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Dynamical systems / *Systèmes dynamiques*

Generalized logistic equation on Networks

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Abstract. In this paper, we consider a general single species model in a heterogeneous environment of n patches ($n \geq 2$), where each patch follows a generalized logistic law. First, we prove the global stability of the model. Second, in the case of perfect mixing, i.e. when the migration rate tends to infinity, the total population follows a generalized logistic law with a carrying capacity which in general is different from the sum of the n carrying capacities. Next, we give some properties of the total equilibrium population and we compute its derivative at no dispersal. 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. Finally, we study an example of two-patch model where the first patch follows a logistic law and the second a Richard's law, we give a complete classification of the model parameter space as to whether dispersal is beneficial or detrimental to the sum of two carrying capacities.

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1. Introduction

The simplest realistic model of population dynamics is the one with exponential growth

$$\frac{dx}{dt} = rx,$$

where r is the intrinsic growth rate. To remove unrestricted growth, Verhulst [39] considered that a stable population would have a saturation level characteristic of the environment. To achieve this the exponential model was augmented by a multiplicative factor $1 - \frac{x}{K}$, which represents the fractional deficiency of the current size from the saturation level K . In Lotka's analysis [29] of the logistic growth concept, the rate of population growth dx/dt , at any moment t is a function of the population size at that moment, $x(t)$, namely,

$$\frac{dx}{dt} = f(x).$$

Since a zero population has zero growth, $x = 0$ is an algebraic root of the function $f(x)$. By expanding f as a Taylor series near $x = 0$ and setting $f(0) = 0$, Lotka obtained the following power series: $f(x) = x(f'(0) + \frac{x}{2}f''(0))$, where higher terms are assumed negligible. By setting $f'(0) = r$ and $f''(0) = -2r/K$, where r is the intrinsic growth rate of the population and K is the carrying capacity, one is led to the Verhulst logistic equation

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right). \quad (1)$$

Turner and co-authors [38] proposed a modified Verhulst logistic equation (1) which they termed the generic growth function. It has the form

$$\frac{dx}{dt} = rx^{1+\mu_2(1-\mu_3)} \left[1 - \left(\frac{x}{K} \right)^{\mu_2} \right]^{\mu_3}, \tag{2}$$

where μ_2, μ_3 are positive exponents and $\mu_2 < 1 + \frac{1}{\mu_3}$.

Blumberg [6] introduced another growth equation based on a modification of the Verhulst logistic growth equation (1) to model population dynamics or organ size evolution. Blumberg observed that the major limitation of the logistic curve was the inflexibility of the inflection point. Blumberg therefore introduced what he called the hyperlogistic function, accordingly

$$\frac{dx}{dt} = rx^{\mu_1} \left(1 - \frac{x}{K} \right)^{\mu_3}. \tag{3}$$

Blumberg's equation (3) is consistent with the Turner and co-author's generic equation (2) when $\mu_1 = 2 - \mu_3, \mu_3 < 2$, and $\mu_2 = 1$. Von Bertalanffy [5] introduced his growth equation to model fish weight growth. He proposed the form given below which can be seen to be a special case of the Bernoulli differential equation:

$$\frac{dx}{dt} = rx^{\frac{2}{3}} \left[1 - \left(\frac{x}{K} \right)^{\frac{1}{3}} \right]. \tag{4}$$

The Turner model does not contain the Bertalanffy one, as the values of the exponents $\mu_1 = 2/3, \mu_2 = 1/3, \mu_3 = 1$, violate the condition $\mu_1 = 1 + \mu_2(1 - \mu_3)$ stipulated by Turner et al. [38]. It cannot therefore be seen as a special case of Blumberg's equation (3). Richards [33] extended the growth equation developed by Von Bertalanffy to fit empirical plant data.

Richards's suggestion was to use the following equation which is also a Bernoulli differential equation

$$\frac{dx}{dt} = rx \left[1 - \left(\frac{x}{K} \right)^{\mu_2} \right]. \tag{5}$$

Unlike its Von Bertalanffy antecedent however, the Richards growth function does follow from the Turner model (2) in the case where $\mu_3 = 1$. For $\mu_2 = 1$, (5) trivially reduces to the Verhulst logistic growth equation (1), but for $\mu_2 > 1$ the maximum slope of the curve is when $x > K/2$, and when $0 < \mu_2 < 1$, the maximum slope of the curve is when $x < K/2$. This allows a wider range of curves to be produced, but as μ_2 tends towards zero, the lowest value of x at the point of inflexion remains greater than K/e , where e represents the universal constant, the base of the natural logarithm. In fact, as μ_2 tends towards zero the Richards growth curve tends towards the Gompertz growth curve, which can be derived from the following form of the logistic equation as a limiting case:

$$\frac{dx}{dt} = \frac{r}{\mu_2^{\mu_3}} x \left[1 - \left(\frac{x}{K} \right)^{\mu_2} \right]^{\mu_3} = \frac{r}{K^{\mu_2\mu_3}} x \left(\frac{K^{\mu_2} - x^{\mu_2}}{\mu_2} \right)^{\mu_3}.$$

When $\mu_2 \rightarrow 0$, we obtain the growth rate modelled by the Gompertz function given by:

$$\frac{dx}{dt} = rx \left[\ln \left(\frac{x}{K} \right) \right]^{\mu_3}, \tag{6}$$

with $\mu_3 > 0$ and $\mu_3 \neq 1$. This special case is more usually known as the hyper Gompertz, generalized ecological growth function, or simply generalized Gompertz function. For $\mu_3 = 1$ the equation (6) is the ordinary Gompertz growth (see [24, 31]).

In [37], Tsoularis et al. proposed a new growth rate that includes all the previous growth rates given by:

$$\frac{dx}{dt} = rx^{\mu_1} \left[1 - \left(\frac{x}{K} \right)^{\mu_2} \right]^{\mu_3}, \tag{7}$$

where μ_1, μ_2 and μ_3 are positive real numbers. Unlike Lotka's derivation of the Verhulst logistic growth equation from the truncation of the Taylor series expansion of $f(x)$ near $x = 0$, (7) cannot be derived from such an expansion unless μ_1, μ_2 and μ_3 are all positive integers.

Many complex systems in sciences and engineering can be modeled by coupled systems of differential equations on networks. A network can be mathematically treated as a weighted digraph (directed graph), consisting of a set of n vertices and a set of directed arcs. In 1977, Freedman and Waltman [18] consider a two-patch model with a single species in logistic population growth as follows:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(x_2 - x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \epsilon(x_1 - x_2), \end{cases} \quad (8)$$

where x_i represents the population density in patch i , the parameter r_i is the intrinsic growth rate, K_i is carrying capacity and ϵ is the dispersal rate. Freedman and Waltman show that under certain conditions, the total population abundance can be larger than the total carrying capacities $K_1 + K_2$. Holt [25] generalized these results to a source-sink system. In 2015, Arditi et al. [1] gave a full mathematical analysis of the model (8) of Freedman and Waltman with symmetric dispersal.

In 2018, Arditi et al. [2] extended the model (8) by considering asymmetric dispersal, i.e. the model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \epsilon(\gamma_{21} x_1 - \gamma_{12} x_2), \end{cases} \quad (9)$$

where $\epsilon\gamma_{12}$ and $\epsilon\gamma_{21}$ with $\gamma_{ij} > 0$, $i \neq j$ and $\epsilon \geq 0$, are the migration terms which describe the flows of individuals from the patch 2 to the patch 1, and from the patch 1 to the patch 2 respectively. These flows can for example depend on the distance between the patches. By noting that the positive equilibrium (x_1^*, x_2^*) of model (9) is the unique positive solution to

$$\begin{cases} r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) = 0, \\ x_2 = \frac{1}{\gamma_{12}} \left(\gamma_{21} x_1 - \frac{r_1}{\epsilon} x_1 \left(1 - \frac{x_1}{K_1}\right)\right), \end{cases}$$

i.e., the intersection of an ellipse and a parabola, they used a graphical method to completely analyze model (9) in order to determine when dispersal is either favorable or unfavorable to total population abundance

In [12], I suggested to study the two-patch coupled model where each patches follows a Richard's law, i.e., the model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \left(\frac{x_1}{K_1}\right)^\mu\right) + \epsilon(\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2}\right)^\mu\right) + \epsilon(\gamma_1 x_1 - \gamma_2 x_2), \end{cases} \quad (10)$$

where x_1 and x_2 represent population densities of the species in patch 1 and 2, respectively. The parameters K_i and r_i represents the carrying capacity and the growth rate respectively. Parameter ϵ represents the dispersal rate and μ is a positive parameter. γ_{12} denote the migration rate from patch 2 to the patch 1 and γ_{21} from patch 1 to patch 2. For this model, I interested in the effect of this choice, which generalize the logistic, on the dynamic of the total population in two patches. I have given a complete classification of the model parameters regarding when the dispersion causes a total biomass smaller or greater than the sum of capacities. I used for this classification, the geometric method of Arditi et al. [2].

In 2021, Elbetch et al. [15] have considered the model of multi-patch logistic growth, coupled by asymmetric linear migration terms

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n, \quad (11)$$

where n is the number of patches in the system. The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity of patch i . The term on the right hand side of the system (11) describes the effect of the linear migration between the patches, where ϵ is the migration rate and $\Gamma := (\gamma_{ij})$ is the matrix representing the migrations between the patches. Note that, the system (11) is studied also by Elbetch et al. [14] and Takeuchi [35] in the case when the matrix Γ is symmetric. We recall that, when the matrix of migration Γ is irreducible, System (11) admits a unique positive equilibrium which is globally asymptotically stable (GAS), see [4, Theorem 1] [3, Theorem 2.2] or [14, Theorem 6.1], when $\epsilon \rightarrow \infty$, this equilibrium tend to

$$\frac{\sum_i \delta_i r_i}{\sum_i \delta_i^2 \alpha_i} (\delta_1, \dots, \delta_n),$$

where $\alpha_i = \frac{r_i}{K_i}$ and $(\delta_1, \dots, \delta_n)^T$ the vector which generate the vector space $\ker \Gamma$ (for more properties of the vector space $\ker \Gamma$, see Subsection 4.1).

In [14, 15], Elbetch et al. have answered in some particular cases of the model (11) to the following important question: Is it possible, depending on the migration rate, that the total equilibrium population be larger than the sum of the capacities $\sum_i K_i$? This question is of ecological importance since the answer gives the conditions under which the linear dispersal is either beneficial or detrimental to total equilibrium population. Note that, this question has been studied by many researches (see [1, 2, 9–11, 14–18, 21], [4, 41] for source-sink models, and [20, 22] for SIS patch-model). They proved that, if all the patches do not differ with respect to the intrinsic growth rate (i.e., $r_1 = \dots = r_n$), then the effect of linear migration is always detrimental. In the case when $(K_1, \dots, K_n)^T \in \ker \Gamma$ (if the matrix Γ is symmetric, the condition $(K_1, \dots, K_n)^T \in \ker \Gamma$ means that the patches do not differ with respect to the carrying capacity), linear migration has no effect on the total equilibrium population. An example when the effect of linear migration is always beneficial, is in the case when Γ is symmetric and all the patches do not differ with respect to the parameter $\alpha = r/K$ quantifying intraspecific competition (i.e., $\alpha_1 = \dots = \alpha_n$) (see also [15, Proposition 4.2]).

For general information of the effects of patchiness and migration in both continuous and discrete cases, and the results beyond the logistic model, the reader is referred to the work of Levin [26, 27], DeAngelis et al. [10, 11] and Freedman et al. [16].

Our aim in this work is to study the model of n patches coupled by migration terms. In particular, we are interested in studying the effect of dispersion and the specific growth rate on the dynamics of population, and to compare some results for the generalized logistic equation with those obtained for multi-patch logistic equation (11). Thus, we extended the result obtained in [14, 15].

This paper is organized as follows: The introduction consists of giving an overview of the different growth models of a population and the links that may exist between them, as well as of the two-patch migration models of a single population and also for n patches. In Section 2, we introduce the mathematical model and we give some definitions and notations. Next, in Section 3, we prove the global stability of the model (12). In Section 4, we study the behavior of the system (12) in the case when the migration rate goes to infinity by direct method and also by using perturbation arguments. In Section 5, we compare the total equilibrium population with the sum of the n carrying capacities for some parameter space. In Section 6, using the method graphic of Arditi et al. [2], we give a complete analysis of two-patch case where the first patch

follows a logistic law and the second Richards law. Two-patch model where one growth rate is much larger than the second one is examined. We ends with a conclusion in Section 7.

2. Mathematical model

Let us consider the growth of single specie which can disperse among n patches described by:

$$\frac{dx_i}{dt} = x_i\varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), \quad i = 1, \dots, n, \tag{12}$$

where x_i represents the population density of the species in the i -th patch and $\varphi_i(x_i)$ represents the specific growth rate of the population in the i -th patch. Since the specific growth rate may depend on each patch environment, the function $\varphi_i(x_i)$ is supposed to be different in each patch. The second term of the right hand side in (12) describes the diffusion effect between patches where ϵ is the growth of migration and $\gamma_{ij} \geq 0$, for all $i \neq j$ is the term of asymmetrical migration which describes the flows of individuals from the patch j to the patch i . These flows can for example depend on the distance between the patches. We list the following hypotheses, the first two of which are standard in single species models (see [16, 35]):

- (H1) All solutions of the initial value problem (12) exist, are unique and are continuable for all positive time.
- (H2) $\varphi_i(0) > 0$, $\frac{d\varphi_i}{dx_i}(x_i) < 0$, there exist $K_i > 0$ such that $\varphi_i(K_i) = 0$ and $x_i\varphi_i(x_i) \rightarrow -\infty$ as $x_i \rightarrow +\infty$ for all $i = 1, \dots, n$.
- (H3) The matrix $\Gamma := (\gamma_{ij})$ where

$$\gamma_{ii} = - \sum_{j=1, j \neq i}^n \gamma_{ji} \tag{13}$$

is irreducible.

In term of graph theory, given a network represented by digraph \mathcal{G} with n vertices, $n \geq 2$, a coupled generalized logistic system can be built on \mathcal{G} by assigning each vertex its own internal dynamics and then coupling these vertex dynamics based on directed arcs in \mathcal{G} (see Figure 1).

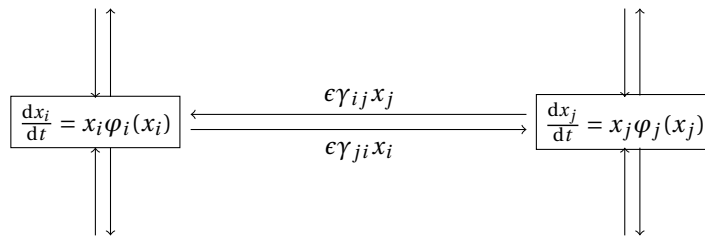


Figure 1. A coupled generalized logistic system on a network

The system (12) can be written in matrix form as follows:

$$\frac{dx}{dt} = \text{diag}(\varphi_1(x_1), \dots, \varphi_n(x_n))x + \epsilon\Gamma x, \tag{14}$$

where $x = (x_1, \dots, x_n)^T$.

In hypothesis (H2), K_i is the carrying capacity of the i -th patch. All patches are source since $\varphi_i(0) > 0$ for all i . We remark that growth functions of patches can be very different; that is, system (12) allows patch-specific population dynamics. To model this specification using continuous space model, one needs to deal with partial differential equations with spatially varying coefficients, which are particularly challenging in stability analysis.

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 , i.e. the irreducibility of matrix Γ implies that every patch in the model (12) is connected by migration term, i.e. the species can reach any i -th patch from any j -patch. For Two-patch model, the matrix Γ is irreducible if and only if γ_{12} and γ_{21} are positives. For Three-patch model, under the irreducibility hypothesis on the matrix Γ , there are five possible cases, modulo permutation of the three patches, see Figures 2 and 3.

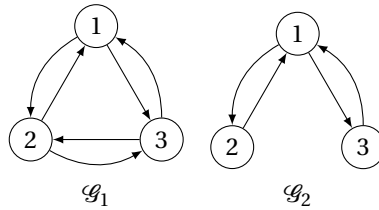


Figure 2. The two graphs \mathcal{G}_1 and \mathcal{G}_2 for which the migration matrix may be symmetric, if $\gamma_{ij} = \gamma_{ji}$.

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

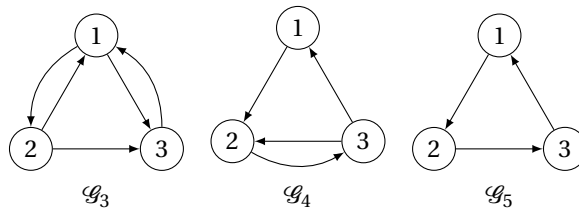


Figure 3. The three graphs $\mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 for which the migration matrix cannot be symmetric.

The model (12) studied in [1, 2, 7, 10, 16, 18, 25] for two patches and logistic growth rate, i.e.

$$\varphi_i(x_i) = r_i - \frac{r_i}{K_i} x_i, \quad i = 1, 2.$$

The same model is studied in [9, 11, 42] for n patches and a logistic growth rate, where the matrix Γ take the following form:

$$\gamma_{1n} = \gamma_{n1} = \gamma_{i,i-1} = \gamma_{i-1,i} = 1 \text{ for } 2 \leq i \leq n \text{ and } \gamma_{ij} = 0 \text{ otherwise.} \tag{15}$$

We have the following result:

Proposition 1. *The domain $\Omega = \{(x_1, \dots, x_n) \in \mathbb{R}^n / x_i \geq 0, i = 1, \dots, n\}$ is positively invariant for the system (12).*

Proof. Assume that $x_i = 0$ and $x_j \geq 0$ for all $j \neq i$. We have

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

Hence, on the boundary of Ω , the vector field associated to (12) either is tangent to Ω , or points inward Ω . According to [34, Proposition B.7, p. 267], no trajectory comes out of Ω .

Therefore, Ω is positively invariant for the system (12). □

3. Global stability

Note that, the model (12) without diffusion (i.e. when $\epsilon = 0$) has a positive globally stable interior equilibrium point (K_1, \dots, K_n) by hypothesis (H2). A boundary equilibrium occur where one or more of the K_i are replaced by zero.

In the next theorem, we prove that the model (12) continues to be globally asymptotically stable for any diffusion rate ϵ . First, we start by giving some definitions.

Definition 2. A matrix $M = (m_{ij})$ is called cooperative if $m_{ij} \geq 0$ for all $i \neq j$. Recall that the differential system

$$\frac{dx}{dt} = F(x),$$

is said to be cooperative, if its jacobian matrix is cooperative, i.e., for all $i \neq j$; $(\partial F_i / \partial x_j) \geq 0$, for all x positive.

Definition 3. The stability modulus of a matrix M is given by

$$s(M) = \max \{ \text{Re}(\lambda) : \lambda \text{ is an eigenvalue of } M \}. \tag{16}$$

We have the following result [32, Lemma 8]:

Lemma 4. 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 $\rho(A) = \lim_{k \rightarrow \infty} \|A^k\|^{\frac{1}{k}}$, we obtain that $\rho(A) \geq \lambda$. \square

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

Lemma 5. Let A be a cooperative 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 cooperative 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 4, we deduce that $\rho(A + hI) \geq \lambda + h$. According to the Perron–Frobenius Theorem [19, Theorem 3, p. 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 $s(A) \geq \lambda$. \square

We have the following result:

Theorem 6. The model (12) has a unique positive equilibrium point which is globally asymptotically stable in the positive cone $\mathbb{R}_+^n \setminus \{0\}$.

Proof. First, System (12) admits a trivial equilibrium $x = 0$, representing the state of species extinction, and its stability can be determined by the Jacobian matrix:

$$A = \epsilon\Gamma + \text{diag}(\varphi_1(0), \dots, \varphi_n(0)), \tag{17}$$

Since Γ is a cooperative and irreducible then A is also. According to a result of Elbetch et al. [14, Theorem 6.1], the stability modulus of the matrix A is positive (just replace $\varphi_i(0)$ by r_i for all i). Indeed, let $u = (1, \dots, 1)^T$. We have

$$A^T u = (\varphi_1(0), \dots, \varphi_n(0))^T \geq \lambda u, \quad \text{where } \lambda = \min\{\varphi_1(0), \dots, \varphi_n(0)\} > 0.$$

Therefore, since A is a cooperative matrix, according to Lemma 5, we have

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

It's follows from Lu and Takeuchi [30, Corollary 1], that the cooperative system (12) possesses a globally asymptotically stable positive equilibrium. \square

In all of this work, the globally asymptotically stable positive equilibrium of the system (12) is denoted by $E_n^*(\epsilon) = (x_1^*(\epsilon), \dots, x_n^*(\epsilon))$, and by $T_n^*(\epsilon)$ the total equilibrium population

$$T_n^*(\epsilon) = \sum_{i=1}^n x_i^*(\epsilon). \tag{18}$$

4. Fast diffusion rate

The goal in the next is to give the behavior of the model (12) when the growth of diffusion tend to infinity (i.e. $\epsilon \rightarrow \infty$).

4.1. Kernel of Γ

First for all, we recall that, if Γ is irreducible, then 0 is a simple eigenvalue of Γ and all non-zero eigenvalues of Γ have negative real part. Moreover, the kernel of the matrix Γ is generated by a positive vector (see [4, Lemma 2]). In all of this paper, we denote by $\delta := (\delta_1, \dots, \delta_n)^T$ this positive vector. For the existence, uniqueness, and positivity of δ see Cosner et al. [7, Lemma 1], and Elbetch et al. [14, Lemma 4.1], [15, Lemma 1]. Note that, if the matrix Γ is symmetric, then $\ker \Gamma$ is generated by $\delta = (1, \dots, 1)^T$. On the other hand, it is shown in Guo et al. [23, Lemma 2.1] and Gao and Dong [21, Lemma 3.1] that the vector $(\Gamma_{11}^*, \dots, \Gamma_{nn}^*)^T$ is a right eigenvector of Γ associated with the zero eigenvalue. Here, Γ_{ii}^* is the cofactor of the i -th diagonal entry of Γ , and $\text{sgn}(\Gamma_{ii}^*) = (-1)^{n-1}$. As in our work, the matrix Γ is assumed to be irreducible, then $(-1)^{n-1}(\Gamma_{11}^*, \dots, \Gamma_{nn}^*)^T$ is strictly positive, i.e. $\delta_i = (-1)^{n-1}\Gamma_{ii}^* > 0$ for all i . Therefore, we have explicit formula for the components of the vector δ , as functions of the coefficients of Γ , at our disposal. For two patches we have $\delta = (\gamma_{12}, \gamma_{21})^T$, and for three patches we have $\delta = (\delta_1, \delta_2, \delta_3)^T$, where

$$\begin{cases} \delta_1 = \gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{32}\gamma_{13}, \\ \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \\ \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32}. \end{cases} \tag{19}$$

Lemma 2.1 of Guo et al. [23] gives explicit formulas of the components of the vector δ , with respect of the coefficients of γ as follow:

$$\delta_k = \sum_{T \in \mathcal{T}_k} \prod_{(i,j) \in E(T)} \gamma_{ij}, \quad k = 1, \dots, n, \tag{20}$$

where \mathcal{T}_k is the set of all directed trees of n vertices rooted at the k -th vertex, and $E(T)$ denotes the set of arcs in a directed tree T .

4.2. The fast dispersal limit

The equilibrium point $E_n^*(\epsilon)$ is the solution of the following system:

$$x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i = 0, \quad i = 1, \dots, n. \tag{21}$$

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

$$\sum_{i=1}^n x_i \varphi_i(x_i) = 0. \tag{22}$$

Therefore $E_n^*(\epsilon)$ belongs to the locus of points described by the equation (22) consists of the origin together with a connected $(n-1)$ -dimension surface denoted by:

$$\mathbb{S} := \left\{ x \in \mathbb{R}_+^n : \Theta(x) := \sum_{i=1}^n x_i \varphi_i(x_i) = 0 \right\}, \tag{23}$$

which passes through all boundary equilibria together with the interior equilibrium (K_1, \dots, K_n) . Note that this surface is independent of the migration terms ϵ and γ_{ij} . In all of the rest, we assume that \mathbb{S} is compact and convex. The following result asserts that when $\epsilon \rightarrow \infty$, the equilibrium $E_n^*(\epsilon)$ converges to an element of $\ker \Gamma$.

Theorem 7. *We have*

$$\lim_{\epsilon \rightarrow +\infty} E_n^*(\epsilon) = \lambda_0 \delta, \tag{24}$$

where $\lambda_0 > 0$ is the unique solution in the positive axis of the following equation:

$$\sum_{i=1}^n \delta_i \varphi_i(\delta_i x) = 0. \tag{25}$$

Proof. The equilibrium point $E_n^*(\epsilon)$ is the solution in the positive cone \mathbb{R}_+^n , of the equation $Y_\epsilon = 0$, where

$$Y_\epsilon(x_1, \dots, x_n) = \left(Y_1(x_1, \dots, x_n), \dots, Y_{n-1}(x_1, \dots, x_n), \sum_{i=1}^n x_i \varphi_i(x_i) \right) \tag{26}$$

with

$$Y_i(x_1, \dots, x_n) = \frac{1}{\epsilon} x_i \varphi_i(x_i) + \sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i, \quad i = 1, \dots, n-1,$$

obtained from (21) by dividing by ϵ the first $n-1$ equations, and replacing the last one by Equation (22), which is the sum of the equations. On the other hand, the limit equations (obtained when $\epsilon \rightarrow \infty$) are given by:

$$Y_\infty(x_1, \dots, x_n) = \left(\sum_{j=1, j \neq 1}^n \gamma_{1j} x_j - \gamma_{j1} x_1, \dots, \sum_{j=1, j \neq n-1}^n \gamma_{n-1,j} x_j - \gamma_{j,n-1} x_{n-1}, \sum_{i=1}^n x_i \varphi_i(x_i) \right) \tag{27}$$

Now, we consider the linear system given by the first $n-1$ equations of (27)

$$\sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i = 0, \quad i = 1, \dots, n-1. \tag{28}$$

According to [15, Lemma 3.4], the system (28) admits a unique solution given by $x_n / \delta_n (\delta_1, \dots, \delta_{n-1})$. Hence, the solution of the equation $Y_\infty = 0$ is given by the solution of the following system:

$$\begin{cases} x_i = \frac{\delta_i}{\delta_n} x_n, & i = 1, \dots, n-1. \\ \sum_{i=1}^n x_i \varphi_i(x_i) = 0. \end{cases} \tag{29}$$

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

$$\frac{1}{\delta_n} x_n \left(\sum_{i=1}^n \delta_i \varphi_i \left(\frac{\delta_i}{\delta_n} x_n \right) \right) = 0. \tag{30}$$

Which admits $x_n = 0$ and $x_n = \lambda_0 \delta_n$ as solutions. So, the equation $Y_\infty = 0$ admits two solutions, 0 and $E^*(\infty) := \lambda_0 (\delta_1, \dots, \delta_n)$.

The surface \mathbb{S} is compact, so the equilibrium $E^*(\epsilon)$ has at least one limit point in \mathbb{S} , when ϵ goes to infinity. To prove the convergence of $E^*(\epsilon)$ to $E^*(\infty)$, it suffices to prove that the origin cannot be a limit point of $E^*(\epsilon)$. We claim that for any ϵ , there exists i such that $x_i^*(\epsilon) \geq K_i$, which entails that $E^*(\epsilon)$ is bounded away from the origin. The coordinates of the vector $\Gamma E^*(\epsilon)$ sum to zero, hence at least one of them, say, the i -th, is non negative. Then $x_i^*(\epsilon) \varphi_i(x_i^*(\epsilon)) \leq 0$, and since $x_i^*(\epsilon)$ cannot be negative or 0, and by hypothesis (H2), $\varphi_i(0) > 0$ and $d\varphi_i/dx_i < 0$, we have $x_i^*(\epsilon) \geq K_i$. By connexity of the arc $\epsilon \rightarrow E^*(\epsilon)$, the point $E^*(\epsilon)$ remains in the surface \mathbb{S} and the limit cannot be the origin. \square

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

Corollary 8. *We have*

$$T_n^*(+\infty) = \lim_{\epsilon \rightarrow +\infty} \sum_{i=1}^n x_i^*(\epsilon) = \left(\sum_{i=1}^n \delta_i \right) \lambda_0. \tag{31}$$

Proof. The sum of the n components of the point $E_n^*(\infty)$ immediately gives (31). □

4.3. Two time scale dynamics

We can use the theory of singular perturbations to obtain a better understanding of the behavior of the system in the case of perfect mixing. We have the following result:

Theorem 9. *Let $(x_1(t, \epsilon), \dots, x_n(t, \epsilon))$ be the solution of the system (12) with initial condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1, \dots, n$. Let $Y(t)$ be the solution of the equation*

$$\sum_{i=1}^n \delta_i \frac{dX}{dt} = X \sum_{i=1}^n \delta_i \varphi_i \left(\frac{\delta_i}{\sum_{i=1}^n \delta_i} X \right), \tag{32}$$

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

$$\sum_{i=1}^n x_i(t, \epsilon) = Y(t) + o(1), \quad \text{uniformly for } t \in [0, +\infty) \tag{33}$$

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

$$x_i(t, \epsilon) = \frac{\delta_i}{\sum_{i=1}^n \delta_i} Y(t) + o(1), \quad i = 1, \dots, n, \text{ uniformly for } t \in [t_0, +\infty). \tag{34}$$

Proof. Let $X(t, \epsilon) = \sum_{i=1}^n x_i(t, \epsilon)$. We rewrite the system (12) using the variables (X, x_1, \dots, x_{n-1}) . One obtains:

$$\begin{cases} \frac{dX}{dt} = \sum_{i=1}^n x_i \varphi_i(x_i), \\ \frac{dx_i}{dt} = x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i, \quad i = 1, \dots, n-1. \end{cases} \tag{35}$$

This system is actually a system in the variables (X, x_1, \dots, x_{n-1}) , since, whenever x_n appears in the right hand side of (35), it should be replaced by

$$x_n = X - \sum_{i=1}^{n-1} x_i. \tag{36}$$

When $\epsilon \rightarrow \infty$, (35) is a *slow-fast* system, with one *slow variable*, X , and $n - 1$ *fast variables*, x_i for $i = 1, \dots, n - 1$. According to Tikhonov's theorem [28, 36, 40] we consider the dynamics of the fast variables in the time scale $\tau = \epsilon t$. One obtains

$$\frac{dx_i}{d\tau} = \frac{1}{\epsilon} x_i \varphi_i(x_i) + \sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i, \quad i = 1, \dots, n-1. \tag{37}$$

where x_n is given by (36). In the limit $\epsilon \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_i}{d\tau} = \sum_{j=1, j \neq i}^n \gamma_{ij} x_j - \gamma_{ji} x_i, \quad i = 1, \dots, n-1. \tag{38}$$

This is an $n - 1$ dimensional linear system differential. According to Lemma 3.9 of Elbetch et al. [15], the slow manifold of system (35), which is the equilibrium point of the fast dynamics (38), is unique and is given by:

$$x_i = \frac{\delta_i}{\sum_{i=1}^n \delta_i} X, \quad i = 1, \dots, n-1. \tag{39}$$

As this manifold is GAS, the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (35) are approximated by the solutions of the *reduced model* which is obtained by replacing (39) into the dynamics of the slow variable, which gives the equation (32). Since (32) admits

$$X^* = \left(\sum_{i=1}^n \delta_i \right) \lambda_0$$

as a positive equilibrium point, which is GAS in the positive axis, the approximation given by Tikhonov’s theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, let $Y(t)$ be the solution of the reduced model (32) of initial condition $Y(0) = X(0, \epsilon) = \sum_{i=1}^n x_i^0$, then, when $\epsilon \rightarrow \infty$, we have the approximations (33) and (34). □

When the movement pattern of individuals among n patches is symmetric, the previous theorem becomes:

Theorem 10. *Assume that the matrix Γ is symmetric. Let $(x_1(t, \epsilon), \dots, x_n(t, \epsilon))$ be the solution of the system (12) with initial condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1, \dots, n$. Let $Y(t)$ be the solution of the equation*

$$\frac{dX}{dt} = \frac{1}{n} X \sum_{i=1}^n \varphi_i \left(\frac{1}{n} X \right), \tag{40}$$

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

$$\sum_{i=1}^n x_i(t, \epsilon) = Y(t) + o(1), \quad \text{uniformly for } t \in [0, +\infty) \tag{41}$$

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

$$x_i(t, \epsilon) = \frac{1}{n} Y(t) + o(1), \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \tag{42}$$

Proof. If the matrix Γ is symmetric, then $\delta = (1, \dots, 1)^T$. □

As a corollary of the previous theorem we obtain the following result which describes the total equilibrium population for perfect mixing when the dispersal is symmetric. We can state this result as follows:

Corollary 11. *The total equilibrium population for perfect mixing $T_n^*(+\infty)$ satisfied:*

$$\sum_{i=1}^n \varphi_i \left(\frac{T_n^*(+\infty)}{n} \right) = 0. \tag{43}$$

Proof. If the matrix Γ is symmetric, then $\delta = (1, \dots, 1)^T$. The equation (40) prove that $T_n^*(+\infty)$ is satisfied by Equation (43). □

We point out the similarity between our expression (43) for the total equilibrium population in the limit $\epsilon \rightarrow \infty$, and the expression obtained in spatial homogenization in [9, Proposition A.2]. The formula (43) is an extension for any growth rate satisfied by the assumption (H2) of the formula obtained by Arditi et al. [1, 2] for two-patch model, and also generalized the result of Elbetch et al. [14, 15] for n -patch model.

5. Total equilibrium population

In this section, our aim is to compare the total equilibrium population T_n^* with the sum of carrying capacities $T_n^*(0) = K_1 + \dots + K_n$, when the rate of migration ϵ varies from zero to infinity. First, we compute the derivative of T_n^* at no dispersal.

Proposition 12. *The derivative of the total equilibrium population T_n^* at $\epsilon = 0$ is given by:*

$$\begin{aligned} \frac{dT_n^*}{d\epsilon}(0) &= - \sum_i \left(\frac{1}{K_i \frac{d\varphi_i}{dx_i}(K_i)} \sum_{j \neq i} \gamma_{ij} K_j - \gamma_{ji} K_i \right) \\ &= - \left(\frac{1}{K_1 \frac{d\varphi_1}{dx_1}(K_1)}, \dots, \frac{1}{K_n \frac{d\varphi_n}{dx_n}(K_n)} \right) \Gamma(K_1, \dots, K_n)^T. \end{aligned} \tag{44}$$

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

$$x_i^*(\epsilon)\varphi_i(x_i^*(\epsilon)) + \epsilon \sum_{j=1, j \neq i}^n \gamma_{ij} x_j^*(\epsilon) - \gamma_{ji} x_i^*(\epsilon) = 0, \quad i = 1, \dots, n. \tag{45}$$

The derivative of (45) with respect to ϵ give:

$$\begin{aligned} \varphi_i(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(\epsilon) + x_i^*(\epsilon) \frac{d\varphi_i}{dx_i^*}(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(\epsilon) + \sum_{j=1, j \neq i}^n \gamma_{ij} x_j^*(\epsilon) - \gamma_{ji} x_i^*(\epsilon) \\ + \epsilon \sum_{j=1, j \neq i}^n \gamma_{ij} \frac{dx_j^*}{d\epsilon}(\epsilon) - \gamma_{ji} \frac{dx_i^*}{d\epsilon}(\epsilon) = 0, \quad i = 1, \dots, n. \end{aligned}$$

For $\epsilon = 0$, we obtain

$$\varphi_i(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(0) + x_i^*(0) \frac{d\varphi_i}{dx_i^*}(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(0) + \sum_{j=1, j \neq i}^n \gamma_{ij} x_j^*(0) - \gamma_{ji} x_i^*(0) = 0.$$

Since $x_i^*(0) = K_i$ and $\varphi_i(K_i) = 0$, then

$$K_i \frac{d\varphi_i}{dx_i^*}(K_i) \frac{dx_i^*}{d\epsilon}(0) + \sum_{j=1, j \neq i}^n \gamma_{ij} K_j - \gamma_{ji} K_i = 0, \quad i = 1, \dots, n.$$

By summing the previous equations for $i = 1, \dots, n$ we then obtain the formula of the derivative (44). □

The formula (44) is an extension of the one obtained by Arditi et al. [1, 2] for two-patch model, and also the result of Elbetch et al. [15, Equation 28] for logistic model.

In the rest of this section, we show that the total equilibrium population, $T_n^*(\epsilon)$, is generally different from the sum of the carrying capacities $T_n^*(0)$. Depending on the intrinsic growth functions and the kernel of the matrix Γ , $T_n^*(\epsilon)$ can either be greater than, smaller than, or equal to the sum of the carrying capacities. Let we start by the following situation:

Proposition 13. *If $K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = K_n \frac{d\varphi_n}{dx_n}(K_n)$, then the total equilibrium population, defined by (18) satisfies $T_n^*(\epsilon) \leq \sum_{i=1}^n K_i$, for all $\epsilon \geq 0$ and $\frac{dT_n^*}{d\epsilon}(0) = 0$. Furthermore, if $(K_1, \dots, K_n)^T$ does not belong in $\ker \Gamma$, then $T_n^*(\epsilon) < \sum_{i=1}^n K_i$, for all $\epsilon > 0$.*

Proof. The equation of the tangent space to the surface \mathbb{S} , defined by (23), at point $\mathcal{A} = (K_1, \dots, K_n)$ is given by

$$\sum_{i=1}^n (x_i - K_i) \frac{\partial \Theta}{\partial x_i}(\mathcal{A}) = 0, \tag{46}$$

where Θ is given by (23). Since $\frac{\partial \Theta}{\partial x_i}(\mathcal{A}) = K_i \frac{d\varphi_i}{dx_i}(K_i)$, (46) can be written as follows:

$$\sum_{i=1}^n K_i \frac{d\varphi_i}{dx_i}(K_i) (x_i - K_i) = 0. \tag{47}$$

If we take $K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = K_n \frac{d\varphi_n}{dx_n}(K_n)$ in (47), we get that the equation of the tangent plane to \mathbb{S} at the point \mathcal{A} is

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

By hypothesis, the surface \mathbb{S} is convex, then any point of \mathbb{S} lies in the half-space defined by the inequation $\sum_{i=1}^n x_i \leq \sum_{i=1}^n K_i$. Therefore $E_n^*(\epsilon)$ satisfies

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

By the convexity of the surface \mathbb{S} , the equality in the previous equation can hold if and only if, $x_i^*(\epsilon) = K_i$. We replace in to (21), we get $\Gamma(K_1, \dots, K_n)^T = 0$. Which gives a contradiction. This completes the proof of the proposition.

According to the hypothesis of the previous proposition and the propriety (13), we conclude that the derivative (44) is equal to 0. □

Note that, the result of the previous proposition is also obtained by Arditi et al. [1, 2] for two-patch model, and by Elbetch et al. [14, 15] for n-patch model with logistic dynamic $\varphi_i(x_i) = r_i - r_i/K_i x_i$. They proved that, if the growth rates r_i are equal in all patches, then the total equilibrium population is always smaller than the sum of the carrying capacities.

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

Proposition 14. *Assume that for all $j < i$, $\frac{d\varphi_i}{dx_i}(K_i)\gamma_{ij} = \frac{d\varphi_j}{dx_j}(K_j)\gamma_{ji}$. Then*

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

Moreover, if there exist i_0 and $j_0 \neq i_0$ such that $K_{i_0} \frac{d\varphi_{i_0}}{dx_{i_0}}(K_{i_0}) \neq K_{j_0} \frac{d\varphi_{j_0}}{dx_{j_0}}(K_{j_0})$, then $T_n^*(\epsilon) > \sum_{i=1}^n K_i$, for all $\epsilon > 0$.

Proof. The equilibrium point $E_n^*(\epsilon)$ satisfies the equation (45). We consider a Taylor series expansion of φ_i in the neighborhood of K_i , i.e.

$$\varphi_i(x_i) = \varphi_i(K_i) + (x_i - K_i) \frac{d\varphi_i}{dx_i}(K_i) + o(x_i - K_i), \quad i = 1, \dots, n.$$

We replace φ_i in (45), we obtain for all i

$$0 = x_i^*(\epsilon) (x_i^*(\epsilon) - K_i) \frac{d\varphi_i}{dx_i^*}(K_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j^*(\epsilon) - \gamma_{ji} x_i^*(\epsilon)) + o(x_i^*(\epsilon)(x_i^*(\epsilon) - K_i)), \tag{48}$$

since $\varphi_i(K_i) = 0$ for all i . Dividing (48) by $\frac{d\varphi_i}{dx_i^*}(K_i)x_i^*(\epsilon)$, one obtains

$$x_i^*(\epsilon) = K_i + \epsilon \sum_{j=1, j \neq i}^n \frac{\gamma_{ij} x_j^*(\epsilon) - \gamma_{ji} x_i^*(\epsilon)}{-\frac{d\varphi_i}{dx_i^*}(K_i)x_i^*(\epsilon)} + o(x_i^*(\epsilon) - K_i).$$

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

$$\begin{aligned}
 T_n^*(\epsilon) &= \sum_{i=1}^n K_i + \epsilon \sum_{i=1}^n \sum_{j=1, j \neq i}^n \frac{\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)}{-\frac{d\varphi_i}{dx_i^*}(K_i)x_i^*(\epsilon)} + o\left(\sum_i x_i^*(\epsilon) - \sum_i K_i\right) \\
 &= \sum_{i=1}^n K_i + \epsilon \sum_{j < i} \left(\frac{\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)}{-\frac{d\varphi_i}{dx_i^*}(K_i)x_i^*(\epsilon)} + \frac{\gamma_{ji}x_i^*(\epsilon) - \gamma_{ij}x_j^*(\epsilon)}{-\frac{d\varphi_j}{dx_j^*}(K_j)x_j^*(\epsilon)} \right) + o\left(\sum_i x_i^*(\epsilon) - \sum_i K_i\right) \\
 &= \sum_{i=1}^n K_i + \epsilon \sum_{j < i} \frac{(\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)) \left(\frac{d\varphi_i}{dx_i^*}(K_i)x_i^*(\epsilon) - \frac{d\varphi_j}{dx_j^*}(K_j)x_j^*(\epsilon) \right)}{\frac{d\varphi_j}{dx_j^*}(K_j) \frac{d\varphi_i}{dx_i^*}(K_i) x_j^*(\epsilon) x_i^*(\epsilon)} \\
 &\hspace{20em} + o\left(\sum_i x_i^*(\epsilon) - \sum_i K_i\right). \tag{49}
 \end{aligned}$$

The conditions $\frac{d\varphi_i}{dx_i^*}(K_i)\gamma_{ij} = \frac{d\varphi_j}{dx_j^*}(K_j)\gamma_{ji}$ can be written $\omega_{ij} := -\frac{d\varphi_i}{dx_i^*}(K_i)/\gamma_{ji} = -\frac{d\varphi_j}{dx_j^*}(K_j)/\gamma_{ij}$ for all $j < i$, such that $\gamma_{ij} \neq 0$ and $\gamma_{ji} \neq 0$. Therefore, there exists $\omega_{ij} > 0$ such that

$$\frac{d\varphi_j}{dx_j^*}(K_j) = -\omega_{ij}\gamma_{ij} \quad \text{and} \quad \frac{d\varphi_i}{dx_i^*}(K_i) = -\omega_{ij}\gamma_{ji} \quad \text{for all } i, j \text{ with } \gamma_{ij} \neq 0 \text{ and } \gamma_{ji} \neq 0.$$

Replacing $\frac{d\varphi_i}{dx_i^*}(K_i)$ and $\frac{d\varphi_j}{dx_j^*}(K_j)$ in (49), one obtains

$$T_n^*(\epsilon) = \sum_{i=1}^n K_i + \epsilon \sum_{j < i} \frac{\omega_{ij} \left(\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon) \right)^2}{\frac{d\varphi_i}{dx_i^*}(K_i) \frac{d\varphi_j}{dx_j^*}(K_j) x_j^*(\epsilon) x_i^*(\epsilon)} + o\left(\sum_i x_i^*(\epsilon) - \sum_i K_i\right) \geq \sum_{i=1}^n K_i. \tag{50}$$

Equality holds if and only if $\epsilon = 0$ or $\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon) = 0$, for all i and j . Let us prove that if $K_i \frac{d\varphi_i}{dx_i^*}(K_i) \neq K_j \frac{d\varphi_j}{dx_j^*}(K_j)$, then equality cannot hold for $\epsilon > 0$. Suppose that there exists $\epsilon^* > 0$ such that the positive equilibrium satisfies

$$\forall i, j, \quad \gamma_{ij}x_j^*(\epsilon^*) = \gamma_{ji}x_i^*(\epsilon^*). \tag{51}$$

Replacing the equation (51) in the system (48), we get that $x_i^*(\epsilon^*) = K_i$, for all i . Therefore, from (51), it is seen that, for all i and j , $K_j\gamma_{ij} = K_i\gamma_{ji}$. From these equations and the conditions $\frac{d\varphi_i}{dx_i^*}(K_i)\gamma_{ij} = \frac{d\varphi_j}{dx_j^*}(K_j)\gamma_{ji}$, we get $K_i \frac{d\varphi_i}{dx_i^*}(K_i) = K_j \frac{d\varphi_j}{dx_j^*}(K_j)$, for all i and j . This is a contradiction with the hypothesis $K_i \frac{d\varphi_i}{dx_i^*}(K_i) \neq K_j \frac{d\varphi_j}{dx_j^*}(K_j)$ of the proposition. Hence the equality in (50) holds if and only if $\epsilon = 0$. □

When the matrix Γ is symmetric, Proposition 14 says that if all $\frac{d\varphi_i}{dx_i^*}(K_i)$ are equal, dispersal enhances population growth. Note that, if φ_i is logistic, then we obtain Proposition 4.2 of [15].

For two-patch logistic model, Prop 14 asserts that if $\alpha_2/\alpha_1 = \gamma_{12}/\gamma_{21}$, then $T_n^*(\epsilon) > K_1 + K_2$, which is a result of Arditi et al. [2, Proposition 2MK(b)].

Now, in the next proposition, we give another important case of the model (12).

Proposition 15.

- (1) If the equilibrium $E_n^*(\epsilon)$ does not depend on ϵ , then $E_n^*(\epsilon) = (K_1, \dots, K_n)$ for all $\epsilon \geq 0$, and $(K_1, \dots, K_n) \in \ker \Gamma$.
- (2) If $(K_1, \dots, K_n) \in \ker \Gamma$ then $E_n^*(\epsilon) = (K_1, \dots, K_n)$ for all $\epsilon \geq 0$, i.e., the total equilibrium population verifies

$$T_n^*(\epsilon) = \sum_{i=1}^n K_i.$$

Proof. $E_n^*(\epsilon)$ is the unique positive solution of the equation

$$\text{diag}(\varphi_1(x_1^*(\epsilon)), \dots, \varphi_n(x_n^*(\epsilon)))E_n^*(\epsilon) + \epsilon \Gamma E_n^*(\epsilon) = 0. \tag{52}$$

(1). Suppose that, the equilibrium $E_n^*(\epsilon)$ does not depend on ϵ , we replace in Equation (52):

$$\text{diag}(\varphi_1(x_1^*(\epsilon)), \dots, \varphi_n(x_n^*(\epsilon)))E_n^* + \epsilon \Gamma E_n^*(\epsilon) = 0. \tag{53}$$

The derivative of (53) with respect to ϵ gives

$$\Gamma E_n^*(\epsilon) = 0. \tag{54}$$

Replacing the equation (54) in the equation (53), we get the matrix equation

$$\text{diag}(\varphi_1(x_1^*), \dots, \varphi_n(x_n^*)) = 0.$$

So, $E_n^*(\epsilon) = (K_1, \dots, K_n)$.

From the equation (54), we conclude that $(K_1, \dots, K_n) \in \ker \Gamma$.

(2). Suppose that $(K_1, \dots, K_n) \in \ker \Gamma$, then (K_1, \dots, K_n) satisfies the equation (52). So, $E_n^* = (K_1, \dots, K_n)$. Which proves that, the total equilibrium population is independent of the migration rates ϵ . □

The result of the previous proposition is same obtained by Elbetch et al. [15] for logistic model.

6. Example of Two-patch model

In this section, we concentrate on the following two-patch model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon (\gamma_{21} x_1 - \gamma_{12} x_2), \end{cases} \tag{55}$$

where the first patch is assumed to follow a logistic law and the second a Richard law (see Figure 4).

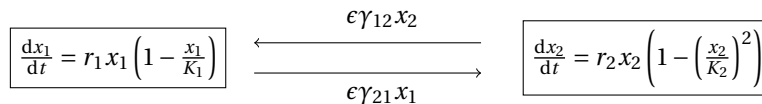


Figure 4. A Tow-patch coupled system

The total equilibrium population of the model (55) in the perfect mixing case (i.e. $\epsilon \rightarrow \infty$) is given by the following formula:

$$T_2^*(+\infty) = (\gamma_{12} + \gamma_{21}) \frac{-r_1 \gamma_{12}^2 K_2 + \sqrt{r_1^2 \gamma_{12}^4 K_2^2 + 4 r_2 \gamma_{21}^3 K_1^2 r_1 \gamma_{12} + 4 r_2^2 \gamma_{21}^4 K_1^2}}{2 r_2 \gamma_{21}^3 K_1} K_2 \tag{56}$$

and the derivative of the total equilibrium population $T_2^*(\epsilon)$ at $\epsilon = 0$ becomes

$$\frac{dT_2^*}{d\epsilon}(0) = (\gamma_{12}K_2 - \gamma_{21}K_1) \left(\frac{1}{r_1} - \frac{1}{2r_2} \right). \tag{57}$$

The equilibrium of the system (55) is the solutions of the following algebraic system:

$$\begin{cases} 0 = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (\gamma_{12} x_2 - \gamma_{21} x_1), \\ 0 = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon (\gamma_{21} x_1 - \gamma_{12} x_2). \end{cases} \tag{58}$$

The sum of two equations of (58) shows that the equilibrium points are in curve noted \mathbb{F} , where its equation is given by:

$$\mathbb{F} : r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + r_2 x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^2 \right) = 0. \tag{59}$$

The curve \mathbb{F} passes through the points $(0, 0)$, $(K_1, 0)$, $(0, K_2)$ and $\mathcal{A} := (K_1, K_2)$. Note that, it is independent of migration rate ϵ and γ_{ij} (shown in red in Figure 5).

Solving the first equation of system (58) for x_2 yields a parabola noted \mathcal{P}_ϵ defined by

$$\mathcal{P}_\epsilon : p_\epsilon(x_1) := \frac{1}{\gamma_{12}} x_1 \left(\gamma_{21} - \frac{r_1}{\epsilon} \left(1 - \frac{x_1}{K_1} \right) \right).$$

As our study is limited in the positive cone, then we are interested only in the positive branch of \mathcal{P}_ϵ . The parabola \mathcal{P}_ϵ (shown in blue in Figure 5) depend on the migration rate ϵ . It always passes through the origin and the point $\mathcal{B} := \left(K_1, \frac{\gamma_{21}}{\gamma_{12}} K_1 \right)$. Notice that, the parabola \mathcal{P}_ϵ intersect the axis (Ox_1) at 0 and a second point $x_1 = -\frac{(\gamma_{21}\epsilon - r_1)K_1}{r_1}$ if $\gamma_{21}\epsilon - r_1 < 0$, which always smaller than K_1 . So, the equilibrium points are the non negative intersection between the curve \mathbb{F} and \mathcal{P}_ϵ . There are two equilibrium points. The first is the trivial point $(0, 0)$ and the second is a non trivial point $E_2^*(\epsilon) = (x_1^*(\epsilon), x_2^*(\epsilon))$ whose position depend on migration rate ϵ (see Figure 5).

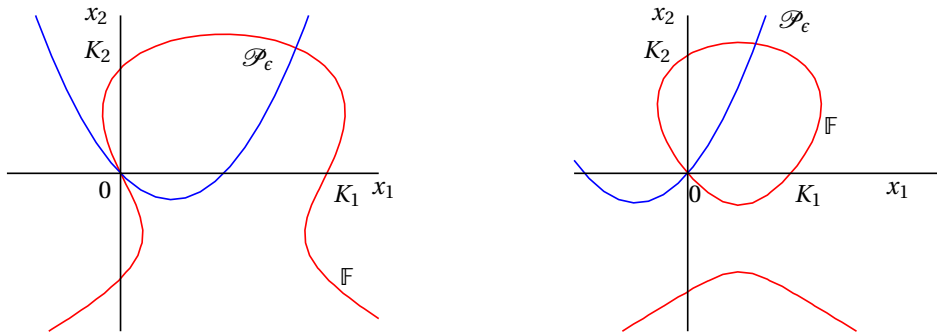


Figure 5. Some examples of the curve \mathbb{F} and the Parabola \mathcal{P}_ϵ . The equilibrium points are the intersection in the positive cone between \mathbb{F} and \mathcal{P}_ϵ , this intersections contains the origin and a second positive point $E^*(\epsilon)$.

When $\epsilon \rightarrow 0$, the left branch of parabola \mathcal{P}_ϵ tend to the vertical line $x_1 = 0$ and the right branch into the vertical line $\mathcal{P}_0 : x_1 = K_1$. Moreover, $\mathbb{F} \cap \mathcal{P}_0 = \{(K_1, 0), (K_1, K_2)\}$. In the case when $\epsilon \rightarrow \infty$, the parabola \mathcal{P}_ϵ tend to the oblique line $\mathcal{P}_\infty : x_2 = \frac{\gamma_{21}}{\gamma_{12}} x_1$. Moreover, $\mathbb{F} \cap \mathcal{P}_\infty = \{(0, 0), (\gamma_{12}\lambda_0, \gamma_{21}\lambda_0)\}$, where

$$\lambda_0 = \frac{-\gamma_{12}r_1K_2 + \sqrt{\gamma_{12}^2r_1^2K_2^2 + 4\gamma_{21}r_2K_1^2\gamma_{12}r_1 + 4\gamma_{21}^2r_2^2K_1^2}}{2\gamma_{21}r_2K_1} K_2.$$

6.1. Effect of dispersal and intrinsic growth rate on total equilibrium population

For two-patch logistic model, it was shown by Arditi et al. [1, Proposition 2, p. 54] that 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 ϵ and detrimental for the higher values. More precisely, it was shown in [1] that, if $n = 2$ in (11), the following trichotomy holds

- If $T_2^*(+\infty) > K_1 + K_2$ then $T_2^*(\epsilon) > K_1 + K_2$ for all $\epsilon > 0$.
- If $\frac{dT_2^*}{d\epsilon}(0) > 0$ and $T_2^*(+\infty) < K_1 + K_2$, then there exists $\epsilon_0 > 0$ such that $T_2^*(\epsilon) > K_1 + K_2$ for $0 < \epsilon < \epsilon_0$, $T_2^*(\epsilon) < K_1 + K_2$ for $\epsilon > \epsilon_0$ and $T_2^*(\epsilon_0) = K_1 + K_2$.
- If $\frac{dT_2^*}{d\epsilon}(0) < 0$, then $T_2^*(\epsilon) < K_1 + K_2$ for all $\epsilon > 0$.

Therefore, the condition $T_2^*(\epsilon) = K_1 + K_2$ holds only for $\epsilon = 0$ and at most for one positive value ϵ_0 . The value ϵ_0 exists if and only if $\frac{dT_2^*}{d\epsilon}(0) > 0$ and $T_2^*(+\infty) < K_1 + K_2$.

In the remainder of this section, we analyze the effect of dispersion and the specific growth rate on the total equilibrium population for the two-patch system (55). Using the method of Arditi et al. [2], we describe the position affects the equilibrium $E^*(\epsilon)$ of (55) when the migration rate varies from zero to infinity, we will give the condition whether T_2^* is greater or smaller than sum of carrying capacity $T_2^*(0) = K_1 + K_2$. We prove there are only three cases as in the 2-patch logistic model can occur. Denote $\sigma = K_2^2(r_2^2K_1^2 + 6r_2K_1K_2r_1 + r_1^2K_2^2 + 4r_1r_2K_1^2)$:

$$\xi_1 = -\frac{-3r_2K_1K_2 - r_1K_2^2 - 2r_2K_1^2 + \sqrt{\sigma}}{2r_2K_1} \quad \xi_2 = \frac{-r_2K_1K_2 - r_1K_2^2 + \sqrt{\sigma}}{2r_2K_1}. \tag{60}$$

Note that, $\xi_1 > 0$ and $\xi_2 > 2$. We consider the regions in the set of the parameters γ_{21} and γ_{12} , denoted \mathcal{J}_0 , \mathcal{J}_1 and \mathcal{J}_2 , depicted in Figure 6 and defined by:

$$\left\{ \begin{array}{l} \mathcal{J}_1 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} > \frac{\xi_2}{\xi_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\xi_2}{\xi_1} \geq \frac{\gamma_{12}}{\gamma_{21}} > \frac{K_1}{K_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{K_1}{K_2} > \frac{\gamma_{12}}{\gamma_{21}} \right\} \end{array} \right. \quad \text{if } 2r_2 > r_1 \tag{61}$$

$$\left\{ \begin{array}{l} \mathcal{J}_1 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} < \frac{\xi_2}{\xi_1} \right\} \\ \mathcal{J}_0 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\xi_2}{\xi_1} \leq \frac{\gamma_{12}}{\gamma_{21}} < \frac{K_1}{K_2} \right\} \\ \mathcal{J}_2 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{K_1}{K_2} < \frac{\gamma_{12}}{\gamma_{21}} \right\} \end{array} \right. \quad \text{if } 2r_2 < r_1$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (55).

Theorem 16. *The total equilibrium population of (55) satisfies the following properties*

- (1) If $r_1 = 2r_2$ then $T_2^*(\epsilon) \leq K_1 + K_2$ for all $\epsilon \geq 0$.
- (2) If $2r_2 \neq r_1$, let \mathcal{J}_0 , \mathcal{J}_1 and \mathcal{J}_2 , be defined by (61). Then we have:
 - if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_0$ then $T_2^*(\epsilon) > K_1 + K_2$ for any $\epsilon > 0$
 - if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_1$ then $T_2^*(\epsilon) > K_1 + K_2$ for $0 < \epsilon < \epsilon_0$ and $T_2^*(\epsilon) < K_1 + K_2$ for $\epsilon > \epsilon_0$, where

$$\epsilon_0 = \frac{r_2K_1}{-\gamma_{12}r_2K_1K_2 - \gamma_{12}r_1K_2^2 - 3\gamma_{21}r_2K_1K_2 - \gamma_{21}r_1K_2^2 - 2\gamma_{21}r_2K_1^2 + (\gamma_{12} + \gamma_{21})\sqrt{\sigma}}.$$

- if $(\gamma_{21}, \gamma_{12}) \in \mathcal{J}_2$ then $T_2^*(\epsilon) < K_1 + K_2$ for any $\epsilon > 0$
- if $\frac{\gamma_{12}}{\gamma_{21}} = \frac{K_1}{K_2}$, then $x_1^*(\epsilon) = K_1$ and $x_2^*(\epsilon) = K_2$ for all $\epsilon \geq 0$. Therefore $T_2^*(\epsilon) = K_1 + K_2$ for all $\epsilon \geq 0$.

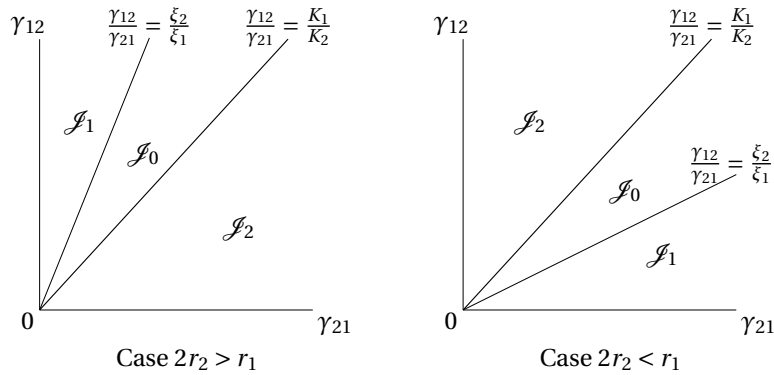


Figure 6. The domains $\mathcal{J}_0, \mathcal{J}_1$ and \mathcal{J}_2 . In the figure $\alpha_1 = r_1 / K_1$ and $\alpha_2 = r_2 / K_2$.

Proof. To facilitate comparison of the total equilibrium population $T_2^*(\epsilon)$ and $T_2^*(0) = K_1 + K_2$, we define a straight line $\Delta : x_1 + x_2 = K_1 + K_2$. If the intersection of the curve \mathbb{F} and the parabola \mathcal{P}_ϵ , i.e., the equilibrium $(x_1^*(\epsilon), x_2^*(\epsilon))$, is on or below the line Δ , then $T_2^*(\epsilon) \leq T_2^*(0)$, whereas if the intersection is above the line, then $T_2^*(\epsilon) \geq T_2^*(0)$. The equilibrium point $E_2^*(\epsilon)$ is always in the curve \mathbb{F} , then, for $\epsilon = 0$, the equilibrium point states at \mathcal{A} , and when ϵ increases, $E_2^*(\epsilon)$ describes an arc of the curve \mathbb{F} and ends at point $E_2^*(\infty)$.

If we take $r_1 = 2r_2$, we get that the equation of tangent space to the curve \mathbb{F} at point \mathcal{A} is the equation of Δ . By Proposition 13, we deduce $T_2^*(\epsilon) \leq T_2^*(0)$ for all $\epsilon \geq 0$.

In the case when $r_1 \neq 2r_2$, direct calculation finds that the curve \mathbb{F} and the line Δ have two intersections:

$$\mathcal{A} = (K_1, K_2), \text{ and } C = (\xi_1, \xi_2).$$

We denote by Σ the straight line joint the origin and C . The slope of Σ is equal to $\frac{\xi_2}{\xi_1}$. We distinguish three cases relative position of the three points $\mathcal{A}, E_2^*(\infty)$, and C , or equivalently, the three lines $[O\mathcal{A}], \mathcal{P}_\infty$ and Σ whose slopes are

$$\frac{K_2}{K_1}, \frac{\gamma_{21}}{\gamma_{12}} \text{ and } \frac{\xi_2}{\xi_1}.$$

By the method graphic of Arditi et al. [2], we conclude the complete proof. □

In general, it is very difficult to give a complete classification for all specific growth rate φ_i under which fragmentation and migration can lead to a total equilibrium population which might be greater or smaller than the sum of carrying capacities and also it is difficult to give the explicit formula of $T_n^*(\infty)$, except in special cases. In the next, we give some examples of the specific growth rates φ_i which we can calculate explicitly the total equilibrium population for perfect mixing and also the its derivative at $\epsilon = 0$.

- Model of Richard: For the Richards's growth rate (5), the total equilibrium population for perfect mixing take the following form:

$$T_n^*(+\infty) = \left(\sum_{i=1}^n \delta_i \right) \left(\frac{\sum_{i=1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^{\mu+1} \frac{r_i}{K_i^\mu}} \right)^{\frac{1}{\mu}} \text{ and } \frac{dT_n^*}{d\epsilon}(0) = \sum_i \left(\frac{1}{\mu r_i} \sum_{j \neq i} \gamma_{ij} K_j - \gamma_{ji} K_i \right).$$

- Model of Gompertz: Consider the ordinary Gompertz growth (6) for $\mu_3 = 1$. The total equilibrium for perfect mixing case and the derivative with no dispersal are given by:

$$T_n^*(\infty) = \left(\sum_{i=1}^n \delta_i \right) \left(\prod_{i=1}^n \left(\frac{K_i}{\delta_i} \right)^{\delta_i r_i} \right)^{\frac{1}{\sum_{i=1}^n \delta_i r_i}} \quad \text{and} \quad \frac{dT_n^*}{d\epsilon}(0) = \infty.$$

6.2. Two-patch model where one growth rate is much larger than the second one

Recently, in [13], Elbetch is interested in some biological situations that can be found in the nature, that is, the case where several sub-populations grow with different speed. Mathematically speaking, he studied the system (11) under the hypothesis that some growth rates tend to infinity (i.e. $r_i \rightarrow \infty$ for some i). In this section, we consider the two-patch model (55) and we assume that the growth rate r_2 (resp. r_1) is much larger than r_1 (resp. r_2).

6.2.1. Case where $r_2 \rightarrow \infty$

In this part, we assume that r_2 is much larger than r_1 . For simplicity we denote $\gamma_2 := \gamma_{12} > 0$ the migration rate from patch 2 to patch 1 and $\gamma_1 := \gamma_{21} > 0$ from patch 1 to patch 2. The model (55) is written:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = \frac{r_2}{\eta} x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon (\gamma_1 x_1 - \gamma_2 x_2), \end{cases} \quad (62)$$

where η is assumed to be a small positive number. Denote $E_2^*(\epsilon, \eta) = (x_1^*(\epsilon, \eta), x_2^*(\epsilon, \eta))$ the positive equilibrium of (62), and $T_2^*(\epsilon, \eta)$, the total equilibrium population. We recall that the derivative of $T_2^*(\epsilon, \eta)$ with respect to ϵ at $\epsilon = 0$ is written as follow:

$$\frac{dT_2^*}{d\epsilon}(0, \eta) = (\gamma_2 K_2 - \gamma_1 K_1) \left(\frac{1}{r_1} - \frac{\eta}{2r_2} \right). \quad (63)$$

The total equilibrium population of the model (62) for perfect mixing (i.e. $\epsilon \rightarrow \infty$) is given by the following formula:

$$T_2^*(+\infty, \eta) = (\gamma_1 + \gamma_2) \frac{-\eta r_1 \gamma_2^2 K_2 + \sqrt{\eta^2 r_1^2 \gamma_2^4 K_2^2 + 4\eta r_2 \gamma_1^3 K_1^2 r_1 \gamma_2 + 4 r_2^2 \gamma_1^4 K_1^2}}{2 r_2 \gamma_1^3 K_1} K_2, \quad (64)$$

First, we have the result:

Theorem 17. *Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of the system (62) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $u(t)$ be the solution of the differential equation*

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (\gamma_2 K_2 - \gamma_1 x_1) =: \varphi(x_1), \quad (65)$$

with initial condition $u(0) = x_1^0$. Then, when $\eta \rightarrow 0$, we have

$$x_1(t, \eta) = u(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (66)$$

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

$$x_2(t, \eta) = K_2 + o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (67)$$

Proof. When $\eta \rightarrow 0$, the system (62) is a *slow-fast* system, with one *slow variable*, x_1 , and one *fast variable*, x_2 . Tikhonov's theorem [28, 36, 40] prompts us to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{\eta} t$. One obtains

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) + \epsilon \eta (\gamma_1 x_1 - \gamma_2 x_2). \quad (68)$$

In the limit $\eta \rightarrow 0$, we find the *fast dynamics*

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(1 - \frac{x_2}{K_2} \right). \tag{69}$$

The slow manifold is given by the positive equilibrium of the system (69), i.e. $x_2 = K_2$, which is GAS in the positive axis. When η goes to zero, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (62) converge to the solutions of the *reduced model* (65), obtained by replacing $x_2 = K_2$ into the dynamics of the slow variable.

The differential equation (65) admits as a positive equilibrium

$$x_1^*(\epsilon, 0^+) := \frac{r_1 - \epsilon \gamma_1 + \sqrt{(r_1 - \epsilon \gamma_1)^2 + 4\epsilon \alpha_1 \gamma_2 K_2}}{2\alpha_1}, \tag{70}$$

where $\alpha_1 = \frac{r_1}{K_1}$. As $\varphi(x_1) > 0$ for all $0 \leq x_1 < x_1^*(\epsilon, 0^+)$ and $\varphi(x_1) < 0$ for all $x_1 > x_1^*(\epsilon, 0^+)$ then, the equilibrium $x_1^*(\epsilon, 0^+)$ is GAS in the positive axis, so, the approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is as small as we want. Therefore, let $u(t)$ be the solution of the reduced model (65) of initial condition $u(0) = x_1^0$, then, when $\epsilon \rightarrow 0$, we have the approximations (66) and (67). \square

As a corollary of the previous theorem, we have the following result which give the limit of the total equilibrium population $T_2^*(\epsilon, \eta)$ of the model (62) when η goes to zero:

Corollary 18. *We have:*

$$\begin{aligned} T_2^*(\epsilon, 0^+) &:= \lim_{\eta \rightarrow 0} T_2^*(\epsilon, \eta) = \lim_{\eta \rightarrow 0} (x_1^*(\epsilon, \eta) + x_2^*(\epsilon, \eta)) \\ &= \frac{r_1 - \epsilon \gamma_1 + \sqrt{(r_1 - \epsilon \gamma_1)^2 + 4\epsilon \alpha_1 \gamma_2 K_2}}{2\alpha_1} + K_2. \end{aligned} \tag{71}$$

Proof. According to the equations (66), (67) and (70), when η goes to zero, the equilibrium $E_2^*(\epsilon, \eta)$ of the model (62) is converge to $E_2^*(\epsilon, 0^+) := (x_1^*(\epsilon, 0^+), K_2)$, where $x_1^*(\epsilon, 0^+)$ is given in (70). The sum of the coordinates of $E_2^*(\epsilon, 0^+)$ gives the formula (71). \square

In the following proposition, we calculate the derivative and the formula of perfect mixing (i.e. when $\epsilon \rightarrow \infty$) of the total equilibrium population defined by (71).

Proposition 19. *Consider the total equilibrium population (71). Then,*

$$\frac{dT_2^*}{d\epsilon}(0, 0^+) := \frac{-\gamma_1 K_1 + \gamma_2 K_2}{r_1}, \tag{72}$$

and

$$T_2^*(+\infty, 0^+) := \frac{\gamma_1 + \gamma_2}{\gamma_1} K_2. \tag{73}$$

Proof. The derivative of the total equilibrium population $T_2^*(\epsilon, 0^+)$ defined by (71) with respect to ϵ is:

$$\begin{aligned} \frac{dT_2^*}{d\epsilon}(\epsilon, 0^+) &= -\frac{K_1}{2\sqrt{K_1(r_1^2 K_1 - 2r_1 K_1 \epsilon \gamma_1 + \epsilon^2 K_1 \gamma_1^2 + 4r_1 \epsilon \gamma_2 K_2)} r_1} \\ &\quad \times \left(\gamma_1 \sqrt{K_1(r_1^2 K_1 - 2r_1 K_1 \epsilon \gamma_1 + \epsilon^2 K_1 \gamma_1^2 + 4r_1 \epsilon \gamma_2 K_2)} + r_1 K_1 \gamma_1 - \epsilon K_1 \gamma_1^2 - 2r_1 \gamma_2 K_2 \right) \end{aligned} \tag{74}$$

In particular, the derivative of the total equilibrium population at $\epsilon = 0$ is given by the formula (72).

By taking the limit of (71) when $\epsilon \rightarrow \infty$, we get that the total equilibrium population $T_2^*(\epsilon, 0^+)$ tend to (73). \square

We consider the regions in the set of the parameters γ_1 and γ_2 , denoted \mathcal{J}_0 and \mathcal{J}_1 defined by:

$$\mathcal{J}_0 = \left\{ (\gamma_1, \gamma_2) : \frac{\gamma_2}{\gamma_1} > \frac{K_1}{K_2} \right\}, \quad \mathcal{J}_1 = \left\{ (\gamma_1, \gamma_2) : \frac{\gamma_2}{\gamma_1} < \frac{K_1}{K_2} \right\}. \tag{75}$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (62) when ϵ goes to zero.

Theorem 20. *Let \mathcal{J}_0 and \mathcal{J}_1 be the domains defined in (75). Consider the total equilibrium population $T_2^*(\epsilon, 0^+)$ given by (71). Then, we have:*

- *If $(\gamma_1, \gamma_2) \in \mathcal{J}_0$ then $T_2^*(\epsilon, 0^+) > K_1 + K_2$, for all $\epsilon > 0$.*
- *If $(\gamma_1, \gamma_2) \in \mathcal{J}_1$ then $T_2^*(\epsilon, 0^+) < K_1 + K_2$, for all $\epsilon > 0$.*
- *If $\frac{\gamma_2}{\gamma_1} = \frac{K_1}{K_2}$, then $x_1^*(\epsilon, 0^+) = K_1$ and $x_2^*(\epsilon, 0^+) = K_2$ for all $\epsilon \geq 0$. Therefore $T_2^*(\epsilon, 0^+) = K_1 + K_2$ for all $\epsilon \geq 0$.*

Proof. First, we try to solve the equation $T_2^*(\epsilon, 0^+) = K_1 + K_2$ with respect to ϵ , the solutions of this last equation give the points of intersection between the curve of the total equilibrium population $\epsilon \mapsto T_2^*(\epsilon, 0^+)$ and the straight line $\epsilon \mapsto K_1 + K_2$. For any $\epsilon > 0$, we have

$$\begin{aligned} T_2^*(\epsilon, 0^+) = K_1 + K_2 &\iff \frac{r_1 - \epsilon\gamma_1 + \sqrt{(r_1 - \epsilon\gamma_1)^2 + 4\epsilon\alpha_1\gamma_2K_2}}{2\alpha_1} = K_1 \\ &\iff -K_1^2(r_1 + \epsilon\gamma_1)^2 + K_1(r_1^2K_1 - 2r_1K_1\epsilon\gamma_1 + \epsilon^2K_1\gamma_1^2 + 4r_1\epsilon\gamma_2K_2) = 0 \\ &\iff -4r_1K_1^2\epsilon\gamma_1 + 4r_1\epsilon K_1\gamma_2K_2 = 0 \\ &\iff \gamma_2K_2 = \gamma_1K_1 \\ &\iff \frac{dT_2^*}{d\epsilon}(0, 0^+) = 0. \end{aligned}$$

So, if $\frac{dT_2^*}{d\epsilon}(0, 0^+) \neq 0$ then $\epsilon = 0$ and the curve of the total equilibrium population intersects the straight line $\epsilon \mapsto K_1 + K_2$ in a unique point which is $(0, K_1 + K_2)$. Therefore, we conclude that the first and second items of the theorem are hold. \square

6.2.2. Case where $r_1 \rightarrow \infty$

In this part, we assume that r_1 is much larger than r_2 . The model (55) is written:

$$\begin{cases} \frac{dx_1}{dt} = \frac{r_1}{\eta} x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon(\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon(\gamma_1 x_1 - \gamma_2 x_2), \end{cases} \tag{76}$$

where η is assumed to be a small positive number. We recall that the derivative of $T_2^*(\epsilon, \eta)$ with respect to ϵ at $\epsilon = 0$ is written as follow:

$$\frac{dT_2^*}{d\epsilon}(0, \eta) = (\gamma_2 K_2 - \gamma_1 K_1) \left(\frac{\eta}{r_1} - \frac{1}{2r_2} \right). \tag{77}$$

The total equilibrium population of the model (62) for perfect mixing (i.e. $\epsilon \rightarrow \infty$) is given by the following formula:

$$T_2^*(+\infty, \eta) = (\gamma_1 + \gamma_2) \frac{-r_1\gamma_2^2K_2 + \sqrt{r_1^2\gamma_2^4K_2^2 + 4\eta r_2\gamma_1^3K_1^2r_1\gamma_2 + 4\eta^2r_2^2\gamma_1^4K_1^2}}{2\eta r_2\gamma_1^3K_1} K_2, \tag{78}$$

We have the result:

Theorem 21. Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of the system (76) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $u(t)$ be the solution of the differential equation

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon (\gamma_1 K_1 - \gamma_2 x_2) =: \varphi(x_1), \tag{79}$$

with initial condition $u(0) = x_2^0$. Then, when $\eta \rightarrow 0$, we have

$$x_2(t, \eta) = u(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \tag{80}$$

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

$$x_1(t, \eta) = K_1 + o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \tag{81}$$

Proof. The proof is the same as in Theorem 17. The differential equation (79) admits unique positive equilibrium $x_2^*(\epsilon, 0^+)$. As $\varphi(x_2) > 0$ for all $0 \leq x_2 < x_2^*(\epsilon, 0^+)$ and $\varphi(x_2) < 0$ for all $x_2 > x_2^*(\epsilon, 0^+)$ then, the equilibrium $x_2^*(\epsilon, 0^+)$ is GAS in the positive axis, so, the approximation given by Tikhonov’s theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is as small as we want. Therefore, let $u(t)$ be the solution of the reduced model (79) of initial condition $u(0) = x_2^0$, then, when $\epsilon \rightarrow 0$, we have the approximations (80) and (81). □

We have the result:

Theorem 22. Let \mathcal{J}_0 and \mathcal{J}_1 be the domains defined in (75). Consider the total equilibrium population $T_2^*(\epsilon, 0^+) = K_1 + x_2^*(\epsilon, 0^+)$ with $x_2^*(\epsilon, 0^+)$ is the unique positive solution of (79). Then, we have:

- If $(\gamma_1, \gamma_2) \in \mathcal{J}_0$ then $T_2^*(\epsilon, 0^+) < K_1 + K_2$, for all $\epsilon > 0$.
- If $(\gamma_1, \gamma_2) \in \mathcal{J}_1$ then $T_2^*(\epsilon, 0^+) > K_1 + K_2$, for all $\epsilon > 0$.
- If $\frac{\gamma_2}{\gamma_1} = \frac{K_1}{K_2}$, then $x_1^*(\epsilon, 0^+) = K_1$ and $x_2^*(\epsilon, 0^+) = K_2$ for all $\epsilon \geq 0$. Therefore $T_2^*(\epsilon, 0^+) = K_1 + K_2$ for all $\epsilon \geq 0$.

Proof. First, we try to solve the equation $T_2^*(\epsilon, 0^+) = K_1 + K_2$ with respect to ϵ , i.e. the equation $x_2^*(\epsilon, 0^+) = K_2$. By (79), we obtain

$$x_2^*(\epsilon, 0^+) = K_2 \iff \sqrt{1 - \epsilon \frac{\gamma_2 x_2 - \gamma_1 K_1}{r_2 x_2}} = 1$$

which implies, for all $\epsilon > 0$:

$$\gamma_2 K_2 = \gamma_1 K_1 \iff \frac{dT_2^*}{d\epsilon}(0, 0^+) = 0.$$

So, if $\frac{dT_2^*}{d\epsilon}(0, 0^+) \neq 0$ then $\epsilon = 0$ and the curve of the total equilibrium population intersects the straight line $\epsilon \mapsto K_1 + K_2$ in a unique point which is $(0, K_1 + K_2)$. Therefore, we conclude that the first and second items of the theorem are hold. □

7. Conclusion

The aim of this paper is to generalize, to a multi-patch model with generalized growth rate, the results obtained in [14, 15] for a multi-patch logistic model.

In Section 3, using the result of Lu and Takeuchi [30, Corollary 1], we prove that the globally asymptotically stable equilibrium still exists for generalized growth rate.

In Section 4, we consider the particular case of perfect mixing, when the migration rate goes to infinity. As in [14] and [15], we implicitly compute the total equilibrium population in that case, and, by perturbation arguments, we prove that the dynamics in this ideal case provides a good approximation to the case when the migration rate is large. Our results generalize those of [1, 2]

for tow-patch logistic model, [14] for n-patch logistic model with dispersal symmetric between patches, and [15] for many patches with movement between patches not necessarily symmetric.

In Section 5, we have shown that if the n patches do not differ with respect to $K_i \frac{d\varphi_i}{dx_i}(K_i)$, then the total equilibrium population on the n connected patches is always less than or equal to the sum of carrying capacity of the isolated patches. This result can be seen as negative but constitutes in our eyes an interesting result. We then addressed this issue in the general case when $K_i \frac{d\varphi_i}{dx_i}(K_i)$ are different, we have determined some conditions for which the total population size of the n connected patches at equilibrium may be greater than the sum of carrying capacities of n isolated patches.

In Section 6, Two-patch model where the first patch is assumed to follow a logistic law and the second a Richard law is studied. As for the logistic case, we have shown that three cases occur : the total equilibrium population is always greater than the sum of carrying capacities (beneficial case), the total equilibrium population is always smaller than the sum of carrying capacities (detrimental case), and finally the effect of dispersal is beneficial to the total population for ϵ less than a critical value ϵ_0 and detrimental for $\epsilon > \epsilon_0$ (Theorem 16). Next, the growth rate in the second (resp. first) patch is supposed to be much larger than that in the first (resp. second) one. We have given then the conditions for which patchiness is beneficial or detrimental for the population in models (62) and (76) when $\eta \rightarrow 0$. In this configuration where the population of one of the patches has a fast growing compared to the other patch, the critical value of migration rate ϵ_0 does not intervene.

Finally, comparisons the present results with previous works [1, 2, 14, 15] indicate that, in general, the generalized growth rate mechanism has an effect on the dynamics of the total equilibrium population. Some questions remain open : is it possible to give a complete classification of the conditions under which dispersal is either beneficial or detrimental to total equilibrium population in the case of two patches (i.e. System (12) for $n = 2$)? Is there a way to make connections between the n patches that increases the total equilibrium population? How these results can be generalized to Source-Sink patch-model?

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