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EFFECTS OF RAPID POPULATION GROWTH ON TOTAL BIOMASS IN MULTI–PATCH ENVIRONMENT

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Abstract. In this work, we study a multi-patch model, where the patches are coupled by asymmetrical migration terms, and each patch follows a logistic law under the assumption that some growth rates are much larger than the other. First, for Two-patch model where one growth rate is much larger than the second one, the total equilibrium population is greater or smaller than the sum of two carrying capacities for all migration rates. Second, we consider Three-patch model in the two cases: (i) where two growth rates are much larger than the third one, and (ii) where one growth rate is much larger than the other two. For both cases, we give a complete classification of all possible situations under which the fragmentation can lead to a total equilibrium population greater or smaller than the sum of the three carrying capacities. Finally, in the general case, we consider the model of n patches with the assumption that: (i) all growth rates but one are much larger than the n th growth rate, (ii) two blocks where the growth rates of the first block are much larger than that of the second one. For the first case, we give a complete classification of all possible situations under which the fragmentation can lead to a total equilibrium population greater or smaller than the sum of the n carrying capacities, and in the second case, we construct a reduced model and we prove its global stability.

1. Introduction

In biology, there are several factors that affect the population growth and its reproduction in a sound manner, for example, the disparity and the large variation in the growth rate between different organisms, which lead to the creation of some imbalances in the environmental milieu. The theoretical paradigm that has been used to treat these problem, is that of a single population fragmented into patches coupled by migration, and the sub population in each patch follows a local logistic law. This system is modeled by a non linear system of differential equation of the following form:

$$\frac{dx}{dt} = f(x) + \beta \Gamma x, \tag{1}$$

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

$$f_i(x_i) = r_i x_i (1 - x_i/K_i), \quad i = 1, \ldots n. \tag{2}$$

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The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity of patch i. It is fundamental in the ecology of population life histories that intrinsic growth rate and carrying capacity are distinct parameters related to a species population, and are not necessarily correlated. The term $\beta\Gamma x$ on the right hand side of the system (1) describes the effect of the migration between the patches, where β is the migration rate and $\Gamma = (\gamma_{ij})$ is the matrix representing the migrations between the patches. For $i \neq j$, $\gamma_{ij} > 0$ denotes the incoming flux from patch j to patch i. If $\gamma_{ij} = 0$, there is no migration. The diagonal entries of Γ satisfy the following equation

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ji}, \qquad i = 1, \cdots, n, \tag{3}$$

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

The model (1), (2), (3) has been studied by many ecologists and mathematicians, for example, Freedman and Waltman [19] and Holt [23] in the case $n = 2$ and Γ such that $\gamma_{12} = \gamma_{21} = 1$, Arditi et al. [1, 2] for two patches and also Poggiale et al. [29] in the case where $\beta \to \infty$.

DeAngelis et al. [7, 10] considered the case of $n > 2$ patches in a circle, with symmetric migration between any patch and its two neighbours:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta (x_{i-1} - 2x_i + x_{i+1}), \qquad i = 1, \ldots, n, \tag{4}$$

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

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

The system (4) is a one-dimensional discrete-patch version of the standard reaction-diffusion model. In [7, 10] the perfect mixing case is described.

Recently, Arditi et al. [1, 2] gave a full mathematical analysis of the two-patch logistic model with symmetric and asymmetric dispersal. Wu et al. [34] generalized their results to a source-sink system, i.e the model (1), (3) for $n = 2$ and

$$f(x_1, x_2) = \left(r_1 x_1 \left(1 - \frac{x_1}{K_1}\right), r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) \right)^T \tag{5}$$

The case of the general symmetric and non symmetric migration was considered by Elbetch et al. in [13] and in [14] respectively. They gave some conditions on the parameters of the model that ensure that migration is beneficial or detrimental to the sum of n carrying capacities. They also calculated the formula of perfect mixing.

Arino et al. [4] also studied a source-sink model of n patches, where the source patch follows a logistic growth rate, and the sink patch with exponential decay, i.e

$$f(x) = \begin{cases} r_i x_i \left(1 - \frac{x_i}{K_i}\right) & \text{if } i = 1, \ldots, m, \\ -r_i x_i & \text{if } i = m+1, \ldots, n. \end{cases} \tag{6}$$

For the model (1), (3), (6), the authors proved the existence of a threshold number of source patches such that the population potentially becomes extinct below the threshold and established above the threshold.

Another important form of f appears in the work of Gao [20] on susceptible-infected-susceptible (SIS) model in n patches connected by human migration:

$$f_i(x_i) = r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \gamma_i x_i, \quad i = 1, \ldots, n, \tag{7}$$

where $\gamma_i > 0$. Note that, if $r_i < \gamma_i$ for some patches i, the system (1), (3), (7) is a source-sink model. For this model, Gao gave the total number of infections at the stable steady state as $\beta \to 0^+$ and $\beta \to \infty$. He also calculated the derivative of the total number of infections at the stable steady for $\beta = 0$. For the two-patch model, Gao gave a complete classification of the model parameter space as to whether dispersal is beneficial or detrimental to disease control.

In [33], Wang considered the model of n patches with Allee effect growth, i.e the system (1), (3) for:

$$f_i(x_i) = r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \frac{\lambda_i \theta_i x_i}{\theta_i + x_i}, \quad i = 1, \ldots, n, \tag{8}$$

where r_i, K_i, λ_i and θ_i are positive constants, the first term in the right-hand side of (8) denote the logistic growth, and the last term describes the mating limitation or predation effect (see [11, 12]). Wang gave the conditions on the global stability of the model (1), (3), (8) in the case of weak Allee effect by using the theory of monotonic dynamical systems.

Recently, Chen et al. [5] considered the two-patch model with additive Allee effect, i.e the system (1), (3) for $n = 2$ and

$$f(x_1, x_2) = \left(-x_1, x_2\left(1 - x_2 - \frac{m}{x_2 + a}\right)\right)^T. \tag{9}$$

The positive parameters m and a are the Allee effect constants. The additive Allee effect consists of two cases, i.e., weak and strong Allee effects. That is, if $0 < m < a$, it is the weak Allee effect; if $m > a$, it is the strong Allee effect. For this model, the authors presented the possible qualitative behavior and bifurcation phenomena, and they also discussed the existence and stability of all non-negative equilibria of this system. They investigated the effect of Allee effect and dispersal on total population abundance. For more details and information on the Allee effect models, the reader is referred to [33].

In [15], I suggested to study the two-patch model where each patch follows a Richard's law, i.e, the model (1), (3) for $n = 2$ and

$$f(x_1, x_2) = \left(r_1 x_1 \left(1 - \left(\frac{x_1}{K_1}\right)^{\mu}\right), r_2 x_2 \left(1 - \left(\frac{x_2}{K_2}\right)^{\mu}\right)\right)^T, \tag{10}$$

where μ is a positive parameter. For this model, I was interested in the effect of this choice, which generalizes the logistic, on the dynamics of the total population in two patches. I gave a complete classification of the model parameter space concerning when dispersal causes smaller or larger total biomass than no dispersal. I used for this classification, the geometric method of Arditi et al. [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. [7, 8, 9, 10], Freedman et al. [18], Zaker et al. [35] and Elbetch et al. [16, 17].

Our aim in the present paper is to study the effect of the migration on the total population with the assumption that some sub populations increase faster than the others. Mathematically, this assumption means that some growth rates in the equation (2) have the form r_i/ε, where ε is assumed to be a small positive number. Under this assumption, the first term in the right hand side of (1) takes the following form:

$$f(x) = \begin{cases} r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) & \text{if } i = 1,\ldots,m, \\ \dfrac{r_i}{\varepsilon} x_i \left(1 - \dfrac{x_i}{K_i}\right) & \text{if } i = m+1,\ldots,n. \end{cases} \tag{11}$$

In our main result of Theorem 4.3, we prove the numerical results of [13] under the assumption that one growth rate is much larger than the other two, i.e the system (1), (3), (11) for $(n,m) = (3,2)$. In particular, we prove the existence of at most two positive values of migration rate, solution of the following equation:

Total equilibrium population = Sum of carrying capacities.

We recall that, the numerical simulations of [13] are given for matrix Γ which is symmetric and irreducible. Note that, in the numerical result of [14], Elbetch et al. proved for three-patch model, when the matrix Γ is irreducible and not necessarily symmetric, the existence of at least three positive values of migration rate for which the total equilibrium population equals its initial state without migration (see Figures 4, 5 and 6 in [14]).

The paper is organized as follows. In Section 2, some proprieties of the model (1), (3), (11) have been recalled as functions of the two parameters ε and β. In Section 3, Two-patch model with one growth rate being much larger than the second one is considered, we compare the total equilibrium population with the sum of two capacities when ε goes to zero. In Section 4, Three-patch model is studied in both cases: the case when two growth rates are much larger than the third one and the case when one growth rate is much larger than the other two. In Section 5, the model in the general case is considered, with the hypothesis that some growth rates are much larger than the others. We have given some comparisons between the total equilibrium population and the sum of carrying capacities. The conclusion is given in Section 6. The paper ends with two appendices A and B, which in the first we show the global stability of the reduced model (44) and in the second, we compute the second derivative of the total equilibrium population of the same model.

2. Model proprieties

Our objective in this section, is to recall some properties of the model (1), (3), (11), and also some essentials results of [13, 14] with respect to parameters β and ε. First, for the non-negativity of the solutions of (1), (3), (11), we have the following proposition [13, Prop. 2.1] and [14, Prop. 2.1]:

PROPOSITION 2.1. *The domain* $\mathbb{R}^n_+ = \{(x_1,\dots,x_n) \in \mathbb{R}^n / x_i \geqslant 0, i = 1,\dots,n\}$ *is positively invariant for the system* (1), (3), (11).

We recall that, when the matrix of migration Γ is irreducible, System (1), (3), (11) admits a unique positive equilibrium which is globally asymptotically stable (GAS), see [3, Theorem 2.2], [4, Theorem 1] or [13, Theorem 6.1]. In what follows, the positive equilibrium point of (1), (3), (11) is denoted by $E^*(\beta,\varepsilon) = (x_1^*(\beta,\varepsilon),\dots,x_n^*(\beta,\varepsilon))$ and the sum of $x_i^*(\beta,\varepsilon)$ for $i = 1,\dots,n$, is denoted by $X_T^*(\beta,\varepsilon)$. Note that, $X_T^*(0,\varepsilon) = K_1+\dots+K_n$. We denote also by $\delta := (\delta_1,\dots,\delta_n)^T$ the positive vector which generates the vector space $\ker\Gamma$. For the existence, uniqueness, and positivity of δ see Lemma 1 of Cosner et al. [6] and Lemma 1 of Elbetch et al. [14]. In [22, Lemma 2.1], Guo et al. gives explicit formulas of the components of the vector δ, with respect of the coefficients of Γ. We denote also in all this article $\alpha_i = r_i/K_i$. We recall the following result of [14, Prop 3.4], which describes the total equilibrium population for perfect mixing (i.e when $\beta \to \infty$ in (1), (3), (11)):

PROPOSITION 2.2. *Consider the system* (1), (3), (11). *We have:*

$$X_T^*(+\infty,\varepsilon) := \lim_{\beta\to\infty} X_T^*(\beta,\varepsilon) = \sum_{i=1}^n \delta_i \frac{\sum_{i=m+1}^n r_i\delta_i + \varepsilon\sum_{i=1}^m \delta_i r_i}{\sum_{i=m+1}^n \alpha_i\delta_i^2 + \varepsilon\sum_{i=1}^m \delta_i^2\alpha_i}. \tag{12}$$

If the matrix Γ is symmetric, the limit (12) specializes to the formula given in [13, Equation (24)]:

$$X_T^*(+\infty,\varepsilon) = n\frac{\sum_{i=m+1}^n r_i + \varepsilon\sum_{i=1}^m r_i}{\sum_{i=m+1}^n \alpha_i + \varepsilon\sum_{i=1}^m \alpha_i}. \tag{13}$$

We recall the formula of the derivative of the total equilibrium population $X_T^*(\beta,\varepsilon)$ given in [14, Prop. 4.7] for Γ non symmetric and in [13, Lemma 3.3] for Γ symmetric:

PROPOSITION 2.3. *The derivative of* X_T^* *with respect to* β *at* $\beta = 0$ *is given by:*

$$\frac{dX_T^*}{d\beta}(0,\varepsilon) = \sum_{i=1}^m \frac{1}{r_i}\sum_{j=1,j\neq i}^n (\gamma_{ij}K_j - \gamma_{ji}K_i) + \varepsilon\sum_{i=m+1}^n \frac{1}{r_i}\sum_{j=1,j\neq i}^n (\gamma_{ij}K_j - \gamma_{ji}K_i). \tag{14}$$

In [13, 14], Elbetch et al. have answered in some particular cases of the model (1), (3), (11) for $n = m$ to the following important question: Is it possible, depending on the migration rate, that the total equilibrium population X_T^* 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 dispersal is either beneficial or detrimental to total equilibrium population. Note that, this last question has been studied by many researches (see [1, 2, 7, 8, 9, 13, 14, 18, 19, 20, 21]). Elbetch et al. [13] proved that, if all the patches do not differ with respect to the intrinsic growth rate (i.e., $r_1 = \ldots = r_n$), then the effect of migration is always detrimental. In the case when $(K_1, \ldots, K_n)^T \in \ker\Gamma$ (if the matrix Γ is symmetric, the condition $(K_1, \ldots, K_n)^T \in \ker\Gamma$ means that the patches do not differ with respect to the carrying capacity), migration has no effect on the total equilibrium population. An example when the effect of 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., $\alpha_1 = \ldots, \alpha_n$) (see also [14, Prop. 4.2] for another example when Γ is non symmetric).

It was shown by Arditi et al. [1, Proposition 2, page 54], for Two-patch model, 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 β and detrimental for the higher values. More precisely, it was shown in [1] that, if $n = 2$ in (1), (3), (11) (i.e the system (15)), the following trichotomy holds

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

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

In [13, Section 5.2], Elbetch et al. have considered the model (1), (3), (11) for $n = 3$ with Γ is symmetric, and shown by numerical simulations the following situations, which do not exist in the two-patch model:

- The case where $\frac{dX_T^*}{d\beta}(0, \varepsilon) < 0$ and $X_T^*(+\infty, \varepsilon) > K_1 + K_2 + K_3$.
- The case where $\frac{dX_T^*}{d\beta}(0, \varepsilon) > 0$ and $X_T^*(+\infty, \varepsilon) > K_1 + K_2 + K_3$ and there exist values of β for which $X_T^*(\beta, \varepsilon) < K_1 + K_2 + K_3$.
- The case where $\frac{dX_T^*}{d\beta}(0, \varepsilon) < 0$ and $X_T^*(+\infty, \varepsilon) < K_1 + K_2 + K_3$ and there exist values of β for which $X_T^*(\beta, \varepsilon) > K_1 + K_2 + K_3$.

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

In [14, Section 6], Elbetch et al. have reconsidered the three-patch model with Γ is not symmetric. The novelty was showing when Γ is not symmetric is the existence of three positive values of migration rate solution of the following equation:

Total equilibrium population = Sum of three carrying capacities,

i.e. the following situation hold:

- The case where $\frac{dX_T^*}{d\beta}(0,\varepsilon) > 0$ and $X_T^*(+\infty,\varepsilon) < K_1+K_2+K_3$, and there exists three values $0 < \beta_1 < \beta_2 < \beta_3$ for which we have:

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

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

In this section, we consider the two-patch model and we assume that the growth rate r_2 is much larger than r_1, i.e the system (1), (3), (11) for $(n,m) = (2,1)$. 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 is written:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right) + \beta\left(\gamma_2x_2 - \gamma_1x_1\right), \\ \dfrac{dx_2}{dt} = \dfrac{r_2}{\varepsilon}x_2\left(1-\dfrac{x_2}{K_2}\right) + \beta\left(\gamma_1x_1 - \gamma_2x_2\right), \end{cases} \tag{15}$$

where ε is assumed to be a small positive number. The derivative of $X_T^*(\beta,\varepsilon)$ with respect to β at $\beta = 0$ becomes:

$$\frac{dX_T^*}{d\beta}(0,\varepsilon) = (\gamma_2K_2 - \gamma_1K_1)\left(\frac{1}{r_1} - \frac{\varepsilon}{r_2}\right), \tag{16}$$

which is the formula [1, Equation A.1] given by Arditi et al with $\varepsilon = 1$ and $\gamma_1 = \gamma_2 = 1$. The behavior of the model (15) for perfect mixing (i.e $\beta \to \infty$) rewritten:

$$X_T^*(+\infty,\varepsilon) = (\gamma_1+\gamma_2)\frac{\varepsilon\gamma_2r_1 + \gamma_1r_2}{\varepsilon\gamma_2^2\alpha_1 + \gamma_1^2\alpha_2}, \tag{17}$$

where $\alpha_i = r_i/K_i$; which is the formula [2, Equation 7] given by Arditi et al with $\varepsilon = 1$.

First, we have the result:

THEOREM 3.1. *Let $(x_1(t,\varepsilon), x_2(t,\varepsilon))$ be the solution of the system (15) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geqslant 0$ for $i = 1,2$. Let $z(t)$ be the solution of the differential equation*

$$\frac{dx_1}{dt} = r_1x_1\left(1-\frac{x_1}{K_1}\right) + \beta(\gamma_2K_2 - \gamma_1x_1) =: \varphi(x_1), \tag{18}$$

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

$$x_1(t,\varepsilon) = z(t) + o_\varepsilon(1), \qquad \textit{uniformly for} \quad t \in [0,+\infty) \tag{19}$$

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

$$x_2(t,\varepsilon) = K_2 + o_\varepsilon(1), \qquad \textit{uniformly for} \quad t \in [t_0,+\infty). \tag{20}$$

Proof. When $\varepsilon \to 0$, the system (15) is a *slow-fast* system, with one *slow variable*, x_1, and one *fast variable*, x_2. Tikhonov's theorem [28, 30, 31] prompts us to consider the dynamics of the fast variable in the time scale $\tau = \frac{1}{\varepsilon}t$. One obtains

$$\frac{dx_2}{d\tau} = r_2 x_2\left(1 - \frac{x_2}{K_2}\right) + \varepsilon\beta(\gamma_1 x_1 - \gamma_2 x_2). \tag{21}$$

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

$$\frac{dx_2}{d\tau} = r_2 x_2\left(1 - \frac{x_2}{K_2}\right). \tag{22}$$

The slow manifold is given by the positive equilibrium of the system (22), 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 (15) converge to the solutions of the *reduced model* (18), obtained by replacing $x_2 = K_2$ into the dynamics of the slow variable.

The differential equation (18) admits as a positive equilibrium

$$x_1^*(\beta,0^+) := \frac{K_1}{2} - \frac{\beta}{2\alpha_1}\gamma_1 + \frac{1}{2\alpha_1}\sqrt{\gamma_1^2\beta^2 + (4\alpha_1\gamma_2K_2 - 2r_1\gamma_1)\beta + r_1^2}. \tag{23}$$

As $\varphi(x_1) > 0$ for all $0 \leqslant x_1 < x_1^*(\beta,0^+)$ and $\varphi(x_1) < 0$ for all $x_1 > x_1^*(\beta,0^+)$ then, the equilibrium $x_1^*(\beta,0^+)$ is GAS in the positive axis, so, the approximation given by Tikhonov's theorem holds for all $t \geqslant 0$ for the slow variable and for all $t \geqslant t_0 > 0$ for the fast variable, where t_0 is as small as we want. Therefore, let $z(t)$ be the solution of the reduced model (18) of initial condition $z(0) = x_1^0$, then, when $\varepsilon \to 0$, we have the approximations (19) and (20). $\square$

As a corollary of the previous theorem, we have the following result, which gives the limit of the total equilibrium population $X_T^*(\beta,\varepsilon)$ of the model (15) when ε goes to zero:

COROLLARY 3.1. *We have:*

$$\begin{aligned} X_T^*(\beta,0^+) &:= \lim_{\varepsilon\to 0} X_T^*(\beta,\varepsilon) = \lim_{\varepsilon\to 0}(x_1^*(\beta,\varepsilon) + x_2^*(\beta,\varepsilon)) \\ &= \frac{K_1}{2} + K_2 - \frac{\beta}{2\alpha_1}\gamma_1 + \frac{1}{2\alpha_1}\sqrt{\gamma_1^2\beta^2 + (4\alpha_1\gamma_2K_2 - 2r_1\gamma_1)\beta + r_1^2}. \end{aligned} \tag{24}$$

Proof. According to the equations (19), (20) and (23), when ε goes to zero, the equilibrium $E^*(\beta,\varepsilon)$ of the model (15) is converge to $E^*(\beta,0^+) := (x_1^*(\beta,0^+),K_2)$, where $x_1^*(\beta,0^+)$ is given in (23).The sum of the coordinates of $E^*(\beta,0^+)$ gives the formula (24). □

In the following proposition, we calculate the derivative and the formula of perfect mixing (i.e when $\beta \to \infty$) of the total equilibrium population defined by (24).

PROPOSITION 3.1. *Consider the total equilibrium population* (24)*. Then,*

$$\frac{dX_T^*}{d\beta}(0,0^+) := \frac{-\gamma_1 K_1 + \gamma_2 K_2}{r_1}, \tag{25}$$

and

$$X_T^*(+\infty,0^+) := \frac{\gamma_1+\gamma_2}{\gamma_1}K_2. \tag{26}$$

Proof. The derivative of the total equilibrium population $X_T^*(\beta,0^+)$ defined by (24) with respect to β is:

$$\frac{dX_T^*}{d\beta}(\beta,0^+) = -\frac{\gamma_1}{2\alpha_1} + \frac{1}{2\alpha_1}\frac{\gamma_1^2\beta + 2\gamma_2 K_2\alpha_1 - \gamma_1 r_1}{\sqrt{\gamma_1^2\beta^2 + (4\gamma_2 K_2\alpha_1 - 2\gamma_1 r_1)\beta + r_1^2}}. \tag{27}$$

In particular, the derivative of the total equilibrium population at $\beta = 0$ is given by the formula (25).

By taking the limit of (24) when $\beta \to \infty$, we get that the total equilibrium population $X_T^*(\beta,0^+)$ tends to (26). □

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

$$\mathscr{J}_0 = \left\{(\gamma_1,\gamma_2) : \frac{\gamma_2}{\gamma_1} > \frac{K_1}{K_2}\right\}, \quad \mathscr{J}_1 = \left\{(\gamma_1,\gamma_2) : \frac{\gamma_2}{\gamma_1} < \frac{K_1}{K_2}\right\}. \tag{28}$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (15) when ε goes to zero.

THEOREM 3.2. *Let* $\mathscr{J}_0$ *and* $\mathscr{J}_1$ *be the domains defined in* (28)*. Consider the total equilibrium population* $X_T^*(\beta,0^+)$ *given by* (24)*. Then, we have:*

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

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

$$
\begin{aligned}
X_T^*(\beta,0^+) = K_1 + K_2 &\Longleftrightarrow \frac{1}{2\alpha_1}\sqrt{\gamma_1^2\beta^2 + [4\alpha_1\gamma_2K_2 - 2r_1\gamma_1]\beta + r_1^2} = \frac{K_1}{2} + \frac{\beta}{2\alpha_1}\gamma_1 \\
&\Longleftrightarrow \sqrt{\gamma_1^2\beta^2 + [4\alpha_1\gamma_2K_2 - 2r_1\gamma_1]\beta + r_1^2} = r_1 + \gamma_1\beta \\
&\Longleftrightarrow 4\alpha_1\gamma_2K_2 - 2r_1\gamma_1 = 2r_1\gamma_1 \\
&\Longleftrightarrow \alpha_1\gamma_2K_2 = r_1\gamma_1 \\
&\Longleftrightarrow \gamma_2K_2 = K_1\gamma_1 \Longleftrightarrow \frac{dX_T^*}{d\beta}(0,0^+) = 0.
\end{aligned}
$$

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

We can also show Theorem 3.2 by using Prop A.1 of [14].

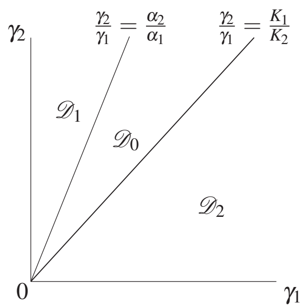

Figure 1: *The domains $\mathscr{D}_0$, $\mathscr{D}_1$ and $\mathscr{D}_2$ where $r_2 > r_1$ (i.e. $\frac{\alpha_2}{\alpha_1} > \frac{K_1}{K_2}$).*

Indeed, if r_2 is much larger than r_1, then the line $\frac{\gamma_2}{\gamma_1} = \frac{r_2K_1}{r_1K_2}$ becomes a vertical line in the set of parameters γ_1 and γ_2. Therefore, the domain $\mathscr{D}_1$ in Fig. 1 (see Fig. 7 of [14]) disappears and there remain the two domains $\mathscr{D}_0$ and $\mathscr{D}_2$ which are the same as the both domains $\mathscr{J}_0$ and $\mathscr{J}_1$ respectively given in (28). So, if $(\gamma_1,\gamma_2) \in \mathscr{D}_0$ then by the item 2 of [14, Prop. A.1], $X_T^*(\beta,0^+) > K_1 + K_2$ for all $\beta > 0$, and if $(\gamma_1,\gamma_2) \in \mathscr{D}_2$ then, $X_T^*(\beta,0^+) < K_1 + K_2$ for all $\beta > 0$.

Note that the critical value $\beta_0 > 0$ of the migration rate given in [14, Prop. A.1] and given also in [1, Prop.2] for the case $\gamma_1 = \gamma_2 = 1$, such that the effect is beneficial for lower values of β on the total equilibrium population and detrimental for the higher values; is written for our model (15) as follows:

$$\beta_0(\varepsilon) = \frac{(r_2 - r_1\varepsilon)\,\alpha_2\alpha_1}{(\alpha_1\varepsilon + \alpha_2)\,(\gamma_2\varepsilon\,\alpha_1 - \gamma_1\alpha_2)}. \tag{29}$$

When $\varepsilon \to 0$, we have $\lim_{\varepsilon\to 0}\beta_0(\varepsilon) = -\frac{\alpha_1 K_2}{\gamma_1} < 0$.

Biologically speaking, the existence of a faster growing sub population compared to the second one causes the critical value of migration rate to disappear. Thus, only three possible situations remain which the total equilibrium population may take instead of four, either the effect is beneficial, detrimental or not to depend on the migration rate.

In the following proposition, we show that, the function $\beta \mapsto X_T^*(\beta, 0^+)$ is monotonic in $[0, +\infty[$.

PROPOSITION 3.2. *If $(\gamma_1, \gamma_2) \in \mathscr{J}_0$ (resp. $(\gamma_1, \gamma_2) \in \mathscr{J}_1$), then the total equilibrium population $X_T^*(\beta, 0^+)$ is increasing (resp. decreasing) in $[0, +\infty[$.*

Proof. By the equation (27), we have:

$$
\begin{aligned}
&\frac{dX_T^*}{d\beta}(\beta, 0^+) = 0 \\
&\iff -1/2\,\frac{\gamma_1\sqrt{r_1{}^2 - 2r_1\beta\gamma_1 + \beta^2\gamma_1{}^2 + 4\alpha_1\beta K_2\gamma_2} + r_1\gamma_1 - \beta\gamma_1{}^2 - 2\alpha_1 K_2\gamma_2}{\sqrt{r_1{}^2 - 2r_1\beta\gamma_1 + \beta^2\gamma_1{}^2 + 4\alpha_1\beta K_2\gamma_2}\,\alpha_1} = 0 \\
&\iff 4r_1\gamma_1\alpha_1 K_2\gamma_2 - 4\alpha_1{}^2 K_2{}^2\gamma_2{}^2 = 0 \\
&\iff \gamma_1 K_1 - K_2\gamma_2 = 0.
\end{aligned}
$$

This last equation prove that $\frac{dX_T^*}{d\beta}(\beta, 0^+) > 0$ for all β if $(\gamma_1, \gamma_2) \in \mathscr{J}_0$, and $\frac{dX_T^*}{d\beta}(\beta, 0^+) < 0$ for all β if $(\gamma_1, \gamma_2) \in \mathscr{J}_1$. □

4. Three-patch model with two time scales dynamics

In this section, we consider the three-patch model, i.e the model (1), (3), (11) for $(n, m) = (3, 1)$. Our aim in what follows is to study the behavior of the model when two growth rates are much larger than the third one and we examine also the case when one growth rate is much larger than the other two. In particular, the aim is to compare the total equilibrium population with the sum of three carrying capacities.

4.1. Two growth rates are much larger than the third one

We assume that the growth rates r_2 and r_3 of the second and the third patches respectively are much larger than r_1. One can write the model (1), (11) for $n = 3$ and $m = 1$ in the following way:

$$
\begin{cases}
\dfrac{dx_1}{dt} = r_1 x_1\left(1 - \dfrac{x_1}{K_1}\right) + \beta(-(\gamma_{21} + \gamma_{31})x_1 + \gamma_{12}x_2 + \gamma_{13}x_3), \\
\dfrac{dx_2}{dt} = \dfrac{r_2}{\varepsilon}x_2\left(1 - \dfrac{x_2}{K_2}\right) + \beta(\gamma_{21}x_1 - (\gamma_{12} + \gamma_{32})x_2 + \gamma_{23}x_3), \\
\dfrac{dx_3}{dt} = \dfrac{r_3}{\varepsilon}x_3\left(1 - \dfrac{x_3}{K_3}\right) + \beta(\gamma_{31}x_1 + \gamma_{32}x_2 - (\gamma_{13} + \gamma_{23})x_3),
\end{cases}
\tag{30}
$$

where ε is assumed to be a small positive number.

First, we have the following result:

THEOREM 4.1. *Let* $(x_1(t,\varepsilon),x_2(t,\varepsilon),x_3(t,\varepsilon))$ *be the solution of the system* (30) *with initial condition* (x_1^0,x_2^0,x_3^0) *satisfying* $x_i^0 \geqslant 0$ *for* $i=1,2,3$. *Let* $z(t)$ *be the solution of the differential equation*

$$\frac{dx_1}{dt} = r_1x_1\left(1-\frac{x_1}{K_1}\right)+\beta(b-ax_1) =: \varphi(x_1), \tag{31}$$

with $a=\gamma_{21}+\gamma_{31}, b=\gamma_{12}K_2+\gamma_{13}K_3$ *and initial condition* $z(0)=x_1^0$. *Then, when* $\varepsilon \to 0$, *we have*

$$x_1(t,\varepsilon) = z(t)+o_\varepsilon(1), \quad \textit{uniformly for} \quad t\in[0,+\infty) \tag{32}$$

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

$$x_i(t,\varepsilon) = K_i+o_\varepsilon(1), \quad i=2,3, \textit{ uniformly for} \quad t\in[t_0,+\infty). \tag{33}$$

Proof. When $\varepsilon \to 0$, the system (30) is a *slow-fast* system, with one *slow variable*, x_1, and two *fast variables*, x_2 and x_3. Tikhonov's theorem [28, 30, 31] prompts us to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{\varepsilon}t$. One obtains

$$\begin{cases} \dfrac{dx_2}{d\tau} = r_2x_2\left(1-\dfrac{x_2}{K_2}\right)+\varepsilon\beta(\gamma_{21}x_1-(\gamma_{12}+\gamma_{32})x_2+\gamma_{23}x_3), \\ \dfrac{dx_3}{d\tau} = r_3x_3\left(1-\dfrac{x_3}{K_3}\right)+\varepsilon\beta(\gamma_{31}x_1+\gamma_{32}x_2-(\gamma_{13}+\gamma_{23})x_3). \end{cases} \tag{34}$$

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

$$\begin{cases} \dfrac{dx_2}{d\tau} = r_2x_2\left(1-\frac{x_2}{K_2}\right), \\ \dfrac{dx_3}{d\tau} = r_3x_3\left(1-\dfrac{x_3}{K_3}\right). \end{cases} \tag{35}$$

The slow manifold is given by the positive equilibrium point of the system (35), i.e $(x_2,x_3)=(K_2,K_3)$, which is GAS in the interior of the positive cone. When ε goes to zero, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (30) converge to solutions of the *reduced model* (31), obtained by replacing $x_2=K_2$ and $x_3=K_3$ into the dynamics of the slow variable.

The differential equation (31) admits

$$x_1^*(\beta,0^+) := \frac{K_1}{2}-\frac{\beta}{2\alpha_1}a+\frac{1}{2\alpha_1}\sqrt{a^2\beta^2+(4\alpha_1 b-2r_1a)\beta+r_1^2}, \tag{36}$$

as a positive equilibrium point, which is GAS in the positive axis by the same reason as the point (23), so, the approximation given by Tikhonov's theorem holds for all

$t \geqslant 0$ for the slow variable and for all $t \geqslant t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, let $z(t)$ be the solution of the reduced model (31) of initial condition $z(0) = x_1^0$, then, when $\varepsilon \to 0$, we have the approximations (32) and (33). □

As a corollary of the previous theorem, we have the following result which gives the limit of the total equilibrium population $X_T^*(\beta, \varepsilon)$ of the model (30) when ε goes to zero:

COROLLARY 4.1. *We have:*

$$X_T^*(\beta, 0^+) := \lim_{\varepsilon \to 0} X_T^*(\beta, \varepsilon) = \lim_{\varepsilon \to 0} (x_1^*(\beta, \varepsilon) + x_2^*(\beta, \varepsilon) + x_3^*(\beta, \varepsilon))$$
$$= \frac{K_1}{2} + K_2 + K_3 - \frac{\beta}{2\alpha_1} a + \frac{1}{2\alpha_1} \sqrt{a^2\beta^2 + (4\alpha_1 b - 2r_1 a)\beta + r_1^2}. \tag{37}$$

Proof. According to the equations (32), (33) and (36), when ε goes to zero, the equilibrium $E^*(\beta, \varepsilon)$ of the model (30) converges to $E^*(\beta, 0^+) := (x_1^*(\beta, 0^+), K_2, K_3)$, where $x_1^*(\beta, 0^+)$ is given in (36).The sum of the coordinates of $E^*(\beta, 0^+)$ gives the formula (37). □

PROPOSITION 4.1. *Consider the total equilibrium* (37). *Then,*

$$\frac{dX_T^*}{d\beta}(0, 0^+) = \frac{-aK_1 + b}{r_1}, \tag{38}$$

and

$$X_T^*(+\infty, 0^+) := K_2 + K_3 + \frac{b}{a}. \tag{39}$$

Proof. The derivative of the total equilibrium population $X_T^*(\beta, 0^+)$ defined in (37) with respect to β is:

$$\frac{dX_T^*}{d\beta}(\beta, 0^+) = -\frac{a}{2\alpha_1} + \frac{1}{2\alpha_1} \frac{a^2\beta + 2b\alpha_1 - ar_1}{\sqrt{a^2\beta^2 + (4b\alpha_1 - 2ar_1)\beta + r_1^2}}. \tag{40}$$

In particular, the derivative of the total equilibrium population at $\beta = 0$ is given by (38).

By taking the limit of (37) when $\beta \to \infty$, we get that the total equilibrium population $X_T^*(\beta, 0^+)$ tend to the limit (39). □

We consider the regions in the set of the parameters a and b, denoted $\mathscr{D}_0$ and $\mathscr{D}_1$ defined by:

$$\mathscr{D}_0 = \{(a, b) : b > aK_1\}, \quad \mathscr{D}_1 = \{(a, b) : b < aK_1\} \tag{41}$$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (30) when ε goes to zero.

COROLLARY 4.2. *Consider the equation* $X_T^*(\beta,0^+)$ *defined in* (37). *Let* $\mathscr{D}_0$ *and* $\mathscr{D}_1$ *be the domains defined by* (41). *Then, we have*

- *If* $(a,b) \in \mathscr{D}_0$ *then* $X_T^*(\beta,0^+) > K_1+K_2+K_3$, *for all* $\beta > 0$.
- *If* $(a,b) \in \mathscr{D}_1$ *then* $X_T^*(\beta,0^+) < K_1+K_2+K_3$, *for all* $\beta > 0$.
- *If* $aK_1 = b$, *then* $x_1^*(\beta,0^+) = K_1, x_2^*(\beta,0^+) = K_2$ *and* $x_2^*(\beta,0^+) = K_3$ *for all* $\beta \geqslant 0$. *Therefore* $X_T^*(\beta,0^+) = K_1+K_2+K_3$ *for all* $\beta \geqslant 0$.

Proof. The result is a consequence of Theorem 3.2. □

REMARK 4.1. When $\varepsilon \to 0$, the condition $aK_1 = b$ is equivalent to $(K_1,K_2,K_3)^T \in \ker\Gamma$. Indeed, if $(K_1,K_2,K_3)^T \in \ker\Gamma$ then

$$\begin{cases} -(\gamma_{21}+\gamma_{31})K_1+\gamma_{12}K_2+\gamma_{13}K_3=0, \\ \gamma_{21}K_1-(\gamma_{12}+\gamma_{32})K_2+\gamma_{23}K_3=0, \\ \gamma_{31}K_1+\gamma_{32}K_2-(\gamma_{13}+\gamma_{23})K_3=0, \end{cases} \tag{42}$$

The first equation of (42) gives $aK_1 = b$.

Now, when $\varepsilon \to 0$, if $aK_1 = b$, then (K_1,K_2,K_3) is an equilibrium of (30), i.e $\Gamma(K_1,K_2,K_3)^T = 0$, so $(K_1,K_2,K_3)^T \in \ker\Gamma$

Note that, Elbetch et al. [14, Prop. 4.5] have shown that the total equilibrium population is independent of the migration rate β if and only if $(K_1,\dots,K_n)^T \in \ker\Gamma$, which is the same with the item 3 of Corollary 4.2.

In [14, Section 6], Elbetch et al. showed that, for the three-patch model, the existence of at least three positive values of migration rate such that $X_T^*(\beta) = K_1+K_2+K_3$. Biologically speaking, the results of Corollary 4.2 prove that the existence of two faster sub populations compared to the third one, causes the all critical values of migration rate to disappear. Thus, when $\varepsilon \to 0$, the total equilibrium population of the model (30) behaves like the total equilibrium population of the two-patch model (15), i.e there are only three possible situations that the total population can take, either the effect is beneficial, detrimental or not to depend on the migration rate.

4.2. One growth rate is much larger than the other two

In this section, we assume that the growth rate r_3 of the third patch is much larger than r_1 and r_2. One can write the model (1), (3), (11) for $(n,m) = (3,2)$ in the following way:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right)+\beta(-(\gamma_{21}+\gamma_{31})x_1+\gamma_{12}x_2+\gamma_{13}x_3), \\ \dfrac{dx_2}{dt} = r_2x_2\left(1-\dfrac{x_2}{K_2}\right)+\beta(\gamma_{21}x_1-(\gamma_{12}+\gamma_{32})x_2+\gamma_{23}x_3), \\ \dfrac{dx_3}{dt} = \dfrac{r_3}{\varepsilon}x_3\left(1-\dfrac{x_3}{K_3}\right)+\beta(\gamma_{31}x_1+\gamma_{32}x_2-(\gamma_{13}+\gamma_{23})x_3), \end{cases} \tag{43}$$

where ε is assumed to be a small positive number.

We have the following theorem:

THEOREM 4.2. *Let* $(x_1(t,\varepsilon),x_2(t,\varepsilon),x_3(t,\varepsilon))$ *be the solution of the system* (43) *with initial condition* (x_1^0,x_2^0,x_3^0) *satisfying* $x_i^0 \geqslant 0$ *for* $i=1,2,3$*. Let* $(z_1(t),z_2(t))$ *be the solution of the system*

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right)+\beta(-(\gamma_{21}+\gamma_{31})x_1+\gamma_{12}x_2+\gamma_{13}K_3) =: f_1(x_1,x_2), \\ \dfrac{dx_2}{dt} = r_2x_2\left(1-\dfrac{x_2}{K_2}\right)+\beta(\gamma_{21}x_1-(\gamma_{12}+\gamma_{32})x_2+\gamma_{23}K_3) =: f_2(x_1,x_2), \end{cases} \tag{44}$$

with initial condition $(z_1(0),z_2(0))=(x_1^0,x_2^0)$*. Then, when* $\varepsilon\to 0$*, we have*

$$x_i(t,\varepsilon)=z_i(t)+o_\varepsilon(1), \qquad i=1,2 \text{ uniformly for } \ t\in[0,+\infty] \tag{45}$$

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

$$x_3(t,\varepsilon)=K_3+o_\varepsilon(1), \text{ uniformly for } \ t\in[t_0,+\infty]. \tag{46}$$

Proof. When $\varepsilon\to 0$, the system (43) is a *slow-fast* system, with two *slow variables*, x_1 and x_2, and one *fast variable* x_3. We consider the dynamics of the fast variable in the time scale $\tau=\frac{1}{\varepsilon}t$. One obtains

$$\frac{dx_3}{d\tau}=r_3x_3\left(1-\frac{x_3}{K_3}\right)+\varepsilon\beta(\gamma_{31}x_1+\gamma_{32}x_2-(\gamma_{13}+\gamma_{23})x_3). \tag{47}$$

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

$$\frac{dx_3}{d\tau}=r_3x_3\left(1-\frac{x_3}{K_3}\right). \tag{48}$$

The slow manifold is given by the positive equilibrium point of the equation (48), i.e $x_3=K_3$, which is GAS in the positive axis. Tikhonov's theorem [28, 30, 31] ensures that after a fast transition toward the slow manifold, the solutions of (43) are approximated by the solutions of the *reduced model* (44), obtained by replacing $x_3=K_3$ into the dynamics of the slow variable. The approximations (45) and (46) follow from Tikhonov's theorem. □

4.2.1. Global stability of the reduced model (44)

For $\beta=0$ the system (44) is uncoupled and there exists an equilibrium (K_1,K_2) interior to the positive quadrant which is GAS. The problem is whether the equilibrium continues to be positive and GAS for any β or not. Clearly, when β is sufficiently small, from elementary perturbation theory it follows that there always exists an interior equilibrium. First, we start by studying the existence of equilibrium of system (44) (see Prop. A.1). Second, in Theorem A.1, we prove the global stability of System (44).

We denoted $\mathscr{E}^*(\beta,0^+):=(x_1^*(\beta,0^+),x_2^*(\beta,0^+))$ the equilibrium of (44) and $X_T^*(\beta,0^+):=x_1^*(\beta,0^+)+x_2^*(\beta,0^+)+K_3$ the total equilibrium population.

4.2.2. Perfect mixing

For the behavior of the reduced model (44) for large migration rate, i.e when $\beta \to \infty$, we prove the following result:

PROPOSITION 4.2. *We have:*

$$\lim_{\beta \to +\infty} \mathscr{E}^*(\beta, 0^+) = \frac{K_3}{\delta_3}(\delta_1, \delta_2),$$

where δ_1, δ_2 and δ_3 are given by:

$$\begin{cases} \delta_1 = \gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{32}\gamma_{13}, \\ \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \\ \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32}. \end{cases} \tag{49}$$

Proof. Denote: $\mathscr{E}^*(\infty, 0^+) = \frac{K_3}{\delta_3}(\delta_1, \delta_2)$. The equilibrium point $\mathscr{E}^*(\beta, 0^+)$ is the solution in the positive cone $\mathbb{R}^2_+$, of the equation $F_\beta = 0$, where

$$F_\beta : \mathbb{R}^2 \to \mathbb{R}^2, \quad (x_1, x_2) \longmapsto (f_1^\beta(x_1, x_2), f_2^\beta(x_1, x_2)),$$

where f_1^β and f_2^β are defined by the first and the second equation of the right hand of (44) respectively. Taking the limit $\beta \to \infty$, of F_β gives

$$F_\infty : \mathbb{R}^2 \to \mathbb{R}^2, \quad (x_1, x_2) \longmapsto (f_1^\infty(x_1, x_2), f_2^\infty(x_1, x_2)),$$

where

$$\begin{cases} f_1^\infty(x_1, x_2) = -(\gamma_{21} + \gamma_{31})x_1 + \gamma_{12}x_2 + \gamma_{13}K_3, \\ f_2^\infty(x_1, x_2) = \gamma_{21}x_1 - (\gamma_{12} + \gamma_{32})x_2 + \gamma_{23}K_3. \end{cases} \tag{50}$$

Since the matrix $\Gamma = (\gamma_{ij})_{3\times 3}$ is irreducible, the solution of the equation $F_\infty = 0$ is given by $\mathscr{E}^*(\infty, 0^+)$. Therefore, when $\beta \to \infty$, the equilibrium $\mathscr{E}^*(\beta, 0^+)$ tend to $\mathscr{E}^*(\infty, 0^+)$. □

COROLLARY 4.3. *Consider the total equilibrium of* (43) *when $\varepsilon \to 0$. Then, when $\beta \to \infty$, the total equilibrium population $X_T^*(\beta, 0^+) := x_1^*(\beta, 0^+) + x_2^*(\beta, 0^+) + x_3^*(\beta, 0^+)$ tends to:*

$$X_T^*(+\infty, 0^+) = \frac{K_3}{\delta_3}(\delta_1 + \delta_2 + \delta_3). \tag{51}$$

Proof. As the equilibrium $\mathscr{E}^*(\beta, 0^+)$ tends to $\frac{K_3}{\delta_3}(\delta_1, \delta_2)$ when $\beta \to \infty$, then

$$\lim_{\beta\to\infty} X_T^*(\beta, 0^+) = \lim_{\beta\to\infty} (x_1^*(\beta, 0^+) + x_2^*(\beta, 0^+) + x_3^*(\beta, 0^+)) = \frac{K_3}{\delta_3}(\delta_1 + \delta_2 + \delta_3). \quad \square$$

4.2.3. Total population abundance

In this part, our aim is to compare the total equilibrium population $X_T^*(\beta,0^+)$ of (43) with the sum of three carrying capacities, by analyzing the stable positive equilibrium $\mathscr{E}^*(\beta,0^+)$ of (44). When there is no migration (i.e $\beta=0$) the total equilibrium population equal to $K_1+K_2+K_3$. First for all, we give some proprieties of the total equilibrium population $X_T^*(\beta,0^+)$.

LEMMA 4.1. *The total equilibrium population $X_T^*(\beta,0^+)$ of (43) satisfies the following relation:*

$$X_T^*(\beta,0^+) = K_1+K_2+K_3+\beta\left(\frac{-(\gamma_{21}+\gamma_{31})x_1^*(\beta,0^+)+\gamma_{12}x_2^*(\beta,0^+)+\gamma_{13}K_3}{\alpha_1 x_1^*(\beta,0^+)}\right.$$
$$\left.+\frac{\gamma_{21}x_1^*(\beta,0^+)-(\gamma_{12}+\gamma_{32})x_2^*(\beta,0^+)+\gamma_{23}K_3)}{\alpha_2 x_2^*(\beta,0^+)}\right). \tag{52}$$

Proof. The equilibrium point $\mathscr{E}^*(\beta,0^+)$ of the reduced model (44) satisfies:

$$\begin{cases} 0 = r_1x_1^*(\beta,0^+)\left(1-\dfrac{x_1^*(\beta,0^+)}{K_1}\right)+\beta(-(\gamma_{21}+\gamma_{31})x_1^*(\beta,0^+) \\ \qquad +\gamma_{12}x_2^*(\beta,0^+)+\gamma_{13}K_3), \\ 0 = r_2x_2^*(\beta,0^+)\left(1-\dfrac{x_2^*(\beta,0^+)}{K_2}\right)+\beta(\gamma_{21}x_1^*(\beta,0^+) \\ \qquad -(\gamma_{12}+\gamma_{32})x_2^*(\beta,0^+)+\gamma_{23}K_3). \end{cases} \tag{53}$$

Dividing the first equation in (53) by $\alpha_1x_1^*(\beta,0^+)$ and the second by $\alpha_2x_2^*(\beta,0^+)$, we obtain

$$\begin{cases} x_1^*(\beta,0^+) = K_1+\beta\dfrac{-(\gamma_{21}+\gamma_{31})x_1^*(\beta,0^+)+\gamma_{12}x_2^*(\beta,0^+)+\gamma_{13}K_3}{\alpha_1x_1^*(\beta,0^+)}, \\ x_2^*(\beta,0^+) = K_2+\beta\dfrac{\gamma_{21}x_1^*(\beta,0^+)-(\gamma_{12}+\gamma_{32})x_2^*(\beta,0^+)+\gamma_{23}K_3}{\alpha_2x_2^*(\beta,0^+)}. \end{cases} \tag{54}$$

Taking the sum of these expressions gives the total equilibrium population for reduced model, and by approximation (46) we deduce the relation (52). □

LEMMA 4.2. *The derivative of the total equilibrium population $X_T^*(\beta,0^+)$ at $\beta=0$ is given by:*

$$\frac{dX_T^*}{d\beta}(0,0^+) = \frac{-(\gamma_{21}+\gamma_{31})K_1+\gamma_{12}K_2+\gamma_{13}K_3}{r_1}+\frac{\gamma_{21}K_1-(\gamma_{12}+\gamma_{32})K_2+\gamma_{23}K_3}{r_2}. \tag{55}$$

Proof. By differentiating the equation (52), at $\beta=0$, we get

$$\frac{dX_T^*}{d\beta}(0,0^+) = \frac{-(\gamma_{21}+\gamma_{31})x_1^*(0,0^+)+\gamma_{12}x_2^*(0,0^+)+\gamma_{13}K_3}{\alpha_1x_1^*(0,0^+)}$$
$$+\frac{\gamma_{21}x_1^*(0,0^+)-(\gamma_{12}+\gamma_{32})x_2^*(0,0^+)+\gamma_{23}K_3)}{\alpha_2x_2^*(0,0^+)}, \tag{56}$$

which gives (55), since $x_1^*(0,0^+) = K_1$ and $x_2^*(0,0^+) = K_2$. □

In the remainder of this section, we denote:

$$\begin{cases} c_1 = K_1 r_2(\gamma_{12}+\gamma_{31}+\gamma_{21}) + K_2 r_1(\gamma_{21}+\gamma_{32}+\gamma_{12}), \\ c_2 = -K_1 r_2\gamma_{21}K_2 - 2K_1 r_2\gamma_{12}K_2 - K_1{}^2 r_2\gamma_{31} - K_1 r_2\gamma_{31}K_2 \\ \qquad -K_1{}^2 r_2\gamma_{21} - K_1 r_2\gamma_{13}K_3 - K_2 r_1\gamma_{32}K_1 - 2K_1{}^2 r_2\gamma_{12} - K_2{}^2 r_1\gamma_{12} \\ \qquad +K_2 r_1\gamma_{23}K_3 - K_2 r_1\gamma_{12}K_1 - K_2{}^2 r_1\gamma_{32}, \\ c_3 = K_1 r_2\gamma_{13}K_3K_2 + K_1 r_2\gamma_{12}K_2{}^2 + K_1{}^3 r_2\gamma_{12} + 2K_1{}^2 r_2\gamma_{12}K_2 + K_1{}^2 r_2\gamma_{13}K_3. \end{cases} \tag{57}$$

As the matrix $\Gamma = (\gamma_{ij})_{3\times 3}$ is irreducible, then $c_1 > 0$ and $c_3 > 0$. We denote: $\xi_1 = \frac{c_2}{c_1}$, $\xi_2 = \frac{c_3}{c_1}$, $\Delta = \xi_1^2 - 4\xi_2$ and m_i, $i = 1,\ldots,5$ are defined as follows:

$$\begin{cases} m_1 = -\xi_1 - \sqrt{\Delta}, \quad m_2 = -\xi_1 + \sqrt{\Delta} \qquad \text{if} \quad \Delta \geqslant 0, \\ m_3 = -2m_1(\gamma_{12}+\gamma_{21}+\gamma_{31}) + 4(\gamma_{12}K_1 + \gamma_{12}K_2 + \gamma_{13}K_3), \\ m_4 = -2m_2(\gamma_{12}+\gamma_{21}+\gamma_{31}) + 4(\gamma_{12}K_1 + \gamma_{12}K_2 + \gamma_{13}K_3), \\ m_5 = 2\xi_1(\gamma_{12}+\gamma_{21}+\gamma_{31}) + 4(\gamma_{12}K_1 + \gamma_{12}K_2 + \gamma_{13}K_3). \end{cases} \tag{58}$$

Notice that: $\xi_2 > 0$, and if $\Delta = 0$ then $m_3 = m_4 = m_5$.

We consider the regions in the set of parameters ξ_1 and ξ_2, denoted $\mathscr{J}_0 := \mathscr{J}_0^- \cup \mathscr{J}_0^+$, $\mathscr{J}_> := \mathscr{J}_>^- \cup \mathscr{J}_>^+$ and $\mathscr{J}_< := \mathscr{J}_<^- \cup \mathscr{J}_<^+$ depicted in Fig. 2 and defined by:

$$\mathscr{J}_0 := \mathscr{J}_0^- \cup \mathscr{J}_0^+ : \begin{cases} \mathscr{J}_0^- = \left\{(\xi_1,\xi_2) : \xi_2 = \frac{\xi_1^2}{4}, \xi_1 < 0\right\}, \\ \mathscr{J}_0^+ = \left\{(\xi_1,\xi_2) : \xi_2 = \frac{\xi_1^2}{4}, \xi_1 > 0\right\}. \end{cases} \tag{59}$$

$$\mathscr{J}_> := \mathscr{J}_>^- \cup \mathscr{J}_>^+ : \begin{cases} \mathscr{J}_>^- = \left\{(\xi_1,\xi_2) : \xi_2 > \frac{\xi_1^2}{4}, \xi_1 < 0\right\}, \\ \mathscr{J}_>^+ = \left\{(\xi_1,\xi_2) : \xi_2 > \frac{\xi_1^2}{4}, \xi_1 \geqslant 0\right\}. \end{cases} \tag{60}$$

$$\mathscr{J}_< := \mathscr{J}_<^- \cup \mathscr{J}_<^+ : \begin{cases} \mathscr{J}_<^- = \left\{(\xi_1,\xi_2) : 0 < \xi_2 < \frac{\xi_1^2}{4}, \xi_1 < 0\right\}, \\ \mathscr{J}_<^+ = \left\{(\xi_1,\xi_2) : 0 < \xi_2 < \frac{\xi_1^2}{4}, \xi_1 > 0\right\}. \end{cases} \tag{61}$$

We can now state our main result:

THEOREM 4.3. *Consider the total equilibrium population $X_T^*(\beta,0^+)$ of (43) when $\varepsilon \to 0$. Let $\frac{dX_T^*}{d\beta}(0,0^+)$ be the derivative of $X_T^*(\beta,0^+)$ at $\beta = 0$ given by (55). Let $\mathscr{J}_0 := \mathscr{J}_0^- \cup \mathscr{J}_0^+$, $\mathscr{J}_> := \mathscr{J}_>^- \cup \mathscr{J}_>^+$ and $\mathscr{J}_< := \mathscr{J}_<^- \cup \mathscr{J}_<^+$ be the domains depicted in Fig. 2 and defined by (59), (60) and (61) respectively. Then,*

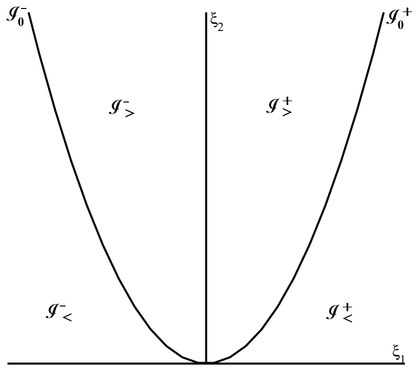

Figure 2: *The domain* $\mathscr{I}_0 := \mathscr{I}_0^- \cup \mathscr{I}_0^+, \mathscr{I}_> := \mathscr{I}_>^- \cup \mathscr{I}_>^+$ *and* $\mathscr{I}_< := \mathscr{I}_<^- \cup \mathscr{I}_<^+$ *in the set of parameters* ξ_1 *and* ξ_2.

1. *if* $(\xi_1,\xi_2) \in \mathscr{I}_< \cup \mathscr{I}_0^+ \cup \mathscr{I}_>^+$, *then, for all* $\beta \geqslant 0$:

$$X_T^*(\beta,0^+) = \begin{cases} > K_1+K_2+K_3 \ \ \text{if} \ \ \frac{dX_T^*}{d\beta}(0,0^+) > 0, \\ < K_1+K_2+K_3 \ \ \text{if} \ \ \frac{dX_T^*}{d\beta}(0,0^+) < 0. \end{cases} \tag{62}$$

2. *Let* $(\xi_1,\xi_2) \in \mathscr{I}_0^-$. *Let* m_5 *be given in* (58).

   (a) *if* $(2K_1+\xi_1)m_5 < 0$ *then there exist unique* $\beta^* = \frac{\alpha_1\xi_1(2K_1+\xi_1)}{m_5} > 0$ *such that:*

$$\begin{cases} \text{if} \ \frac{dX_T^*}{d\beta}(0,0^+) > 0 \ \text{then} \ X_T^*(\beta,0^+) = \begin{cases} > K_1+K_2+K_3 \ \ \text{if} \ \ 0 \leqslant \beta \leqslant \beta^*, \\ < K_1+K_2+K_3 \ \ \text{if} \ \ \beta \geqslant \beta^*. \end{cases} \\ \text{if} \ \frac{dX_T^*}{d\beta}(0,0^+) < 0 \ \text{then} \ X_T^*(\beta,0^+) = \begin{cases} < K_1+K_2+K_3 \ \ \text{if} \ \ 0 \leqslant \beta \leqslant \beta^*, \\ > K_1+K_2+K_3 \ \ \text{if} \ \ \beta \geqslant \beta^*. \end{cases} \end{cases} \tag{63}$$

   (b) *if* $(2K_1+\xi_1)m_5 \geqslant 0$ *with* $m_5 \neq 0$ *then the total equilibrium population* $X_T^*(\beta,0^+)$ *satisfies to* (62).

   (c) *if* $m_5 = 0$, *then* $x_1^*(\beta,0^+) = K_1, x_2^*(\beta,0^+) = K_2$ *and* $x_3^*(\beta,0^+) = K_3$ *for all* $\beta \geqslant 0$. *Therefore,* $X_T^*(\beta,0^+) = K_1+K_2+K_3$ *for all* β.

3. *Let* $(\xi_1,\xi_2) \in \mathscr{I}_>^-$. *Let* m_1, m_2, m_3 *and* m_4 *be given in* (58).

   (a) *if* $m_3(m_1-2K_1) > 0$ *and* $m_4(m_2-2K_1) > 0$, *then there exist two values of migration rate* $\beta_1^* = \frac{\alpha_1 m_1(m_1-2K_1)}{m_3} > 0$ *and* $\beta_2^* = \frac{\alpha_1 m_2(m_2-2K_1)}{m_4} > 0$ *such* *that:*

$$\begin{cases} \text{if } \frac{dX_T^*}{d\beta}(0,0^+) > 0 \text{ then } X_T^*(\beta,0^+) = \begin{cases} > K_1+K_2+K_3 \\ \quad \text{if } \beta \in [0,\beta_1] \cup [\beta_2,\infty[, \\ < K_1+K_2+K_3 \\ \quad \text{if } \beta \in [\beta_1,\beta_2]. \end{cases} \\ \text{if } \frac{dX_T^*}{d\beta}(0,0^+) < 0 \text{ then } X_T^*(\beta,0^+) = \begin{cases} < K_1+K_2+K_3 \\ \quad \text{if } \beta \in [0,\beta_1] \cup [\beta_2,\infty[, \\ > K_1+K_2+K_3 \\ \quad \text{if } \beta \in [\beta_1,\beta_2]. \end{cases} \end{cases} \tag{64}$$

(b) if $m_3(m_1-2K_1) \leqslant 0$ with $m_3 \neq 0$ and $m_4(m_2-2K_1) > 0$ or $m_3(m_1-2K_1) > 0$ and $m_4(m_2-2K_1) \leqslant 0$ with $m_4 \neq 0$ then there exist unique β^* such that, the total equilibrium population $X_T^*(\beta,0^+)$ satisfies to (63).

(c) if $m_3(m_1-2K_1) \leqslant 0$ and $m_4(m_2-2K_1) \leqslant 0$ with $m_3 \neq 0$ and $m_4 \neq 0$ then, the total equilibrium population $X_T^*(\beta,0^+)$ satisfies to (62).

(d) if $m_3 = 0$ or $m_4 = 0$, then $x_1^*(\beta,0^+) = K_1, x_2^*(\beta,0^+) = K_2$ and $x_3^*(\beta,0^+) = K_3$ for all $\beta \geqslant 0$. Therefore, $X_T^*(\beta,0^+) = K_1+K_2+K_3$ for all β.

Proof. By Equation (52), the equality $X_T^* = K_1+K_2+K_3$ is equivalent to $\beta = 0$ or

$$\begin{aligned} &-(\gamma_{21}K_1r_2+\gamma_{31}K_1r_2+\gamma_{12}K_2r_1+\gamma_{32}K_2r_1)x_1^*x_2^*+\gamma_{12}K_1r_2{x_2^*}^2 \\ &+\gamma_{13}K_3K_1r_2x_2^*+\gamma_{21}K_2r_1{x_1^*}^2+\gamma_{23}K_3K_2r_1x_1^* = 0 \end{aligned} \tag{65}$$

Thus (x_1^*,x_2^*) is the solution of the following algebraic system:

$$\begin{cases} -(\gamma_{21}K_1r_2+\gamma_{31}K_1r_2+\gamma_{12}K_2r_1+\gamma_{32}K_2r_1)x_1^*x_2^*+\gamma_{12}K_1r_2{x_2^*}^2 \\ +\gamma_{13}K_3K_1r_2x_2^*+\gamma_{21}K_2r_1{x_1^*}^2+\gamma_{23}K_3K_2r_1x_1^* = 0, \\ x_1^*+x_2^* = K_1+K_2. \end{cases} \tag{66}$$

By the second equation of (66), we get $x_2^* = K_1+K_2-x_1^*$. Substitute x_2^* into the first equation in (66) to obtain the following quadratic equation of x_1^*:

$$(x_1^*)^2+\xi_1x_1^*+\xi_2 = 0, \tag{67}$$

where the coefficients $\xi_1 = c_2/c_1$ and $\xi_2 = c_3/c_1$ are given in (57).

(1) If $(\xi_1,\xi_2) \in \mathscr{J}_<$, then $\Delta < 0$, and the equation (67) admits no solutions, therefore, the system (66) admits no solutions. If $(\xi_1,\xi_2) \in \mathscr{J}_0^+$, then $\Delta = 0$, so the equation (67) admits $x_1^* = -\xi_1/2$ as solution which is negative. The case where $(\xi_1,\xi_2) \in \mathscr{J}_>^+$, we have $\Delta > 0$ and the equation (67) admits two negative solutions. Thus, if $(\xi_1,\xi_2) \in \mathscr{J}_< \cup \mathscr{J}_0^+ \cup \mathscr{J}_>^+$, then, the inequalities (62) are satisfied.

(2) Let $(\xi_1,\xi_2) \in \mathscr{J}_0^-$. The equation (67) admits the positive solution $x_1^* = -\xi_1/2$. By the second equation of (66), we deduce that $x_2^* = K_1 + K_2 + \frac{\xi_1}{2}$. So the system (66) admits a unique solution given by $(\frac{-\xi_1}{2}, K_1 + K_2 + \frac{\xi_1}{2})$. If we replace this last solution in the first equation of (44) we obtain $\beta^* = \frac{\alpha_1\xi_1(2K_1+\xi_1)}{m_5}$ with $m_5 \neq 0$. So, if $\frac{2K_1+\xi_1}{m_5} > 0$ then β^* is positive and the inequalities (63) are satisfied, otherwise, $\beta = 0$ is the unique solution of the equation $X_T^* = K_1 + K_2 + K_3$, and (62) is satisfied. If $m_5 = 0$, then if we replace the solution $(\frac{-\xi_1}{2}, K_1 + K_2 + \frac{\xi_1}{2})$ in the first equation of (44) we obtain $\frac{-\xi_1}{2} = K_1$. Thus $X_T^*(\beta,0^+) = K_1 + K_2 + K_3$ for all β.

(3) Let $(\xi_1,\xi_2) \in \mathscr{J}_>^-$, therefore, $\Delta > 0$ and $c_2 < 0$, then the equation (67) admits two positive solutions given by $x_{11}^* = \frac{m_2}{2}$ and $x_{12}^* = \frac{m_1}{2}$. By the second equation of (66), we deduce: $x_{21}^* = K_1 + K_2 - \frac{m_2}{2}$, and $x_{22}^* = K_1 + K_2 - \frac{m_1}{2}$ respectively. So the system (66) admits two positive solutions given by: (x_{11}^*, x_{21}^*) and (x_{12}^*, x_{22}^*). If we replace the first (resp. the second) solution in the first equation of (44) we obtain $\beta_1^* = \frac{\alpha_1 m_1(m_1-2K_1)}{m_3}$ (resp. $\beta_2^* = \frac{\alpha_1 m_2(m_2-2K_1)}{m_4}$).

We discuss the existence of β_1^* and β_2^* with respect to signs of $\frac{m_1(m_1-2K_1)}{m_3}$ and $\frac{m_2(m_2-2K_1)}{m_4}$ respectively. In particular, if β_1^* and β_2^* are positive then the inequalities (64) are satisfied. If $m_3 = 0$ (resp. $m_4 = 0$), then if we replace the solution $(\frac{m_1}{2}, K_1 + K_2 + \frac{m_1}{2})$ (resp. $(\frac{m_2}{2}, K_1 + K_2 + \frac{m_2}{2})$) in the first equation of (44), we obtain that $\frac{m_1}{2} = K_1$ (resp. $\frac{m_2}{2} = K_1$). Thus, $X_T^*(\beta,0^+) = K_1 + K_2 + K_3$ for all β. $\square$

Let $\mathscr{S}$ be a set of the non negative solutions of the equation $X_T^*(\beta,0^+) = K_1 + K_2 + K_3$, which can be summarized as follows:

$$
\text{If } \Delta > 0 \text{ then } \begin{cases} \text{If } \xi_1 \geqslant 0 \text{ then } \mathscr{S} = \{0\}, \\ \text{If } \xi_1 < 0 \text{ then } \begin{cases} \text{If } m_3(m_1-2K_1) \leqslant 0, \text{ with } m_3 \neq 0 \text{ and} \\ m_4(m_2-2K_1) \leqslant 0 \text{ with } m_4 \neq 0, \text{ then } \mathscr{S} = \{0\}, \\ \text{If } m_3(m_1-2K_1) > 0 \text{ and } m_4(m_2-2K_1) \leqslant 0) \text{ or} \\ (m_3(m_1-2K_1) \leqslant 0 \text{ and } m_4(m_2-2K_1) > 0 \\ \text{then } \mathscr{S} = \left\{0, \alpha_1 m_1 \frac{(m_1-2K_1)}{m_3}\right\} \text{ or} \\ \mathscr{S} = \left\{0, \alpha_1 m_2 \frac{(m_2-2K_1)}{m_4}\right\} \text{ respectively .} \\ \text{If } m_3(m_1-2K_1) > 0 \text{ and } m_4(m_2-2K_1) > 0 \text{ then} \\ \mathscr{S} = \{0, \alpha_1 m_1 \frac{(m_1-2K_1)}{m_3}, \alpha_1 m_2 \frac{(m_2-2K_1)}{m_4}\}, \\ \text{If } m_3 = 0 \text{ or } m_4 = 0 \text{ then } \mathscr{S} = \mathbb{R}^+. \end{cases} \end{cases}
$$

$$
\text{If } \Delta = 0 \text{ then } \begin{cases} \text{If } \xi_1 < 0 \text{ then } \begin{cases} \text{If } m_5(2K_1+\xi_1) \geqslant 0 \text{ with } m_5 \neq 0 \text{ then } \mathscr{S} = \{0\}, \\ \text{If } m_5(2K_1+\xi_1) < 0, \text{ then } \mathscr{S} = \left\{0, \alpha_1 \xi_1 \frac{2K_1+\xi_1}{m_5}\right\}, \\ \text{If } m_5 = 0 \text{ then } \mathscr{S} = \mathbb{R}^+. \end{cases} \\ \text{If } \xi_1 \geqslant 0 \text{ then } \mathscr{S} = \{0\}. \end{cases}
$$

$$
\text{If } \Delta < 0 \text{ then } \mathscr{S} = \{0\}.
$$

REMARK 4.2. In Theorem 4.3, if $\frac{dX_T^*}{d\beta}(0,0^+) = 0$, then we discuss according to the sign of the second derivative of the total equilibrium population. In the appendix B, we have added the explicit calculations of the second derivative of X_T^* defined by (52).

In our result of Theorem 4.3, we prove the numerical results of [13] under the assumption that one growth rate is much larger than the other two. In particular, we prove the existence of two positive values of β solutions of $X_T^* = K_1 + K_2 + K_3$.

In [14, Prop. 4.5], Elbetch et al. have shown that, the equilibrium $E^*(\beta,\varepsilon)$ of (1), (2), (3) does not depend on β if and only if $(K_1,\dots,K_n)^T \in \ker\Gamma$. In this case we have $E^*(\beta,\varepsilon) = (K_1,\dots,K_n)$ for all β and for all $\varepsilon > 0$. Therefore, for three-patch model (43), we have the result:

PROPOSITION 4.3. *Consider the domains* $\mathscr{J}_0^-$ *and* $\mathscr{J}_>^-$ *defined in* (59) *and* (60) *respectively. Let* m_3, m_4 *and* m_5 *be given in* (58). *We have*

1. *Let* $(\xi_1,\xi_2) \in \mathscr{J}_0^-$. *The hypothesis in item 2 (c) of Theorem* 4.3 *is equivalent to* $(K_1,K_2,K_3)^T \in \ker\Gamma$, *i.e* $m_5 = 0$ *if and only if* $(K_1,K_2,K_3)^T \in \ker\Gamma$.
2. *Let* $(\xi_1,\xi_2) \in \mathscr{J}_>^-$. *The hypothesis in item 3 (d) of Theorem* 4.3 *is equivalent to* $(K_1,K_2,K_3)^T \in \ker\Gamma$, *i.e* $m_3 = 0$ *or* $m_4 = 0$ *if and only if* $(K_1,K_2,K_3)^T \in \ker\Gamma$.

Proof. For the proof, we prove the first point, the second is shown in the same way as the first. If $(\xi_1,\xi_2) \in \mathscr{J}_0^-$, then the system (66) admits unique solution given by $(\frac{-\xi_1}{2}, K_1 + K_2 + \frac{\xi_1}{2})$. Suppose that $m_5 = 0$ i.e

$$\xi_1(\gamma_{12} + \gamma_{21} + \gamma_{31}) + 2(\gamma_{12}K_1 + \gamma_{12}K_2 + \gamma_{13}K_3) = 0. \tag{68}$$

As $\xi_1 = -2K_1$, so the equation (68) becomes

$$-(\gamma_{21} + \gamma_{31})K_1 + \gamma_{12}K_2 + \gamma_{13}K_3 = 0. \tag{69}$$

By the second equation of the reduced model (44) at equilibrium, we obtain:

$$\gamma_{21}K_1 - (\gamma_{12} + \gamma_{32})K_2 + \gamma_{23}K_3 = 0. \tag{70}$$

The sum of Equation (70) and (69) gives

$$\gamma_{31}K_1 + \gamma_{32}K_2 - (\gamma_{13} + \gamma_{23})K_3 = 0. \tag{71}$$

The equations (69), (70) and (71) show that $(K_1,K_2,K_3)^T \in \ker\Gamma$.

Now, suppose that $(K_1,K_2,K_3)^T \in \ker\Gamma$, then by the equation (69) we have:

$$\begin{aligned} 0 = -(\gamma_{21} + \gamma_{31})K_1 + \gamma_{12}K_2 + \gamma_{13}K_3 &= \frac{1}{2}\left((\gamma_{21} + \gamma_{31})\xi_1 + 2(\gamma_{12}K_2 + \gamma_{13}K_3)\right) \\ = \frac{1}{2}\left(\xi_1(\gamma_{12} + \gamma_{21} + \gamma_{31}) + 2(\gamma_{12}K_1 + \gamma_{12}K_2 + \gamma_{13}K_3)\right) &= \frac{1}{2}m_5. \end{aligned}$$

Hence, $m_5 = 0$, which completes the demonstration of the first point. □

5. The general case

In this section, we consider the model of multi-patch logistic growth, coupled by asymmetric migration terms (1), (3), (11). Our goal is to generalize some results of the previous sections. First, we start by the following situation:

5.1. All growth rates but one are much larger than the last one

We assume that the growth rates $r_2,\dots,r_n$ are much larger than r_1. The model (1), (3), (11) is written under this assumption as:

$$\begin{cases} \dfrac{dx_1}{dt} = r_1x_1\left(1-\dfrac{x_1}{K_1}\right)+\beta\sum_{j=1,j\neq 1}^{n}\left(\gamma_{1j}x_j-\gamma_{j1}x_1\right), \\ \dfrac{dx_i}{dt} = \dfrac{r_i}{\varepsilon}x_i\left(1-\dfrac{x_i}{K_i}\right)+\beta\sum_{j=1,j\neq 1}^{n}\left(\gamma_{ij}x_j-\gamma_{ji}x_i\right), \qquad i=2,\cdots,n, \end{cases} \tag{72}$$

where ε is assumed to be a small positive number.

We have the following theorem:

THEOREM 5.1. *Let $(x_1(t,\varepsilon),\dots,x_n(t,\varepsilon))$ be the solution of the system (72) with initial condition $(x_1^0,\dots,x_n^0)$ satisfying $x_i^0\geqslant 0$ for $i=1,\dots,n$. Let $z(t)$ be the solution of the differential equation*

$$\frac{dx_1}{dt} = r_1x_1\left(1-\frac{x_1}{K_1}\right)+\beta(\xi-\mu x_1) =: \varphi(x_1), \tag{73}$$

with $\mu=\sum_{j=2}^{n}\gamma_{j1}, \xi=\sum_{j=2}^{n}\gamma_{1j}K_j$ and initial condition $z(0)=x_1^0$. Then, when $\varepsilon\to 0$, we have

$$x_1(t,\varepsilon)=z(t)+o_\varepsilon(1), \quad \textit{uniformly for} \quad t\in[0,+\infty) \tag{74}$$

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

$$x_i(t,\varepsilon)=K_i+o_\varepsilon(1), \quad i=2,\dots,n, \ \textit{uniformly for} \quad t\in[t_0,+\infty). \tag{75}$$

Proof. Consequence direct of proof of Theorem 4.1. □

As a corollary of the previous theorem, we have the following result which gives the limit of the total equilibrium population $X_T^*(\beta,\varepsilon)$ of the model (72) when ε goes to zero:

COROLLARY 5.1. *We have:*

$$\begin{aligned} X_T^*(\beta,0^+) := \lim_{\varepsilon\to 0}X_T^*(\beta,\varepsilon) = {} & \frac{K_1}{2}+K_2+\dots+K_n-\frac{\beta}{2\alpha_1}\mu \\ & +\frac{1}{2\alpha_1}\sqrt{\mu^2\beta^2+(4\alpha_1\xi-2r_1\mu)\beta+r_1^2}. \end{aligned} \tag{76}$$

In particular, the derivative of the total equilibrium population (76) at $\beta = 0$ is given by:

$$\frac{dX_T^*}{d\beta}(0,0^+) = \frac{-\mu K_1 + \xi}{r_1}. \tag{77}$$

By taking the limit of (76) when $\beta \to \infty$, we get that the total equilibrium population $X_T^*(\beta,0^+)$ tends to:

$$X_T^*(+\infty,0^+) = K_2 + \ldots + K_n + \frac{\xi}{\mu}. \tag{78}$$

We consider the regions in the set of the parameters μ and ξ, denoted $\mathscr{J}_0$ and $\mathscr{J}_1$ defined by:

$$\mathscr{J}_0 = \{(\mu,\xi) : \xi > \mu K_1\}, \quad \mathscr{J}_1 = \{(\mu,\xi) : \xi < \mu K_1\} \tag{79}$$

We have the following result which gives the conditions for which the patchiness is beneficial or detrimental in the model (72) when ε goes to zero.

COROLLARY 5.2. *Consider the total equilibrium population $X_T^*(\beta,0^+)$ defined in (76). Let $\mathscr{J}_0$ and $\mathscr{J}_1$ be the domains defined by (79). Then, we have*

- *If $(\mu,\xi) \in \mathscr{J}_0$ then $X_T^*(\beta,0^+) > \sum_{i=1}^n K_i$, for all $\beta > 0$.*
- *If $(\mu,\xi) \in \mathscr{J}_1$ then $X_T^*(\beta,0^+) < \sum_{i=1}^n K_i$, for all $\beta < 0$.*
- *If $\xi = \mu K_1$, then $x_i^*(\beta,0^+) = K_i, i = 1,\ldots,n$, for all $\beta \geqslant 0$. Therefore $X_T^*(\beta,0^+)$ $= \sum_{i=1}^n K_i$ for all $\beta \geqslant 0$.*

REMARK 5.1. The condition $\mu K_1 = \xi$ is equivalent to $(K_1,\ldots,K_n)^T \in \ker\Gamma$. Indeed, if $(K_1,\ldots,K_n)^T \in \ker\Gamma$ then

$$\sum_{j=1,j\neq i}^{n} \gamma_{ij}K_j - \gamma_{ji}K_i = 0, \tag{80}$$

The first equation of (80) gives $\mu K_1 = \xi$.

Now, when $\varepsilon \to 0$, if $\mu K_1 = \xi$, then $(K_1,\ldots,K_n)$ is a equilibrium of (72), i.e $\Gamma(K_1,\ldots,K_n)^T = 0$, so $(K_1,\ldots,K_n)^T \in \ker T$.

5.2. One growth rate is much larger than all others

We propose here to study the model (1), (3), (11) with the hypothesis that r_n much larger than $r_1,\ldots,r_{n-1}$. On can write the model in the following way:

$$\begin{cases} \dfrac{dx_i}{dt} = r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + \beta \sum_{j=1,j\neq n}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), & i = 1,\cdots,n-1, \\ \dfrac{dx_n}{dt} = \dfrac{r_n}{\varepsilon} x_n \left(1 - \dfrac{x_n}{K_n}\right) + \beta \sum_{j=1,j\neq i}^n (\gamma_{nj}x_j - \gamma_{jn}x_n), & \end{cases} \tag{81}$$

where ε is assumed to be small positive number.

We have the theorem:

THEOREM 5.2. *Let $(x_1(t,\varepsilon),\ldots,x_n(t,\varepsilon))$ be the solution of the system (81) with initial condition $(x_1^0,\ldots,x_n^0)$ satisfying $x_i^0 \geqslant 0$ for $i=1,\ldots,n$. Let $z(t)$ be the solution of the system:*

$$\dot{x} = \psi(x) + \beta(Lx + K_n V) =: \Upsilon(x), \tag{82}$$

with initial condition $z_i(0) = x_i^0$ for $i=1,\ldots,n-1$, $x=(x_1,\ldots,x_{n-1})^T$, $L := (\gamma_{ij})_{n-1\times n-1}$ is the sub matrix of the matrix Γ, obtained by dropping the last row and the last column of Γ, V is the vector defined by $V := (\gamma_{in})_{n-1\times 1}$ and

$$\psi(x) = (r_1 x_1(1-x_1/K_1),\cdots,r_{n-1}x_{n-1}(1-x_{n-1}/K_{n-1}))^T. \tag{83}$$

Then, when $\varepsilon \to 0$, we have

$$x_i(t,\varepsilon) = z_i(t) + o_\varepsilon(1), \quad i=1,\ldots,n-1 \quad \text{uniformly for} \quad t\in[0,+\infty) \tag{84}$$

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

$$x_n(t,\varepsilon) = K_n + o_\varepsilon(1), \quad \text{uniformly for} \quad t\in[t_0,+\infty). \tag{85}$$

Proof. The same proof of Theorem 4.1. □

5.2.1. Global stability of the reduced model (82)

Our goal in this part, is to prove the global stability of the system (82). First, we start by the following proposition:

PROPOSITION 5.1. *The positive cone $\mathbb{R}_+^{n-1}$ is positively invariant for (82).*

Proof. Assume that $x_j \geqslant 0$ for all j and there exist i such that $x_i = 0$. We have

$$\frac{dx_i}{dt} = \beta\left(\sum_{i\neq j}\gamma_{ij}x_j + \gamma_{in}K_n\right) \geqslant 0. \tag{86}$$

Hence, on the boundary of $\mathbb{R}_+^{n-1}$, the vector field associated to (82) either is tangent to the boundary of $\mathbb{R}_+^{n-1}$, or points inward. The system (82) is cooperative. Indeed, it has a jacobian matrix with no negative off-diagonal elements, given by:

$$\mathbb{J}\Upsilon(x) = \operatorname{diag}(r_i - 2\alpha_i x_i) + \beta L. \tag{87}$$

According to [32, Proposition B.7, page 267], no trajectory comes out of $\mathbb{R}_+^{n-1}$. Therefore, $\mathbb{R}_+^{n-1}$ is positively invariant for (82). □

For the boundedness of the solutions of the reduced model (82) we prove:

PROPOSITION 5.2. *For any non-negative initial condition, the solutions of System (82) remain bounded, for all $t \geqslant 0$. Moreover, the set*

$$\Lambda_{n-1} = \left\{ (x_1, \dots, x_{n-1}) : x_1 + \dots + x_{n-1} \leqslant \frac{\mu_2^*}{\mu_1^*} \right\}, \tag{88}$$

where $\mu_1^* = \min_i \{1 + \beta \gamma_{ni}\}$ and $\mu_2^* = \sum_{i=1}^{n-1} \frac{(r_i+1)^2}{\alpha_i} + \beta \gamma_{in} K_n$, is positively invariant and is a global attractor for the system (82).

Proof. To show that all solutions are bounded, we consider the quantity defined by $X_T(t) = x_1(t) + \dots + x_{n-1}(t)$. So, we have

$$\dot{X}_T(t) = \sum_{i=1}^{n-1} r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \beta \sum_{i=1}^{n-1} \gamma_{ni} x_i + \beta \left(\sum_{i=1}^{n-1} \gamma_{in}\right) K_n. \tag{89}$$

By Equation (107), the equation (89) becomes

$$\dot{X}_T(t) \leqslant \sum_{i=1}^{n-1} -x_i + \frac{(r_i+1)^2}{\alpha_i} - \beta \sum_{i=1}^{n-1} \gamma_{ni} x_i + \beta \left(\sum_{i=1}^{n-1} \gamma_{in}\right) K_n. \tag{90}$$

Therefore

$$\dot{X}_T(t) \leqslant -\mu_1^* X_T(t) + \mu_2^*, \qquad \text{for all } t \geqslant 0, \tag{91}$$

which gives

$$X_T(t) \leqslant \left(X_T(0) - \frac{\mu_2^*}{\mu_1^*}\right) e^{-\mu_1^* t} + \frac{\mu_2^*}{\mu_1^*}, \qquad \text{for all } t \geqslant 0. \tag{92}$$

Hence

$$X_T(t) \leqslant \max\left(X_T(0), \frac{\mu_2^*}{\mu_1^*}\right), \qquad \text{for all } t \geqslant 0. \tag{93}$$

Therefore, the solutions of System (82) are positively bounded and defined for all $t \geqslant 0$. From (92) it can be deduced that the set Λ_{n-1} is positively invariant and it is a global attractor for the system (82). □

LEMMA 5.1. *Assume that the matrix Γ is irreducible. The reduced model (82) does not admits the origin as equilibrium.*

Proof. We suppose that the origin is an equilibrium of (82), then $\Upsilon(0) = 0$, which equivalent to $V^T = 0$, i.e $\gamma_{1n} = \dots = \gamma_{n-1,n} = 0$. So, we obtain a contradiction since Γ is irreducible. □

THEOREM 5.3. *Assume that the two matrices L and Γ are irreducible. The reduced model (82) admits unique equilibrium point in the interior of the positive cone $\mathbb{R}_+^{n-1} \setminus \{0\}$ which is GAS.*

Proof. To show the global stability of the reduced model (82) in this case, we use the following result of Hirsch [25]. If the cooperative system

$$\dot{x} = F(x), \tag{94}$$

has the following proprieties:

- $\mathbb{J}F(x)$ is irreducible for any $x \geqslant 0$,
- $\mathbb{J}F(x) \leqslant \mathbb{J}F(y)$ for any $x \geqslant y \geqslant 0$, and
- all solutions are bounded,

then either the origin is globally stable or else there exists a unique positive equilibrium point and all the trajectories in $\mathbb{R}^n_+ \setminus \{0\}$ tend to it. Here $\mathbb{J}F(x)$ is the Jacobian of $F(x)$.

The jacobian matrix of the reduced model (82) is given by (87), which is irreducible because L is also. Moreover, if $\mathbb{J}\Upsilon(x) \leqslant \mathbb{J}\Upsilon(y)$ then $\mathrm{diag}(r_i - 2\alpha_i x_i) \leqslant \mathrm{diag}(r_i - 2\alpha_i y_i)$ which gives $x_i \geqslant y_i$ for all i, i.e $x \geqslant y \geqslant 0$. By Lemma 5.2, all solutions are bounded and the reduced model (82) does not admit the origin as equilibrium by Lemma 5.1. Hence, the reduced model (82) is globally stable according to Hirsch [25]. We denote by $\mathscr{E}^*_{n-1}(\beta, 0^+)$ this equilibrium. □

5.2.2. Perfect mixing

For the behavior of the reduced model (82) for large migration rate, i.e when $\beta \to \infty$, we obtain:

PROPOSITION 5.3. *we have:*

$$\lim_{\beta \to +\infty} \mathscr{E}_{n-1}(\beta, 0^+) = \frac{K_n}{\delta_n}(\delta_1, \ldots, \delta_{n-1}).$$

Proof. Denote $\mathscr{E}_{n-1}(\infty, 0^+) = \frac{K_n}{\delta_n}(\delta_1, \ldots, \delta_{n-1})$. The equilibrium point $\mathscr{E}_{n-1}(\beta, 0^+)$ is the unique solution in the positive cone of the equation $\Psi_\beta = 0$, where

$$\Psi_\beta(x) := \psi(x) + \beta(Lx + K_n V) = 0. \tag{95}$$

Taking the limit $\beta \to \infty$, in (95) we get

$$\Psi_\infty(x) := Lx + K_n V = 0. \tag{96}$$

By Lemma 2 of Elbetch et al. [14], the equation $\Psi_\infty = 0$ admits $\mathscr{E}_{n-1}(\infty, 0^+)$ as unique solution. Therefore, when $\beta \to \infty$, the equilibrium $\mathscr{E}_{n-1}(\beta, 0^+)$ tend to $\mathscr{E}_{n-1}(\infty, 0^+)$. □

As a corollary of the previous proposition, we obtain

COROLLARY 5.3. *The total equilibrium population* $X_T^*(\beta,0^+)$ *of* (81) *satisfies:*

$$X_T^*(+\infty,0^+) = \frac{K_n}{\delta_n}\sum_{i=1}^{n}\delta_i.$$

Moreover, if the matrix Γ *is symmetric, then* $X_T^*(+\infty,0^+) = nK_n$.

Proof. Consequence direct of the formula $\mathscr{E}_{n-1}(\infty,0^+)$ and the approximation (85). □

5.3. Two blocks of patches, where the growth rates of the first block are much larger than of the second one

We propose here to study the model (1), (3), (11).

We have the theorem:

THEOREM 5.4. *Let* $(x_1(t,\varepsilon),\dots,x_n(t,\varepsilon))$ *be the solution of the system* (1), (11) *with initial condition* $(x_1^0,\dots,x_n^0)$ *satisfying* $x_i^0 \geqslant 0$ *for* $i=1,\dots,n$. *Let* $z(t)$ *be the solution of the system:*

$$\dot{x} = \psi(x) + \beta(Lx+UK) =: \Upsilon(x), \tag{97}$$

with initial condition $z_i(0) = x_i^0$ *for* $i=1,\dots,m$, $x=(x_1,\dots,x_m)^T$, $L := (\gamma_{ij})_{m\times m}$ *is the sub matrix of the matrix* Γ, *obtained by dropping the* $n-m$ *last row and the* $n-m$ *last column of* Γ, $U := (\gamma_{ij})_{m\times(n-m)}$ *is the sub matrix of the matrix* Γ, *obtained by dropping the* $n-m$ *last row and the* m *first column of* Γ, K *is the vector defined by* $K := (K_{m+1},\dots,K_n)^T$, *and*

$$\psi(x) = \left(r_1x_1(1-x_1/K_1),\cdots,r_mx_m(1-x_m/K_m)\right)^T. \tag{98}$$

Then, when $\varepsilon\to 0$, *we have*

$$x_i(t,\varepsilon) = z_i(t) + o_\varepsilon(1), \quad i=1,\dots,m \quad \text{uniformly for} \quad t\in[0,+\infty) \tag{99}$$

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

$$x_i(t,\varepsilon) = K_i + o_\varepsilon(1), \quad i=m+1,\dots,n \quad \text{uniformly for} \quad t\in[t_0,+\infty). \tag{100}$$

Proof. The same proof of Theorem 4.1. □

5.3.1. Study of the reduced model (97)

It is clear that the positive cone $\mathbb{R}_+^m$ is positively invariant for the model (97), and for any non-negative initial condition, the solution of the reduced model is bounded, for all $t\geqslant 0$. Now, we prove the result:

LEMMA 5.2. *Assume that the matrix* Γ *is irreducible. The reduced model* (97) *does not admits the origin as equilibrium.*

Proof. We suppose that the origin is a equilibrium of (97), then $\Upsilon(0) = 0$, which equivalent to $UK = 0$, i.e $\gamma_{ij} = 0$ for all $i \in \{1,\ldots,m\}$ and $j \in \{m+1,\ldots,n\}$. So, we obtain a contradiction since Γ is irreducible. □

THEOREM 5.5. *Assume that the two matrices L and Γ are irreducible. The reduced model (97) admits unique equilibrium point in the interior of the positive cone $\mathbb{R}^m_+ \setminus \{0\}$ which is GAS, denoted by $\mathscr{E}_m(\beta, 0^+)$.*

Proof. We use Theorem of Hirsch [25] as in proof of Theorem 5.3. □

The behavior of the reduced model (97) for large migration rate, i.e $\beta \to \infty$, is given by:

PROPOSITION 5.4. *we have:*

$$\lim_{\beta \to +\infty} \mathscr{E}_m(\beta, 0^+) = -L^{-1}UK.$$

Proof. Denote $\mathscr{E}_m(\infty, 0^+) := -L^{-1}UK$. The equilibrium point $\mathscr{E}_m(\beta, 0^+)$ is the unique solution in the positive cone of the equation $\Psi_\beta = 0$, where

$$\Psi_\beta(x) := \psi(x) + \beta(Lx + UK) = 0. \tag{101}$$

Taking the limit $\beta \to \infty$, in (101) we get

$$\Psi_\infty(x) := Lx + UK = 0. \tag{102}$$

Since, the matrix L is invertible, then the equation $\Psi_\infty = 0$ admits $\mathscr{E}_m(\infty, 0^+)$ as unique solution. Therefore, when $\beta \to \infty$, the equilibrium $\mathscr{E}_m(\beta, 0^+)$ tend to $\mathscr{E}_m(\infty, 0^+)$. □

6. Conclusion

The aim of this paper is to study the effect of the dispersal on the dynamics of the total equilibrium population under the assumption that some growth rates are much larger than others in the multi-patch logistic model.

In Section 3, we consider the two-patch model in the case when one growth rate is much larger than the second one. First, by perturbation arguments, we give a approximation of the solutions of the system in this case. Next, we compare the total equilibrium population with the sum of two carrying capacities.

In Section 4, first, we study a three-patch model under the assumption that two growth rates are much larger than the third one. We compute the derivative at $\beta = 0$ of the total equilibrium population and also we give the formula of perfect mixing. Next, we compare the total equilibrium population with the sum of the three carrying capacities. Second, we study three-patch model under the assumption that one growth rate is much larger than the two others. Our results prove the numerical simulation of

[13]. In particular, we prove, under certain conditions on the parameters of the system, the existence of two positive values of β solutions of the following equation:

Total equilibrium population=Sum of three carrying capacities.

In Section 5, we generalize some results of the sections 3 and 4. In particular, we determine the reduced models and we prove their global stability using Hirsch's theorem [25] in the following cases:

- All growth rates but one are much larger than the last one.
- One growth rate is much larger than all others.
- Two blocks of patches, with the growth rates of the first block being much larger than of the second one.

We give also the formula of the perfect mixing for the three previous cases.

Some questions important remain open: for example, for three-patch logistic model, is it possible to a complete comparison between the total equilibrium population and the sum of the three carrying capacities without the assumption that some growth rates are much larger than the other. I think this question is difficult and requires a lot of work and mathematical tools.

A. Global stability of the reduced model (44)

In this section, we prove the global stability of the reduced model (44). First, we start by study the existence and uniqueness of equilibrium points. We have the result:

PROPOSITION A.1. *Assume that the matrices* $\Gamma = (\gamma_{ij})_{3\times 3}$ *and*

$$L = \begin{bmatrix} -(\gamma_{21}+\gamma_{31}) & \gamma_{12}, \\ \gamma_{21} & -(\gamma_{12}+\gamma_{32}) \end{bmatrix}$$

are irreducible. Then, the reduced model (44) *admits a unique equilibrium in the interior of the positive cone* $\mathbb{R}^2_+ \setminus \{0\}$ *for all* β.

Proof. The equilibrium of (44) is a solution of the following system of equations:

$$\begin{cases} 0 = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right) + \beta(-(\gamma_{21}+\gamma_{31})x_1 + \gamma_{12}x_2 + \gamma_{13}K_3), \\ 0 = r_2 x_2 \left(1 - \dfrac{x_2}{K_2}\right) + \beta(\gamma_{21}x_1 - (\gamma_{12}+\gamma_{32})x_2 + \gamma_{23}K_3). \end{cases} \tag{103}$$

The system (103) does not admits the origin as solution. Indeed, we suppose that the origin is a solution of (103), then $\gamma_{13} = \gamma_{23} = 0$. So, we obtain a contradiction since Γ is irreducible. Note that, as the matrix L is irreducible, then $\gamma_{12} \neq 0$ and $\gamma_{21} \neq 0$.

Solving the first equation of (103) with respect to x_2 and the second with respect to x_1 we get:

$$\begin{cases} \mathscr{P}_1: \quad x_2 = \dfrac{\alpha_1}{\beta\gamma_{12}}x_1^2 + \dfrac{\beta(\gamma_{21}+\gamma_{31})-r_1}{\beta\gamma_{12}}x_1 - \dfrac{\gamma_{13}}{\gamma_{12}}K_3, \\ \mathscr{P}_2: \quad x_1 = \dfrac{\alpha_2}{\beta\gamma_{21}}x_2^2 + \dfrac{\beta(\gamma_{12}+\gamma_{32})-r_2}{\beta\gamma_{21}}x_2 - \dfrac{\gamma_{23}}{\gamma_{21}}K_3. \end{cases} \tag{104}$$

The two equations of (104) define simply the two isoclines of (44). The isocline $\mathscr{P}_1$ is a parabola, which is convex downward and intersect the first axis in two points. Indeed, the equation $\mathscr{P}_1(x_1) = 0$ must have two real roots and one of them must be a non-positive root and the other is non-negative. Likewise for the other isocline, $\mathscr{P}_2$ is a parabola, which is convex leftward and intersect the second axis in two points, one is non-positive and the other is non-negative. So, these two isoclines have a unique intersection in the interior of the positive cone denoted $\mathscr{E}^*(\beta,0^+)$ which is depend a the migration rate (see figure 3).

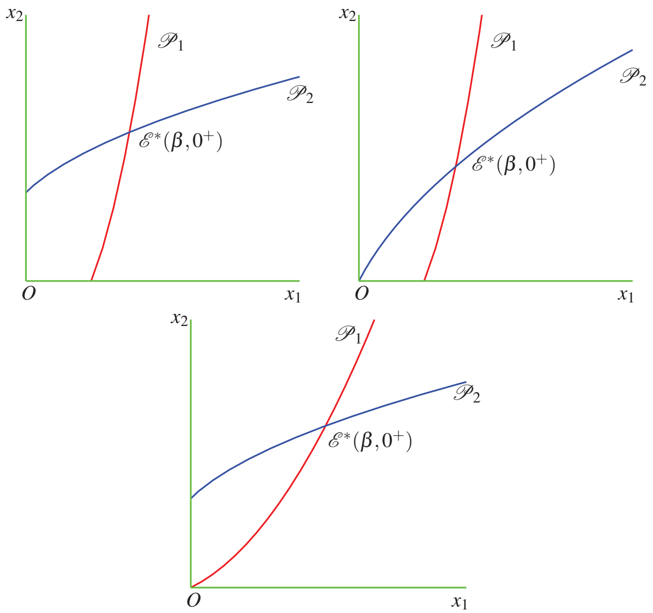

Figure 3: *All possible configurations for the isoclines of the system* (103) *(in red for* x_1 *and in blue foor* x_2 *) for certain parameters. The equilibrium points are the intersection between these two isoclines, this intersections contains the positive point* $\mathscr{E}^*(\beta,0^+)$.

□

In the following, our aim is to show the global stability of the equilibrium $\mathscr{E}^*(\beta,0^+)$. For this, we need some results. First, for the non-negativity and boundedness of the solutions of the reduced model (44), we have the following result:

LEMMA A.1. *For any non-negative initial condition, the solutions of system* (44) *remain bounded, for all* $t \geqslant 0$. *Moreover, the set*

$$\Lambda = \left\{ (x_1, x_2) : x_1 + x_2 \leqslant \frac{\xi_2^*}{\xi_1^*} \right\}, \tag{105}$$

where $\xi_1^* = \min\{1 + \beta\gamma_{31}, 1 + \beta\gamma_{32}\}$ *and* $\xi_2^* = \frac{(r_1+1)^2}{\alpha_1} + \frac{(r_2+1)^2}{\alpha_2} + \beta(\gamma_{13} + \gamma_{23})K_3$, *is positively invariant and is a global attractor for the system* (44).

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

$$\dot{X}_T(t) = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta(-\gamma_{31}x_1 - \gamma_{32}x_2 + (\gamma_{13} + \gamma_{23})K_3). \tag{106}$$

For all r_i and K_i positive, we have the following inequality

$$r_i x_i \left(1 - \frac{x_i}{K_i}\right) \leqslant -x_i + \frac{(r_i+1)^2}{\alpha_i} \qquad i = 1, 2. \tag{107}$$

Substituting Equation (107) in the equation (106), we get

$$\dot{X}_T(t) \leqslant -x_1 + \frac{(r_1+1)^2}{\alpha_1} - x_2 + \frac{(r_2+1)^2}{\alpha_2} + \beta(-\gamma_{31}x_1 - \gamma_{32}x_2 + (\gamma_{13} + \gamma_{23})K_3). \tag{108}$$

Therefore

$$\dot{X}_T(t) \leqslant -\xi_1^* X_T(t) + \xi_2^*, \qquad \text{for all } t \geqslant 0, \tag{109}$$

which gives

$$X_T(t) \leqslant \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*}\right) e^{-\xi_1^* t} + \frac{\xi_2^*}{\xi_1^*}, \qquad \text{for all } t \geqslant 0. \tag{110}$$

Hence

$$X_T(t) \leqslant \max\left(X_T(0), \frac{\xi_2^*}{\xi_1^*}\right), \qquad \text{for all } t \geqslant 0. \tag{111}$$

Therefore, the solutions of system (44) are positively bounded and defined for all $t \geqslant 0$. From (110) it can be deduced that the set Λ is positively invariant and it is a global attractor for the system (44). □

We have also the following property:

LEMMA A.2. *System* (44) *admits no periodic solution.*

Proof. Let f_i be the right hand side of the system (44). Then

$$\begin{aligned} \frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} &= r_1 + r_2 - 2(\alpha_1 x_1 + \alpha_2 x_2) - \beta(\gamma_{21} + \gamma_{31} + \gamma_{12} + \gamma_{32}) \\ &= -\left(\frac{d\mathscr{P}_1}{dx_1} + \frac{d\mathscr{P}_2}{dx_2}\right) < 0. \end{aligned}$$

So, by Dulac's Criterion [24, Theorem 4.1.1], the system (44) admits no periodic solution. □

THEOREM A.1. *The equilibrium $\mathscr{E}^*(\beta,0^+)$ of (44) is GAS for all β.*

Proof. The Jacobian matrix of the system (44) at $\mathscr{E}^*(\beta,0^+)$ is given by:

$$\mathbb{J}(\mathscr{E}^*) = \begin{bmatrix} \theta_1 & \beta\gamma_{12} \\ \beta\gamma_{21} & \theta_2 \end{bmatrix}, \tag{112}$$

where $\theta_1 = r_1 - 2\frac{r_1}{K_1}x_1^*(\beta,0^+) - \beta(\gamma_{21}+\gamma_{31})$, and $\theta_2 = r_2 - 2\frac{r_2}{K_2}x_2^*(\beta,0^+) - \beta(\gamma_{12}+\gamma_{32})$.

We have:

$$\begin{aligned} 0 < \frac{d\mathscr{P}_1}{dx_1}(x_1^*(\beta,0^+),x_2^*(\beta,0^+)) &= 2\frac{\alpha_1}{\beta\gamma_{12}}x_1^*(\beta,0^+) + \frac{\beta(\gamma_{21}+\gamma_{31})-r_1}{\beta\gamma_{12}}, \\ &= -\frac{1}{\beta\gamma_{12}}\left(r_1 - 2\frac{r_1}{K_1}x_1^*(\beta,0^+) - \beta(\gamma_{21}+\gamma_{31})\right), \\ &= -\frac{1}{\beta\gamma_{12}}\theta_1. \end{aligned}$$

Therefore, $\theta_1 < 0$. By the same method, we obtain that $\theta_2 < 0$. This implies that $\mathrm{tr}(\mathbb{J}(\mathscr{E}^*)) = \theta_1 + \theta_2 < 0$, where tr means the trace.

It's clear that, at the equilibrium $\mathscr{E}^*$:

$$\frac{d\mathscr{P}_1}{dx_1}(\mathscr{E}^*) > \left(\frac{d\mathscr{P}_2}{dx_2}(\mathscr{E}^*)\right)^{-1}, \tag{113}$$

which gives

$$\frac{\theta_1}{-\beta\gamma_{12}} > \frac{-\beta\gamma_{21}}{\theta_2}. \tag{114}$$

Thus, $\det\mathbb{J}(\mathscr{E}^*) = \theta_1\theta_2 - \beta^2\gamma_{12}\gamma_{21} > 0$. Hence by the Routh-Hurwitz criteria for stability, the real parts of the the eigenvalues value of the Jacobian matrix are negative, proving that $\mathscr{E}^*$ is asymptotically stable. Lemmas A.1 and A.2 imply that there cannot be any non-trivial closed paths lying in the interior of the positive quadrant and hence the stability must be global. □

B. The second derivative of the total equilibrium population (52) at $\beta = 0$

We consider the reduced model (44). The steady state $(x_1^*(\beta,0^+),x_2^*(\beta,0^+))$ is the solution of the set of algebraic equations:

$$\begin{cases} 0 = r_1x_1^*(\beta,0^+)\left(1 - \dfrac{x_1^*(\beta,0^+)}{K_1}\right) + \beta(-(\gamma_{21}+\gamma_{31})x_1^*(\beta,0^+) + \gamma_{12}x_2^*(\beta,0^+) + \gamma_{13}K_3), \\ 0 = r_2x_2^*(\beta,0^+)\left(1 - \dfrac{x_2^*(\beta,0^+)}{K_2}\right) + \beta(\gamma_{21}x_1^*(\beta,0^+) - (\gamma_{12}+\gamma_{32})x_2^*(\beta,0^+) + \gamma_{23}K_3). \end{cases} \tag{115}$$

The derivative of (115) with respect to β gives

$$\begin{cases} 0=\left[r_1-2\dfrac{r_1}{K_1}x_1^*(\beta,0^+)-\beta(\gamma_{21}+\gamma_{31})\right]\dfrac{dx_1^*}{d\beta}(\beta,0^+)+\beta\dfrac{dx_2^*}{d\beta}(\beta,0^+) \\ \qquad -(\gamma_{21}+\gamma_{31})x_1^*(\beta,0^+)+\gamma_{12}x_2^*(\beta,0^+)+\gamma_{13}K_3, \\ 0=\left[r_2-2\dfrac{r_2}{K_2}x_2^*(\beta,0^+)-\beta(\gamma_{12}+\gamma_{32})\right]\dfrac{dx_2^*}{d\beta}(\beta,0^+)+\beta\dfrac{dx_1^*}{d\beta}(\beta,0^+) \\ \qquad +\gamma_{21}x_1^*(\beta,0^+)-(\gamma_{12}+\gamma_{32})x_2^*(\beta,0^+)+\gamma_{23}K_3. \end{cases} \tag{116}$$

For $\beta=0$, $x_1^*(0,0^+)=K_1$ and $x_2^*(0,0^+)=K_2$, the equations (116) become

$$\begin{cases} 0=-r_1\dfrac{dx_1^*}{d\beta}(0,0^+)-(\gamma_{21}+\gamma_{31})K_1+\gamma_{12}K_2+\gamma_{13}K_3, \\ 0=-r_2\dfrac{dx_2^*}{d\beta}(0,0^+)+\gamma_{21}K_1-(\gamma_{12}+\gamma_{32})K_2+\gamma_{23}K_3. \end{cases} \tag{117}$$

Therefore

$$\begin{cases} \dfrac{dx_1^*}{d\beta}(0,0^+)=\dfrac{1}{r_1}\left(-(\gamma_{21}+\gamma_{31})K_1+\gamma_{12}K_2+\gamma_{13}K_3\right), \\ \dfrac{dx_2^*}{d\beta}(0,0^+)=\dfrac{1}{r_2}\left(\gamma_{21}K_1-(\gamma_{12}+\gamma_{32})K_2+\gamma_{23}K_3\right). \end{cases} \tag{118}$$

The derivative of (116) with respect to β gives

$$\begin{cases} 0=\left[r_1-2\dfrac{r_1}{K_1}x_1^*(\beta,0^+)-\beta(\gamma_{21}+\gamma_{31})\right]\dfrac{d^2x_1^*}{d\beta^2}(\beta,0^+)-2\dfrac{r_1}{K_1}\left(\dfrac{dx_1^*}{d\beta}(\beta,0^+)\right)^2 \\ \qquad -(\gamma_{21}+\gamma_{31})\dfrac{dx_1^*}{d\beta}(\beta,0^+)+\beta\dfrac{d^2x_2^*}{d\beta^2}(\beta,0^+)+\dfrac{dx_2^*}{d\beta}(\beta,0^+) \\ \qquad -(\gamma_{21}+\gamma_{31})\dfrac{dx_1^*}{d\beta}(\beta,0^+)+\gamma_{12}\dfrac{dx_2^*}{d\beta}(\beta,0^+), \\ 0=\left[r_2-2\dfrac{r_2}{K_2}x_2^*(\beta,0^+)-\beta(\gamma_{12}+\gamma_{32})\right]\dfrac{d^2x_2^*}{d\beta^2}(\beta,0^+)-2\dfrac{r_2}{K_2}\left(\dfrac{dx_2^*}{d\beta}(\beta,0^+)\right)^2 \\ \qquad -(\gamma_{12}+\gamma_{32})\dfrac{dx_2^*}{d\beta}(\beta,0^+)+\beta\dfrac{d^2x_1^*}{d\beta^2}(\beta,0^+)+\dfrac{dx_1^*}{d\beta}(\beta,0^+) \\ \qquad -(\gamma_{12}+\gamma_{32})\dfrac{dx_2^*}{d\beta}(\beta,0^+)+\gamma_{21}\dfrac{dx_2^*}{d\beta}(\beta,0^+). \end{cases} \tag{119}$$

Hence

$$\begin{cases} 0=\left[r_1-2\frac{r_1}{K_1}x_1^*(\beta,0^+)-\beta(\gamma_{21}+\gamma_{31})\right]\frac{d^2x_1^*}{d\beta^2}(\beta,0^+)+\beta\frac{d^2x_2^*}{d\beta^2}(\beta,0^+) \\ \qquad -2\frac{r_1}{K_1}\left(\frac{dx_1^*}{d\beta}(\beta,0^+)\right)^2-2(\gamma_{21}+\gamma_{31})\frac{dx_1^*}{d\beta}(\beta,0^+)+(1+\gamma_{12})\frac{dx_2^*}{d\beta}(\beta,0^+), \\ 0=\left[r_2-2\frac{r_2}{K_2}x_2^*(\beta,0^+)-\beta(\gamma_{12}+\gamma_{13})\right]\frac{d^2x_2^*}{d\beta^2}(\beta,0^+)+\beta\frac{d^2x_1^*}{d\beta^2}(\beta,0^+) \\ \qquad -2\frac{r_2}{K_2}\left(\frac{dx_2^*}{d\beta}(\beta,0^+)\right)^2-2(\gamma_{12}+\gamma_{32})\frac{dx_2^*}{d\beta}(\beta,0^+)+(1+\gamma_{21})\frac{dx_1^*}{d\beta}(\beta,0^+). \end{cases} \tag{120}$$

For $\beta=0, x_1^*(0,0^+)=K_1$ and $x_2^*(0,0^+)=K_2$, the equations (120) become

$$\begin{cases} 0=-r_1\frac{d^2x_1^*}{d\beta^2}(0,0^+)+2\frac{r_1}{K_1}\left(\frac{dx_1^*}{d\beta}(0,0^+)\right)^2-2(\gamma_{21}+\gamma_{31})\frac{dx_1^*}{d\beta}(0,0^+) \\ \qquad +(1+\gamma_{12})\frac{dx_2^*}{d\beta}(0,0^+), \\ 0=-r_2\frac{d^2x_2^*}{d\beta^2}(0,0^+)-2\frac{r_2}{K_2}\left(\frac{dx_2^*}{d\beta}(0,0^+)\right)^2-2(\gamma_{12}+\gamma_{32})\frac{dx_2^*}{d\beta}(0,0^+) \\ \qquad +(1+\gamma_{21})\frac{dx_1^*}{d\beta}(0,0^+), \end{cases} \tag{121}$$

where $\frac{dx_1^*}{d\beta}(0,0^+)$ and $\frac{dx_2^*}{d\beta}(0,0^+)$ are given by (118). Therefore

$$\begin{cases} \frac{d^2x_1^*}{d\beta^2}(0,0^+)=\frac{2}{K_1}\left(\frac{dx_1^*}{d\beta}(0,0^+)\right)^2-\frac{2}{r_1}(\gamma_{21}+\gamma_{31})\frac{dx_1^*}{d\beta}(0,0^+)+\frac{1}{r_1}(1+\gamma_{12})\frac{dx_2^*}{d\beta}(0,0^+), \\ \frac{d^2x_2^*}{d\beta^2}(0,0^+)=\frac{2}{K_2}\left(\frac{dx_2^*}{d\beta}(0,0^+)\right)^2-\frac{2}{r_2}(\gamma_{12}+\gamma_{32})\frac{dx_2^*}{d\beta}(0,0^+)+\frac{1}{r_2}(1+\gamma_{21})\frac{dx_1^*}{d\beta}(0,0^+). \end{cases} \tag{122}$$

The sum of the equations in (122) give the second derivative of the total equilibrium.

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