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Effect of dispersal in two-patch environment with Richards growth on population dynamics

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Abstract. In this paper, we consider a two-patch model coupled by migration terms, where each patch follows a Richards law. First, we prove the global stability of the model. Second, in the case when the migration rate tends to infinity, the total carrying capacity is given, which in general is different from the sum of the two carrying capacities and depends on the parameters of the growth rate and also on the migration terms. Using the theory of singular perturbations, we give an approximation of the solutions of the system in this case. Finally, 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 two carrying capacities and we give a complete classification for all possible cases. The total equilibrium population formula for a large migration rate plays an important role in this classification. We show that this choice of local dynamics has an influence on the effect of dispersal. Comparing the dynamics of the total equilibrium population as a function of the migration rate with that of the logistic model, we obtain the same behavior. In particular, we have only three situations that the total equilibrium population can occur: it is always greater than the sum of two carrying capacities, always smaller, and a third case, where the effect of dispersal is beneficial for lower values of the migration rate and detrimental for the higher values. We end by examining the two-patch model where one growth rate is much larger than the second one, we compare the total equilibrium population with the sum of the two carrying capacities.

Keywords: Population dynamics, Richards Model, Asymmetric dispersal, Singular Perturbation.

2020 Mathematics Subject Classification: 92B05, 92D25, 34D15, 34D05.

1 Introduction

Population dynamics is a wide field of mathematics, which contains many problems, among them the effect of migration on the general dynamics of the population. Bibliographies can be found in the work of Levin [18, 19] and Holt [15]. There are ecological situations that motivate the representation of space as a finite set of patches connected by migrations, for

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instance, an archipelago with bird populations and predators. It is an example of insular biogeography. A reference work on mathematical models is the book of Levin, Powell and Steele [20], whereas Hanski and Gilpin [13] give a more ecological account of the subject. The standard question in this type of biomathematical problem 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.

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 [33] 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 [21] 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

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right). \tag{1.1}$$

Turner and co-authors [32] proposed a modified Verhulst logistic equation (1.1) which they termed the generic growth function. It has the form

$$\frac{dx}{dt} = rx^{1+\mu_2(1-\mu_3)}\left[1 - \left(\frac{x}{K}\right)^{\mu_2}\right]^{\mu_3}, \tag{1.2}$$

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

Blumberg [4] introduced another growth equation based on a modification of the Verhulst logistic growth equation (1.1) 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

$$\frac{dx}{dt} = rx^{\mu_1}\left(1 - \frac{x}{K}\right)^{\mu_3}. \tag{1.3}$$

Blumberg's equation (1.3) is consistent with the Turner and co-author's generic equation (1.2) when $\mu_1 = 2 - \mu_3, \mu_3 < 2$, and $\mu_2 = 1$. Von Bertalanffy [3] 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:

$$\frac{dx}{dt} = rx^{\frac{2}{3}}\left[1 - \left(\frac{x}{K}\right)^{\frac{1}{3}}\right]. \tag{1.4}$$

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. [32]. It cannot therefore be seen as a special case of Blumberg's equation (1.3). Richards [27] 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

$$\frac{dx}{dt} = rx\left[1 - \left(\frac{x}{K}\right)^{\mu_2}\right]. \tag{1.5}$$

Unlike its Von Bertalanffy antecedent however, the Richards growth function does follow from the Turner model (1.2) in the case where $\mu_3 = 1$. For $\mu_2 = 1$, (1.5) trivially reduces to the Verhulst logistic growth equation (1.1), 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 $\mu_2 \to 0$, we obtain the growth rate modeled by the Gompertz function given by:

$$\frac{dx}{dt} = rx\left[\ln\left(\frac{x}{K}\right)\right]^{\mu_3}, \tag{1.6}$$

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 (1.6) is the ordinary Gompertz growth (see [12,24]).

In [31], Tsoularis et al. proposed a new growth rate that includes all the previous growth rates given by:

$$\frac{dx}{dt} = rx^{\mu_1}\left[1 - \left(\frac{x}{K}\right)^{\mu_2}\right]^{\mu_3}, \tag{1.7}$$

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 $x = 0$, (1.7) cannot be derived from such an expansion unless μ_1, μ_2 and μ_3 are all positive integers.

In 1977, Freedman and Waltman [9] consider a two-patch model with a single species in logistic population growth as follows:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1 x_1\left(1 - \dfrac{x_1}{K_1}\right) + m(x_2 - x_1), \\ \dfrac{dx_2}{dt} = r_2 x_2\left(1 - \dfrac{x_2}{K_2}\right) + m(x_1 - x_2), \end{cases} \tag{1.8}$$

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 m 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 [15] generalized these results to a source-sink system. In 2015, Arditi et al. [1] gave a full mathematical analysis of the model (1.8) of Freedman and Waltman with symmetric dispersal.

In 2018, Arditi et al. [2] extended the model (1.8) by considering asymmetric dispersal, i.e. the model:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right) + m(m_{12}x_2 - m_{21}x_1), \\ \dfrac{dx_2}{dt} = r_2x_2\left(1-\dfrac{x_2}{K_2}\right) + m(m_{21}x_1 - m_{12}x_2), \end{cases} \tag{1.9}$$

where mm_{12} and mm_{21} with $m_{ij} > 0, i \neq j$ and $m \geq 0$, 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 (1.9) is the unique positive solution to

$$\begin{cases} r_1x_1\left(1-\dfrac{x_1}{K_1}\right) + r_2x_2\left(1-\dfrac{x_2}{K_2}\right) = 0, \\ x_2 = \frac{1}{m_{12}}\left(m_{21}x_1 - \frac{r_1}{m}x_1\left(1-\dfrac{x_1}{K_1}\right)\right), \end{cases}$$

i.e., the intersection of an ellipse and a parabola, they used a graphical method to completely analyze model (1.9) in order to determine when dispersal is either favorable or unfavorable to total population abundance (see Appendix B).

Wu et al. [35] studied the following two-patch source-sink model:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right) + m(x_2 - sx_1), \\ \dfrac{dx_2}{dt} = r_2x_2\left(-1-\dfrac{x_2}{K_2}\right) + m(sx_1 - x_2), \end{cases} \tag{1.10}$$

where the parameter s reflects the dispersal asymmetry. The authors show that the dispersal asymmetry can lead to either an increased total size of the species population in two patches, a decreased total size with persistence in the patches, or even extinction in both patches. They show also that for a large growth rate of the species in the source and a fixed dispersal intensity:

- If the asymmetry is small, the population would persist in both patches and reach a density higher than that without dispersal, in which the population approaches its maximal density at an appropriate asymmetry.
- If the asymmetry is intermediate, the population persists in both patches but reaches a density less than that without dispersal.
- If the asymmetry is large, the population goes to extinction in both patches, and asymmetric dispersal is more favorable than symmetric dispersal under certain conditions.

Kang et al. [16] have considered a two-patch model with Allee effect and dispersal:

$$\begin{cases} \frac{dx_1}{dt} = r_1x_1\left(x_1-\theta\right)\left(1-x_1\right) + m(x_2 - x_1), \\ \frac{dx_2}{dt} = r_2x_2\left(x_2-\theta\right)\left(1-x_2\right) + m(x_1 - x_2), \end{cases} \tag{1.11}$$

where x_1 and x_2 denote the population density in two patches. The parameters $m \in [0,1]$ and θ represent the dispersal intensity and Allee threshold, respectively. It was shown that the dispersal parameter m and the Allee threshold θ will affect the global dynamics. Another important two-patch model with additive Allee effect is proposed and studied in [5], given by:

$$\begin{cases} \dfrac{dx_1}{dt} = -x_1 + m(m_{12}x_2 - m_{21}x_1), \\ \dfrac{dx_2}{dt} = x_2\left(1 - x_2 - \dfrac{\sigma}{x_2 + a}\right) + m(m_{21}x_1 - m_{12}x_2), \end{cases} \tag{1.12}$$

where the positive parameters σ and a are the Allee effect constants. Note that, the additive Allee effect consists of two cases, i.e., weak and strong Allee effects. That is, if $0 < \sigma < a$, it is the weak Allee effect; if $\sigma > a$, it is the strong Allee effect. The authors show that dispersal and Allee effect may lead to persistence or extinction in both patches. Also, by mathematical analysis with numerical simulation, they verified that the total population abundance will increase when the Allee effect constant a increases or σ decreases. And the total population density increases when the dispersal rate m_{12} increases or the dispersal rate m_{21} decreases. The reader may refer to [16, 22, 23, 25, 28] for more references and details on the effects of dispersal on the total population in discrete space additive Allee effect. For more details and information on the maximization of the total population with logistic growth in a multi-patchy environment, the reader is referred to [7, 8, 11] and the references therein.

This paper is organized as follows: in Section 2, we introduce Richard's model in two patches. Next, in Section 3, we study the behavior of the system (2.1) in the case when the migration rate goes to infinity using perturbation arguments. In Section 4, we compare the total equilibrium population with the sum of the two carrying capacities for all parameter space by using the same method as Arditi et al. [2]. In Section 5, two-patch model (2.1) where one growth rate is much larger than the second one is considered, we compare the total equilibrium population with the sum of two capacities in this case. In Appendix A, we analyze the existence of equilibrium point by geometrical method and we prove also the global stability of the system (2.1) and in Appendix B, we recall some result on two-patch logistic model.

2 Two-patch Richards model

Taking the case of two patches, coupled by asymmetric migration terms, and assuming that each patch follows the same Richards law (1.5), the two-patch Richards model can be written in the following form:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left[1 - \left(\dfrac{x_1}{K_1}\right)^{\mu}\right] + m(m_{12}x_2 - m_{21}x_1), \\ \dfrac{dx_2}{dt} = r_2x_2\left[1 - \left(\dfrac{x_2}{K_2}\right)^{\mu}\right] + m(m_{21}x_1 - m_{12}x_2), \end{cases} \tag{2.1}$$

where x_i is the population in the patch i, the parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity in the patch i, and μ is a positive number. The parameters mm_{12} and mm_{21} with $m_{12} > 0$ and $m_{21} > 0$, represent 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. For $\mu = 1$, the system (2.1) trivially reduces to Two-patch logistic model (1.9). Note that the system (1.9) is studied in [1, 6, 9, 10, 15] in the case where the migration rates satisfy $m_{12} = m_{21}$, and in [2, 26] for general migration rates. Model (2.1) has always a unique positive equilibrium, again denoted by $\mathcal{E}^*(m) := (x_1^*(m), x_2^*(m))$ which satisfies

$$\begin{cases} 0 = r_1 x_1^*(m)\left[1-\left(\frac{x_1^*(m)}{K_1}\right)^{\mu}\right] + m(m_{12}x_2^*(m) - m_{21}x_1^*(m)), \\ 0 = r_2 x_2^*(m)\left[1-\left(\frac{x_2^*(m)}{K_2}\right)^{\mu}\right] + m(m_{21}x_1^*(m) - m_{12}x_2^*(m)). \end{cases}$$

The equilibrium $\mathcal{E}^*$ is GAS in $\mathbb{R}^2 \setminus \{0\}$ (see Appendix A). We thus define the total equilibrium population at the positive equilibrium under dispersal rate , i.e.

$$X_T^*(m) = x_1^*(m) + x_2^*(m), \tag{2.2}$$

as the total realized asymptotic population abundance.

The main aim of this paper is to study the effect of population dispersal on total population size and to perform the mathematical analysis of the two-patch Richards model (2.1) in the full parameter space. Thus, we extend [1,2] by considering the case $\mu \neq 1$.

3 The behavior of the model for a large migration rate

In this section, we aim to study the behavior of the system (2.1) for a large migration rate, i.e. when $m \to \infty$. We have the following result:

Theorem 3.1. Let $\mathcal{E}^*(m)$ be the positive equilibrium of the system (2.1). We then have :

$$\lim_{m\to\infty} \mathcal{E}^*(m) = \left(\frac{m_{12}r_1 + m_{21}r_2}{m_{12}^{\mu+1}\frac{r_1}{K_1^{\mu}} + m_{21}^{\mu+1}\frac{r_2}{K_2^{\mu}}}\right)^{\frac{1}{\mu}} (m_{12}, m_{21})\,. \tag{3.1}$$

Proof. Denote $\mathcal{E}^*(\infty)$ the limit (3.1). The equilibrium point $\mathcal{E}^*(m)$ of the system (2.1) is the solution of the equation $F_m = 0$, where:

$$F_m(x_1,x_2) = \left(r_1x_1\left[1-\left(\tfrac{x_1}{K_1}\right)^{\mu}\right] + r_2x_2\left[1-\left(\tfrac{x_2}{K_2}\right)^{\mu}\right], r_2x_2\left[1-\left(\tfrac{x_2}{K_2}\right)^{\mu}\right] + m(m_{21}x_1 - m_{12}x_2) \right). \tag{3.2}$$

When $m \to \infty$, Equation (3.2) becomes:

$$F_\infty(x_1,x_2) = \left(r_1x_1\left[1-\left(\tfrac{x_1}{K_1}\right)^{\mu}\right] + r_2x_2\left[1-\left(\tfrac{x_2}{K_2}\right)^{\mu}\right], m_{21}x_1 - m_{12}x_2 \right). \tag{3.3}$$

The solutions of the equation $F_\infty = 0$ are given by 0 and $\mathcal{E}^*(\infty)$. Therefore, to prove the convergence of $\mathcal{E}^*(m)$ to $\mathcal{E}^*(\infty)$, it suffices to prove that the origin cannot be a limit point of $\mathcal{E}^*(m)$. We claim that for any m, there exists $i \in \{1,2\}$ such that $x_i^*(m) \geq K_i$, which entails that $E^*(m)$ is bounded away from the origin. If $m_{12}x_2^*(m) \leq m_{21}x_1^*(m)$ then we have

$$r_2x_2^*(m)\left[1-\left(\frac{x_2^*(m)}{K_2}\right)^{\mu}\right] \leq 0,$$

and since x_2^* cannot be negative or 0, we have $x_2^*(m) \geq K_2$. Therefore, $\mathcal{E}^*(m) \to \mathcal{E}^*(+\infty)$ as $m \to \infty$. □

As a first corollary of the previous theorem we obtain the following result which describes the total equilibrium population when $m \to \infty$:

Corollary 3.2. Consider the total equilibrium population (2.2). We have:

$$X_T^*(+\infty) = (m_{12}+m_{21})\left(\frac{m_{12}r_1+m_{21}r_2}{m_{12}^{\mu+1}\frac{r_1}{K_1^\mu}+m_{21}^{\mu+1}\frac{r_2}{K_2^\mu}}\right)^{\frac{1}{\mu}}. \tag{3.4}$$

Notice that, the formula (3.4) shows that the total equilibrium population depends on the migration terms m_{12}, m_{21} and the parameter μ . For $\mu = 1$, this formula was obtained for the 2-patch logistic model (1.9) by Freedman and Waltman [10, Theorem 1]. It was also obtained by Arditi et al. [1, Formula (A.13)]. If the migration is symmetric (i.e. $m_{12} = m_{21}$), then the total equilibrium population (3.4) does not depend on the flux of migration m_{12} and m_{21} and (3.4) becomes:

$$X_T^*(+\infty) = 2\left(\frac{r_1+r_2}{\frac{r_1}{K_1^\mu}+\frac{r_2}{K_2^\mu}}\right)^{\frac{1}{\mu}}.$$

In [1], Arditi et al. also obtained the formula (3.4), in the 2-patch case with logistic model and symmetric migration, (i.e. the system (1.9) with $m_{12} = m_{21} = 1$) by using singular perturbation theory, see [1, Formula (A.13)]. They showed that, if $(x_1(t,m), x_2(t,m))$ is the solution of (1.9), with initial condition (x_1^0, x_2^0), then, when $m \to \infty$, the total population $x_1(t,m) + x_2(t,m)$ is approximated by $X(t)$, the solution of the logistic equation:

$$\begin{cases} \dfrac{dX}{dt} = rX\left(1-\dfrac{X}{2K}\right), \\ X(0) = x_1^0 + x_2^0, \end{cases} \tag{3.5}$$

where $r = \frac{r_1+r_2}{2}, K = \frac{r_1+r_2}{\alpha_1+\alpha_2}$ and $\alpha_i = \frac{r_i}{K_i}$. Therefore the total population behaves like the unique logistic equation given by (3.5). In addition, one obtains the following property: with the exception of a small initial interval, the populations density $x_1(t,m)$ and $x_2(t,m)$ are both approximated by $X(t)/2$, see [1, Proposition 3]. Therefore, this approximation shows that, when t and m tend to ∞, the density population $x_i(t,m)$ tends toward $\frac{r_1+r_2}{\alpha_1+\alpha 2}$, and in addition, $x_i(t,m)$ quickly jumps from its initial condition x_i^0 to the average $X_0/2$ and then is very close to $X(t)/2$. Our aim is to generalize this result for the 2-patch model (2.1) for all μ positive. To avoid any confusion with $X(t)$, which is the total population, we denote $Z(t)$ the solution of the equation (3.6), and we prove that $X(t)$ is asymptotically equivalent, when m goes to infinity, to $Z(t)$. We have the following result

Theorem 3.3. Let $(x_1(t,m), x_2(t,m))$ be the solution of the system (2.1) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $Z(t)$ be the solution of the Richards equation

$$\begin{cases} \dfrac{dX}{dt} = rX\left[1-\left(\dfrac{X}{(m_{12}+m_{21})K}\right)^{\mu}\right], \\ X(0) = x_1^0 + x_2^0, \end{cases} \tag{3.6}$$

where $r = \frac{m_{12}r_1+m_{21}r_2}{m_{12}+m_{21}}$ and $K = \left[\frac{m_{12}r_1+m_{21}r_2}{m_{12}^{\mu+1}\frac{r_1}{K_1^\mu}+m_{21}^{\mu+1}\frac{r_2}{K_2^\mu}}\right]^{\frac{1}{\mu}}$. Then, when $m \to \infty$, we have

$$x_1(t,m) + x_2(t,m) = Z(t) + o_m(1), \quad \text{uniformly for } t \in [0, +\infty) \tag{3.7}$$

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

$$\begin{cases} x_1(t,m) = \dfrac{m_{12}}{m_{12}+m_{21}} Z(t) + o_m(1), \\ x_2(t,m) = \dfrac{m_{21}}{m_{12}+m_{21}} Z(t) + o_m(1) \quad \text{uniformly for } t \in [t_0, +\infty). \end{cases} \tag{3.8}$$

Proof. Let $X(t,m) = x_1(t,m) + x_2(t,m)$. We rewrite the system (2.1) using the variables (X, x_1). One obtains:

$$\begin{cases} \dfrac{dX}{dt} = r_1 x_1 \left[1 - \left(\dfrac{x_1}{K_1}\right)^{\mu}\right] + r_2 (X - x_1) \left[1 - \left(\dfrac{X - x_1}{K_2}\right)^{\mu}\right], \\ \dfrac{dx_1}{dt} = r_1 x_1 \left[1 - \left(\dfrac{x_1}{K_1}\right)^{\mu}\right] + m\left(m_{12} X - (m_{12}+m_{21}) x_1\right). \end{cases} \tag{3.9}$$

When $m \to \infty$, (3.9) is a *slow-fast* system, with one *slow variable*, X, and one *fast variable* x_1. According to Tikhonov's Theorem [17, 30, 34] we consider the dynamics of the fast variable in the time scale $\tau = mt$. One obtains

$$\frac{dx_1}{d\tau} = \frac{1}{m} r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^{\mu}\right] + m_{12} X - (m_{12}+m_{21}) x_1.$$

In the limit $m \to \infty$, we find the *fast dynamics*

$$\frac{dx_1}{d\tau} = m_{12} X - (m_{12}+m_{21}) x_1. \tag{3.10}$$

The *slow manifold* is formed by the equilibrium points of the fast equation (3.10), which given by:

$$x_1^* = \frac{m_{12}}{m_{12}+m_{21}} X. \tag{3.11}$$

Since x_1^* is GAS for the system (3.10), the Theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (3.9) are approximated by the solutions of the *reduced model* which is obtained by replacing (3.11) into the dynamics of the slow variable, that is:

$$\frac{dX}{dt} = r_1 \frac{m_{12}}{m_{12}+m_{21}} X \left[1 - \left(\frac{m_{12} X}{(m_{12}+m_{21}) K_1}\right)^{\mu}\right] + r_2 \frac{m_{21}}{m_{12}+m_{21}} X \left[1 - \left(\frac{m_{21} X}{(m_{12}+m_{21}) K_2}\right)^{\mu}\right], \tag{3.12}$$

which gives the equation (3.6). Since (3.6) admits

$$X^* = (m_{12}+m_{21}) K = (m_{12}+m_{21}) \left[\frac{m_{12} r_1 + m_{21} r_2}{m_{12}^{\mu+1} \frac{r_1}{K_1^{\mu}} + m_{21}^{\mu+1} \frac{r_2}{K_2^{\mu}}}\right]^{\frac{1}{\mu}}$$

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 variable, where t_0 is small as we want. Therefore, let $Z(t)$ be the solution of the reduced model (3.12) of initial condition $Z(0) = X(0,m) = x_1^0 + x_2^0$, then, when $m \to \infty$, we have the approximations (3.7) and (3.8). □

In the case where the migration rate tends to infinity, the approximation (3.7) shows that the total population behaves like a unique equation of Richards (3.6) and then, when t and m tend to ∞, the total population $x_1(t,m) + x_2(t,m)$ tends towards $X_T^*(\infty)$ defined by (3.4) as stated in Corollary 3.2. The approximation (3.8) shows that, with the exception of a thin initial boundary layer, where the density population $x_1(t,m)$ and $x_2(t,m)$ quickly jumps from its initial condition x_1^0 and x_2^0 to $m_{12}X_0/(m_{12}+m_{12})$ and $m_{21}X_0/(m_{12}+m_{12})$ respectively. The first (resp. second) patch behaves like the single Richards equation

$$\frac{dz}{dt} = rz\left[1-\left(\frac{z}{m_{12}K}\right)^{\mu}\right] \quad \left(\text{resp.} \quad \frac{dz}{dt} = rz\left[1-\left(\frac{z}{m_{21}K}\right)^{\mu}\right]\right), \tag{3.13}$$

where r and K are defined in (3.6). Hence, when t and m tend to ∞, the density population $x_1(t,m)$ and $x_2(t,m)$ tends toward $m_{12}K$ and $m_{21}K$ respectively, as stated in Theorem 3.1.

4 Influence of dispersal on the total population size

In [2], Arditi et al. have considered the system (1.9) and they showed that there are only three cases that 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 dispersal is beneficial for lower values of the migration rate m and detrimental for the higher values. More precisely, it was shown in [2], that the following trichotomy holds

- If $X_T^*(+\infty) > K_1 + K_2$ then $X_T^*(m) > K_1 + K_2$ for all $m > 0$.
- If $\frac{d}{dm}X_T^*(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$, then there exists $m_0 > 0$ such that $X_T^*(m) > K_1 + K_2$ for $0 < m < m_0$, $X_T^*(m) < K_1 + K_2$ for $m > m_0$ and $X_T^*(m_0) = K_1 + K_2$.
- If $\frac{d}{dm}X_T^*(0) < 0$, then $X_T^*(m) < K_1 + K_2$ for all $m > 0$.

Therefore, the condition $X_T^*(m) = K_1 + K_2$ holds only for $m = 0$ and at most for one positive value $m = m_0$. The value m_0 exists if and only if $\frac{d}{dm}X_T^*(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$.

In this section, we generalize the result of Arditi et al. [2] by considering the case where $\mu \neq 1$ in the system (2.1). We analyze the effect of dispersal on the total equilibrium population for the Richards system (2.1). Using the method of Arditi et al. [2], we describe the position affects the equilibrium $\mathcal{E}^*(m)$ of (2.1) when the migration rate varies from zero to infinity. The total equilibrium population $X_T^*(+\infty)$, given by equation (3.4), play a vary important role in the characterization of the different possible positions of the equilibrium $\mathcal{E}^*$. As for the 2-patch logistic model (1.9), we prove that exactly three cases can occur. More precisely we have the following theorem:

Theorem 4.1. Consider the system (2.1). Let $X_T^*(\infty)$ be defined by (3.4). Then,

1. If $r_1 = r_2$, then $X_T^*(m) \leq K_1 + K_2$ for all $m \geq 0$.
2. If $r_1 < r_2$, then
    (a) If $\frac{m_{21}}{m_{12}} < \frac{K_1}{K_2}$, then
        i. If $X_T^*(\infty) \geq K_1 + K_2$, then $X_T^*(m) \geq K_1 + K_2$ for all $m \geq 0$.
        ii. If $X_T^*(\infty) < K_1 + K_2$, there is an $m_0 > 0$ such that:
            A. If $m < m_0$, then $X_T^*(m) \geq K_1 + K_2$.

            B. If $m \geq m_0$, then $X_T^*(m) \leq K_1 + K_2$.
    - (b) If $\frac{m_{21}}{m_{12}} > \frac{K_1}{K_2}$, then $X_T^*(m) \leq K_1 + K_2$ for all $m \geq 0$.
    - (c) If $\frac{m_{21}}{m_{12}} = \frac{K_1}{K_2}$, then $X_T^*(m) = K_1 + K_2$ for all $m \geq 0$, i.e. the equilibrium $\mathcal{E}^*$ does not depend on m.

3. If $r_1 > r_2$, then
    - (a) If $\frac{m_{21}}{m_{12}} > \frac{K_1}{K_2}$, then
        - i. If $X_T^*(\infty) \geq K_1 + K_2$, then $X_T^*(m) \geq K_1 + K_2$.
        - ii. If $X_T^*(\infty) < K_1 + K_2$, there is a $m_0 > 0$ such that:
            - A. If $m < m_0$, then $X_T^*(m) \geq K_1 + K_2$.
            - B. If $m \geq m_0$, then $X_T^*(m) \leq K_1 + K_2$.
    - (b) If $\frac{m_{21}}{m_{12}} < \frac{K_1}{K_2}$, then $X_T^*(m) \leq K_1 + K_2$ for all $m \geq 0$.
    - (c) If $\frac{m_{21}}{m_{12}} = \frac{K_1}{K_2}$, then $X_T^*(m) = K_1 + K_2$ for all $m \geq 0$, i.e. the equilibrium $\mathcal{E}^*$ does not depend on m.

Proof. First, we consider the line Δ with Cartesian equation $x_1 + x_2 = K_1 + K_2$, of slope -1 and passing through the point $A = (K_1, K_2)$. The equilibrium point $\mathcal{E}^*$ is always on the curve $\mathcal{C}_\mu$ (see Appendix A). For $m = 0$, $\mathcal{E}^*$ coincides with A. When m increases, $\mathcal{E}^*$ describes an arc of the curve $\mathcal{C}_\mu$ and ends at point $\mathcal{E}^*(\infty)$ given in equation (3.1).

1. The equation of the tangent line to the curve $\mathcal{C}_\mu$ at the point $\mathcal{A}$ is given by:

$$(x_1 - K_1)\frac{\partial \Phi_\mu}{\partial x_1}(\mathcal{A}) + (x_2 - K_2)\frac{\partial \Phi_\mu}{\partial x_2}(\mathcal{A}) = 0, \tag{4.1}$$

   where the function Φ_μ is given by the equation (A.2). Since $\frac{\partial \Phi_\mu}{\partial x_1}(\mathcal{A}) = -\mu r_1$ and $\frac{\partial \Phi_\mu}{\partial x_2}(\mathcal{A}) = -\mu r_2$, Equation (4.1) becomes simply

$$r_1 x_1 + r_2 x_2 = r_1 K_1 + r_2 K_2. \tag{4.2}$$

   If $r_1 = r_2$ in the equation (4.2), the tangent space to the the curve $\mathcal{C}_\mu$ at $\mathcal{A}$ is the line Δ. By the concavity of $\mathcal{C}_\mu$, any point of $\mathcal{C}_\mu$ lies below the line Δ. Therefore $\mathcal{E}^*(m)$ satisfies $x_1^*(m) + x_2^*(m) \leq K_1 + K_2$, for all $m \geq 0$ (see figure 4.1), which completes the proof of item 1.

2. We suppose now that $r_1 < r_2$, then the line Δ makes a second intersection with the curve $\mathcal{C}_\mu$ at a point noted C. This intersection is below the line $\Sigma : x_2 = \dfrac{K_2}{K_1}x_1$ (as shown in the figures 4.2, 4.3 and 4.4). When $m \to \infty$, the curve $M_{m,\mu}$ defined by (A.3), goes to the oblique line $M_{\infty,\mu} : x_2 = \frac{m_{21}}{m_{12}}x_1$. The intersection points between the line $M_{\infty,\mu}$ and the curve $\mathcal{C}_\mu$ are the origin and $\mathcal{E}^*(\infty)$. If the line $M_{\infty,\mu}$ is below the line Σ, that is $m_{21}/m_{12} < K_1/K_2$, we have two possible cases for the relative positions of the point $\mathcal{E}^*(\infty)$ and the line Δ. In the case where $\mathcal{E}^*(\infty)$ is above the line Δ, that is $X_T^*(\infty) \geq K_1 + K_2$, then the equilibrium point start at point A and when m increases from 0 to ∞, $\mathcal{E}^*(m)$ moves along the curve $\mathcal{C}_\mu$ and ends at the point $\mathcal{E}^*(\infty)$. Equivalently, the total equilibrium population start, for $m = 0$, with the value $K_1 + K_2$ and satisfies

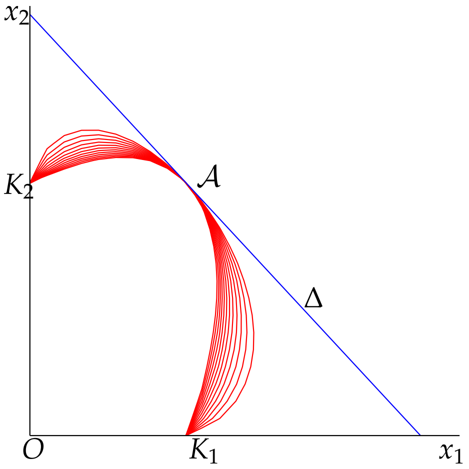

Figure 4.1: The illustration of item 1 of Theorem 4.1. The curve $\mathcal{C}_\mu$ is shown in red for some values of μ and the straight line Δ in blue. The total equilibrium population is always smaller than $K_1 + K_2$ for all m because it belongs to the curve $\mathcal{C}_\mu$.

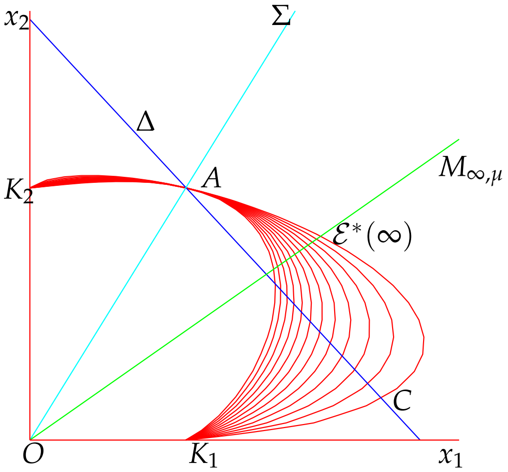

Figure 4.2: The illustration of item (2.a.i) of Theorem 4.1. The curve $\mathcal{C}_\mu$ is shown in red for some values of μ, the straight lines Δ, Σ and $M_{\infty,\mu}$ are shown in blue, cyan and green respectively. The total equilibrium point is always greater than $K_1 + K_2$ for all m, because it belongs to the curve $\mathcal{C}_\mu$ and the limit point $\mathcal{E}^*(\infty)$ is above Δ. As the migration rate increases from 0 to ∞, the equilibrium point varies along the curve $\mathcal{C}_\mu$ from A to $\mathcal{E}^*(\infty)$.

the inequality $x_1^*(m) + x_2^*(m) \geq K_1 + K_2$ for all m, which completes the proof of item (2.a.i). (see figure 4.2).

In the case where $\mathcal{E}^*(\infty)$ is below the line Δ, that is $X_T^*(\infty) < K_1 + K_2$, the equilibrium point $\mathcal{E}^*(m)$ start, for $m = 0$, at point A and when m increases from 0 to ∞, it moves along the curve $\mathcal{C}_\mu$, passes through the point $\mathcal{C}$ for a certain m_0 and ends at the point $\mathcal{E}^*(\infty)$. Therefore, the total equilibrium is greater than $K_1 + K_2$ for $m < m_0$ and smaller than $K_1 + K_2$ for all $m \geq m_0$, which completes the proof of item (2.a.ii) (see figure 4.3).

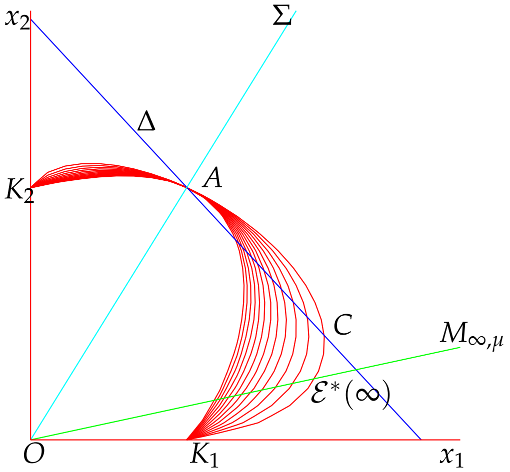

Figure 4.3: The illustration of item (2.a-ii) of Theorem 4.1. The curve $\mathcal{C}_\mu$ is shown in red for some values of μ, the straight lines Δ, Σ and $M_{\infty,\mu}$ are shown in blue, cyan and green respectively. As the limit point $\mathcal{E}^*(\infty)$ is above Δ, then, when the migration rate increases from 0 to ∞, the equilibrium point varies along the curve $\mathcal{C}_\mu$ from A to $\mathcal{E}^*(\infty)$, passing through the point C which is the other point of intersection between the curve $\mathcal{C}_\mu$ and the line Δ.

If the line $M_{\infty,\mu}$ is above the line Σ, that is $m_{21}/m_{12} > K_1/K_2$, then the total equilibrium population is smaller than the sum of carrying capacities for all m. This completes the proof of item (2.b). (see figure 4.4).

It is clear that if the two lines Σ and $M_{\infty,\mu}$ are identical, i.e. $\mathcal{A} = \mathcal{E}^*(\infty)$, then the total equilibrium population does not depend on migration rate m. Therefore, $x_1^*(m) = K_1$ and $x_2^*(m) = K_2$ for all $m \geq 0$. This gives the proof of item (2.c).

3. As the role of the variables of the system (2.1) is symmetrical, this case is analogous to case 2.

□

According to the previous theorem, we concluded that, the dispersal can lead to an increased or decreased the total equilibrium population with persistence in each patch.

Proposition 4.2. The derivative of the total equilibrium population X_T^* at $m = 0$ is given by:

$$\frac{dX_T^*}{dm}(0) = \frac{1}{\mu}\left(m_{12}K_2 - m_{21}K_1\right)\left(\frac{1}{r_1} - \frac{1}{r_2}\right). \tag{4.3}$$

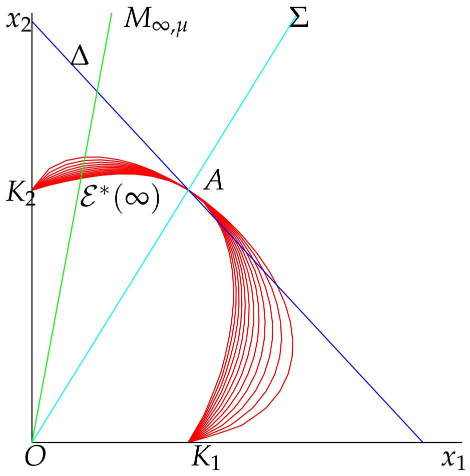

Figure 4.4: The illustration of item (b) of Theorem 4.1. The curve $\mathcal{C}_\mu$ is shown in red for some values of μ, the straight lines Δ, Σ and $M_{\infty,\mu}$ are shown in blue, cyan and green respectively. The total equilibrium is always smaller than $K_1 + K_2$ for all m.

In particular, $\frac{dX_T^*}{dm}(0) = 0$ if and only if, $r_1 = r_2$ or $\frac{K_1}{K_2} = \frac{m_{12}}{m_{21}}$.

Proof. The equilibrium point $\mathcal{E}^*(m)$ satisfies the system

$$\begin{cases} 0 = r_1 x_1^*(m)\left[1 - \left(\frac{x_1^*(m)}{K_1}\right)^\mu\right] + m(m_{12}x_2^*(m) - m_{21}x_1^*(m)), \\ 0 = r_2 x_2^*(m)\left[1 - \left(\frac{x_2^*(m)}{K_2}\right)^\mu\right] + m(m_{21}x_1^*(m) - m_{12}x_2^*(m)). \end{cases} \tag{4.4}$$

Dividing the first and the second equation by $\frac{r_1}{K_1^\mu}x_1^*(m)$ and $\frac{r_2}{K_2^\mu}x_2^*(m)$ respectively, one obtains

$$\begin{cases} x_1^*(m) = \left(K_1^\mu + m\dfrac{m_{12}x_2^*(m) - m_{21}x_1^*(m)}{\frac{r_1}{K_1^\mu}x_1^*(m)}\right)^{\frac{1}{\mu}}, \\ x_2^*(m) = \left(K_2^\mu + m\dfrac{m_{21}x_1^*(m) - m_{12}x_2^*(m)}{\frac{r_2}{K_2^\mu}x_2^*(m)}\right)^{\frac{1}{\mu}}. \end{cases} \tag{4.5}$$

Hence, the total equilibrium population X_T^* is given by

$$X_T^*(m) = \left(K_1^\mu + m\frac{m_{12}x_2^*(m) - m_{21}x_1^*(m)}{\frac{r_1}{K_1^\mu}x_1^*(m)}\right)^{\frac{1}{\mu}} + \left(K_2^\mu + m\frac{m_{21}x_1^*(m) - m_{12}x_2^*(m)}{\frac{r_2}{K_2^\mu}x_2^*(m)}\right)^{\frac{1}{\mu}}. \tag{4.6}$$

By differentiating the equation (4.6) at $m = 0$, we get:

$$\frac{dX_T^*}{dm}(0) = \frac{1}{\mu}\left(\frac{m_{12}x_2^*(0) - m_{21}x_1^*(0)}{\frac{r_1}{K_1^\mu}x_1^*(0)}\right)K_1^{1-\mu} + \frac{1}{\mu}\left(\frac{m_{21}x_1^*(0) - m_{12}x_2^*(0)}{\frac{r_2}{K_2^\mu}x_2^*(0)}\right)K_2^{1-\mu}, \tag{4.7}$$

which gives (4.3), since $x_1^*(0) = K_1$ and $x_2^*(0) = K_2$. □

Note that, the derivative (4.3) is dependent on all the parameters of the model. it is equal to zero if and only if both patches have the same growth rates or $m_{12}K_2 = m_{21}K_1$, positive if $r_1 < r_2$ and $m_{12}K_2 > m_{21}K_1$, or $r_1 > r_2$ and $m_{12}K_2 < m_{21}K_1$.

As a corollary of the previous theorem, we have the result:

Corollary 4.3. Let $\mu_i, i = 1, \dots, n,$ be a positive number such that $0 < \mu_0 < \dots < \mu_n$. Consider the following systems:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1 x_1 \left[1 - \left(\dfrac{x_1}{K_1}\right)^{\mu_i}\right] + m(m_{12}x_2 - m_{21}x_1), \\ \dfrac{dx_2}{dt} = r_2 x_2 \left[1 - \left(\dfrac{x_2}{K_2}\right)^{\mu_i}\right] + m(m_{21}x_1 - m_{12}x_2), \end{cases} \tag{4.8}$$

where the parameters r_i, K_i, m_{12} and m_{21} are as in (2.1). Let $X_T^*(m, \mu_i), i = 1, \dots, n$ be the total equilibrium population of (4.8). Then, the sequence $(X_T^*(m, \mu_i))_{1 \le i \le n}$ is increasing. In particular, when $m \to \infty$, we have:

$$X_T^*(\infty, \mu_1) < \dots < X_T^*(\infty, \mu_n).$$

Proof. The equilibrium point of the system (4.8) is always on the curve noted $\mathcal{C}_{\mu_i}$ given by

$$\mathcal{C}_{\mu_i}: \quad r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^{\mu_i}\right] + r_2 x_2 \left[1 - \left(\frac{x_2}{K_2}\right)^{\mu_i}\right] = 0.$$

These curves intersect at four points $(0, 0), (0, K_2), (K_1, 0)$ and (K_1, K_2). If $\mu_i < \mu_j$ for some i and j, then the curve $\mathcal{C}_{\mu_i}$ is below the curve $\mathcal{C}_{\mu_j}$ as shown in the figure A.1 and in the others figures 4.1, 4.2, 4.3 and 4.4. Therefore, the total equilibrium population $X_T^*(m, \mu_i) < X_T^*(m, \mu_j)$ for all $m > 0$ and for all $i, j \in \{1, \dots, n\}$. □

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

In this section, we consider the two-patch model (2.1) and we assume that the growth rate in the second patch is much larger than in the first. For simplicity we denote $m_2 := m_{12} > 0$ the migration rate from patch 2 to patch 1 and $m_1 := m_{21} > 0$ from patch 1 to patch 2. Mathematically, the model (2.1) is written under this assumption as follows:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^{\mu}\right] + m\left(m_2 x_2 - m_1 x_1\right), \\ \frac{dx_2}{dt} = \frac{r_2}{\epsilon} x_2 \left[1 - \left(\frac{x_2}{K_2}\right)^{\mu}\right] + m\left(m_1 x_1 - m_2 x_2\right), \end{cases} \tag{5.1}$$

where ϵ is assumed to be a small positive number. We denote $E^*(m, \epsilon) = (x_1^*(m, \epsilon), x_2^*(m, \epsilon))$, the positive equilibrium of (5.1), which is GAS, and $X_T^*(m, \epsilon) := x_1^*(m, \epsilon) + x_2^*(m, \epsilon)$ the total equilibrium. The behavior of the model (5.1) for perfect mixing (i.e. $m \to \infty$) is given by the following formula:

$$X_T^*(+\infty, \epsilon) = (m_1 + m_2) \left(\frac{\epsilon m_2 r_1 + m_1 r_2}{\epsilon m_2^{\mu+1} r_1 / K_1^{\mu} + m_1^{\mu+1} r_2 / K_2^{\mu}} \right)^{\frac{1}{\mu}}, \tag{5.2}$$

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

$$\frac{dX_T^*}{dt}(0,\epsilon)=\frac{1}{\mu}\left(m_{12}K_2-m_{21}K_1\right)\left(\frac{1}{r_1}-\frac{\epsilon}{r_2}\right). \tag{5.3}$$

First, we have the result:

Theorem 5.1. Let $(x_1(t,\epsilon),x_2(t,\epsilon))$ be the solution of the system (5.1) with initial condition (x_1^0,x_2^0) satisfying $x_i^0\geq 0$ for $i=1,2$. Let $z(t)$ be the solution of the differential equation

$$\frac{dx_1}{dt}=r_1x_1\left[1-\left(\frac{x_1}{K_1}\right)^{\mu}\right]+m(m_2K_2-m_1x_1)=:\varphi_\mu(x_1), \tag{5.4}$$

with initial condition $z(0)=x_1^0$. Then, when $\epsilon\to 0$, we have

$$x_1(t,\epsilon)=z(t)+o_\epsilon(1),\qquad \text{uniformly for } t\in[0,+\infty) \tag{5.5}$$

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

$$x_2(t,\epsilon)=K_2+o_\epsilon(1),\quad \text{uniformly for}\quad t\in[t_0,+\infty). \tag{5.6}$$

Proof. When $\epsilon\to 0$, the system (5.1) is a *slow-fast* system, with one *slow variable*, x_1, and one *fast variable*, x_2. Tikhonov's Theorem [17,30,34] prompts us to consider the dynamics of the fast variable in the time scale $\tau=\frac{1}{\epsilon}t$. One obtains

$$\frac{dx_2}{d\tau}=r_2x_2\left[1-\left(\frac{x_2}{K_2}\right)^{\mu}\right]+\epsilon m(m_1x_1-m_2x_2).$$

In the limit $\epsilon\to 0$, we find the *fast dynamics*

$$\frac{dx_2}{d\tau}=r_2x_2\left[1-\left(\frac{x_2}{K_2}\right)^{\mu}\right]. \tag{5.7}$$

The slow manifold is given by the positive equilibrium of the system (5.7), i.e. $x_2=K_2$, which is GAS in the positive axis. When ϵ goes to zero, Tikhonov's Theorem ensures that after a fast transition toward the slow manifold, the solutions of (5.1) converge to the solutions of the *reduced model* (5.4), obtained by replacing $x_2=K_2$ into the dynamics of the slow variable.

The differential equation (5.4) admits unique positive equilibrium, which is GAS. Indeed, we distinguish two cases according to sign of r_1-mm_1. First, note that, if $r_1-mm_1=0$, then $\frac{d\varphi_\mu}{dx_1}(x_1)=-(\mu+1)\frac{r_1}{K_1^\mu}x_1^\mu+r_1-mm_1=0$ if and only if $x_1=0$.

If $r_1-mm_1<0$, then $\frac{d\varphi_\mu}{dx_1}(x_1)=-(\mu+1)\frac{r_1}{K_1^\mu}x_1^\mu+r_1-mm_1<0$, for all $x_1\geq 0$. In addition, $\varphi_\mu(0)>0$ and $\varphi_\mu\to-\infty$ when x_1 goes to infinity. So, there exists a unique positive solution of $\varphi_\mu(x_1)=0$. Denote $x_1^*(m,0^+)$ this solution. As $\varphi_\mu(x_1)>0$ for all $0\leq x_1<x_1^*(m,0^+)$ and $\varphi_\mu(x_1)<0$ for all $x_1>x_1^*(m,0^+)$ then, the equilibrium $x_1^*(m,0^+)$ is GAS in the positive axis.

If $r_1-mm_1>0$, then $\frac{d\varphi_\mu}{dx_1}(x_1)=0$ implies $\tilde{x_1}:=\left(\frac{r_1-mm_1}{(\mu+1)r_1/K_1^\mu}\right)^{\frac{1}{\mu}}>0$. So φ_μ is increasing on $[0,\tilde{x_1}[$ and decreasing on $]\tilde{x_1},\infty[$. In addition, $\varphi_\mu(0)>0$ and $\varphi_\mu\to-\infty$ when x_1 goes to infinity. So, there exists unique positive solution of $\varphi_\mu(x_1)=0$ denoted $x_1^*(m,0^+)$. As $\varphi_\mu(x_1)>0$ for all $0\leq x_1<x_1^*(m,0^+)$ and $\varphi_\mu(x_1)<0$ for all $x_1>x_1^*(m,0^+)$ then, the equilibrium $x_1^*(m,0^+)$ is GAS in the positive axis. Therefore, 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, if $z(t)$ is the solution of the reduced model (5.4) of initial condition $z(0)=x_1^0$, then, when $\epsilon\to 0$, we have the approximations (5.5) and (5.6). □

As a corollary of the previous theorem, we have the following result which gives the limit of the total equilibrium population $X_T^*(m,\epsilon)$ of the model (5.1) when ϵ goes to zero:

Corollary 5.2. We have:

$$X_T^*(m,0^+) := \lim_{\epsilon\to 0} X_T^*(m,\epsilon) = \lim_{\epsilon\to 0}(x_1^*(m,\epsilon)+x_2^*(m,\epsilon)) = x_1^*(m,0^+)+K_2, \tag{5.8}$$

where $x_1^*(m,0^+)$ is the equilibrium of the reduced model (5.4).

Proposition 5.3. Consider the total equilibrium population (5.8). Then,

$$\frac{dX_T^*}{dm}(0,0^+) := \frac{1}{\mu}\frac{-m_1K_1+m_2K_2}{r_1}, \tag{5.9}$$

and

$$X_T^*(+\infty,0^+) := \frac{m_1+m_2}{m_1}K_2. \tag{5.10}$$

Proof. The equilibrium $x_1^*(m,0^+)$ satisfies:

$$r_1x_1^*(m,0^+)\left[1-\left(\frac{x_1^*(m,0^+)}{K_1}\right)^{\mu}\right]+m(m_2K_2-m_1x_1^*(m,0^+))=0. \tag{5.11}$$

Dividing (5.11) by $\frac{r_1}{K_1^{\mu}}x_1^*(m,0^+)$, we obtain:

$$x_1^*(m,0^+) = \left[K_1{}^{\mu}+m\frac{m_2K_2-m_1x_1^*(m,0^+)}{\frac{r_1}{K_1^{\mu}}x_1^*(m,0^+)}\right]^{\frac{1}{\mu}}. \tag{5.12}$$

The derivative of (5.12) with respect to m, gives

$$\begin{aligned}\frac{dx_1^*}{dm}(m,0^+) = \frac{1}{\mu}&\left[m\frac{d}{dm}\left(\frac{m_2K_2-m_1x_1^*(m,0^+)}{\frac{r_1}{K_1^{\mu}}x_1^*(m,0^+)}\right)\right.\\ &\left.+\frac{m_2K_2-m_1x_1^*(m,0^+)}{\frac{r_1}{K_1^{\mu}}x_1^*(m,0^+)}\right]\left[K_1{}^{\mu}+m\frac{m_2K_2-m_1x_1^*(m,0^+)}{\frac{r_1}{K_1^{\mu}}x_1^*(m,0^+)}\right]^{\frac{1}{\mu}-1}.\end{aligned} \tag{5.13}$$

For $m=0$, we have $x_1^*(0,0^+)=K_1$, therefore, the equation (5.13) gives the derivative (5.9).

For the formula of perfect mixing, dividing (5.11) by m, and taking the limit when $m\to\infty$, we get:

$$m_2K_2-m_1x_1^*(+\infty,0^+)=0,$$

Hence, as $x_2^*(+\infty,0^+)=K_2$, the sum of $x_1^*(+\infty,0^+)$ and $x_2^*(+\infty,0^+)$ gives the formula (5.10). □

Remark 5.4. We can deduce the formula of perfect mixing $X_T^*(+\infty,0^+)$ and the derivative of the total equilibrium population $\frac{dX_T^*}{dm}(0,0^+)$ by computing the limit of the equations (5.2) and (5.3) when ϵ goes to zero respectively.

We consider the regions in the set of the parameters m_1 and m_2, denoted $\mathcal{J}_0$ and $\mathcal{J}_1$ defined by:

$$\mathcal{J}_0 = \left\{(m_1, m_2) : \frac{m_2}{m_1} > \frac{K_1}{K_2}\right\}, \quad \mathcal{J}_1 = \left\{(m_1, m_2) : \frac{m_2}{m_1} < \frac{K_1}{K_2}\right\}. \tag{5.14}$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (5.1) when ϵ goes to zero.

Theorem 5.5. Let $\mathcal{J}_0$ and $\mathcal{J}_1$ be the domains defined in (5.14). Consider the total equilibrium population $X_T^*(m, 0^+)$ given by (5.8). Then, we have:

- If $(m_1, m_2) \in \mathcal{J}_0$ then $X_T^*(m, 0^+) > K_1 + K_2$, for all $m > 0$.
- If $(m_1, m_2) \in \mathcal{J}_1$ then $X_T^*(m, 0^+) < K_1 + K_2$, for all $m > 0$.
- If $\frac{m_2}{m_1} = \frac{K_1}{K_2}$, then $x_1^*(m, 0^+) = K_1$ and $x_2^*(m, 0^+) = K_2$ for all $m \geq 0$. Therefore $X_T^*(m, 0^+) = K_1 + K_2$ for all $m \geq 0$.

Proof. First, we try to solve the equation $X_T^*(m, 0^+) = K_1 + K_2$ with respect to m, to obtain the intersection points between the curve of the total equilibrium population $m \mapsto X_T^*(m, 0^+)$ and the straight line $m \mapsto K_1 + K_2$. For any $m > 0$, we have

$$\begin{aligned} x_1^*(m, 0^+) = K_1 \iff & \left[{K_1}^{\mu} + m \frac{m_2 K_2 - m_1 x_1^*(m, 0^+)}{\frac{r_1}{K_1^{\mu}} x_1^*(m, 0^+)} \right]^{\frac{1}{\mu}} = K_1 \\ \iff & m_2 K_2 = m_1 x_1^*(m, 0^+) \\ \iff & m_2 K_2 = K_1 m_1 \iff \frac{dX_T^*}{dm}(0, 0^+) = 0. \end{aligned}$$

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

Biologically speaking, according to the result of the previous theorem, the existence of a faster growing sub-population compared to the second one causes the critical value of migration rate m_0 (see Theorem 4.1) to disappear.

6 Conclusion

The goal of this paper was to generalize to some general growth rates the results obtained in [2] for a two-patch logistic model. In particular, we considered the model of two patches with Richards growth rate.

In Section 3, we looked at the case when migration rate goes to infinity. We computed the equilibrium in this situation (Theorem 3.1) and we proved that the dynamics of the system (3.6) provide a good approximation of the model (2.1) by using singular perturbation arguments (Theorem 3.3). In Section 4, we have given a complete classification of the conditions under which dispersal is either beneficial or detrimental to total equilibrium population. The important result is, even with more general dynamics, the effect of migration is the same as with logistic dynamic: either patchiness always has a beneficial effect on the total equilibrium population, or this effect is always detrimental, or there exists a critical value m_0 of the migration rate m, such that, the effect is beneficial for $m < m_0$, and detrimental for $m < m_0$ (see Theorem 4.1). In Section 5, we considered the two-patch model (2.1), in the case where one growth rate is much larger than the last. First, by perturbation arguments, we have given an approximation of the solutions of the system in this case. Next, we compared the total equilibrium population with the sum of two carrying capacities.

Some question remains open: how do our results generalize to situations with more than two patches? If we consider a more general growth dynamic than the growth of Richards (1.5), this has an effect on the total equilibrium population. I think these questions are difficult to answer, and require a lot of work and mathematical tools.

Appendix

A Equilibria and stability of (2.1)

In this section, our goal is to prove the global stability of the positive equilibrium of the system (2.1). In the absence of migration, i.e. the case where $m = 0$, the system (2.1) admits (K_1, K_2) as a non trivial equilibrium point, which furthermore is globally asymptotically stable (GAS) in the interior of the positive cone $\mathbb{R}^2_+$. The problem is whether the equilibrium continues to be positive and globally stable for any $m > 0$ or not. We first prove the non negativity of the solution of System (2.1). We have the following proposition:

Proposition A.1. The positive cone $\mathbb{R}^2_+$ is positively invariant for the system (2.1).

Proof. Suppose that, at a given time t, one of the state variables of the system (2.1) is at a boundary of $\mathbb{R}^2_+$, meaning that at least one population is at 0. We suppose first that $x_1 = 0$, and $x_2 \geq 0$, then the dynamics of x_1 is given by $\frac{dx_1}{dt} = m_{21}x_2 \geq 0$, and, if $x_2 = 0$, and $x_1 \geq 0$, then we have $\frac{dx_2}{dt} = m_{12}x_1 \geq 0$. So each trajectory initiated at a boundary of $\mathbb{R}^2_+$ either remains at the boundary or goes to the interior of $\mathbb{R}^2_+$. According to [29, Proposition B.7, page 267], no trajectory comes out of $\mathbb{R}^2_+$. Therefore, $\mathbb{R}^2_+$ is positively invariant for (2.1). □

The equilibrium of the system (2.1) is the solutions of the following algebraic system:

$$\begin{cases} 0 = r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^{\mu}\right] + m(m_{12}x_2 - m_{21}x_1), \\ 0 = r_2 x_2 \left[1 - \left(\frac{x_2}{K_2}\right)^{\mu}\right] + m(m_{21}x_1 - m_{12}x_2). \end{cases} \tag{A.1}$$

The sum of the two equations of (A.1) shows that the equilibrium points are in a curve noted $\mathcal{C}_\mu$, which its equation is given by:

$$\Phi_\mu(x_1, x_2) := r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^{\mu}\right] + r_2 x_2 \left[1 - \left(\frac{x_2}{K_2}\right)^{\mu}\right] = 0. \tag{A.2}$$

The curve $\mathcal{C}_\mu$ passes through the points $(0,0), (K_1, 0), (0, K_2)$ and $\mathcal{A} := (K_1, K_2)$ for all value positive of parameter μ. Note that, it is independent of migration rate m and m_{ij}. For the particular value $\mu = 1$, the curve $\mathcal{C}_1$ is an ellipse centered in $\left(\frac{K_1}{2}, \frac{K_2}{2}\right)$ (shown in black in Figure A.1). For $\mu > 1$, the curve $\mathcal{C}_\mu$ is below the ellipse $\mathcal{C}_1$ (shown in green and brown in the figure A.1) and for $0 < \mu < 1$, the curve $\mathcal{C}_\mu$ is above the ellipse $\mathcal{C}_1$ (shown in red and blue in Figure A.1). The function $\Phi_\mu(x_1, x_2) = \Phi_{\mu,1}(x_1) + \Phi_{\mu,2}(x_2)$, with $\Phi_{\mu,i}(x_i) = r_i x_i \left[1 - \left(\frac{x_i}{K_i}\right)^\mu\right]$ is concave since $\Phi_{\mu,1}$ and $\Phi_{\mu,2}$ are two concave functions. Another property of the curve $\mathcal{C}_\mu$, if is that if a point (x_1, x_2) belongs to $\mathcal{C}_\mu$ with $x_1 < K_1$ (resp. $x_2 > K_2$) then $x_2 > K_2$ (resp. $x_1 < K_1$) (see figure A.1).

Solving the first equation of system (A.1) for x_2 yields a curve noted $M_{m,\mu}$ of equation $x_2 = \varphi_{m,\mu}(x_1)$, where the function $\varphi_{m,\mu}$ is given by the following equation:

$$\varphi_{m,\mu}(x_1) := \frac{1}{m_{12}} \left(m_{21} x_1 - \frac{r_1}{m} x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^\mu\right]\right). \tag{A.3}$$

The curve $M_{m,\mu}$ (shown in the figure A.1 for some values of μ) depends on the migration rate m and the parameter μ. It always passes through the origin and the point $\mathcal{B} := \left(K_1, \frac{m_{21}}{m_{12}} K_2\right)$. So, the equilibrium points are the non-negative intersection between the curves $\mathcal{C}_\mu$ and $M_{m,\mu}$. There are two equilibrium points. The first is the trivial point $(0, 0)$ and the second is a non trivial point noted $\mathcal{E}^*(m) := (x_1^*(m), x_2^*(m))$ whose position depend on migration rate m (see Figure A.2).

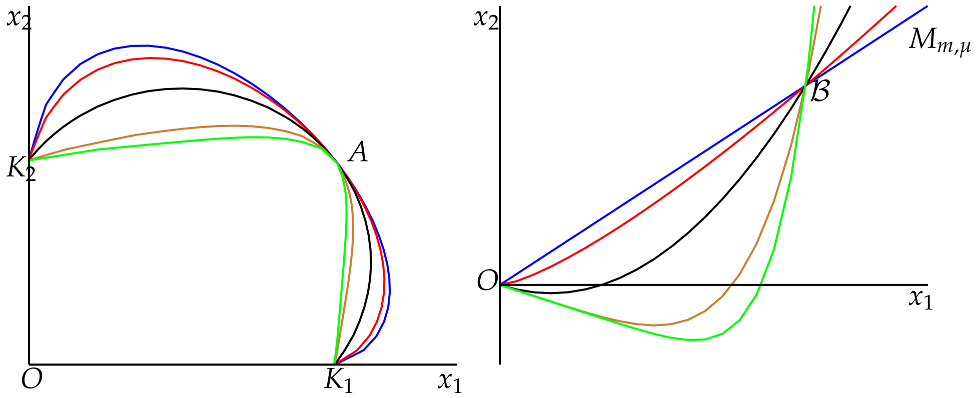

Figure A.1: The curves $\mathcal{C}_\mu$ (left) and $M_{m,\mu}$ (right) for $r_1 = 3, r_2 = 2, K_1 = 5, K_2 = 4, m_{12} = m_{21} = m = 1$ and $\mu = 0.001$ (green curves), $\mu = 0.2$ (gold curves), $\mu = 1$ (black curves), $\mu = 4$ (red curves) and $\mu = 7$ (blue curves).

In the following, our aim is to show the global stability of the equilibrium $\mathcal{E}^*(m)$. For this, we need some results. First, for the non-negativity and boundedness of the solution of the system (2.1), we have the following result:

Lemma A.2. For any non-negative initial condition, the solutions of the system (2.1) remain bounded, for all $t \geq 0$. Moreover, the set

$$\Sigma = \left\{ (x_1, x_2) \in \mathbb{R}_+^2 / x_1 + x_2 \leq \frac{\xi_2^*}{\xi_1^*} \right\},$$

where $\xi_1^* = \mu \min\{r_1, r_2\}$ and $\xi_2^* = \mu(r_1 K_1 + r_2 K_2)$, is positively invariant and is a global attractor for the system (2.1).

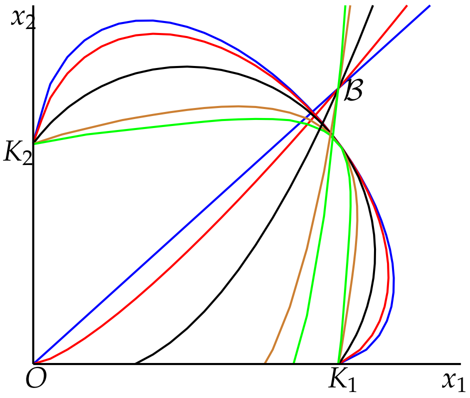

Figure A.2: Intersection between $\mathcal{C}_\mu$ and $M_{m,\mu}$, which are drawn in the same color.

Proof. To show that all solutions are bounded, we consider the quantity defined by $X_T(t) = x_1(t) + x_2(t)$. So, we have

$$\dot{X}_T(t) = r_1 x_1(t)\left[1-\left(\frac{x_1(t)}{K_1}\right)^{\mu}\right] + r_2 x_2(t)\left[1-\left(\frac{x_2(t)}{K_2}\right)^{\mu}\right]. \tag{A.4}$$

For all r_i and K_i, we have the inequality:

$$r_i x_i\left[1-\left(\frac{x_i}{K_i}\right)^{\mu}\right] \le \mu r_i (K_i - x_i), \quad i = 1,2. \tag{A.5}$$

Substituting Equation (A.5) into (A.4), we get

$$\dot{X}_T(t) \le -\xi_1^* X_T(t) + \xi_2^* \qquad \text{for all } t \ge 0,$$

which gives

$$X_T(t) \le \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*}\right) e^{-\xi_1 t} + \frac{\xi_2^*}{\xi_1^*}, \qquad \text{for all } t \ge 0. \tag{A.6}$$

Hence,

$$X_T(t) \le \max\left(X_T(0), \frac{\xi_2^*}{\xi_1^*}\right), \qquad \text{for all } t \ge 0.$$

Therefore, the solutions of System (2.1) are positively bounded and defined for all $t \ge 0$. From (A.6), it can be deduced that the set Σ is positively invariant and it is a global attractor for the system (2.1). □

We have also the following property:

Lemma A.3. System (2.1) admits no periodic solution.

Proof. The isoclines of the system (2.1) are given by the two equations:

$$\begin{cases} \mathcal{P}_1(x_1) = -\frac{r_1}{mm_{12}}x_1\left[1-\left(\frac{x_1}{K_1}\right)^{\mu}\right] + \frac{m_{21}}{m_{12}}x_1, \\ \mathcal{P}_2(x_2) = -\frac{r_2}{mm_{21}}x_2\left[1-\left(\frac{x_2}{K_2}\right)^{\mu}\right] + \frac{m_{12}}{m_{21}}x_2. \end{cases}$$

Let f_i be the right hand side of the system (2.1). Then, for all m we have:

$$\begin{aligned} \frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} &= r_1 + r_2 - (\mu+1)\left[r_1\left(\frac{x_1}{K_1}\right)^{\mu} + r_2\left(\frac{x_2}{K_2}\right)^{\mu}\right] \\ &\quad - m(m_{21}+m_{12}) = -m\left(m_{12}\frac{d\mathcal{P}_1}{dx_1} + m_{21}\frac{d\mathcal{P}_2}{dx_2}\right) < 0. \end{aligned}$$

So, by Dulac's Criterion [14, Theorem 4.1.1], the system (2.1) admits no periodic solution. □

Theorem A.4. The equilibrium $\mathcal{E}^*(m)$ of (2.1) is GAS in the positive cone $\mathbb{R}^2_+ \setminus \{0\}$.

Proof. The Jacobian matrix of the system (2.1) at $\mathcal{E}^*(m)$ is given by:

$$\mathbb{J}(\mathcal{E}^*) = \begin{bmatrix} \kappa_1 & mm_{12} \\ mm_{21} & \kappa_2 \end{bmatrix},$$

where $\kappa_1 = r_1 - (\mu+1)r_1\left(\frac{x_1^*(m)}{K_1}\right)^{\mu} - mm_{21}$, and $\kappa_2 = r_2 - (\mu+1)r_2\left(\frac{x_2^*(m)}{K_2}\right)^{\mu} - mm_{12}$. We have: $0 < \frac{d\mathcal{P}_1}{dx_1}(x_1^*(m), x_2^*(m)) = -\frac{1}{mm_{12}}\kappa_1$, and $0 < \frac{d\mathcal{P}_2}{dx_2}(x_1^*(m), x_2^*(m)) = -\frac{1}{mm_{21}}\kappa_2$. Therefore, $\kappa_1 < 0$ and $\kappa_2 < 0$. This implies that $\mathrm{tr}(\mathbb{J}(\mathcal{E}^*)) = \kappa_1 + \kappa_2 < 0$, where tr means the trace.
It's clear that, in the figures A.3, at the equilibrium $\mathcal{E}^*$, we have: $\frac{d\mathcal{P}_1}{dx_1}(\mathcal{E}^*) > \left(\frac{d\mathcal{P}_2}{dx_2}(\mathcal{E}^*)\right)^{-1}$, which gives $\frac{\kappa_1}{-mm_{12}} > \frac{-mm_{21}}{\kappa_2}$. Thus, $\det \mathbb{J}(\mathcal{E}^*) = \kappa_1\kappa_2 - m^2 m_{12}m_{21} > 0$.
Hence by the Routh-Hurwitz criteria for stability, the real parts of the eigenvalues value of the Jacobian matrix $\mathbb{J}(\mathcal{E}^*)$ are negative, proving that $\mathcal{E}^*$ is asymptotically stable. Lemmas A.2 and A.3 imply that there cannot be any non-trivial closed paths lying in the interior of the positive quadrant and hence the asymptotic stability must be global. □

B Two-patch logistic model

We consider the 2-patch logistic equation with asymmetric migrations. We denote by m_{12} the migration rate from patch 2 to patch 1, m_{21} from patch 1 to patch 2, and m is the dispersal rate between two patches. The model is written:

$$\begin{cases} \frac{dx_1}{dt} = r_1x_1\left(1-\frac{x_1}{K_1}\right) + m\left(m_{12}x_2 - m_{21}x_1\right), \\ \frac{dx_2}{dt} = r_2x_2\left(1-\frac{x_2}{K_2}\right) + m\left(m_{21}x_1 - m_{12}x_2\right). \end{cases} \tag{B.1}$$

Note that the system (B.1) is studied in [1,6,9,10,15] in the case where the migration rates satisfy $m_{21} = m_{12}$, and in [2] for general migration rates. If we denote $\gamma = \frac{m_{12}}{m_{21}}$, then the system (B.1) becomes:

$$\begin{cases} \frac{dx_1}{dt} = r_1x_1\left(1-\frac{x_1}{K_1}\right) + m\left(\gamma x_2 - x_1\right), \\ \frac{dx_2}{dt} = r_2x_2\left(1-\frac{x_2}{K_2}\right) + m\left(x_1 - \gamma x_2\right), \end{cases} \tag{B.2}$$

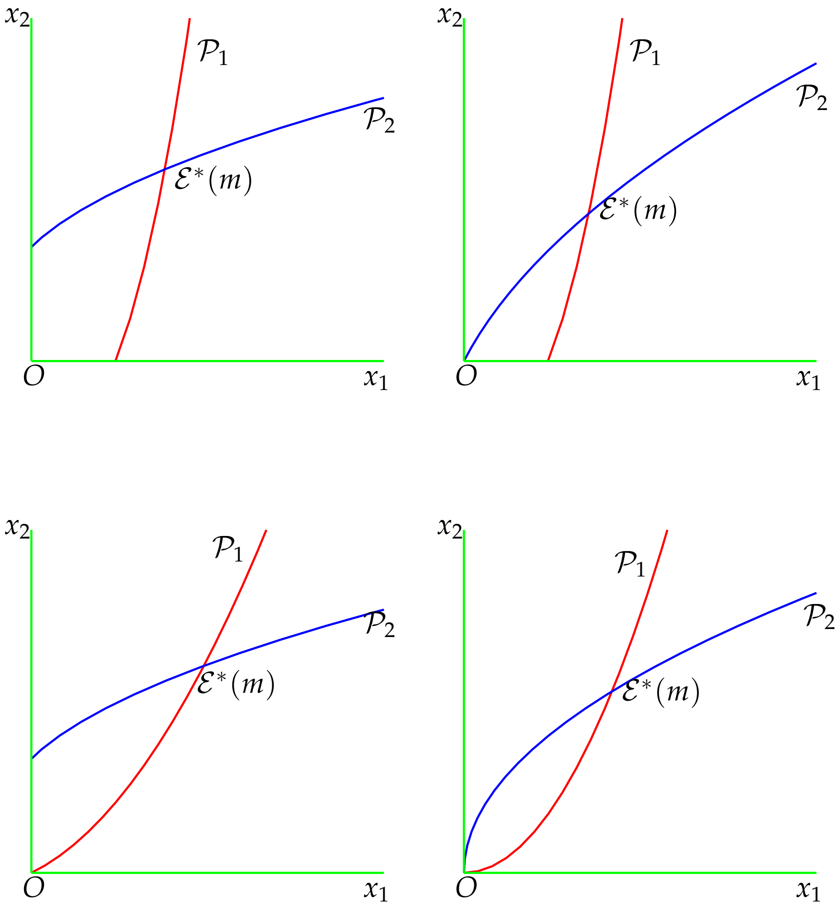

Figure A.3: All possible configurations for the isoclines of the system (2.1) (in red for x_1 and in blue for x_2) for certain parameters. The equilibrium points are the intersection between these two isoclines: the origin and the positive equilibrium $\mathcal{E}^*(m)$.

The system (B.2) has always a unique positive equilibrium, still denoted by $E^*(m,\gamma) = (x_1^*(m,\gamma), x_2^*(m,\gamma))$, which is GAS in the interior of positive cone $\mathbb{R}^2 \setminus \{0\}$. We thus define the total population abundance at the positive equilibrium under dispersal rate m and dispersal asymmetry γ by

$$X_T^*(m,\gamma) = x_1^*(m,\gamma) + x_2^*(m,\gamma),$$

as the total realized asymptotic population abundance.

B.1 Total population size for fixed γ

In all of this part, we assume that γ is positive and fixed parameter and m varies in $[0,\infty[$. We recall that the derivative of $X_T^*(m,\gamma)$ with respect to m at $m=0$ is given by the following formula [8]:

$$\frac{dX_T^*}{dm}(0,\gamma) = (\gamma K_2 - K_1)\left(\frac{1}{r_1} - \frac{1}{r_2}\right). \tag{B.3}$$

The behavior of the model (B.2) for perfect mixing (i.e. $m \to \infty$) is given by the following formula [2,8]:

$$X_T^*(\infty,\gamma) = (1+\gamma)\frac{\gamma r_1 + r_2}{\gamma^2\alpha_1 + \alpha_2}, \qquad \text{where } \alpha_i = r_i/K_i. \tag{B.4}$$

We consider the regions in the set of the parameter γ denoted $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$, defined by:

$$\begin{cases} \text{If } r_2 > r_1 \text{ then } \begin{cases} \mathcal{J}_1 = \left\{\gamma : \gamma > \frac{\alpha_2}{\alpha_1}\right\}, \\ \mathcal{J}_0 = \left\{\gamma : \frac{\alpha_2}{\alpha_1} \geq \gamma > \frac{K_1}{K_2}\right\}, \\ \mathcal{J}_2 = \left\{\gamma : \frac{K_1}{K_2} > \gamma\right\}. \end{cases} \\ \text{If } r_2 < r_1 \text{ then } \begin{cases} \mathcal{J}_1 = \left\{\gamma : \gamma < \frac{\alpha_2}{\alpha_1}\right\}, \\ \mathcal{J}_0 = \left\{\gamma : \frac{\alpha_2}{\alpha_1} \leq \gamma < \frac{K_1}{K_2}\right\}, \\ \mathcal{J}_2 = \left\{\gamma : \frac{K_1}{K_2} < \gamma\right\}. \end{cases} \end{cases} \tag{B.5}$$

We recall the following result of Arditi et al. [2] which gives the conditions for which patchiness is beneficial or detrimental in model (B.2).

Proposition B.1. The total equilibrium population X_T^* of (B.2) for γ fixed satisfies the following properties

1. If $r_1 = r_2$ then $X_T^*(m,\gamma) \leq K_1 + K_2$ for all $m \geq 0$.
2. If $r_2 \neq r_1$, let $\mathcal{J}_0$, $\mathcal{J}_1$ and $\mathcal{J}_2$, be defined by (B.5). Then we have:
   - if $\gamma \in \mathcal{J}_0$ then $X_T^*(m,\gamma) > K_1 + K_2$ for all $m > 0$
   - if $\gamma \in \mathcal{J}_1$ then $X_T^*(m,\gamma) > K_1 + K_2$ for $0 < m < m_0$ and $X_T^*(m,\gamma) < K_1 + K_2$ for $m > m_0$, where
     $$m_0 = \frac{r_2 - r_1}{\frac{\gamma}{\alpha_2} - \frac{1}{\alpha_1}}\frac{1}{\alpha_1 + \alpha_2}.$$
   - if $\gamma \in \mathcal{J}_2$ then $X_T^*(m,\gamma) < K_1 + K_2$ for any $m > 0$
   - If $\gamma = \frac{K_1}{K_2}$, then $x_1^*(m,\gamma) = K_1$ and $x_2^*(m,\gamma) = K_2$ for all $m \geq 0$. Therefore $X_T^*(m,\gamma) = K_1 + K_2$ for all $m \geq 0$.

B.2 Total population size for fixed m

In all of this section, we assume that m is fixed parameter and γ varies from 0 to ∞.

B.2.1 The model when $\gamma \to 0$

We have the following result

Proposition B.2. Consider the system (B.2). Then,

$$\lim_{\gamma\to 0} E^*(m,\gamma) = \begin{cases} (0,K_2), & if \quad m \geq r_1, \\ \left(\left(1-\frac{m}{r_1}\right)K_1, \frac{1}{2}K_2 + \frac{1}{2\alpha_2}\sqrt{r_2^2 + 4m\alpha_2\left(1-\frac{m}{r_1}\right)K_1}\right), & if \quad m < r_1. \end{cases} \tag{B.6}$$

Proof. Denote $E^*(m,0^+) = (x_1^*(m,0^+), x_2^*(m,0^+)) := \lim_{\gamma\to 0} E^*(m,\gamma)$. When $\gamma \to 0$, the equilibrium equations of (B.2) take the following form:

$$\begin{cases} 0 = r_1 x_1^*(m,0^+)\left(1 - \dfrac{x_1^*(m,0^+)}{K_1}\right) - m x_1^*(m,0^+), \\ 0 = r_2 x_2^*(m,0^+)\left(1 - \dfrac{x_2^*(m,0^+)}{K_2}\right) + m x_1^*(m,0^+), \end{cases} \tag{B.7}$$

which implies

$$\begin{cases} 0 = (r_1 - m)x_1^*(m,0^+) - \alpha_1(x_1^*(m,0^+))^2 = 0, \\ -\alpha_1(x_2^*(m,0^+))^2 + m x_1^*(m,0^+) + r_2 x_2^*(m,0^+) = 0. \end{cases} \tag{B.8}$$

If $m \geq r_1$, then the system (B.8) admits $(0,0)$ and $(0,K_2)$ as solutions. Since $(0,0)$ is unstable for (B.2), then $E^*(m,\gamma) \to (0,K_2)$ as $\gamma \to 0$.

If $m < r_1$, the first equation in (B.8) gives $x_1^*(m,0^+) = 0$ or $x_1^*(m,0^+) = \frac{r_1-m}{\alpha_1}$. If we replace $x_1^*(m,0^+) = 0$ in the second equation of (B.8) we get $x_2^*(m,0^+) = 0$ or $x_2^*(m,0^+) = K_2$, and if we replace $x_1^*(m,0^+) = \frac{r_1-m}{\alpha_1}$ in the second equation of (B.8) we obtain the following equation:

$$-\alpha_2(x_2^*(m,0^+))^2 + r_2 x_2^*(m,0^+) + \frac{m\,(r_1-m)}{\alpha_1} = 0, \tag{B.9}$$

which admits as positive solution

$$x_2^*(m,0^+) = \frac{1}{2}K_2 + \frac{1}{2\alpha_2}\sqrt{r_2^2 + 4m\alpha_2\left(1-\frac{m}{r_1}\right)K_1}.$$

Therefore, if $r_1 > m$, then the system (B.8) admits three solutions: $(0,0)$, $(0,K_2)$ and

$$E^*(m,0^+) := \left(\left(1-\frac{m}{r_1}\right)K_1, \frac{1}{2}K_2 + \frac{1}{2\alpha_2}\sqrt{r_2^2 + 4m\alpha_2\left(1-\frac{m}{r_1}\right)K_1}\right), \tag{B.10}$$

Since, $(0,0)$, and $(0,K_2)$ are unstable, so $E^*(m,\lambda)$ converge to $E^*(m,0^+)$ as $\gamma \to 0$. □

As a corollary of the previous proposition, we obtain the following result which describes the total equilibrium population $X_T^*(m,\gamma)$ when $\gamma \to 0$.

Corollary B.3. we have:

$$\lim_{\gamma\to 0} X_T^*(m,\gamma) := X_T^*(m,0^+) = \begin{cases} K_2, & if \quad m \geq r_1, \\ \left(1-\frac{m}{r_1}\right)K_1 + \frac{1}{2}K_2 + \frac{1}{2\alpha_2}\sqrt{r_2^2 + 4m\alpha_2\left(1-\frac{m}{r_1}\right)K_1}, & if \quad m < r_1. \end{cases} \tag{B.11}$$

B.2.2 The model when $\gamma \to \infty$

In the next theorem, we give the behavior of the model (B.2) when $\gamma \to \infty$.

Proposition B.4. Let $(x_1(t,\gamma), x_2(t,\gamma))$ be the solution of the system (B.2) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1,2$. Let $z(t)$ be the solution of the differential equation

$$\frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K_1}\right), \tag{B.12}$$

with initial condition $z(0) = x_1^0 + x_1^0$. Then, when $\gamma \to \infty$, we have

$$x_1(t,\gamma) + x_2(t,\gamma) = z(t) + o_\gamma(1), \qquad \text{uniformly for } t \in [0, +\infty) \tag{B.13}$$

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

$$\begin{cases} x_1(t,\gamma) = z(t) + o_\gamma(1), \\ x_2(t,\gamma) = o_\gamma(1), \end{cases} \quad \text{uniformly for} \quad t \in [t_0, +\infty). \tag{B.14}$$

Proof. Let $X = x_1 + x_2$. We rewrite the system (B.2) using the variables (X, x_1), and get:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right) + m\left(\gamma(X - x_1) - x_1\right), \\ \dfrac{dX}{dt} = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right) + r_2(X - x_1)\left(1 - \dfrac{(X - x_1)}{K_2}\right). \end{cases} \tag{B.15}$$

When $\gamma \to \infty$, (B.15) is a slow-fast system, with one slow variable, X, and one fast variable x_1. As suggested by Tikhonov's Theorem [17, 30, 34] we consider the dynamics of the fast variable in the time scale $\tau = \gamma t$. One obtains

$$\frac{dx_1}{d\tau} = m(X - x_1). \tag{B.16}$$

The *slow manifold*, which is the equilibrium point of the fast dynamics (B.16), is given by $x_1 = X$. As this manifold is GAS for the system (B.16), the Theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (B.15) are approximated by the solutions of the *reduced model* which is obtained by replacing $x_1 = X$ into the dynamics of the slow variable, which gives (B.12).

Since (B.12) admits $X = K_1$ 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 variable, where t_0 is small as we want. Therefore, let $z(t)$ be the solution of the reduced model (B.12) of initial condition $z(0) = X(0,\gamma) = x_1^0 + x_2^0$, then, when $m \to \infty$, we have the approximations (B.13) and (B.14). □

According to previous proposition, when $\gamma \to \infty$, the equilibrium $E^*(m,\gamma)$ converge to $(K_1, 0)$ and $X_T^*(m, +\infty) = K_1$.

For more details on the effects of dispersal intensity and dispersal asymmetry on the total population abundance, the reader may refer to the recent work of Gao et al. [11].

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Conflict of Interest

The author has no conflicts of interest to declare.

References

[1] R. Arditi, C. Lobry and T. Sari, *In dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation*, Theor. Popul. Biol., **106** (2015), 45-59. DOI

[2] R. Arditi, C. Lobry and T.Sari, *Asymmetric dispersal in the multi-patch logistic equation*, Theor. Popul. Biol., **1206** (2018), 11-15. DOI

[3] L. Von. Bertalanffyi, *A quantitative theory of organic growth*, Human Biology., **10**(2) (1938), 181-213. DOI

[4] A. A. Blumberg, *Logistic Growth rate functions*, J. Theor. Biol., **21** (1968), 42-443. DOI

[5] L. Chen, T. Liu and F. Chen, *Stability and bifurcation in a two-patch model with additive Allee effect*, AIMS Math., **7**(1) (2021), 536-551. DOI

[6] D. L. DeAngelis, C. C. Travis and W. M. Post, *Persistence and stability of seed-dispersel species in a patchy environment*. Theor. Popul. Biol., **16** (1979), 107-125. DOI

[7] B. Elbetch, T. Benzekri, D. Massart and T. Sari, *The multi-patch logistic equation*. Discrete Contin. Dyn. Syst. - B., **26**(12) (2020), 6405-6424. DOI

[8] B. Elbetch, T. Benzekri, D. Massart and T. Sari, *The multi-patch logistic equation with asymmetric migration*, Rev. Integr. Temas Mat., **40**(1) (2022), 25-57. DOI

[9] H. I. Freedman and P. Waltman, *Mathematical Models of Population Interactions with Dispersal I: Stability of two habitats with and without a predator*. SIAM J. Appl Math., **32** (1977), 631-648. DOI

[10] H. I. Freedman, B. Rai and P. Waltman, *Mathematical Models of Population Interactions with Dispersal II: Differential Survival in a Change of Habitat*. J. Math. Anal. Appl., **115** (1986), 140-154. DOI

[11] D. Gao and Y. Lou, *Total biomass of a single population in two-patch environments*. Theor. Popul. Biol., **(146)** (2022), 1-14. DOI

[12] J. W. Haefner, *Modelling Biological Systems: Principles and Applications*, ITP Chapman and Hall, New York, 1996. URL

[13] I. A. Hanski and M. E. Gilpin, *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, 1997.

[14] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, 1998. URL

[15] R. D. Holt, *Population dynamics in two patch environments: some anomalous consequences of an optimal habitat distribution*. Theor. Popul. Biol., **28** (1985), 181-201. DOI

[16] Y. Kang and N. Lanchier, *Expansion or extinction: Deterministic and stochastic two-patch models with Allee effects*, J. Math. Biol., **62** (2011), 925-973. DOI

[17] C. Lobry, T. Sari and S. Touhami, *On Tykhonov's theorem for convergence of solutions of slow and fast systems*. Electron. J. Differ. Equ., **19**(1998), 1-22. URL

[18] S. A. Levin, *Dispersion and population interactions*. Amer. Natur., **108** (1974), 207-228. DOI

[19] S. A. Levin, *Spatial patterning and the structure of ecological communities, in Some Mathematical Questions in Biology VII*. American Mathematical Society, 1976. URL

[20] S. A. Levin, T. M. Powell and J. H. Steele, *Patch Dynamics*, volume **96** of Lecture Notes in Biomathematics. Springer-Verlag, 1993. DOI

[21] A. J. Lotka, *Elements of Mathematical Biology*. DOVER, New York, 1956. URL

[22] Y. Y. Lv, L. J. Chen and F. D. Chen, *Stability and bifurcation in a single species logistic model with additive Allee effect and feedback control*, Adv. Differ. Equ., **8** (2020), 2686-2697. DOI

[23] Y. Y. Lv, L. J. Chen, F. D. Chen and Z. Li, *Stability and bifurcation in an SI epidemic model with additive Allee effect and time delay*, Int. J. Bifurcat. Chaos, **31**(2021), 2150060. DOI

[24] H. McCallum, *Population Parameters: Estimation for Ecological Models*, Blackwell Science, UK 2008. URL

[25] D. Pal and G. P. Samanta, *Effects of dispersal speed and strong Allee effect on stability of a two-patch predator-prey model*, Int. J. Dyn. Control, **6** (2018), 1484-1495. DOI

[26] J.-C. Poggiale, P. Auger, D. Nérini, C. Manté and F. Gilbert, *Global production increased spatial heterogeneity in a population dynamics model*. Acta Biotheor., **53** (2005), 359-370. DOI

[27] F. J. Richards, *A Flexible Growth Function for Empirical Use*, J. Exp. Bot., **10**(29) (1959), 290-300. DOI

[28] S. Saha and G. P. Samanta, *Influence of dispersal and strong Allee effect on a two-patch predator-prey model*, Int. J. Dyn. Control, **7** (2009), 1321-1349. DOI

[29] H. L. Smith and P. Waltman, *The Theory of the Chemostat : Dynamics of Microbial Competition*, Cambridge Studies in Mathematical Biology, **13** (1995). DOI

[30] A. N. Tikhonov, *Systems of differential equations containing small parameters in the derivatives*. Mat. Sb. (N.S.), **31**(73):3 (1952), 575-586. URL

[31] A. Tsoularis and J. Wallace, *Analysis of Logistic Growth Models*. Math. Biosci., **179** (2002), 21-55. DOI

[32] M. E. Turner, E. Bradley , K. Kirk and K. Pruitt, *A Theory of Growth*. Math. Biosci., **29** (1976), 367-373. DOI

[33] P. F. Verhulst, *Notice sur la loi que la population suit dans son accroissement*. Corr. Math. Physics, **10**(1838), 113. DOI

[34] W. R. Wasow, *Asymptotic Expansions for Ordinary Differential Equations*. Robert E. Krieger Publishing Company, Huntington, New York, 1976.

[35] H. Wu, Y. Wang, Y. Li and D. DeAngelis, *Dispersal asymmetry in a two-patch system with source-sink populations*. Theor. Popul. Biol., **131** (2020), 54-65. DOI