], that it has a unique solution (x^*, x_n^*), satisfying

$$K < x^* < x_n^* < K_n \text{ if } K < K_n, \text{and } K > x^* > x_n^* > K_n \text{ if } K > K_n. \tag{55}$$



(a) $K < K_n$ (b) $K > K_n$

FIGURE 5. The intersection point (x^*, x_n^*), between Ellipse $\mathcal{E}$ and Parabola $\mathcal{P}$, lies in the interior of triangle ABC. (a): the case $K < K_n$. (b): the case $K > K_n$.

For the convenience of the reader, we give here the details of the proof of (55). Adding the equations of (54) we get

$$r(n-1)x\left(1-\frac{x}{K}\right)+r_nx_n\left(1-\frac{x_n}{K_n}\right)=0, \tag{56}$$

which is the equation of an ellipse $\mathcal{E}$ passing through the points $(0,0)$, $(K,0)$, $(0,K_n)$ and $A = (K, K_n)$. The first equation of (54) represents a parabola $\mathcal{P}$ of equation $x_n = P(x)$, where

$$P(x) = x\left(1-\frac{r}{\beta\gamma}+\frac{r}{\beta\gamma K}x\right). \tag{57}$$

So, the solutions of system (54) are defined by the intersection points between Ellipse $\mathcal{E}$ and Parabola $\mathcal{P}$, as it is shown in Fig. 5. Since $P'(K) = 1 + \frac{r}{\beta\gamma} > 1$, this intersection lies in the triangle ABC, where $A = (K, K_n)$, $B = (K, K)$ and $C = (K_n, K_n)$, which proves (55). □

Lemma A.4. The derivative of the total equilibrium population $X_T^*(\beta)$ at $\beta = 0$, is given by

$$\frac{dX_T^*}{d\beta}(0) = \sum_{i=1}^{n} \frac{1}{r_i} \sum_{j=1, j\neq i}^{n} \gamma_{ij} \left(K_j - K_i\right). \tag{58}$$

Proof. By differentiating the equation (49), at $\beta = 0$, we get:

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

which gives (58), since $x_i^*(0) = K_i$ for $i = 1 \cdots n$. □

Appendix B. **Stability modulus of a Metzler matrix.** For the ease of the reader, we recall in this section the proof of a result which gives a minoration of the stability modulus of a Metzler matrix, see Lemma B.2. This Lemma is a corollary of result which gives a minoration of the spectral radius of a non negative matrix, see Lemma B.1. Recall that the spectral radius of matrix A is defined as

$$\rho(A) = \max\left\{|\lambda| : \lambda \text{ is an eigenvalue of } A\right\}. \tag{59}$$

We have the following result [15, Lemma 8]:

Lemma B.1. Let A be a non negative matrix. Let $u \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$. If $Au \geq \lambda u$ then $\rho(A) \geq \lambda$.

Proof. If $Au \geq \lambda u$ then, since A is non negative, $A^k u \geq \lambda^k u$ for all k. Therefore $\|A^k\| \geq \lambda^k$ for any matricial norm. Using the Gelfand formula $\rho(A) = \lim_{k\to\infty} \|A^k\|^{\frac{1}{k}}$, we obtain that $\rho(A) \geq \lambda$. □

Recall that the stability modulus of a matrix A is given by

$$s(A) = \max\left\{\mathrm{Re}(\lambda) : \lambda \text{ is an eigenvalue of } A\right\}. \tag{60}$$

A matrix $A = (a_{ij})$ is said to be Metzler if $a_{ij} \geq 0$ for $i \neq j$. We have the following result [3, Lemma 8]:

Lemma B.2. Let A be a Metzler matrix. Let $u \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$. If $Au \geq \lambda u$ then $s(A) \geq \lambda$.

Proof. Let A be a Metzler matrix, there exists $h > 0$ such that $A + hI$, where I is the identity matrix, is non negative. Let u and λ be such that $Au \geq \lambda u$. Since $(A + hI)u \geq (\lambda + h)u$, using Lemma B.1, we deduce that $\rho(A + hI) \geq \lambda + h$. According to the Perron-Frobenius Theorem [9, Theorem 3, page 66], we have

$$s(A + hI) = \rho(A + hI).$$

Therefore we have $s(A + hI) \geq \lambda + h$. Using $s(A + hI) = s(A) + h$, we obtain $s(A) \geq \lambda$. □

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Received xxxx 20xx; revised xxxx 20xx.

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