Effect of dispersal in single-species discrete diffusion systems with source-sink patches

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Abstract

A multi-patch source-sink model with and without intraspecific competition in the sink patches is considered. First, we study the dynamics of the model when the matrix of migration is irreducible and reducible. We show that, there is a threshold number of source patches such that the population potentially becomes extinct below the threshold and established above the threshold. Next, used the theory of perturbation singular and theorem of Tikhonov, in the case of perfect mixing, i.e. when the diffusion rate tends to infinity, we calculate the equilibrium of the model and we give a good approximations of the solutions in this case. Second, we determine, in some particular cases, the conditions under which fragmentation and the existence of sinks patches can lead to a total equilibrium population greater or smaller than the sum of the carrying capacities of the source patches. Finally, we study the effect of the rapid growth source population and rapid death sink population on the dynamics of the total equilibrium population and on the coexistence of the species.

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Contents

1 Introduction

Population dynamics is a wide field of mathematics, which contains many problems, for example fragmentation of population and the effect of migration in the general dynamics of population. Bibliographies can be found in the work of Levin [30, 31] and Holt [26]. There are ecological situations that motivate the representation of space as a finite set of patches connected by migrations, for instance an archipelago with bird population and predators. It is an example of insular bio-geography. A reference work on mathematical models is the book of Levin, Powell and Steele [28], whereas Hanski and Gilpin [24] give a more ecological account of the subject. The standard question in this type of biomathematical problems, is to study the effect of migration on the general population dynamics, and the consequences of fragmentation on the persistence or extinction of the population.

In 2019, Wu et al. [38] studied the following Two-patch Source-Sink model:

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

where x_1 and x_2 represent population densities of the species in patch 1 and 2, respectively. The parameters K_i and r_i are positives. Parameter D represents the dispersal intensity while 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.

Arino et al. [3] 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 the model

$$\begin{cases} \dfrac{dx_i}{dt} = r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n} \gamma_{ij} x_j, & i = 1, \ldots, s, \\ \dfrac{dx_i}{dt} = -r_i x_i + D\sum_{j=1, j\neq i}^{n} \gamma_{ij} x_j, & i = s+1, \ldots, n, \end{cases} \tag{2}$$

where x_i represent population densities of the species in the patch i. The parameter D represents the dispersion rate of the population, $\gamma_{ij} \geq 0$ denote the flux between patches j and i for $i \neq j$. We denote Γ the matrix $\Gamma = (\gamma_{ij})_{n\times n}$. For the model (2), 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.

In [11, 12], Elbetch et al. have answered in the particular case of the n-Source 0-Sink patch model (i.e the system (2) for $n = s$), which rewritten as:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + D \sum_{j=1, j\neq i}^{n} \gamma_{ij} x_j, \qquad i = 1, \ldots, n, \tag{3}$$

to the following important question:

Question 1.1 *Is it possible, depending on the migration rate D, that the total equilibrium population $X_T^* = \sum_i x_i^*$, where $(x_1^*, \ldots, x_n^*)$ the positive equilibrium of* (3) *be larger than the sum of the capacities $\sum_i K_i$?*

Note that, the system (3) is studied also by Elbetch et al. [11] and Takeuchi [35] in the case when the matrix Γ is symmetric. We recall that, when the matrix of migration Γ is irreducible, System (3) admits a unique positive equilibrium which is globally asymptotically stable (GAS), see [4, Theorem 2.2], [3, Theorem 1] or [11, Theorem 6.1], when $D \to \infty$, this equilibrium tend to

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

where $\alpha_i = \frac{r_i}{K_i}$ and $(\delta_1, \ldots, \delta_n)^T$ the vector which generate the vector space $\ker\Gamma$. The question 1.1 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 least question has been studied by many researches (see [1, 2, 5, 7, 8, 9, 10, 11, 12, 13, 16, 18, 19, 20, 40], [14] for effect of nonlinear diffusion on the total biomass, and [21, 22] for susceptible-infectedsusceptible (SIS) patch-model). Elbetch et al. [11] 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 [12, 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-Source, 0-Sink 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 D and detrimental for the higher values. More precisely, it was shown in [1] that, if $n = 2$ in (3), the following trichotomy holds

- If $X_T^*(+\infty, \varepsilon) > K_1 + K_2$ then $X_T^*(D) > K_1 + K_2$ for all $\beta > 0$ and $\varepsilon > 0$.
- If $\frac{dX_T^*}{dD}(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$, then there exists $D_0(\varepsilon) > 0$ such that $X_T^*(D) > K_1 + K_2$ for $0 < D < D_0$, $X_T^*(D) < K_1 + K_2$ for $D > D_0$ and $X_T^*(D_0) = K_1 + K_2$.
- If $\frac{dX_T^*}{dD}(0) < 0$, then $X_T^*(D) < K_1 + K_2$ for all $D > 0$.

Therefore, the condition $X_T^*(D) = K_1 + K_2$ holds only for $D = 0$ and at most for one positive value $D = D_0$. The value D_0 exists if and only if $\frac{d}{dD}X_T^*(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2$.

In [11, Section 5.2], Elbetch et al. have considered the model (3) 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 $\frac{dX_T^*}{dD}(0) < 0$ and $X_T^*(+\infty) > K_1 + K_2 + K_3$.
- The case where $\frac{dX_T^*}{dD}(0) > 0$ and $X_T^*(+\infty) > K_1 + K_2 + K_3$ and there exist values of D for which $X_T^*(D) < K_1 + K_2 + K_3$.
- The case where $\frac{dX_T^*}{dD}(0) < 0$ and $X_T^*(+\infty) < K_1 + K_2 + K_3$ and there exist values of D for which $X_T^*(D) > K_1 + K_2 + K_3$.

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

In [12, Section 6], Elbetch et al. have reconsidered the three-patch model with Γ is not symmetric. The novelty when Γ is not symmetric is the existence of three positive values of migration rate solution of the following equation:

$$\text{Total equilibrium population = Sum of three carrying capacities,}$$

i.e. the following situation hold:

- The case where $\frac{dX_T^*}{dD}(0) > 0$ and $X_T^*(+\infty) < K_1 + K_2 + K_3$, and there exists three values $0 < D_1 < D_2 < D_3$ for which we have:

$$X_T^*(D) = \begin{cases} > K_1 + K_2 + K_3 & \text{for} \quad D \in]0, D_1[\cup]D_2, D_3[, \\ < K_1 + K_2 + K_3 & \text{for} \quad D \in]D_1, D_2[\cup]D_3, \infty[. \end{cases}$$

For more details and the proof of the previous numerical results, see the recent work of Elbetch [15], where it is studied the model (3) under the assumption that some growth rates are much larger than the other.

Recently, Yu et al. [39] considered a consumer-resource patch model, where the consumer moves between multiple source-sink patches with both resource and toxicant given by the following system:

$$\begin{cases} \dfrac{dx_i}{dt} = N_{0i} - \mu_i x_i - \dfrac{r_i x_i y_i}{\Gamma_i (k_i + x_i)}, & i = 1, \ldots, n, \\ \dfrac{dy_i}{dt} = y_i \left(\dfrac{r_i x_i}{k_i + x_i} - m_i - g_i y_i \right) - D \left(s_i y_i - \dfrac{1}{2} s_{i-1} y_{i-1} - \dfrac{1}{2} s_{i+1} + y_{i+1} \right), \end{cases} \tag{4}$$

where $i = i$ mod n, and "mod" means modula [41]. For example, $y_0 = y_n$ and $y_{n+1} = y_1$. Variable x_i represents the nutrient concentration and y_i is the consumer's population density in patch i. Parameter N_{0i} represents the nutrient input, μ_i is the dilution rate of nutrient, Γ_i is the yield, or fraction of nutrient per unit biomass. Parameter r_i represents the consumer's maximal growth rate with infinite resource, k_i is the half saturation coefficient, m_i is the mortality rate, and g_i is the density-dependent loss rate. Parameter D represents the diffusion rate, while s_i is the asymmetry in diffusion. Note that, when $s_i = 1$ for all i, the diffusion is symmetric. Yu et al. [39] showed the global stability of positive equilibria in the system (4). They have shown also that diffusion could make the consumer persist in sinks, even make it reach total population abundance larger than if non-diffusing. It is also shown that under certain conditions, diffusion could make the total abundance less than if non-diffusing, even make the consumer go into extinction in all patches.

An important result proven by Yu et al. [39] is that when toxicants are distributed homogeneously, asymmetric diffusion always makes the total abundance less than if non-diffusing. For general information on the effect of asymmetric diffusion, toxicant distribution, and geographic pattern of patches on the total population abundance of the consumer, and also in the continuous and discrete cases of (4), the reader is referred to the work of Yu et al. [39] and Zhang et al. [41].

Our aim of the present paper, is to study the effect of the migration on the total population with the assumption that some patches among the n patches are sinks. Thus we generalize some results of [11, 12] for n-Source, 0-Sink patch model to s-Source, (n-s)-Sink patch model and also we extend the results proved by Wu et al. [38] for One-Source, One-Sink patch model.

The paper is organized as follows. In Section 2, some proprieties of One-Source, One-Sink patch model (1) have been recalled as a function of the two parameters γ_1 and γ_2. Two-patch model with the growth (resp. death) rate is much larger than the death (resp. growth) rate is considered. In both last cases, we compare the total equilibrium population with the capacity. In Section 3, Multi-patch Source-Sink model with intraspecific competition in the sink patches is being described. We prove that there exists a threshold number of source patches such that the population becomes extinct below the threshold and established above the threshold. The behavior of the model for large migration rate is studied. Total population abundance is analyzed also in some homogeneous and heterogeneous particular case. The following both cases: death rates are much larger than the growth rates and growth rates are much larger than the death rates are considered. In Section 4, Multi-patch Source-Sink model without intraspecific competition in the sink patches is considered. In Appendix A, we give some properties of the total equilibrium population. In Appendix B, we give some background concepts and preliminaries results which used in the analysis of the global stability of our model.

2 Some preliminaries results in the two-patch model with source-sink populations

In this section, we consider the 2-patch system with source-sink dynamics given by:

$$\begin{cases} \dfrac{dx_1}{dt} &= a_1 x_1 \left(1 - \dfrac{x_1}{L_1}\right) + D\left(\gamma_2 x_2 - \gamma_1 x_1\right), \\ \dfrac{dx_2}{dt} &= a_2 x_2 \left(-1 - \dfrac{x_2}{L_2}\right) + D\left(\gamma_1 x_1 - \gamma_2 x_2\right), \end{cases} \tag{5}$$

where x_1 and x_2 represent population densities of the species in patch 1 and 2, respectively. Patch 1 is assumed to be the source but patch 2 is the sink, i.e $a_1, a_2 > 0$. The parameters $\alpha_i := a_i/L_i$ are the intraspecific competition degree. Parameter D represents the dispersal intensity. We denote γ_2 the migration rate from source patch 2 to the sink patch 1 and γ_1 from sink patch 1 to source patch 2, the dispersal is symmetric if $\gamma_1 = \gamma_2$. This system is studied in [38]. We propose here to recall some essential results of [38]. First of all, let's start by recalling the global dynamics of the system (5).

2.1 Global dynamics

We consider the following regions in the set of parameters γ_1 and γ_2, denoted $\mathscr{D}_0, \mathscr{D}_1$ and $\mathscr{D}_2$ depicted in Figure 1 and defined by:

$$\begin{cases} \mathscr{D}_0 = \left\{ (\gamma_1, \gamma_2) : \quad \gamma_2 \geq \dfrac{a_2}{a_1}\gamma_1 \right\}, \\ \mathscr{D}_1 = \left\{ (\gamma_1, \gamma_2) : \quad \dfrac{a_2}{a_1}\gamma_1 < \gamma_2 < \dfrac{a_2 D}{a_1 a_2 + D a_1}\gamma_1 \right\}, \\ \mathscr{D}_2 = \left\{ (\gamma_1, \gamma_2) : \quad \gamma_2 \geq \dfrac{a_2 D}{a_1 a_2 + D a_1}\gamma_1 \right\}. \end{cases} \tag{6}$$

The global dynamic of the system (5) is shown as follows.

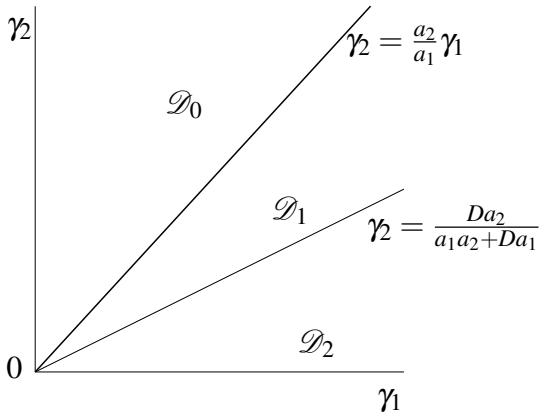


Figure 1: Global stability of the model (5). In $\mathscr{D}_0$ and $\mathscr{D}_1$ the system admits unique equilibrium $E^*(D)$ which is GAS. In the region $\mathscr{D}_2$, the system admits the origin as unique equilibrium which is GAS.

Theorem 2.1 (Prop. 5.5 in [38]) *Consider the model* (5)*. Then, if* $(\gamma_1, \gamma_2) \in \mathscr{D}_0 \cup \mathscr{D}_1$*, the system* (5) *admits unique equilibrium in* $\mathbb{R}^2 \backslash \{0\}$ *denoted* $E^*(D)$*, which is GAS, and if* $(\gamma_1, \gamma_2) \in \mathscr{D}_2$*, then the origin is GAS.*

2.2 Total population abundance

In this section, we recall the comparison given in [38, Proposition 5.11], between the total equilibrium population

$$X_T^*(D) = x_1^*(D) + x_2^*(D), \qquad E^*(D) = (x_1^*(D), x_2^*(D)),$$

of (5) and L_1, by analyzing the stable positive equilibrium $E^*(D)$. Note that, when there is no dispersal (i.e., $D = 0$), the total equilibrium population is $X_T^*(0) = L_1$. We consider the

regions in the set of the parameters γ_1 and γ_2, denoted $\mathscr{L}_0$, $\mathscr{L}_1, \mathscr{L}_2$, $\mathscr{L}_3$ and $\mathscr{J}_4$, depicted in Figure 2 and defined by:

$$\begin{cases} \text{If } a_2 \geq a_1 \text{ then } \begin{cases} \mathscr{L}_0 = \left\{(\gamma_1,\gamma_2): \quad \frac{\gamma_2}{\gamma_1} < \frac{a_2}{a_1}\right\}, \\ \mathscr{L}_1 = \left\{(\gamma_1,\gamma_2): \quad \frac{\gamma_2}{\gamma_1} \geq \frac{a_2}{a_1}\right\}. \end{cases} \\ \text{If } a_2 < a_1 \text{ then } \begin{cases} \mathscr{L}_2 = \left\{(\gamma_1,\gamma_2): \quad \frac{\gamma_2}{\gamma_1} \leq \frac{a_2}{a_1}\right\}, \\ \mathscr{L}_3 = \left\{(\gamma_1,\gamma_2): \quad \frac{a_2}{a_1} < \frac{\gamma_2}{\gamma_1} < \frac{L_2(a_1-a_2)}{a_2(L_1+L_2)}\right\}, \\ \mathscr{L}_4 = \left\{(\gamma_1,\gamma_2): \quad \frac{\gamma_2}{\gamma_1} \geq \frac{L_2(a_1-a_2)}{a_2(L_1+L_2)}\right\}. \end{cases} \end{cases} \tag{7}$$

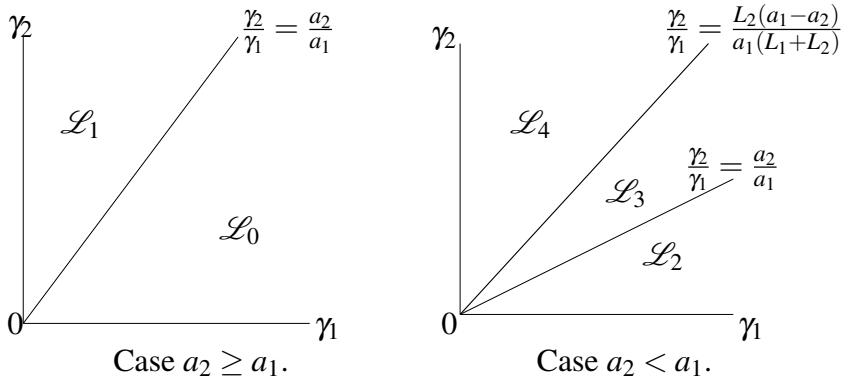


Figure 2: Qualitative properties of source-sink model (5). In $\mathscr{L}_0$ and $\mathscr{L}_1$ the effect is detrimental with extinction in two patches for $\mathscr{L}_0$ and persistence for $\mathscr{L}_1$. In $\mathscr{L}_2$ and $\mathscr{L}_3$, the effect is beneficial for $D < D_0$ and detrimental for $D > D_0$ with persistence of the population in the region $\mathscr{L}_2$ and extinction in the region $\mathscr{L}_3$. In $\mathscr{L}_4$, patchiness has a beneficial effect on the total equilibrium population.

Theorem 2.2 *The total equilibrium population of* (5) *satisfies the following properties*

1. *If $a_2 \geq a_1$, let $\mathscr{L}_0$ and $\mathscr{L}_1$ be defined by (7). Then we have:*

   - *if $(\gamma_1,\gamma_2) \in \mathscr{L}_0$ then $X_T^*(D) \leq L_1$ for all $D \geq 0$. More precisely, there is $D^* = \frac{\gamma_2 a_1 a_2}{\gamma_1 a_2 - \gamma_2 a_1}$, such that:*

   $$\begin{cases} 0 < X_T^*(D) \leq L_1 & \text{If} \quad D < D^*, \\ X_T^*(D) = 0 & \text{If} \quad D \geq D^*. \end{cases} \tag{8}$$

   - *if $(\gamma_1,\gamma_2) \in \mathscr{L}_1$ then $0 < X_T^*(D) \leq L_1$ for all $D \geq 0$.*

2. *If $a_2 < a_1$, let $\mathscr{L}_2, \mathscr{L}_3$ and $\mathscr{L}_4$ be defined by (7). Then we have:*

   - *if $(\gamma_1,\gamma_2) \in \mathscr{L}_2$ then $X_T^*(D) > L_1$ for $D < D_0$ and $X_T^*(D) < L_1$ for all $D > D_0$. where*

   $$D_0 = \frac{(a_1 - a_2)(L_1 + L_2)}{(\gamma_2(a_2 - a_1) + \gamma_1 \alpha_1 (L_1 + L_2))(\alpha_1{}^{-1} + \alpha_2{}^{-1})}, \qquad \text{with } \alpha_i = a_i/L_i. \tag{9}$$

   Moreover, there is $D^* \geq D_0$ such that $X_T^*(D) = 0$ for all $D \geq D^*$.

- *if* $(\gamma_1, \gamma_2) \in \mathscr{L}_3$ *then we have*

$$\begin{cases} X_T^*(D) \geq L_1 & If \quad D \leq D^*, \\ 0 < X_T^*(D) < L_1 & If \quad D > D^*. \end{cases} \tag{10}$$

- *if* $(\gamma_1, \gamma_2) \in \mathscr{L}_4$, *then* $X_T^*(D) \geq L_1$ *for all* $D \geq 0$.

Proof 1 *The all results were established by Wu at al. [38, Proposition 5.11]. Note that, the explicit expression* (9) *of* D_0 *was not given in [38].*

In biological terms, the results of the previous theorem for One-Source One-Sink patch shows that, the dispersal asymmetry can lead to an increased total size of the species in two patches, a decreased total size with persistence in the patches, and even extinction in both patches. Comparing these results with that of Arditi et al. [1, 2] for One-source One-source patch model, we deduce that the existence of a sink patch among the two patches, can cause an extinction of the total population in the two patches.

In the case of perfect mixing (i.e $D \to \infty$), we have the following result [38, Proposition 5.10]:

Proposition 2.1 *We have:*

$$X_T^*(\infty) := \lim_{D\to\infty} X_T^*(D) = \begin{cases} (\gamma_1+\gamma_2)\dfrac{\gamma_2 a_1 - \gamma_1 a_2}{\gamma_2^2 a_1/L_1 + \gamma_1^2 a_2/L_2} & if \quad \gamma_1/\gamma_2 < a_1/a_2, \\ 0 \quad otherwise. \end{cases} \tag{11}$$

Wu et al. [38] proved that large dispersal intensity (i.e., $D \to \infty$), the intermediate asymmetry γ_1/γ_2 can lead to population density higher than that without dispersal, and extremely small asymmetry is still favorable, while extremely large asymmetry is unfavorable: (i) When the dispersal asymmetry is small, the species can approach a density larger than that without dispersal, while it reaches its maximum value at an intermediate asymmetry $\frac{\gamma_1}{\gamma_2} = \frac{a_1-a_2}{2\alpha_2(L_1+L_2)}$. (ii) When γ_1/γ_2 is extremely large, the species goes to extinction in both patches. Mathematically speaking, we can rewrite the following result [38, Proposition 5.10]:

Proposition 2.2 *[38, Proposition 5.10] Assume that* $\frac{\gamma_1}{\gamma_2} < \frac{a_1}{a_2}$. *Consider the total equilibrium population for* $D \to \infty$ *given in* (11). *We have:*

$$X_T^*(+\infty) \begin{cases} > L_1 & if \quad \frac{\gamma_1}{\gamma_2} < \frac{a_1-a_2}{\alpha_2(L_1+L_2)}, \\ = L_1 & if \quad \frac{\gamma_1}{\gamma_2} = \frac{a_1-a_2}{\alpha_2(L_1+L_2)}, \\ < L_1 & if \quad \frac{\gamma_1}{\gamma_2} > \frac{a_1-a_2}{\alpha_2(L_1+L_2)}. \end{cases} \tag{12}$$

Moreover, $X_T^*(+\infty)$ *approaches its maximum value*

$$\gamma_2^2 a_2 L_1 \frac{L_1+L_2}{4(\gamma_2^2 a_1 L_2 + \gamma_1^2 a_2 L_1)} \left(\frac{a_1-a_2}{\alpha_2(L_1+L_2)}\right)^2$$

at $\frac{\gamma_1}{\gamma_2} = \frac{a_1-a_2}{2\alpha_2(L_1+L_2)}$.

In the remainder of this section, we present our first result in this work. More precisely, we study the effect of the rapid growth source population and rapid death sink population on the dynamics of the total equilibrium population and on the coexistence of the species. Note that, these situations were not examined in [3, 38]. Here, we study

the total equilibrium population as a function of the migration rate in the case where the growth (resp. death) rate is much larger than the death (resp. growth) rate. In particular, we explicitly calculate the total equilibrium in the both situations, its derivative in the absence of the migration, its limit for large migration rate and we compare the total equilibrium population with the carrying capacity of the source patch. First, we start by the following situation:

2.3 The death rate is much larger than the growth rate

In this part, we consider the two-patch model (5) and we assume that the death rate a_2 is much larger than the growth rate a_1. On can write the model in the following way:

$$\left\{\begin{array}{rcl} \dfrac{dx_1}{dt} & = & a_1x_1\left(1-\dfrac{x_1}{L_1}\right)+D\left(\gamma_2x_2-\gamma_1x_1\right), \\ \dfrac{dx_2}{dt} & = & \dfrac{a_2}{\varepsilon}x_2\left(-1-\dfrac{x_2}{L_2}\right)+D\left(\gamma_1x_1-\gamma_2x_2\right), \end{array}\right. \tag{13}$$

where ε is assumed to be a small positive number. First, we have the following result:

Theorem 2.3 *Let $(x_1(t,\varepsilon),x_2(t,\varepsilon))$ be the solution of the system* (13) *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*

$$\frac{dx_1}{dt}=a_1x_1\left(1-\frac{x_1}{L_1}\right)-D\gamma_1x_1=:\varphi(x_1), \tag{14}$$

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

$$x_1(t,\varepsilon)=z(t)+o_\varepsilon(1), \qquad \text{uniformly for } t\in[0,+\infty) \tag{15}$$

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

$$x_2(t,\varepsilon)=o_\varepsilon(1), \quad \text{uniformly for} \quad t\in[t_0,+\infty). \tag{16}$$

Proof 2 *When $\varepsilon\to 0$, the system* (13) *is a slow-fast system, with one slow variable, x_1, and one fast variable, x_2. Tikhonov's theorem [29, 36, 37] prompts us to consider the dynamics of the fast variables in the time scale $\tau=\frac{1}{D}t$. One obtains*

$$\frac{dx_2}{d\tau}=a_2x_2\left(-1-\frac{x_2}{L_2}\right)+\varepsilon D(\gamma_1x_1-\gamma_2x_2). \tag{17}$$

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

$$\frac{dx_2}{d\tau}=a_2x_2\left(-1-\frac{x_2}{L_2}\right). \tag{18}$$

The slow manifold is given by the equilibrium of the system (18)*, i.e $x_2=0$, 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* (13) *converge to the solutions of the reduced model* (14)*, obtained by replacing $x_2=0$ into the dynamics of the slow variable.*

If $a_1-D\gamma_1\leq 0$, then, the differential equation (14) *admits $x_1^*(D,0^+)=0$ for all D, as equilibrium, which is GAS. If $a_1-D\gamma_1>0$, then, the differential equation* (14) *admits as a positive equilibrium*

$$x_1^*(D,0^+):=\frac{L_1(a_1-D\gamma_1)}{a_1}. \tag{19}$$

As $\varphi(x_1) > 0$ *for all* $0 \leq x_1 < x_1^*(D,0^+)$ *and* $\varphi(x_1) < 0$ *for all* $x_1 > x_1^*(D,0^+)$ *then, the equilibrium* $x_1^*(D,0^+)$ *is GAS in the positive axis, so, the approximation given by Tikhonov's theorem holds for all* $t \geq 0$ *for the slow variable and for all* $t \geq t_0 > 0$ *for the fast variable, where* t_0 *is as small as we want. Therefore, let* $z(t)$ *be the solution of the reduced model* (14) *of initial condition* $z(0) = x_1^0$*, then, when* $\varepsilon \to 0$*, we have the approximations* (15) *and* (16).

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (13) when ε goes to zero.

Corollary 2.1 *Consider the total equilibrium population* $x_1^*(D,0^+)$ *of the model* (13) *when* $\varepsilon \to 0$*, given by* (19)*. Then,* $0 < x_1^*(D,0^+) < L_1$ *for* $D < \frac{\gamma_1}{a_1}$*, and* $x_1^*(D,0^+) = 0$ *for* $D \geq \frac{\gamma_1}{a_1}$.

2.4 The growth rate is much larger than the death rate

In this part, we consider the two-patch model (5) and we assume that the growth rate a_1 is much larger than the death rate a_2. On can write the model in the following way:

$$\left\{\begin{array}{rcl} \dfrac{dx_1}{dt} & = & \dfrac{a_1}{\varepsilon}x_1\left(1-\dfrac{x_1}{L_1}\right)+D\left(\gamma_2 x_2-\gamma_1 x_1\right), \\ \dfrac{dx_2}{dt} & = & a_2 x_2\left(-1-\dfrac{x_2}{L_2}\right)+D\left(\gamma_1 x_1-\gamma_2 x_2\right), \end{array}\right. \tag{20}$$

where ε is assumed to be a small positive number. We prove the following result:

Theorem 2.4 *Let* $(x_1(t,\varepsilon),x_2(t,\varepsilon))$ *be the solution of the system* (20) *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*

$$\frac{dx_2}{dt} = a_2 x_2\left(-1-\frac{x_2}{L_2}\right)+D(\gamma_1 L_1-\gamma_2 x_2) =: \psi(x_2), \tag{21}$$

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

$$x_2(t,\varepsilon) = z(t)+o_\varepsilon(1), \qquad \textit{uniformly for } t \in [0,+\infty) \tag{22}$$

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

$$x_1(t,\varepsilon) = L_1+o_\varepsilon(1), \quad \textit{uniformly for} \quad t \in [t_0,+\infty). \tag{23}$$

Proof 3 *When* $\varepsilon \to 0$*, the system* (20) *is a slow-fast system, with one slow variable,* x_2*, and one fast variable,* x_1*. Tikhonov's theorem [29, 36, 37] prompts us to consider the dynamics of the fast variables in the time scale* $\tau = \frac{1}{D}t$*. One obtains*

$$\frac{dx_1}{d\tau} = a_1 x_1\left(1-\frac{x_1}{L_1}\right)+\varepsilon D(-\gamma_1 x_1+\gamma_2 x_2). \tag{24}$$

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

$$\frac{dx_1}{d\tau} = a_1 x_1\left(1-\frac{x_1}{L_1}\right). \tag{25}$$

The slow manifold is given by the equilibrium of the system (18)*, i.e* $x_1 = L_1$*, 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 (20) *converge to the solutions of the reduced model* (21)*, obtained by replacing* $x_1 = L_1$ *into the dynamics of the slow variable.*
The differential equation (14) *admits as a positive equilibrium*

$$x_1^*(D,0^+) := -\frac{L_2}{2} - \frac{DL_2}{2a_2}\gamma_2 + \frac{1}{2a_2}\sqrt{L_2^2\gamma_2^2D^2 + (2a_2L_2^2\gamma_2 + 4a_2L_2L_1\gamma_1)D + a_2^2L_2^2}. \quad (26)$$

As $\psi(x_1) > 0$ *for all* $0 \leq x_1 < x_1^*(D,0^+)$ *and* $\psi(x_1) < 0$ *for all* $x_1 > x_1^*(D,0^+)$ *then, the equilibrium* $x_1^*(D,0^+)$ *is GAS in the positive axis, so, the approximation given by Tikhonov's theorem holds for all* $t \geq 0$ *for the slow variable and for all* $t \geq t_0 > 0$ *for the fast variable, where* t_0 *is as small as we want. Therefore, let* $z(t)$ *be the solution of the reduced model* (21) *of initial condition* $z(0) = x_1^0$*, then, when* $\varepsilon \to 0$*, we have the approximations* (22) *and* (23)*.*

As a corollary of the previous theorem, we have the following result which give the limit of the total equilibrium population $X_T^*(D,\varepsilon)$ of the model (20) when ε goes to zero:

Corollary 2.2 *We have:*

$$X_T^*(D,0^+) := L_1 - \frac{L_2}{2} - \frac{DL_2}{2a_2}\gamma_2 + \frac{1}{2a_2}\sqrt{L_2^2\gamma_2^2D^2 + (2a_2L_2^2\gamma_2 + 4a_2L_2L_1\gamma_1)D + a_2^2L_2^2}. \quad (27)$$

In the following proposition, we calculate the derivative of $X_T^*(D,0^+)$ at $D = 0$ and the formula of perfect mixing (i.e when $D \to \infty$) of the total equilibrium population defined by (27).

Proposition 2.3 *Consider the total equilibrium population* (27)*. Then,*

$$\frac{dX_T^*}{dD}(0,0^+) = \frac{\gamma_1 L_1}{a_2}, \quad (28)$$

and

$$X_T^*(+\infty,0^+) = \frac{\gamma_1+\gamma_2}{\gamma_2}L_1. \quad (29)$$

Proof 4 *The derivative of the total equilibrium population* $X_T^*(D,0^+)$ *defined by* (27) *with respect to D is:*

$$\frac{dX_T^*}{dD}(D,0^+) = -\frac{L_2\gamma_2}{2a_2} + 1/4\,\frac{2\,a_2{L_2}^2\gamma_2 + 2\,D{L_2}^2{\gamma_2}^2 + 4\,a_2L_2\gamma_1L_1}{a_2\sqrt{{a_2}^2{L_2}^2 + 2\,a_2{L_2}^2D\gamma_2 + D^2{L_2}^2{\gamma_2}^2 + 4\,a_2DL_2\gamma_1L_1}}. \quad (30)$$

In particular, the derivative of the total equilibrium population at $D = 0$ *is given by the formula* (28)*.*

By taking the limit of (27) *when* $D \to \infty$*, we get that the total equilibrium population* $X_T^*(D,0^+)$ *tend to* (29)*.*

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (20) when ε goes to zero.

Theorem 2.5 *Consider the total equilibrium population* $X_T^*(D,0^+)$ *given by* (27)*. Then,* $X_T^*(D,0^+) \geq L_1$*, for all* $D \geq 0$*.*

Proof 5 *First, we try to solve the equation $X_T^*(D,0^+) = L_1$ with respect to D, the solutions of this last equation give the points of intersection between the curve of the total equilibrium population $D \mapsto X_T^*(D,0^+)$ and the straight line $D \mapsto L_1$. For any $D \geq 0$, we have*

$$\begin{aligned} X_T^*(D,0^+) = L_1 &\Longleftrightarrow \frac{1}{2a_2}\sqrt{L_2^2\gamma_2^2D^2 + (2a_2L_2^2\gamma_2 + 4a_2L_2L_1\gamma_1)D + a_2^2L_2^2} = \frac{L_2}{2} + \frac{DL_2}{2a_2}\gamma_2 \\ &\Longleftrightarrow \sqrt{L_2^2\gamma_2^2D^2 + (2a_2L_2^2\gamma_2 + 4a_2L_2L_1\gamma_1)D + a_2^2L_2^2} = a_2L_2 + \gamma_2DL_2 \\ &\Longleftrightarrow 4a_2\gamma_1L_1L_2D = 0 \\ &\Longleftrightarrow D = 0. \end{aligned}$$

So, since $\frac{dX_T^*}{dD}(0,0^+) > 0$, the curve of the total equilibrium population intersects the straight line $D \mapsto L_1 + L_2$ in a unique point which is $(0,L_1)$. Therefore, $X_T^*(D,0^+) \geq L_1$, for all $D \geq 0$.

Biologically speaking, from Sections 2.4 and 2.3, we conclude that, the rapid increase in the source population results in persistence in the both patches with increased total size population, and the rapid sink population results in extinction in both patches.

3 Multi-patch Source-sink model with intraspecific competition in the sink patches

In this section, we consider the model of n patches, with s source patches and $n-s$ sink patches given by:

$$\frac{dx_i}{dt} = x_i(a_i - \alpha_i x_i) + D\sum_{j=1, j\neq i}^{n}(\gamma_{ij}x_j - \gamma_{ji}x_i), \qquad i = 1,\ldots,n, \tag{31}$$

where x_i represent population densities of the species in the patch i. Without loss of generality, the s first patches are assumed to be the source (i.e $a_i > 0$ for all $i = 1,\ldots,s$) and the other $n-s$ patches, assumed to bet the sink (i.e $a_i < 0$ for all $i = s+1,\ldots,n$). The parameter α_i is positive for all i and represent the intraspecific competition for the i-th patch. The parameter D represents the dispersion rate of the population, $\gamma_{ij} \geq 0$ denote the flux between patches j and i for $i \neq j$. If $\gamma_{ij} = 0$ then non direct flux from j to i and if $\gamma_{ij} > 0$ there is a flux of migration from patch j to patch i. We assume that, there exists intraspecific competition in $n-s$ sink patches, i.e $\alpha_i > 0$ for all $i = s+1,\ldots,n$. If we denote:

$$a_i = \begin{cases} r_i & \text{if} \quad i = 1,\ldots,s, \\ -r_i & \text{if} \quad i = s+1,\ldots,n, \end{cases}$$

where $r_i > 0$ for all i, and $K_i = r_i/\alpha_i$ for all $i = 1,\ldots,n$, then the system (31) can be written as:

$$\begin{cases} \dfrac{dx_i}{dt} = r_ix_i\left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n}(\gamma_{ij}x_j - \gamma_{ji}x_i), & i = 1,\ldots,s, \\ \dfrac{dx_i}{dt} = r_ix_i\left(-1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n}(\gamma_{ij}x_j - \gamma_{ji}x_i), & i = s+1,\ldots,n, \end{cases} \tag{32}$$

where the parameters $r_i > 0$ is the both growth rate in the case of source (i.e $i \leq s$) patches and the death rate in the case of sink (i.e $s+1 \leq i \leq n$), $K_i > 0$ is the carrying capacity of

source patches. The system (32) can be written:

$$\begin{cases} \dfrac{dx_i}{dt} = r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n} \gamma_{ij} x_j, & i = 1, \ldots, s, \\ \dfrac{dx_i}{dt} = r_i x_i \left(-1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n} \gamma_{ij} x_j, & i = s+1, \ldots, n, \end{cases} \tag{33}$$

where the term γ_{ii} accounts for the flux out of patch i and takes the form:

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ji}. \tag{34}$$

We denote by Γ the matrix $\Gamma := (\gamma_{ij})_{n\times n}$. We call Γ the movement matrix of the system (32). Its columns sum to 0 since the diagonal elements γ_{ii} are defined by (34) in such a way that each row sums to 0 and Γ is cooperative matrix. If Γ is irreducible, then 0 is a simple eigenvalue of Γ and all non-zero eigenvalues of Γ have negative real part, i.e., the stability modulus of a matrix Γ equal to zero. Moreover, the kernel of the matrix Γ is generated by a positive vector (see Lemma 2 in [3]). In all of this paper, we denote by $\delta := (\delta_1, \ldots, \delta_n)^T$ this positive vector. Note that, if the matrix Γ is symmetric, then $\ker\Gamma$ is generated by $\delta = (1, \ldots, 1)^T$. The matrix

$$\Gamma_0 := \Gamma - \mathrm{diag}(\gamma_{11}, \ldots, \gamma_{nn}) \tag{35}$$

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

Remark 3.1 *For the existence , uniqueness, and positivity of δ see Lemma 1 of Cosner et al. [7], Lemma 4.1 and Lemma 1 of Elbetch et al. [11, 12]. On the other hand, it is shown in Guo et al. [22, Lemma 2.1] and Gao and Dong [20, Lemma 3.1] that the vector $(\Gamma^*_{11}, \ldots, \Gamma^*_{nn})^T$ is a right eigenvector of Γ associated with the zero eigenvalue. Here, Γ^*_{ii} is the cofactor of the i-th diagonal entry of Γ, and $sgn(\Gamma^*_{ii}) = (-1)^{n-1}$. For two patches we have $\delta = (\gamma_{12}, \gamma_{21})^T$, and for three patches we have $\delta = (\delta_1, \delta_2, \delta_3)^T$, where*

$$\begin{cases} \delta_1 = \gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{32}\gamma_{13}, \\ \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \\ \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32}. \end{cases} \tag{36}$$

In Lemma 2.1 of Guo et al [22] gives explicit formulas of the components of the vector δ, with respect of the coefficients of Γ as follow:

$$\delta_k = \sum_{T\in\mathscr{T}_k} \prod_{(i,j)\in E(T)} \gamma_{ij}, \qquad k = 1, \ldots, n, \tag{37}$$

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

The system (32) can be also rewritten in matrix form as follow:

$$\begin{cases} \dot{X}_s = \mathrm{diag}\left(r_1 - \frac{r_1}{K_1}x_1, \cdots, r_s - \frac{r_s}{K_s}x_s\right) X_s + D\left(\Gamma_{ss}X_s + \Gamma_{sp}X_p\right), \\ \dot{X}_p = \mathrm{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}, \cdots, -r_n - \frac{r_n}{K_n}x_n\right) X_p + D\left(\Gamma_{ps}X_s + \Gamma_{pp}X_p\right), \end{cases} \tag{38}$$

where $X_s = (x_1, \ldots, x_s)^T, X_p = (x_{s+1}, \ldots, x_p)^T$ and the matrix $\Gamma_{ss}, \Gamma_{pp}, \Gamma_{sp}, \Gamma_{ps}$ describe the flux within and between source and sink patches. They are obtained by writing the matrix Γ in block form as

$$\Gamma = \begin{bmatrix} \Gamma_{ss} & \Gamma_{sp} \\ \Gamma_{ps} & \Gamma_{pp} \end{bmatrix}. \tag{39}$$

The model (32) studied in [38] for two patches, i.e $n = 2$ and $s = 1$. The same model studied in [3] for n patches where the sink population flow at the death rate: $\dot{x}_i = -r_i x_i$ for all $s+1 \leq i \leq n$.

3.1 Global dynamics

In this part, our goal is to study the dynamics of the system (32). Note that, in the absence of migration, i.e. the case where $D = 0$, the system (32) admits $(K_1, \ldots, K_s, 0, \ldots, 0)$ as a non trivial equilibrium point, which furthermore is GAS, and the origin as trivial equilibrium which is unstable. The problem is whether or not, the equilibrium continues to exist and GAS for any $D > 0$. The Jacobian matrix of the system (32) evaluated at $x = 0$ is given by:

$$\mathbb{J}_s(0) = \mathrm{diag}(\mathrm{r_1}, \ldots, \mathrm{r_s}, -\mathrm{r_{s+1}}, \ldots, -\mathrm{r_n}) + \mathrm{D}\Gamma, \tag{40}$$

which is the same as the matrix obtained by Arino et al. [3, Equation 7] for the model (2). The matrix $\mathbb{J}_s(0)$ is cooperative. We have the following result:

Lemma 3.1 *Consider the matrix $\mathbb{J}_s(0)$. Then, if $s = 0$, $S(\mathbb{J}_0(0)) < 0$, and if $s = n$, $S(\mathbb{J}_n(0)) > 0$.*

Proof 6 *If $s = 0$, then the matrix $\mathbb{J}_0(0)$ becomes*

$$\mathbb{J}_0(0) = \mathrm{diag}(-\mathrm{r_1}, \ldots, -\mathrm{r_n}) + \mathrm{D}\Gamma. \tag{41}$$

Let $u = (1, \cdots, 1)^T$. We have

$$\mathbb{J}_0(0)^T u = (-r_1, \cdots, -r_n)^T \leq \lambda u, \quad \textit{where} \quad \lambda = \max\{-r_1, \cdots, -r_n\} < 0.$$

Therefore, since $\mathbb{J}_0(0)$ is a cooperative matrix, according to Lemma B.4, we have

$$S(\mathbb{J}_0(0)) = S(\mathbb{J}_0(0)^T) \leq \lambda < 0.$$

If $s = n$, then the matrix $\mathbb{J}_n(0)$ becomes

$$\mathbb{J}_n(0) = \mathrm{diag}(\mathrm{r_1}, \ldots, \mathrm{r_n}) + \mathrm{D}\Gamma. \tag{42}$$

Let $u = (1, \cdots, 1)^T$. We have

$$\mathbb{J}_n(0)^T u = (r_1, \cdots, r_n)^T \geq \lambda u, \quad \textit{where} \quad \lambda = \min\{r_1, \cdots, r_n\} > 0.$$

Therefore, since $\mathbb{J}_n(0)$ is a cooperative matrix, according to Lemma B.4, we have

$$S(\mathbb{J}_n(0)) = S(\mathbb{J}_n(0)^T) \geq \lambda < 0.$$

This completes the proof of the lemma.

We have also the following result:

Lemma 3.2 *The stability modulus of the matrix $\mathbb{J}_s(0)$ is a non-decreasing function of s. Moreover, if the matrix of movement Γ is irreducible, then $\mathbb{J}_s(0)$ is an increasing function of s.*

Proof 7 *See proof of Proposition 6 in [3].*

The dynamics of the system (32) in the case where Γ is reducible, is given as follow:

Theorem 3.3 *Consider the system* (32)*. Assume that* Γ *is irreducible. Then, there exists a unique interval* $\mathscr{I} \subset]0,n[\subset \mathbb{R}$*, such that:*

- *If* $s < \min \mathscr{I}$*, then the origin is LAS, and*
- *if* $s > \max \mathscr{I}$*, then the origin is unstable.*

Proof 8 *Since* $S(\mathbb{J}_0(0)) < 0$*, and* $S(\mathbb{J}_n(0)) > 0$ *by Lemma 3.1. Moreover, the function* $s \mapsto S(\mathbb{J}_s(0))$ *is non-decreasing by Lemma 3.2 and continues (See [27, Theorem 2.4.9.2]). So by the intermediate value theorem, there exists an interval* $\mathscr{I}$*, possibly reduced to a single point, such that* $S(\mathbb{J}_s(0)) = 0$ *for all* $s \in \mathscr{I}$*. Criteria for local asymptotic stability and instability of equilibria gives the completes proof of the theorem.*

Our goal in the remainder of this section is to study the dynamics of the model (32) in the case when the matrix Γ is irreducible. First, it is clear that the solutions of (32) exist for all $t \geq 0$ and remain non negative for non negative initial conditions. Thus, the positive cone $\mathbb{R}^n_+$ is invariant under the flow of the system (32). To establish the boundedness of solutions, we have the following result:

Proposition 3.1 *For any non negative initial condition, the solutions of the system* (32) *remain non negative and positively bounded. Moreover, the set*

$$\Lambda = \left\{ (x_1, \ldots, x_n) \in \mathbb{R}^n : 0 \leq \sum_{i=1}^{n} x_i \leq \frac{\xi_2^*}{\xi_1^*} \right\} \tag{43}$$

is positively invariant and is a global attractor for (32)*, where* $\xi_1^* = \min_{1 \leq i \leq n} r_i$ *and* $\xi_2^* = \sum_{s=1}^{s} r_i K_i$*.*

Proof 9 *To show that all solutions are bounded, we consider the quantity defined by* $X_T(t) = \sum_{i=1}^{n} x_i(t)$*. So, we have*

$$\dot{X}_T(t) = \sum_{i=1}^{s} r_i x_i(t) \left(1 - \frac{x_i(t)}{K_i}\right) + \sum_{i=s+1}^{n} r_i x_i(t) \left(-1 - \frac{x_i(t)}{K_i}\right). \tag{44}$$

For all $r_i, K_i \in \mathbb{R}^*_+$*, we have the following inequality:*

$$\begin{aligned} r_i x_i \left(1 - \tfrac{x_i}{K_i}\right) &\leq r_i (K_i - x_i), \quad i = 1, \ldots, s, \\ r_i x_i \left(-1 - \tfrac{x_i}{K_i}\right) &\leq -r_i x_i, \quad i = s+1, \ldots, n. \end{aligned} \tag{45}$$

Substituting Equation (45) *into* (44)*, we get*

$$\dot{X}_T(t) \leq -\xi_1^* X_T(t) + \xi_2^* \qquad \forall t \geq 0, \tag{46}$$

which gives

$$X_T(t) \leq \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*}\right) e^{-\xi_1^* t} + \frac{\xi_2^*}{\xi_1^*}, \qquad \text{for all } t \geq 0. \tag{47}$$

Hence,

$$X_T(t) \leq \max\left(X_T(0), \frac{\xi_2^*}{\xi_1^*}\right), \qquad \text{for all } t \geq 0. \tag{48}$$

Therefore, the solutions of system (32) *are positively bounded and defined for all* $t \geq 0$*. From* (47) *it can be deduced that the set* Λ *is positively invariant and it is a global attractor for the system* (32)*.*

We have the result:

Theorem 3.4 *Consider the system* (32)*. Assume that the matrix* Γ *(or equivalently, the connectivity matrix* Γ_0*) is irreducible, then, thre exists a unique point* $\mathscr{I}^* \in]0,n[$*, such that:*

- *If* $s < \mathscr{I}^*$*, then the origin is GAS, and*
- *if* $s > \mathscr{I}^*$*, then the model has a unique equilibrium point* $E^*(D)$*, which is GAS in the interior of the positive cone* $\mathbb{R}^n \setminus \{0\}$*.*

Proof 10 *If the matrix* Γ *is irreducible, then the interval* $\mathscr{I}$ *reduced to a single point* $\mathscr{I}^*$*, such that: if* $s < \mathscr{I}^*$*, then* $S(\mathbb{J}_s(0)) < 0$*, and if* $s > \mathscr{I}^*$*, then* $S(\mathbb{J}_s(0)) > 0$*. According to [32, Theorem 1], if* $S(\mathbb{J}_s(0)) < 0$*, the origin is GAS. If* $S(\mathbb{J}_s(0)) > 0$*, then, the model* (32) *is persistent for any* $D > 0$*, that is, any solution* $x(t)$ *satisfies* $\lim_{t\to\infty} inf\, x_i(t) > 0$*, for all i, and furthermore, since all the solutions to* (32) *are bounded, there exists a positive equilibrium point. We note* $(x_1^*(D),\ldots,x_n^*(D))$ *an equilibrium of* (32)*. Now, define the map:*

$$\Upsilon_i :]0,+\infty[\to \mathbb{R}, \qquad \Upsilon_i(\xi) = \Psi_i(\xi E^*(D)),$$

where $\Psi = (\Psi_1,\ldots,\Psi_n)$ *denote the vector field associated to* (32)*. We have,*

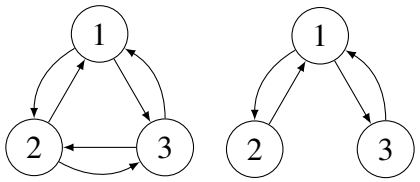
$$\Upsilon_i(\xi) = \frac{r_i}{K_i}\left(x_i^*(D)\right)^2 \xi(1-\xi), \qquad i = 1,\ldots,n.$$

Therefore, according to Theorem B.6, we conclude the proof of theorem.

As a corollary of the previous theorem we obtain the following result which proven in [11, Theorem 6.1]:

Corollary 3.1 *If* $s = n$*, the model* (32) *has a unique equilibrium point in the interior of the positive cone, which is GAS.*

Remark 3.2 *The assumption that the matrix* Γ *is irreducible, implies that the species can reach any i-th patch from any j-patch. For One-Source, One-Sink patch model, the matrix* Γ *is irreducible if and only if* γ_{12} *and* γ_{21} *are positives. For Three-patch model, under the irreducibility hypothesis on the matrix* Γ*, there are five possible cases, modulo permutation of the three patches, see Figures 3 and 4.*



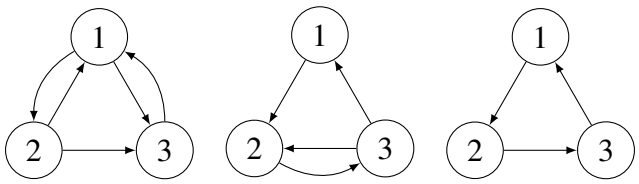
$\mathscr{G}_1$ $\mathscr{G}_2$

Figure 3: The two graphs $\mathscr{G}_1$ and $\mathscr{G}_2$ for which the migration matrix may be symmetric, if $\gamma_{ij} = \gamma_{ji}$.

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

In all of this work, we denote $E^*(D)$ the unique equilibrium in the interior of the positive cone of the system (32) if it exists, and $X_T^*(D)$, the total equilibrium population:

$$X_T^*(D) = \sum_{i=1}^{n} x_i^*(D), \qquad E^*(D) = (x_1^*(D),\ldots,x_n^*(D)). \tag{49}$$



$\mathscr{G}_3$ $\mathscr{G}_4$ $\mathscr{G}_5$

Figure 4: The three graphs $\mathscr{G}_3, \mathscr{G}_4$ and $\mathscr{G}_5$ for which the migration matrix cannot be symmetric.

3.2 The behavior of the model for large migration rate

In this section, our aim is to study the behavior of the system (32) for large migration rate, i.e. when $D \to \infty$. We use the theory of singular perturbations and Tikhonov's theorem [29, 36, 37] to obtain a better understanding of the behavior of the system in the case of perfect mixing. We have the following result:

Theorem 3.5 *Let $(x_1(t,D),\dots,x_n(t,D))$ be the solution of the system* (32) *with initial condition $(x_1^0,\cdots,x_n^0)$ satisfying $x_i^0 \geq 0$ for $i = 1\cdots n$. Let $Y(t)$ be the solution of the equation*

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{(\sum_{i=1}^n \delta_i)\,K}\right), \tag{50}$$

where

$$r = \frac{\sum_{i=1}^s \delta_i r_i - \sum_{i=s+1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i}, \quad K = \frac{\sum_{i=1}^s \delta_i r_i - \sum_{i=s+1}^n \delta_i r_i}{\sum_{i=1}^n \delta_i^2 \alpha_i} \quad \text{and} \quad \alpha_i = r_i/K_i. \tag{51}$$

Then, when $D \to \infty$, we have

$$\sum_{i=1}^n x_i(t,D) = Y(t) + o_D(1) \qquad \text{uniformly for } t \in [0,+\infty) \tag{52}$$

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

$$x_i(t,D) = \frac{\delta_i}{\sum_{i=1}^n \delta_i} Y(t) + o_D(1) \qquad i = 1,\dots,n, \text{ uniformly for } \quad t \in [t_0,+\infty). \tag{53}$$

Proof 11 *Let $X(t,D) = \sum_{i=1}^n x_i(t,D)$. We rewrite the system* (32) *using the variables $(X, x_1, \cdots, x_{n-1})$, and get:*

$$\begin{cases} \dfrac{dX}{dt} = \displaystyle\sum_{i=1}^s r_i x_i\left(1 - \frac{x_i}{K_i}\right) - \sum_{i=s+1}^n r_i x_i\left(1 + \frac{x_i}{K_i}\right), \\ \dfrac{dx_i}{dt} = r_i x_i\left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1,j\neq i}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), \qquad i = 1,\dots,s, \\ \dfrac{dx_i}{dt} = r_i x_i\left(-1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1,j\neq i}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), \qquad i = s+1,\dots,n-1. \end{cases} \tag{54}$$

This system is actually a system in the variables $(X, x_1, \cdots, x_{n-1})$, since, whenever x_n appears in the right hand side of (56)*, it should be replaced by*

$$x_n = X - \sum_{i=1}^{n-1} x_i. \tag{55}$$

When $D \to \infty$, (56) *is a slow-fast system, with one slow variable, X, and $n-1$ fast variables, x_i for $i = 1 \dots n-1$. As suggested by Tikhonov's theorem [29, 36, 37], we consider the dynamics of the fast variables in the time scale $\tau = Dt$. We get*

$$\begin{cases} \dfrac{dx_i}{d\tau} = \dfrac{1}{D} r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + \sum_{j=1, j\neq i}^{n} (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = 1, \dots, s, \\ \dfrac{dx_i}{d\tau} = \dfrac{1}{D} r_i x_i \left(-1 - \dfrac{x_i}{K_i}\right) + \sum_{j=1, j\neq i}^{n} (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = s+1, \dots, n-1. \end{cases} \tag{56}$$

where x_n is given by (55)*. In the limit $D \to \infty$, we find the fast dynamics*

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

This is an $(n-1)$-dimensional linear differential system. According to [12, Lemma B.1], this system admits unique equilibrium GAS given by

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

Thus, the slow manifold of System (56) *is given by*

$$x_i = \frac{\delta_i}{\sum_{i=1}^n \delta_i} X, \qquad i = 1, \dots, n-1. \tag{57}$$

As this manifold is GAS, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (56) *are approximated by the solutions of the reduced model, which is obtained by replacing* (57) *into the dynamics of the slow variable, that is:*

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

where r and K are defined in (51)*. Therefore, the reduced model is* (50)*. If $\sum_{i=1}^s \delta_i r_i > \sum_{i=s+1}^n \delta_i r_i$,* (50) *admits*

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

as a positive equilibrium point, which is GAS in the positive axis, and if $\sum_{i=1}^s \delta_i r_i \leq \sum_{i=s+1}^n \delta_i r_i$, (50) *admits the origin as unique equilibrium point, which is GAS. The approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, letting $Y(t)$ be the solution of the reduced model* (50) *with initial condition $Y(0) = X(0, D) = \sum_{i=1}^n x_i^0$, then, then $D \to \infty$, we have the approximations* (52) *and* (53)*.*

Note that, in the case of perfect mixing, the approximation (52) shows that:

- If $\sum_{i=1}^s \delta_i r_i > \sum_{i=s+1}^n \delta_i r_i$, then the total population behaves like the unique logistic equation (50) and then, when t and D tend to ∞, the total population $\sum x_i(t, D)$ tends toward $(\sum_{i=1}^n \delta_i) K = (\sum_{i=1}^n \delta_i) \frac{\sum_{i=1}^s \delta_i r_i - \sum_{i=s+1}^n \delta_i r_i}{\sum \delta_i^2 \alpha_i}$.

- If $\sum_{i=1}^{s} \delta_i r_i \leq \sum_{i=s+1}^{n} \delta_i r_i$, then the equation (50) admit the origin as unique equilibrium, and then, when t and D tend to ∞, the total population $\sum x_i(t,D)$ tends toward 0

The approximation (53) shows that, with the exception of a thin initial boundary layer, where the density population $x_i(t,D)$ quickly jumps from its initial condition x_i^0 to the average $\delta_i X_0 / \sum_{i=1}^{n} \delta_i$, each patch of the n-patch source-sink model behaves like the single logistic equation

$$\frac{du}{dt} = \begin{cases} ru\left(1 - \dfrac{u}{\delta_i K}\right) & \text{if} \quad \sum_{i=1}^{s} \delta_i r_i > \sum_{i=s+1}^{n} \delta_i r_i, \\ \tilde{r}u\left(-1 - \dfrac{u}{\delta_i \tilde{K}}\right) & \text{otherwise,} \end{cases}$$

where $\tilde{r} = -r, \tilde{K} = -K$, r and K are given in (51).

Hence, when t and D tend to ∞, the density population $x_i(t,D)$ tends toward $K = \delta_i \frac{\sum_{i=1}^{s} \delta_i r_i - \sum_{i=s+1}^{n} \delta_i r_i}{\sum \delta_i^2 \alpha_i}$ if $\sum_{i=1}^{s} \delta_i r_i > \sum_{i=s+1}^{n} \delta_i r_i$, and $x_i(t,D)$ tends toward 0 if $\sum_{i=1}^{s} \delta_i r_i \leq \sum_{i=s+1}^{n} \delta_i r_i$.

According to the previous theorem, we obtain the limit $E^*(\infty)$ of $E^*(D)$ when $D \to \infty$:

Corollary 3.2 *We have:*

$$\lim_{D \to +\infty} E^*(D) = \begin{cases} \dfrac{\sum_{i=1}^{s} \delta_i r_i - \sum_{i=s+1}^{n} \delta_i r_i}{\sum_{i=1}^{n} \delta_i^2 \alpha_i} (\delta_1, \ldots, \delta_n), & \text{if } \sum_{i=1}^{s} \delta_i r_i > \sum_{i=s+1}^{n} \delta_i r_i, \\ 0 & \text{otherwise,} \end{cases} \tag{58}$$

where $\alpha_i = r_i / K_i$ and $(\delta_1, \ldots, \delta_n)$ the vector which generate the kernel of Γ. Moreover, if the matrix Γ is symmetric, then:

$$\lim_{D \to +\infty} E^*(D) = \begin{cases} \dfrac{\sum_{i=1}^{s} r_i - \sum_{i=s+1}^{n} r_i}{\sum_{i=1}^{n} \alpha_i} (1, \ldots, 1), & \text{if } \sum_{i=1}^{s} r_i > \sum_{i=s+1}^{n} r_i, \\ 0 & \text{otherwise.} \end{cases} \tag{59}$$

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

Corollary 3.3 *We have*

$$X_T^*(+\infty) = \begin{cases} \sum_{i=1}^{n} \delta_i \dfrac{\sum_{i=1}^{s} \delta_i r_i - \sum_{i=s+1}^{n} \delta_i r_i}{\sum_{i=1}^{n} \delta_i^2 \alpha_i} & \text{if} \quad \sum_{i=1}^{s} \delta_i r_i > \sum_{i=s+1}^{n} \delta_i r_i, \\ 0 & \text{otherwise} \quad . \end{cases} \tag{60}$$

Moreover, if the matrix Γ is symmetric, then:

$$X_T^*(+\infty) = \begin{cases} n \dfrac{\sum_{i=1}^{s} r_i - \sum_{i=s+1}^{n} r_i}{\sum_{i=1}^{n} \alpha_i}, & \text{if} \quad \sum_{i=1}^{s} r_i > \sum_{i=s+1}^{n} r_i, \\ 0 & \text{otherwise} \quad . \end{cases} \tag{61}$$

Proof 12 *The sum of the n components of the point $E^*(\infty)$ immediately gives the equation* (60).

In the case $n=2$ and $s=1$, one has $\delta_1=\gamma_{12}$ and $\delta_2=\gamma_{21}$. Therefore (60) becomes

$$X_T^*(+\infty)=\begin{cases}(\gamma_{12}+\gamma_{21})\dfrac{\gamma_{12}r_1-\gamma_{21}r_2}{\gamma_{12}^2\alpha_1+\gamma_{21}^2\alpha_2} & if \qquad \gamma_{21}/\gamma_{12}<r_1/r_2,\\ 0 & otherwise.\end{cases}$$

which is the formula given by Wu et al. [38, Equation 5.8]. In the case $n=s=2$, the formula (60) becomes

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

which is the formula given by Arditi et al. [2, Equation 7] and by Poggiale et al. [34, page 362].

In the case of the multi-patch logistic model with asymmetric migration, i.e the model (32) with $s=n$, the formula (60) becomes

$$X_T^*(+\infty)=\left(\sum_{i=1}^n\delta_i\right)\frac{\sum_{i=1}^n\delta_i r_i}{\sum_{i=1}^n\delta_i^2\alpha_i},$$

which is the formula given by Elbetch et al. [12, Equation 13].

As a corollary of the previous theorem we obtain the following result which describes the behavior of the system (32) for perfect mixing and symmetrical dispersal:

Corollary 3.4 *Assume that the matrix Γ is symmetric. Let $(x_1(t,D),\ldots,x_n(t,D))$ be the solution of the system* (32) *with initial condition $(x_1^0,\cdots,x_n^0)$ satisfying $x_i^0\geq 0$ for $i=1\cdots n$. Let $Y(t)$ be the solution of the equation*

$$\frac{dX}{dt}=rX\left(1-\frac{X}{nK}\right), \tag{62}$$

where

$$r=\frac{\sum_{i=1}^s r_i-\sum_{i=s+1}^n r_i}{n},\quad K=\frac{\sum_{i=1}^s r_i-\sum_{i=s+1}^n r_i}{\sum_{i=1}^n\alpha_i}\quad and\quad \alpha_i=r_i/K_i. \tag{63}$$

Then, when $D\to\infty$, we have

$$\sum_{i=1}^n x_i(t,D)=Y(t)+o_D(1)\qquad uniformly\ for\ t\in[0,+\infty) \tag{64}$$

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

$$x_i(t,D)=\frac{Y(t)}{n}+o_D(1)\qquad i=1,\ldots,n,\ uniformly\ for\quad t\in[t_0,+\infty). \tag{65}$$

Proof 13 *If Γ is symmetric, one has $\delta_i=1$ for all i. Therefore, the formulas* (50), (51), *and the approximations* (52), (53) *for $\delta_i=1$, give the proof of the corollary.*

3.3 Total population size

In this section, Our aim is to compare the total equilibrium population

$$X_T^*(D)=x_1^*(D)+\ldots+x_n^*(D), \tag{66}$$

with the sum of carrying capacities $K_1+\ldots+K_s$, when the migration rate D varies from zero to infinity. First, we start by the following case.

3.3.1 Homogeneous Source-Sink System

Let we consider a Source-Sink patch model (32) when the patches have a homogeneous structure in the sense that the growth rates and death rates are independent of the patch. In the next proposition, we show that, if the growth rates in source patches, and the death rates in the sink patches, are equal, then the total equilibrium population is smaller than the sum of carrying capacities. Moreover, under some conditions, we can have a persistent in all the patches, or extinction in all the patches from a positive value of the migration rate. Mathematically speaking, we have the result:

Proposition 3.2 *Consider the system* (32)*. If* $r_1 = \ldots = r_n$*, then* $X_T^*(D) \leq \sum_{i=1}^{s} K_i$ *for all* $D \geq 0$*, and* $\frac{dX_T^*}{dD}(0) = 0$*. Moreover,*

- *If* $\sum_{i=1}^{s} \delta_i r_i \leq \sum_{i=s+1}^{n} \delta_i r_i$*, then there is* $D^* > 0$ *such that,* $X_T^*(D) > 0$ *for* $D < D^*$*, and* $X_T^*(D) = 0$*, for* $D \geq D^*$*.*
- *If* $\sum_{i=1}^{s} \delta_i r_i > \sum_{i=s+1}^{n} \delta_i r_i$*, then* $X_T^*(D) > 0$ *for all* $D \geq 0$*.*

Proof 14 *If the equilibrium* $E^*(D)$ *exist, then it is a solution of the algebraic system:*

$$\begin{cases} 0 = r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n} (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = 1, \ldots, s, \\ 0 = r_i x_i \left(-1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n} (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = s+1, \ldots, n. \end{cases} \tag{67}$$

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

$$\sum_{i=1}^{s} r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \sum_{i=s+1}^{n} r_i x_i \left(1 + \frac{x_i}{K_i}\right) = 0. \tag{68}$$

Therefore $E^*(D)$ *belongs to the ellipsoid:*

$$\mathbb{E}_s^{n-1} := \left\{ x \in \mathbb{R}^n : \Theta(x) := \sum_{i=1}^{s} r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \sum_{i=s+1}^{n} r_i x_i \left(1 + \frac{x_i}{K_i}\right) = 0 \right\}. \tag{69}$$

Note that, this ellipsoid is independent of the migration terms D and γ_{ij}*. It depends on the number of the sources and sinks patches. The ellipsoid* $\mathbb{E}_s^{n-1}$ *passes through the points O,* $(K_1, \ldots, K_s, 0, \ldots, 0)$ *and* $(0, \ldots, 0, -K_{s+1}, \ldots, K_n)$*.*

The equation of the tangent space to the ellipsoid $\mathbb{E}_s^{n-1}$*, defined by* (69)*, at point* $\mathscr{A}_s = (K_1, \ldots, K_s, 0, \ldots, 0)$ *is given by*

$$\sum_{i=1}^{s} (x_i - K_i) \frac{\partial \Theta}{\partial x_i}(\mathscr{A}_s) + \sum_{i=s+1}^{n} x_i \frac{\partial \Theta}{\partial x_i}(\mathscr{A}_s) = 0, \tag{70}$$

where Θ *is given by the equation* (69)*. Since* $\frac{\partial \Theta}{\partial x_i}(\mathscr{A}_s) = -r_i$ *for all* $i = 1, \ldots, n$*, the equation* (70) *can be written as follows:*

$$\sum_{i=1}^{n} r_i x_i = \sum_{i=1}^{s} r_i K_i. \tag{71}$$

If we take $r_1 = \ldots = r_n$*, in Equation* (71)*, we get that the equation of the tangent plane to* $\mathbb{E}_s^{n-1}$ *at the point* $\mathscr{A}_s$ *is*

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

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

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

Now, according to the formula of perfect mixing (60)*, we can see immediately that $X_T^*(+\infty) = 0$ if and only if $\sum_{i=1}^s \delta_i r_i = \sum_{i=s+1}^n \delta_i r_i$.*

If $r_1 = \ldots = r_n =: r$, then the formula of the derivative (118) *at $D = 0$ becomes*

$$\frac{dX_T^*}{dD}(0) = \frac{1}{r}(1,\ldots,1)\,\Gamma\,(K_1,\ldots,K_s,0,\ldots,0)^T = 0,$$

since Γ verify the relation (34)*. This completes the proof of the proposition.*

In the case when $s = n$, the previous proposition becomes: if $r_1 = \ldots = r_s$, then $0 < X_T^*(D) \leq \sum_i K_i$, which is [11, Prop. 3.1 and Prop. 6.2].

3.3.2 Heterogeneous Source-Sink system

In the next proposition we give sufficient and necessary conditions for the total equilibrium population not to depend on the migration rate. More precisely, we show that, the only situation where the total equilibrium population is independent with respect to dispersal, is when all the patches are sources and the vector of the carrying capacities lies in the vector space $\ker\Gamma$. That is, if there is at least one sink patch, or we have n sources patches and the vector of the carrying capacities does not belong in the vector space $\ker\Gamma$, then the total equilibrium population is depends on the dispersion.

Proposition 3.3 *The equilibrium $E^*(D)$ does not depend on D if and only if, $s = n$ and $(K_1,\ldots,K_n) \in \ker\Gamma$. In this case $E^*(D) = (K_1,\ldots,K_n)$ for all $D > 0$.*

Proof 15 *The equilibrium $E^*(D) := (X_s^*(D); X_p^*(D))$, where $X_s^*(D) = (x_1^*(D),\ldots,x_s^*(D))$ and $X_p^*(D) = (x_{s+1}^*(D),\ldots,x_n^*(D))$, is the unique positive solution of the system:*

$$\begin{cases} 0 = \operatorname{diag}\left(r_1 - \frac{r_1}{K_1}x_1,\cdots,r_s - \frac{r_s}{K_s}x_s\right)X_s + D\left(\Gamma_{ss}X_s + \Gamma_{sp}X_p\right), \\ 0 = \operatorname{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1},\cdots,-r_n - \frac{r_n}{K_n}x_n\right)X_p \\ \quad + D\left(\Gamma_{ps}X_s + \Gamma_{pp}X_p\right), \end{cases} \tag{72}$$

Suppose that the equilibrium $E^*(D)$ does not depend on D, then we replace in Equation (72)*:*

$$\begin{cases} 0 = \operatorname{diag}\left(r_1 - \frac{r_1}{K_1}x_1^*(D),\cdots,r_s - \frac{r_s}{K_s}x_s^*(D)\right)X_s^*(D) \\ \quad + D\left(\Gamma_{ss}X_s^*(D) + \Gamma_{sp}X_p^*(D)\right), \\ 0 = \operatorname{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}^*(D),\cdots,-r_n - \frac{r_n}{K_n}x_n^*(D)\right)X_p^*(D) \\ \quad + D\left(\Gamma_{ps}X_s^*(D) + \Gamma_{pp}X_p^*(D)\right). \end{cases} \tag{73}$$

The derivative of (73) *with respect to D gives:*

$$\Gamma E^*(D) = 0. \tag{74}$$

Replacing the equation (74) *in the equation* (73)*, we get $E^*(D) = (K_1,\ldots,K_s,0,\ldots,0)$. From the equation* (74)*, we conclude that*

$(K_1,\dots,K_s,0,\dots,0) \in \ker\Gamma$. *Since the vector space* $\ker\Gamma$ *is generate by a positive vector, then* $(K_1,\dots,K_s,0,\dots,0) \in \ker\Gamma$ *is hold if and only if,* $s = n$.

Now, suppose that $s = n$ *and* $(K_1,\dots,K_n) \in \ker\Gamma$, *then* $(K_1,\dots,K_n)$ *satisfies the equation* (72)*, for all* $D \geq 0$. *So,* $E^*(D) = (K_1,\dots,K_n)$*, for all* $D \geq 0$*, which proves that the total equilibrium population is independent of the migration rate D.*

it is also clear that when all the patches are sources and the vector of the carrying capacities lies in the vector space $\ker\Gamma$, we obtain the results proved by Elbetch et al. [11, Prop. 3.2] and [12, Prop. 4.5].

3.3.3 Two blocks of identical source and sink patches

we consider the model of source-sink patches (32) and we assume that we have one block of source patches and one block for the sink patches. We denote by $I_{so} = \{1,\dots,s\}$ and $I_{si} = \{s+1,\dots,n\}$ for the block of the source patches and sink patches respectively such that $I_{so} \cup I_{si} = \{1,\dots,n\}$. The source patches being identical means that they have the same growth rate r_i and carrying capacity K_i. Therefore, we have

$$r_1 = \dots = r_s =: r_{so}, \quad K_1 = \dots = K_s =: K_{so}. \tag{75}$$

The same for the sink patches, we suppose that:

$$r_{s+1} = \dots = r_n =: r_{si}, \quad K_{s+1} = \dots = K_n =: K_{si}. \tag{76}$$

First, we give some definitions:

Definition 3.6 *Let the flux*

$$\Gamma_{iI_{si}} = \sum_{j\in I_{si}} \gamma_{ij}, \Gamma_{jI_{so}} = \sum_{i\in I_{so}} \gamma_{ij}, \Gamma_{I_{so}I_{si}} = \sum_{i\in I_{so}, j\in I_{si}} \gamma_{ij}, \text{and} \quad \Gamma_{I_{si}I_{so}} = \sum_{i\in I_{so}, j\in I_{si}} \gamma_{ji}.$$

- *For* $i \in I_{so}, \Gamma_{iI_{si}}$ *is the flux from block* I_{si} *to patch i, i.e. the sum of the migration rates* γ_{ij} *from patch* $j \in I_{si}$ *to patch i.*
- *For* $j \in I_{si}, \Gamma_{jI_{so}}$ *is the flux from block* I_{so} *to patch j, i.e. the sum of the migration rates* γ_{ji} *from patch* $i \in I_{so}$ *to patch j.*
- $\Gamma_{I_{so}I_{si}}$ *is the flux from block* I_{si} *to block* I_{so}*, i.e. the sum of the migration rates* γ_{ij} *from patch* $j \in I_{si}$*, to patch* $i \in I_{so}$.
- $\Gamma_{I_{si}I_{so}}$ *is the flux from block* I_{so} *to block* I_{si}*, i.e. the sum of the migration rates* γ_{ji} *from patch* $i \in I_{so}$*, to patch* $j \in I_{si}$.

For each patch i we denote by $\mathscr{T}_i$ the sum of all migration rates γ_{ji} from patch i to another patch $j \neq i$ (i.e. the outgoing flux of patch i) minus the sum of the migration rates γ_{ik} from patch k to patch i, where k belongs to the same block as i. Hence, we have:

$$\begin{aligned} &\text{If } i \in I_{so}, \quad \mathscr{T}_i = \sum_{j\in I_{si}} \gamma_{ji} + \sum_{k\in I_{so}\setminus\{i\}} (\gamma_{ki} - \gamma_{ik}) \\ &\text{If } j \in I_{si}, \quad \mathscr{T}_j = \sum_{i\in I_{so}} \gamma_{ij} + \sum_{k\in I_{si}\setminus\{j\}} (\gamma_{kj} - \gamma_{jk}) \end{aligned} \tag{77}$$

We make the following assumption on the migration rates

$$\begin{aligned} &\Gamma_{1I_{si}} = \dots = \Gamma_{sI_{si}}, \qquad \Gamma_{(s+1)I_{so}} = \dots = \Gamma_{nI_{so}} \\ &\mathscr{T}_1 = \dots = \mathscr{T}_s, \qquad \mathscr{T}_{s+1} = \dots = \mathscr{T}_n \end{aligned} \tag{78}$$

If the conditions (78) are satisfied, then, according to [12, Lemma 4.6], we have for all $i \in I_{so}$ and $j \in I_{si}$ one has

$$\Gamma_{iI_{si}} = \Gamma_{I_{so}I_{si}}/s, \quad \Gamma_{jI_{so}} = \Gamma_{I_{si}I_{so}}/\bar{s}, \quad \mathscr{T}_i = \Gamma_{I_{si}I_{so}}/s, \quad \mathscr{T}_j = \Gamma_{I_{so}I_{si}}/\bar{s}. \tag{79}$$

where $\bar{s} = n - s, \Gamma_{I_{so}I_{si}}$ and $\Gamma_{I_{si}I_{so}}$ are defined in Definition 3.6.

We consider the following regions in the set of parameters $\Gamma_{I_{si}I_{so}}$ and $\Gamma_{I_{so}I_{si}}$, denoted $\mathscr{Z}_0, \mathscr{Z}_1$ and $\mathscr{Z}_2$ depicted in Figure 5 and defined by:

$$\begin{cases} \mathscr{Z}_0 = \left\{ (\Gamma_{I_{si}I_{so}}, \Gamma_{I_{so}I_{si}}) : \quad \Gamma_{I_{so}I_{si}} \geq \dfrac{r_{si}}{r_{so}} \Gamma_{I_{si}I_{so}} \right\}, \\ \mathscr{Z}_1 = \left\{ (\Gamma_{I_{si}I_{so}}, \Gamma_{I_{so}I_{si}}) : \quad \dfrac{r_{si}}{r_{so}} \Gamma_{I_{si}I_{so}} < \Gamma_{I_{so}I_{si}} < \dfrac{r_{si}D}{r_{so}r_{si} + Dr_{so}} \Gamma_{I_{si}I_{so}} \right\}, \\ \mathscr{Z}_2 = \left\{ (\Gamma_{I_{si}I_{so}}, \Gamma_{I_{so}I_{si}}) : \quad \Gamma_{I_{so}I_{si}} \geq \dfrac{r_{si}D}{r_{so}r_{si} + Dr_{so}} \Gamma_{I_{si}I_{so}} \right\}. \end{cases} \tag{80}$$

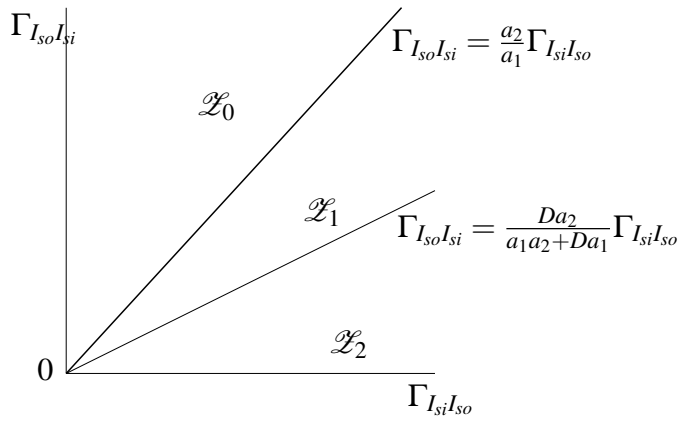


Figure 5: The regions $\mathscr{Z}_0, \mathscr{Z}_1$ and $\mathscr{Z}_2$ in the set of parameters $\Gamma_{I_{si}I_{so}}$ and $\Gamma_{I_{so}I_{si}}$.

We can state now our main result

Theorem 3.7 *Consider the regions $\mathscr{Z}_0, \mathscr{Z}_1$ and $\mathscr{Z}_2$ depicted in Figure 5 and defined by* (80)*. Assume that the conditions* (75),(76) *and (78) are satisfied. If $(\Gamma_{I_{si}I_{so}}, \Gamma_{I_{so}I_{si}}) \in \mathscr{Z}_2$, then the model* (32) *admits the origin as unique equilibrium point, which is GAS, and if $(\Gamma_{I_{si}I_{so}}, \Gamma_{I_{so}I_{si}}) \in \mathscr{Z}_0 \cup \mathscr{Z}_1$, the model* (32) *admits unique equilibrium point in the interior of the positive cone, which is of the form*

$$x_1 = x_1^*, \ldots, x_s = x_{so}^*, \quad x_{s+1} = x_n^*, \ldots, x_n = x_{si}^*$$

where (x_{so}^*, x_{si}^*) is the interior equilibrium point of the 2-patch source -sink model

$$\begin{cases} \dfrac{dx_{so}}{dt} &= sr_{so}x_{so}\left(1 - \dfrac{x_{so}}{K_{so}}\right) + D\left(\Gamma_{I_{so}I_{si}}x_{si} - \Gamma_{I_{si}I_{so}}x_{so}\right), \\ \dfrac{dx_{si}}{dt} &= \bar{s}r_{si}x_{si}\left(-1 - \dfrac{x_{si}}{K_{si}}\right) + D\left(\Gamma_{I_{si}I_{so}}x_{so} - \Gamma_{I_{so}I_{si}}x_{si}\right), \end{cases} \tag{81}$$

with specific growth rates sr_{so} and death rate $\bar{s}r_{si}$, carrying capacities K_{so} for the source patch, parameter K_{si} due to the intraspecific competition in the sink patch and migration rates $\Gamma_{I_{si}I_{so}}$ from source patch to the sink patch and $\Gamma_{I_{so}I_{si}}$ from the sink patch to the source patch.

Proof 16 *Assume that the conditions (75) and* (76) *are satisfied. Then, if the interior equilibrium point of (32) exist, it is the unique positive solution of the set of algebraic equations*

$$\begin{cases} r_{so}x_i\left(1-\dfrac{x_i}{K_{so}}\right)+D\displaystyle\sum_{k=1,k\neq i}^{n}(\gamma_{ik}x_k-\gamma_{ki}x_i)=0, & i=1,\cdots,s,\\ r_{si}x_j\left(-1-\dfrac{x_j}{K_{si}}\right)+D\displaystyle\sum_{k=1,k\neq j}^{n}(\gamma_{jk}x_k-\gamma_{kj}x_j)=0, & j=s+1,\cdots,n. \end{cases} \tag{82}$$

We consider the following set of algebraic equations obtained from (82) by replacing $x_i = x_{so}$ *for* $i = 1,\ldots,s$ *and* $x_i = x_{si}$ *for* $i = s+1,\ldots,n$*:*

$$\begin{cases} r_{so}x_{so}\left(1-\dfrac{x_{so}}{K_{so}}\right)+D\left(\Gamma_{iI_{si}}x_{si}-\mathscr{T}_i x_{so}\right)=0, & i=1,\cdots,s,\\ r_{si}x_n\left(-1-\dfrac{x_{si}}{K_{si}}\right)+D\left(\Gamma_{jI_{so}}x_{so}-\mathscr{T}_j x_{si}\right)=0, & j=s+1,\cdots,n. \end{cases} \tag{83}$$

Now, using the assumptions (78), together with the relations (79), we see that the system (83) is equivalent to the set of two algebraic equations:

$$\begin{cases} r_{so}x_{so}\left(1-\dfrac{x_{so}}{K_{so}}\right)+D\left(\dfrac{\Gamma_{I_{so}I_{si}}}{s}x_{si}-\dfrac{\Gamma_{I_{si}I_{so}}}{s}x_{so}\right)=0,\\ r_{si}x_{si}\left(-1-\dfrac{x_{si}}{K_{si}}\right)+D\left(\dfrac{\Gamma_{I_{si}I_{so}}}{\bar{s}}x_{so}-\dfrac{\Gamma_{I_{so}I_{si}}}{\bar{s}}x_{si}\right)=0. \end{cases} \tag{84}$$

We first notice that if $x_{so} = x_{so}^*$, $x_{si} = x_{si}^*$ *is a positive solution of (84) then* $x_i = x_{so}^*$ *for* $i = 1,\ldots,s$ *and* $x_i = x_{si}^*$ *for* $i = s+1,\ldots,n$ *is a positive solution of (82). According to Proposition 2.1, If* $(\Gamma_{I_{si}I_{so}},\Gamma_{I_{so}I_{si}}) \in \mathscr{Z}_2$*, then the model* (84) *admits the origin as unique equilibrium point, which is GAS, and if* $(\Gamma_{I_{si}I_{so}},\Gamma_{I_{so}I_{si}}) \in \mathscr{Z}_0 \cup \mathscr{Z}_1$*, the model* (84) *admits unique equilibrium point in the interior of the positive cone.*

As a corollary of the previous theorem:

Corollary 3.5 *Assume that the conditions (75), (76) and (78) are satisfied. Then the total equilibrium population* $X_T^*(D) = sx_{so}^*(D) + \bar{s}x_{si}^*(D)$ *of (32) behaves like the total equilibrium population of the 2-patch source-sink model*

$$\begin{cases} \dfrac{dy_{so}}{dt} &= r_{so}y_{so}\left(1-\dfrac{y_{so}}{sK_{so}}\right)+D\left(\gamma_2 y_{si}-\gamma_1 y_{so}\right),\\ \dfrac{dy_{si}}{dt} &= r_{si}y_{si}\left(-1-\dfrac{y_{si}}{\bar{s}K_{si}}\right)+D\left(\gamma_1 y_{so}-\gamma_2 y_{si}\right). \end{cases} \tag{85}$$

with specific growth rate r_{so}*, death rate* r_{si}*, carrying capacities* sK_{so}*, parameter* K_{si} *due to the intraspecific competition in the sink patch and migration rates* $\gamma_1 = \frac{\Gamma_{I_{si}I_{so}}}{s}$, $\gamma_2 = \frac{\Gamma_{I_{so}I_{si}}}{\bar{s}}$.

Proof 17 *The equilibrium point* (x_{so}^*, x_{si}^*) *is the positive solution of the following system:*

$$\begin{cases} sr_{so}x_{so}\left(1-\dfrac{x_{so}}{K_{so}}\right)+D\left(\Gamma_{I_{so}I_{si}}x_{si}-\Gamma_{I_{si}I_{so}}x_{so}\right)=0,\\ \bar{s}r_{si}x_{si}\left(-1-\dfrac{x_{si}}{K_{si}}\right)+D\left(\Gamma_{I_{si}I_{so}}x_{so}-\Gamma_{I_{so}I_{si}}x_{si}\right)=0. \end{cases} \tag{86}$$

Therefore $(y^*_{so} = sx^*_{so}, y^*_{si} = \bar{s}x^*_{si})$ *is the solution of the set of equations*

$$\begin{cases} r_{so}y_{so}\left(1-\dfrac{y_{so}}{sK_{so}}\right)+D\left(\gamma_2 y_{si}-\gamma_1 y_{so}\right)=0, \\ r_{si}y_{si}\left(-1-\dfrac{y_{si}}{\bar{s}K_{si}}\right)+D\left(\gamma_1 y_{so}-\gamma_2 y_{si}\right)=0, \end{cases} \tag{87}$$

obtained from (86) by using the change of variables $y_{so} = sx_{so}$, $y_{si} = \bar{s}x_{si}$.

We can describe the conditions for which, under the conditions (75), (76) and (78), patchiness is beneficial or detrimental in model (32). We consider the regions in the set of the parameters $\Gamma_{I_{so}I_{si}}$ and $\Gamma_{I_{si}I_{so}}$, denoted $\mathscr{L}_0$, $\mathscr{L}_1, \mathscr{L}_2$, $\mathscr{L}_3$ and $\mathscr{L}_4$, depicted in Fig. 6 and defined by:

$$\begin{cases} \text{If } r_{si} \geq r_{so} \text{ then } \begin{cases} \mathscr{L}_0 = \left\{(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) : \dfrac{\Gamma_{I_{si}I_{so}}}{\Gamma_{I_{so}I_{si}}} < \dfrac{r_{si}}{r_{so}}\right\} \\ \mathscr{L}_1 = \left\{(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) : \dfrac{\Gamma_{I_{si}I_{so}}}{\Gamma_{I_{so}I_{si}}} \geq \dfrac{r_{si}}{r_{so}}\right\} \end{cases} \\ \text{If } r_{si} < r_{so} \text{ then } \begin{cases} \mathscr{L}_2 = \left\{(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) : \dfrac{\Gamma_{I_{so}I_{si}}}{\Gamma_{I_{si}I_{so}}} \leq \dfrac{r_{so}}{r_{si}}\right\} \\ \mathscr{L}_3 = \left\{(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) : \dfrac{r_{si}}{r_{so}} < \dfrac{\Gamma_{I_{si}I_{so}}}{\Gamma_{I_{so}I_{si}}} < \dfrac{K_{si}(r_{so}-r_{si})}{r_{so}(K_{so}+K_{si})}\right\} \\ \mathscr{L}_4 = \left\{(\Gamma_{I_{so}I_{si}}, \Gamma_{I_sI_{so}}) : \dfrac{\Gamma_{I_{si}I_{so}}}{\Gamma_{I_{so}I_{si}}} \geq \dfrac{K_{si}(r_{so}-r_{si})}{r_{so}(K_{so}+K_{si})}\right\} \end{cases} \end{cases} \tag{88}$$

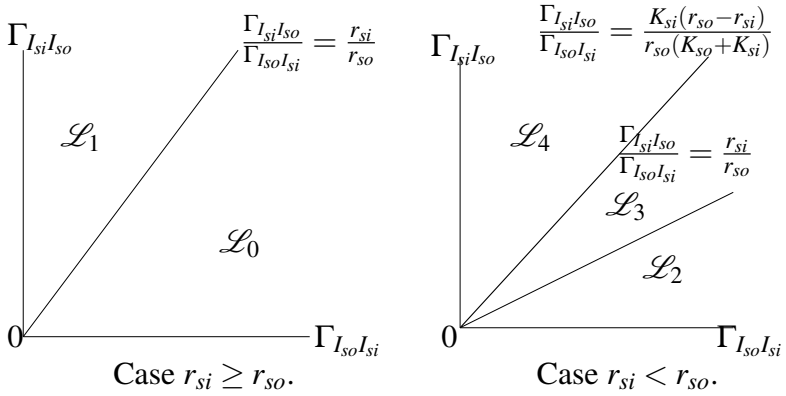


Figure 6: Qualitative properties of source-sink model (32) under the conditions (75),(76) and (78). In $\mathscr{L}_0$ and $\mathscr{L}_1$ the effect is detrimental with extinction in two patches for $\mathscr{L}_0$ and persistence for $\mathscr{L}_1$. In $\mathscr{L}_4$, patchiness has a beneficial effect on total equilibrium population. In $\mathscr{L}_2$ and $\mathscr{L}_3$, the effect is beneficial for $D < D_0$ and detrimental for $D > D_0$ with persistence of the population in the region $\mathscr{L}_2$ and extinction in the region $\mathscr{L}_3$.

Proposition 3.4 *Assume that the conditions* (75),(76) *and (78) are satisfied, then, the total equilibrium population* $X^*_T(D) = sx^*_{so}(D) + \bar{s}x^*_{si}(D)$ *of (32) satisfies the following properties*

1. *If* $r_{si} \geq r_{so}$, *let* $\mathscr{L}_0$ *and* $\mathscr{L}_1$ *be defined by (88) and depicted in Figure 6. Denote* $D^* = \dfrac{\Gamma_{I_{si}I_{so}} r_{so} r_{si}}{\Gamma_{I_{so}I_{si}} r_{si} - \Gamma_{I_{si}I_{so}} r_{so}}$. *Then we have:*

- *if* $(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) \in \mathscr{L}_0$ *then* $X_T^*(D) \leq sK_{so}$ *for all* $D \geq 0$. *More precisely,*

$$\begin{cases} 0 < X_T^*(D) \leq sK_{so} & \text{If} \quad D < D^*, \\ X_T^*(D) = 0 & \text{If} \quad D \geq D^*. \end{cases} \tag{89}$$

- *if* $(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) \in \mathscr{L}_1$ *then* $0 < X_T^*(D) \leq sK_{so}$ *for* $D \geq 0$.

2. *If* $r_{si} < r_{so}$, *let* $\mathscr{L}_2, \mathscr{L}_3$ *and* $\mathscr{L}_4$ *be defined by (88) and depicted in Figure 6. Then we have:*

   - *if* $(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) \in \mathscr{L}_2$ *then* $X_T^*(D) > sK_{so}$ *for* $D < D_0$ *and* $X_T^*(D) < sK_{so}$ *for all* $D > D_0$. *where*

$$D_0 = \frac{(r_{so} - r_{si})(sK_{so} + \bar{s}K_{si})}{\left(\Gamma_{I_{si}I_{so}}(r_{si} - r_{so}) + \frac{1}{s}\Gamma_{I_{so}I_{si}}\alpha_{so}(sK_{so} + \bar{s}K_{si})\right)\left((s\alpha_{so})^{-1} + (\bar{s}\alpha_{si})^{-1}\right)}, \tag{90}$$

   with $\alpha_{so} = r_{so}/K_{so}$ *and* $\alpha_{si} = r_{si}/K_{si}$. *Moreover,* $X_T^*(D) = 0$ *for all* $D \geq D^*$.

   - *if* $(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) \in \mathscr{L}_3$ *then we have*

$$\begin{cases} X_T^*(D) \geq sK_{so} & \text{If} \quad D \leq D^*, \\ 0 < X_T^*(D) < sK_{so} & \text{If} \quad D > D^*. \end{cases} \tag{91}$$

   - *if* $(\Gamma_{I_{so}I_{si}}, \Gamma_{I_{si}I_{so}}) \in \mathscr{L}_4$, *then* $X_T^*(D) \geq sK_{so}$ *for any* $D \geq 0$.

Proof 18 *The result is a consequence of Theorem 2.2 and Corollary 3.5.*

3.4 Death rates are much larger than the growth rates

In this part, we consider the multi-patch Source-Sink model (32) and we assume that the death rates of the sink patches are much larger than the growth rates of the source patches. Under this assumption, one can write the model in the matrix form as follow:

$$\begin{cases} \dot{X}_s = \text{diag}\left(r_1 - \frac{r_1}{K_1}x_1, \cdots, r_s - \frac{r_s}{K_s}x_s\right) X_s + D\left(\Gamma_{ss}X_s + \Gamma_{sp}X_p\right), \\ \dot{X}_p = \frac{1}{\varepsilon}\text{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}, \cdots, -r_n - \frac{r_n}{K_n}x_n\right) X_p + D\left(\Gamma_{ps}X_s + \Gamma_{pp}X_p\right), \end{cases} \tag{92}$$

where ε is assumed to be a small positive number. We have the following result:

Theorem 3.8 *Let* $(x_1(t,\varepsilon), \ldots, x_n(t,\varepsilon))$ *be the solution of the system* (92) *with initial condition* $(x_1^0, \ldots, x_n^0)$ *satisfying* $x_i^0 \geq 0$ *for* $i = 1, \ldots, n$. *Let* $u(t) = (u_1(t), \ldots, u_s(t))$ *be the solution of the following differential system*

$$\dot{X}_s = \text{diag}\left(\mathrm{r_1} - \frac{\mathrm{r_1}}{\mathrm{K_1}}\mathrm{x_1}, \ldots, \mathrm{r_s} - \frac{\mathrm{r_s}}{\mathrm{K_s}}\mathrm{x_s}\right) \mathrm{X_s} + \mathrm{D}\Gamma_{\mathrm{ss}}, \tag{93}$$

with initial condition $u(0) = (x_1^0, \ldots, x_s^0)$, $X_s = (x_1, \ldots, x_s)^T$ *and* Γ_{ss} *is the sub matrix of* Γ *defined by* (39). *Then, when* $\varepsilon \to 0$, *we have*

$$x_i(t,\varepsilon) = u_i(t) + o_\varepsilon(1), \quad i = 1, \ldots, s \qquad \text{uniformly for } t \in [0, +\infty) \tag{94}$$

and

$$x_i(t,\varepsilon) = o_\varepsilon(1), \quad i = s+1, \ldots, n, \tag{95}$$

uniformly for $t \in [t_0, T]$, *where* $0 < t_0 < T$ *are arbitrary but fixed and independent of* ε. *If the solution* $u_s(t)$ *of the reduced problem converges to an asymptotically stable equilibrium, then we can put* $T = +\infty$ *in the approximations* (94) *and* (95).

Proof 19 *When $\varepsilon \to 0$, the system* (92) *is a slow-fast system, with $x_1, \ldots, x_s$ are slow variables, and $x_{s+1}, \ldots, x_n$ fast variable. Tikhonov's theorem [29, 36, 37] prompts us to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{D}t$. One obtains*

$$\dot{X}_p = \operatorname{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}, \cdots, -r_n - \frac{r_n}{K_n}x_n\right) X_p + \varepsilon D\left(\Gamma_{ps}X_s + \Gamma_{pp}X_p\right) \tag{96}$$

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

$$\dot{X}_p = \operatorname{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}, \cdots, -r_n - \frac{r_n}{K_n}x_n\right) X_p. \tag{97}$$

The slow manifold is given by the equilibrium of the system (97)*, i.e $X_p = 0$, 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* (92) *converge to the solutions of the reduced model* (93)*, obtained by replacing $X_p = 0$ into the dynamics of the slow variable. The approximations* (94) *and* (95) *follow from Tikhonov's Theorem. Recall that when the reduced problem* (93) *has an asymptotically stable equilibrium, then these approximations hold for all $t > 0$ and not only on a compact interval $[0, T]$. Recall also that there is a boundary layer for the fast variables, that is the approximations* (95) *hold only for $t > t_0$ where $t_0 > 0$ can be arbitrarily small but fixed.*

For the dynamics of the reduced model (93), we have the following result:

Theorem 3.9 *Consider the model* (93)*. Let A be the matrix defined by*

$$A := \operatorname{diag}(\mathrm{r}_1, \ldots, \mathrm{r}_\mathrm{s}) + \mathrm{D}\Gamma_{\mathrm{ss}}.$$

Assume that the matrix Γ_{ss} is irreducible, then we have:

- *if $S(A) \leq 0$, the origin is GAS for* (93)*, and*
- *if $S(A) > 0$, the reduced model has a GAS positive equilibrium.*

Proof 20 *As the matrix Γ_{ss} is irreducible, then the matrix A is also. Note that, the matrix A is the Jacobian matrix of the reduced model* (93) *evaluated at $X_s = 0$. According to [32, Corollary 1], we conclude the complete proof.*

Remark 3.3 *Under the assumption that the matrix Γ_{ss} is irreducible, the approximations* (94) *and* (95) *hold for all $t > 0$ and not only on a compact interval $[0, T]$.*

Note that, we ca written the reduced model (93) as follow:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \gamma_i x_i + D\sum_{j=1}^{s} \gamma_{ij} x_j, \ldots i = 1, \ldots, s, \tag{98}$$

where $\gamma_i = D\sum_{j=s+1}^{n} \gamma_{ji}$ for $i = 1, \ldots, s$. We denote $\tilde{\Gamma} := (\gamma_{ij})_{1 \leq i,j \leq s}$ the matrix which represent the migration between the source patches. In [19, Theorem 2.1], Gao have considered the model (98)and proved under the assumptions $\gamma_i > 0$, $(K_1, \ldots, K_s) \in \ker \tilde{T}$ and $\tilde{\Gamma}$ is irreducible, that, if $\mathscr{R}_0 \leq 0$, the origin is GAS for (93), and if $\mathscr{R}_0 > 0$, there exist unique positive equilibrium which is GAS. Here $\mathscr{R}_0$ is the basic reproduction number of the reduced model (93) defined as:

$$\mathscr{R}_0 = \rho(FV^{-1}), \text{ with } F = \operatorname{diag}(\mathrm{r}_1, \ldots, \mathrm{r}_\mathrm{s}) \text{ and } \mathrm{V} = \operatorname{diag}(\gamma_1, \ldots, \gamma_\mathrm{s}) - \mathrm{D}\tilde{\Gamma},$$

where ρ is the spectral radius.

3.5 Growth rates are much larger than the death rates

In this part, we consider the multi-patch Source-Sink model (32) and we assume that the growth rates of the source patches are much larger than the death rates of the sink patches. Under this assumption, one can write the model in the matrix form as follow:

$$\begin{cases} \dot{X}_s = \frac{1}{\varepsilon}\text{diag}\left(r_1 - \frac{r_1}{K_1}x_1, \cdots, r_s - \frac{r_s}{K_s}x_s\right)X_s + D\left(\Gamma_{ss}X_s + \Gamma_{sp}X_p\right), \\ \dot{X}_p = \text{diag}\left(-r_{s+1} - \frac{r_{s+1}}{K_{s+1}}x_{s+1}, \cdots, -r_n - \frac{r_n}{K_n}x_n\right)X_p + D\left(\Gamma_{ps}X_s + \Gamma_{pp}X_p\right), \end{cases} \tag{99}$$

where ε is assumed to be a small positive number. We have the following result:

Theorem 3.10 *Let $(x_1(t,\varepsilon),\ldots,x_n(t,\varepsilon))$ be the solution of the system* (92) *with initial condition $(x_1^0,\ldots,x_n^0)$ satisfying $x_i^0 \geq 0$ for $i = 1,\ldots,n$.*
Let $u(t) = (u_1(t),\ldots,u_p(t))$ be the solution of the differential system

$$\dot{X}_p = \text{diag}\left(-\mathrm{r_{s+1}} - \frac{\mathrm{r_{s+1}}}{\mathrm{K_{s+1}}}\mathrm{x_{s+1}},\ldots,-\mathrm{r_n} - \frac{\mathrm{r_n}}{\mathrm{K_n}}\mathrm{x_n}\right)\mathrm{X_p} + \mathrm{D}\left(\Gamma_{\mathrm{ps}}\mathscr{K}_{\mathrm{s}} + \Gamma_{\mathrm{pp}}\mathrm{X_p}\right), \tag{100}$$

with initial condition $(x_{s+1}^0,\ldots,x_n^0)$, $X_p = (x_{s+1},\ldots,x_n)^T$, $\mathscr{K}_s = (K_1,\ldots,K_s)^T$, Γ_{pp} and Γ_{ps} are the sub matrix of Γ defined by (39)*. Then, when $\varepsilon \to 0$, we have*

$$x_i(t,\varepsilon) = K_i + o_\varepsilon(1), \quad i = 1,\ldots,s \qquad \text{uniformly for } t \in [0,+\infty) \tag{101}$$

and

$$x_i(t,\varepsilon) = u_i(t) + o_\varepsilon(1), \quad i = s+1,\ldots,n, \tag{102}$$

uniformly for $t \in [t_0,T]$, where $0 < t_0 < T$ are arbitrary but fixed and independent of ε. If the solution $u_p(t)$ of the reduced problem converges to an asymptotically stable equilibrium, then we can put $T = +\infty$ in the approximations (101) *and* (102)*.*

Proof 21 *The proof is the same as Theorem 3.8.*

Our goal in next, is to prove the global stability of the reduced model (100). First, we start by the following lemma:

Lemma 3.11 *Assume that the matrix Γ is irreducible. The reduced model* (100) *does not admits the origin as equilibrium.*

Proof 22 *We suppose that the origin is a equilibrium of* (100)*, then $\Gamma_{ps}\mathscr{K}_s = 0$, which equivalent to $\Gamma_{ps} = 0$. So, we obtain a contradiction since Γ is irreducible.*

Theorem 3.12 *Assume that the two matrices Γ_{pp} and Γ are irreducible. The reduced model* (100) *admits unique equilibrium point in the interior of the positive cone $\mathbb{R}_+^{n-s}\setminus\{0\}$ which is GAS.*

Proof 23 *To show the global stability of the reduced model* (100) *in this case, we use the result of Hirsch [25] recalled in Theorem B.7.*

The jacobian matrix of the reduced model (100) *is given by*

$$G(X_p) := -\text{diag}\left(\mathrm{r_{s+1}} + 2\frac{\mathrm{r_{s+1}}}{\mathrm{K_{s+1}}}\mathrm{x_{s+1}},\ldots,\mathrm{r_n} + 2\frac{\mathrm{r_n}}{\mathrm{K_n}}\mathrm{x_n}\right) + \mathrm{D}\Gamma_{\mathrm{pp}},$$

which is irreducible because Γ_{pp} is also. Moreover, if $G(X_p) \leq G(Y_p)$ then $diag(-r_i - 2\alpha_i x_i) \leq diag(-r_i - 2\alpha_i y_i)$ which gives $x_i \geq y_i$ for all i, i.e $X_p \geq Y_p \geq 0$. All solutions are bounded and the reduced model (100) *does not admits the origin as equilibrium by Lemma 3.11. Hence, the reduced model* (100) *is globally stable according to Hirsch [25].*

4 Multi-patch Source-sink model without intraspecific competition in the sink patches

In this section, we assume that, there is no intraspecific competition in $n-s$ sink patches, i.e $\alpha_i = 0$ for all $i \geq s+1$ in the model (31). Under this assumption, the system (31) is rewritten as follow:

$$\begin{cases} \dfrac{dx_i}{dt} = r_i x_i \left(1 - \dfrac{x_i}{K_i}\right) + D\sum_{j=1, j\neq i}^{n}(\gamma_{ij}x_j - \gamma_{ji}x_i), & i = 1, \ldots, s, \\ \dfrac{dx_i}{dt} = -r_i x_i + D\sum_{j=1, j\neq i}^{n}(\gamma_{ij}x_j - \gamma_{ji}x_i), & i = s+1, \ldots, n. \end{cases} \tag{103}$$

The model (103) is studied by Arino et al. [3] for n patches connected by migration terms and also by Wu et al. [38] for two patches. The global dynamics of (103) is given in [3, Theorem 1]. In all of this section, we denote $\mathscr{E}^*(D)$ the positive equilibrium of (103) if it exists, and $\mathscr{X}_T^*(D)$, the total equilibrium population.

4.1 The large migration rate

We have the following result which is a consequence of Theorem 3.2.

Corollary 4.1 *We have:*

$$\lim_{D\to+\infty} \mathscr{E}^*(D) = \begin{cases} \dfrac{\sum_{i=1}^{s}\delta_i r_i - \sum_{i=s+1}^{n}\delta_i r_i}{\sum_{i=1}^{s}\delta_i^2\alpha_i}(\delta_1, \ldots, \delta_n), & \text{if} \quad \sum_{i=1}^{s}\delta_i r_i > \sum_{i=s+1}^{n}\delta_i r_i, \\ 0 & \text{otherwise,} \end{cases} \tag{104}$$

where $\alpha_i = r_i/K_i$. Moreover, if the matrix Γ is symmetric, then:

$$\lim_{D\to+\infty} \mathscr{E}^*(D) = \begin{cases} \dfrac{\sum_{i=1}^{s} r_i - \sum_{i=s+1}^{n} r_i}{\sum_{i=1}^{s}\alpha_i}(1, \ldots, 1), & \text{if} \quad \sum_{i=1}^{s} r_i > \sum_{i=s+1}^{n} r_i, \\ 0 & \text{otherwise.} \end{cases} \tag{105}$$

Proof 24 *Just replace $\alpha_i = 0$ for $i = s+1, \ldots, n$ in Theorem 3.2.*

According to the previous corollary, we obtain the formula of the total equilibrium population for perfect mixing:

$$\mathscr{X}_T^*(+\infty) = \begin{cases} \sum_{i=1}^{n}\delta_i \dfrac{\sum_{i=1}^{s}\delta_i r_i - \sum_{i=s+1}^{n}\delta_i r_i}{\sum_{i=1}^{s}\delta_i^2\alpha_i} & \text{if} \quad \sum_{i=1}^{s}\delta_i r_i > \sum_{i=s+1}^{n}\delta_i r_i, \\ 0 & \text{otherwise.} \end{cases} \tag{106}$$

Moreover, if the matrix Γ is symmetric, then:

$$\mathscr{X}_T^*(+\infty) = \begin{cases} n\dfrac{\sum_{i=1}^{s} r_i - \sum_{i=s+1}^{n} r_i}{\sum_{i=1}^{s}\alpha_i}, & \text{if} \quad \sum_{i=1}^{s} r_i > \sum_{i=s+1}^{n} r_i, \\ 0 & \text{otherwise} \quad . \end{cases} \tag{107}$$

4.2 Derivative of the total equilibrium population

In this section, Our aim is to calculate the derivative of the total equilibrium population of the model (103) at $D = 0$. First, we start by giving the following result:

Lemma 4.1 *Consider the model* (103)*. The total equilibrium population $\mathscr{X}_T^*$ satisfies the following relation:*

$$\mathscr{X}_T^*(D) = \sum_{i=1}^{s} K_i + D\left(\sum_{i=1}^{s}\sum_{i=1,j\neq i}^{n} \frac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{\alpha_i x_i^*(D)} + \sum_{i=s+1}^{n}\sum_{i=1,j\neq i}^{n} \frac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{r_i}\right). \tag{108}$$

Proof 25 *If the system* (103) *admits unique equilibrium $\mathscr{E}^*(D)$ in the interior of the positive cone, then it satisfies the following system:*

$$\begin{cases} 0 = r_i x_i^*(D)\left(1 - \dfrac{x_i^*(D)}{K_i}\right) + D\sum_{j=1,j\neq i}^{n}(\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)), & i = 1,\ldots,s, \\ 0 = -r_i x_i^*(D) + D\sum_{j=1,j\neq i}^{n}(\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)), & i = s+1,\ldots,n. \end{cases} \tag{109}$$

Dividing the first s equations in (109) *by $\alpha_i x_i^*(D)$, and the last $n-s$ equations by r_i, one obtain*

$$\begin{cases} x_i^*(D) = K_i + D\sum_{i=1,j\neq i}^{n} \frac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{\alpha_i x_i^*(D)} & i = 1,\ldots,s, \\ x_i^*(D) = D\sum_{i=1,j\neq i}^{n} \frac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{r_i} & i = s+1,\ldots,n. \end{cases} \tag{110}$$

Taking the sum of these expressions gives (108)*.*

Proposition 4.1 *The derivative of the total equilibrium population $\mathscr{X}_T^*$ at $D = 0$, is given by:*

$$\frac{d\mathscr{X}_T^*}{dD}(0) = \left(\frac{1}{r_1},\ldots,\frac{1}{r_n}\right)\Gamma(K_1,\ldots,K_s,0,\ldots,0)^T. \tag{111}$$

Proof 26 *Using matrix notation, the relation* (109) *is written as follow:*

$$\mathscr{X}_T^*(D) = \sum_{i=1}^{s} K_i + D\left(\frac{1}{\alpha_1 x_i^*(D)},\ldots,\frac{1}{\alpha_s x_s^*(D)},\frac{1}{r_{s+1}},\ldots,\frac{1}{r_n}\right)\Gamma(x_1^*(D),\ldots,x_n^*(D))^T. \tag{112}$$

By differentiating the equation (112) *at $D = 0$, we get:*

$$\frac{d\mathscr{X}_T^*}{dD}(0) = \left(\frac{1}{\alpha_1 x_i^*(0)},\ldots,\frac{1}{\alpha_s x_s^*(0)},\frac{1}{r_{s+1}},\ldots,\frac{1}{r_n}\right)\Gamma(x_1^*(0),\ldots,x_n^*(0))^T, \tag{113}$$

which gives (118)*, since $x_i^*(0) = K_i$ for all $i = 1,\ldots,s$, and $x_i^*(0) = 0$ for all $i = s+1,\ldots,n$.*

4.3 Comparison between results on (32) and the results on (103)

In this part, our aim is to compare the result on (32) and the results on (103). We focus on two results on the total equilibrium population, the formulas of perfect mixing and the derivatives of the total equilibrium population at $D = 0$. We have the following result:

Corollary 4.2 *Consider the models* (32) *and* (103) *with the total equilibrium population $X_T^*(D)$ and $\mathscr{X}_T^*(D)$ respectively. Then,*

$$\frac{dX_T^*}{dD}(0) = \frac{d\mathscr{X}_T^*}{dD}(0), \quad \text{and} \quad \mathscr{X}_{\mathrm{T}}^*(+\infty) - \mathrm{X}_{\mathrm{T}}^*(+\infty)\begin{cases} > 0, & \text{if } \sum_{i=1}^{s}\delta_i r_i > \sum_{i=s+1}^{n}\delta_i r_i, \\ = 0 & \text{otherwise.} \end{cases}$$

5 Conclusion

The goal of this paper was to generalize to a multi-patch source-sink model the results obtained in [38] for a two-patch source-sink model and also the results of [11, 12] for mutipatch logistic model i.e. n-source 0-sink patch model. The diffusion between patches is modeled by a cooperative matrix. When this last matrix is irreducible, the system has a unique equilibrium, which furthermore is globally asymptotically stable (see Subsection 3.1).

In Subsection 3.2 we considered the particular case of perfect mixing, i.e. when the diffusion rate goes to infinity, that is, individuals may travel freely between patches. As in [38] for Two-patch model and [11, 12], we compute the total equilibrium population in that case as a function of the number of the source patches, and, by perturbation arguments, we proved that the dynamics in this ideal case provides a good approximation for the case when the diffusion rate is large.

In Subsection 3.3 we considered the total equilibrium population in the n patches. We gave a complete solution in the case when the source and sink patches are partitioned into two blocks of identical patches (source patches are identical and sink patches also). Our results mirror those of [38], which deals with the two-patch source-sink case (see Section 2). As shown in Proposition 3.2, diffusion could make total abundance small than if non-diffusing and also the extinction in both patches.

In Subsections 3.4 and 3.5, we study the total equilibrium population of the source-sink patch model (32) as a function of the diffusion rate in the case where the growth (resp. death) rate is much larger than the death (resp. growth) rate.

Some questions important remain open: Is there a way to make connections between the sources and sinks patches that increases the total equilibrium population? Mathematically speaking, are there conditions on the parameters of the model in which the following:

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

is positive for all positive diffusion rate D? Anther problem, for example, for three-patch logistic model (One-source Two-sink, Two-source One-sink), is it possible to give a complete comparison between the total equilibrium population and the sum of the carrying capacities. I think this question is difficult and requires a lot of work and mathematical tools.

A Derivative of the total equilibrium population of (32)

First, we start by the following result:

Lemma A.1 *Consider the model* (32)*. The total equilibrium population X_T^* satisfies the following relation:*

$$X_T^*(D)=\sum_{i=1}^{s}K_i+D\left(\sum_{i=1}^{s}\sum_{i=1,j\neq i}^{n}\frac{\gamma_{ij}x_j^*(D)-\gamma_{ji}x_i^*(D)}{\alpha_i x_i^*(D)}+\sum_{i=s+1}^{n}\sum_{i=1,j\neq i}^{n}\frac{\gamma_{ij}x_j^*(D)-\gamma_{ji}x_i^*(D)}{\alpha_i(K_i+x_i^*(D))}\right). \tag{114}$$

Proof 27 *If the system* (32) *admits unique equilibrium $E^*(D)$ in the interior of the positive cone, then it satisfies the following system:*

$$\begin{cases} 0=r_i x_i^*(D)\left(1-\dfrac{x_i^*(D)}{K_i}\right)+D\sum_{j=1,j\neq i}^{n}(\gamma_{ij}x_j^*(D)-\gamma_{ji}x_i^*(D)), \quad i=1,\ldots,s,\\ 0=r_i x_i^*(D)\left(-1-\dfrac{x_i^*(D)}{K_i}\right)+D\sum_{j=1,j\neq i}^{n}(\gamma_{ij}x_j^*(D)-\gamma_{ji}x_i^*(D)), i=s+1,\ldots,n. \end{cases} \tag{115}$$

Dividing the first s equations in (115) *by* $\alpha_i x_i^*(D)$*, and the last* $n-s$ *equations by* $\alpha_i(K_i + x_i^*(D))$*, one obtain*

$$\begin{cases} x_i^*(D) = K_i + D\sum_{i=1, j\neq i}^{n} \dfrac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{\alpha_i x_i^*(D)} & i = 1,\ldots,s, \\ x_i^*(D) = D\sum_{i=1, j\neq i}^{n} \dfrac{\gamma_{ij}x_j^*(D) - \gamma_{ji}x_i^*(D)}{\alpha_i(K_i + x_i^*(D))} & i = s+1,\ldots,n. \end{cases} \tag{116}$$

Taking the sum of these expressions gives (114)*.*

Remark A.1 *Using matrix notation, the relation* (115) *is written as follow:*

$$X_T^*(D) = \sum_{i=1}^{s} K_i + Dv^T(D)\Gamma\left(x_1^*(D),\ldots,x_n^*(D)\right)^T, \tag{117}$$

where $v^T(D) = \left(\frac{1}{\alpha_1 x_i^*(D)},\ldots,\frac{1}{\alpha_s x_s^*(D)}, \frac{1}{\alpha_{s+1}(K_{s+1}+x_{s+1}^*(D))},\ldots,\frac{1}{\alpha_n(K_n+x_n^*(D))}\right)$*.*

Proposition A.1 *The derivative of the total equilibrium population at* $D = 0$*, is given by:*

$$\frac{dX_T^*}{dD}(0) = \left(\frac{1}{r_1},\ldots,\frac{1}{r_n}\right)\Gamma\left(K_1,\ldots,K_s,0,\ldots,0\right)^T. \tag{118}$$

Proof 28 *By differentiating the equation* (117) *at* $D = 0$*, we get:*

$$\frac{dX_T^*}{dD}(0) = v^T(0)\Gamma\left(x_1^*(0),\ldots,x_n^*(0)\right)^T. \tag{119}$$

which gives (118)*, since* $x_i^*(0) = K_i$ *for all* $i = 1,\ldots,s$*, and* $x_i^*(0) = 0$ *for all* $i = s+1,\ldots,n$*.*

For $s = n$, the derivative (118) becomes

$$\frac{dX_T^*}{dD}(0) = \left(\frac{1}{r_1},\ldots,\frac{1}{r_n}\right)\Gamma\left(K_1,\ldots,K_n\right)^T, \tag{120}$$

which is the formula [11, Equation 28]. Note that, the formula (118) show that, the derivative of the total equilibrium population at $D = 0$ is depend on growth and death rates r_i, the carrying capacities K_i for all $i = 1,\ldots,s$, and the sub matrix Γ_{ss}, Γ_{ps} of the matrix Γ. It is independents of the parameters K_i with $i = s+1,\ldots,n$, and the sub matrix Γ_{pp}, Γ_{sp} of the matrix Γ

B Background concepts and preliminaries results

In this section, our goal is to recall some concepts and results which we need in this work. Proofs of some results are given here and the others we refer interested readers to references.

Definition B.1 *A matrix* $A = (a_{ij})$ *is called cooperative if* $a_{ij} \geq 0$ *for all* $i \neq j$*.*

Definition B.2 *The stability modulus of a matrix A is given by*

$$S(A) = \max\left\{\mathrm{Re}(\lambda) : \quad \lambda \text{ is an eigenvalue of } A\right\}, \tag{121}$$

and the spectral radius of A is

$$\rho(A) = \max\{\mid \lambda \mid : \quad \lambda \text{ is an eigenvalue of } A\}. \tag{122}$$

We have the following result [33, Lemma 8]:

Lemma B.3 *Let A be a non negative matrix. Let $u \in \mathbb{R}^n$ be a non-zero vector and $\lambda \in \mathbb{R}$ be a real number. If $Au \geq \lambda u$ then $\rho(A) \geq \lambda$. If for a strictly positive vector u we have $Au \leq \lambda u$ then $\rho(A) \leq \lambda$.*

Proof 29 *If $Au \geq \lambda u$ then, since A is non negative, $A^k u \geq \lambda^k u$ for all k. Therefore $\|A^k\| \geq \lambda^k$ for any matricial norm. Using the Gelfand formula $\rho(A) = \lim_{k\to\infty} \|A^k\|^{\frac{1}{k}}$, we obtain that $\rho(A) \geq \lambda$. The second statement is a simple consequence of the representation (2) in [33].*

We have also the following result [6, Lemma 8]:

Lemma B.4 *Let A be a cooperative matrix. Let $u \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$. If $Au \geq \lambda u$ then $S(A) \geq \lambda$. If for a strictly positive vector u we have $Au \leq \lambda u$ then $S(A) \leq \lambda$.*

Proof 30 *Let A be a cooperative matrix, there exists $h > 0$ such that $A + hI$, where I is the identity matrix, is non negative. Let u and λ be such that $Au \geq \lambda u$. Since $S(A + hI)u \geq (\lambda + h)u$, using Lemma B.3, we deduce that $\rho(A + hI) \geq \lambda + h$. According to the Perron-Frobenius Theorem [23, Theorem 3, page 66], we have*

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

Therefore we have $S(A + hI) \geq \lambda + h$. Using $S(A + hI) = S(A) + h$, we obtain $S(A) \geq \lambda$. By the same method, we prove the second statement.

Let we consider the autonomous system:

$$\dot{x} = \Psi(x), \tag{123}$$

where $\dot{x}$ denote the derivative of x, $\Psi = (\Psi_1, \ldots, \Psi_n)$ is $\mathscr{C}^1$ on a domain $\mathbb{R}^n_+$.

Definition B.5 *The system* (123) *is called cooperative if the Jacobian matrix $\mathbb{J}\Psi(x)$ is a cooperative matrix for all $x \in \mathbb{R}^n_+$.*

To prove the global stability of the system cooperative (123), generally, the following result is used:

Theorem B.6 *[17, 35] If system* (123) *possesses a positive equilibrium point x^* satisfying*

$$\Psi_i(\xi x^*) \begin{cases} > 0 & \text{for} \quad \xi \in]0,1[, \\ < 0 & \text{for} \quad \xi > 1, \end{cases} \tag{124}$$

then x^* is globally stable.

We have also the following result of Hirsch [25]:

Theorem B.7 *If the cooperative system* (123) *has the following proprieties:*

- *$\mathbb{J}\Psi(x)$ is irreducible for any $x \geq 0$,*
- *$\mathbb{J}\Psi(x) \leq \mathbb{J}\Psi(y)$ for any $x \geq y \geq 0$, 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.

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