

NONLINEAR ASYMMETRIC DISPERSAL IN TWO-PATCH SOURCE-SINK HETEROGENEOUS ENVIRONMENT

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ABSTRACT. This paper analyzes a source-sink system with nonlinear asymmetric dispersal between two patches, where populations grow logistically in the source patch and decays logistically in the sink patch. First, using the theory of cooperative differential systems, we prove the global stability of the model. Next, applying the theory of singular perturbations and Tikhonov's theorem, we study the case of perfect mixing, i.e., when the diffusion rate tends to infinity. In this regime, we compute the equilibrium of the model, which differs from the carrying capacity of the source patch, and provide accurate approximation of the solutions. Furthermore, a complete analysis of the model demonstrates a mechanism by which nonlinear asymmetric dispersal may lead to: (i) an increase in the total population size across the two patches, (ii) a decrease in the total population size with persistence in both patches, or (iii) extinction in both patches when the migration rate becomes infinite. We also perform numerical comparisons, for specific parameter values, between the total equilibrium populations of models with linear and nonlinear asymmetric dispersal. These results show that the two populations are generally different, although they may coincide for certain migration rates. Finally, we investigate the effect of rapid growth in the source patch and rapid decline in the sink patch on the dynamics of the total equilibrium population and on the coexistence of populations in both patches.

KEYWORDS: Population Dynamics, Nonlinear dispersal, Migration rate, Source-sink model, Logistic growth, Global stability, Slow-fast systems, Tikhonov's theorem.

AMS Subject Classification: :37N25 92D25 34D23 34D15.

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 [23, 24] and Holt [22]. There are ecological situations that motivate the representation of space as a finite set

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Article history : Received 31/07/2024 Accepted 20/02/2026.

DOI : <https://doi.org/10.69650/jnao.2026.17.1.3146>.

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 et al. [25], whereas Hanski and Gaggiotti [20] 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.

An ecological model is used to describe population changes in two habitats, both occupied by the same species. One habitat is of high quality and allows a population to increase, leading to a surplus. This is the source. The other habitat is of low quality, leading to a deficit that ordinarily would lead to the habitat being abandoned. This is the sink. The source-sink model was first proposed by biologist Crick [7]. In population ecology, the source-sink model is used to describe how variation in habitat quality may affect the population growth or decline of organisms.

In 2019, Wu et al. [32] studied the following two-patch source-sink model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(x_2 - s x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon(s x_1 - x_2), \end{cases} \quad (1.1)$$

where x_1 and x_2 represent population densities of the species in patch 1 and 2, respectively. The parameters $r_i > 0$ and $K_i > 0$ are respectively the intrinsic growth rate and the carrying capacity of patch i . Parameter ϵ 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 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: (i) If the asymmetry is small, the population would persist in both patches and reach a density higher than that without dispersal and the population approaches its maximal density at an appropriate asymmetry, (ii) If the asymmetry is intermediate, the population persists in both patches but reaches a density less than that without dispersal, (iii) If the asymmetry is large, the population goes to extinction in both patches.

Arino et al. [5] also studied a source-sink model of n patches, where the source patch follows a logistic growth rate, and the sink patch follows exponential decay and they proved the existence of a threshold number of source patches such that the population potentially becomes extinct below and persistent above the threshold.

In [2], Allen considered the n -patch general model given by the following equations:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \Gamma_i(x), \quad i = 1, \dots, n, \quad (1.2)$$

where r_i and K_i are positive constants; $x = (x_1, \dots, x_n)^T$ where x_i represents the population density in the i -th patch. The function Γ_i represent one of the three types of different mechanisms. The mechanism for linear diffusion is given by:

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} (x_j - \theta_{ij} x_i), \quad i = 1, \dots, n, \quad (1.3)$$

where ϵ_{ij} and θ_{ij} are positive constants. Dispersal by linear diffusion implies that the species is able to move to all locations within its environment with equal probability. The mechanism for biased diffusion is given by:

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} x_i (x_j - \theta_{ij} x_i), \quad i = 1, \dots, n, \quad (1.4)$$

where ϵ_{ij} and θ_{ij} are positive constants. Note that, the term 'biased' means that the diffusion rate is a function of population density. The diffusion rate is regulated by population density, increasing for large populations and decreasing for small populations. The third

type of mechanism, is the directed diffusion which is formulated by Gurney and Nisbet [19], given by:

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} (x_j^2 - \theta_{ij} x_i^2), \quad i = 1, \dots, n, \quad (1.5)$$

where ϵ_{ij} and θ_{ij} are positive constants. Dispersal by directed diffusion implies that the individuals move from high population concentration to low ones, i.e., the movement is a function of species density. For more information on the biological interpretation and also the continuous version of those types of diffusion, we refer the readers to [1] and [19]. The objective of the work of Allen [2] is to study the effect of different types of the dispersion on the persistence and extinction of the species. The persistence and extinction behavior is completely determined in a two-patch model (1.2)(1.3) for $n = 2$ (see Theorem 1 in [2]). For model (1.2)(1.4), Allen [2, Theorem 2] showed that a population modelled with biased diffusion is always persistent and in fact represents a strongly persistent population. For more details on the results of persistence and extinction, see Theorem 3 of [2] for n -patch model (1.2)(1.4) and Proposition 1 of [2] for 2-patch case; Theorem 4 of [2] for the n -patch model (1.2)(1.5). In [27, 30], Lu and Takeuchi generalized some results of Allen for the model (1.2) with generalized growth rate.

In [11], Elbetich and Moussaoui considered the following two-patch model coupled by nonlinear terms of migration:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2). \end{cases} \quad (1.6)$$

For system (1.6), the authors have given a complete classification of the model parameter space as to whether nonlinear dispersal is beneficial or detrimental to the sum of two carrying capacities. They studied also the model (1.6) in the case where one growth rate is much larger than the second one. For general information on the effect of asymmetric and nonlinear diffusion on the total population abundance for the n -patch model, the reader is referred to [11].

This paper is organized as follows: In Section 2, some properties of Two-patch source-sink model with linear asymmetric dispersal (Model (2.1)) are recalled as a function of the two parameters θ_1 and θ_2 , Theorem 2.1 for the global dynamic, Theorem 2.2 for the effect of linear asymmetric dispersal on the dynamic of the total equilibrium population in two patches, Proposition 2.2 give the perfect mixing formula and our first result for this model is given in Theorem 2.3, which we studied the model in two time scales different using Tykhonov's theorem [26, 29, 31, 6]. In Section 3, we introduce the two-patch source-sink model coupled by nonlinear asymmetric terms of migration. In Subsection 3.1, we prove their global stability in the interior of the positive cone. Next, in Subsection 3.2, we study the behavior of the model in the case when the migration rate goes to infinity using singular perturbation arguments and Tykhonov's theorem (see Theorems 3.2 and 3.3). In Subsection 3.3, we compare the total equilibrium population with the carrying capacity of source patch for all parameter space by using the same method as in the works of Arditi et al. [4] and Wu et al. [32] (see Theorem 3.4 and Corollary 3.2). In subsections 3.4 and 3.5, Two-patch model with the growth (resp. death) rate much larger than the death (resp. growth) rate is considered. In Section 4, some numerical examples illustrate, confirm and extend our results are given. Section 5 concludes the paper and describes the future works suggestion. The rest of the paper contains appendices, in Appendix A, we demonstrate nonnegativeness and boundedness of the solutions, we give also the detailed proof of the existence and stability of the equilibrium point of (1.1). In Appendices B and C, we have calculated the derivatives of the total equilibrium population of (2.1), T_1^* , and also of (3.1), T_2^* respectively, with respect of ϵ .

2. TWO-PATCH SOURCE-SINK MODEL WITH LINEAR DISPERSION

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

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2 - \theta_1 x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1 - \theta_2 x_2), \end{cases} \quad (2.1)$$

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. $r_1, r_2 > 0$. The parameter $\alpha_i := r_i/K_i$ is the intraspecific competition degree. Parameter ϵ represents the dispersal intensity. We denote θ_2 the migration rate from source patch to the sink patch and θ_1 from sink patch to source patch, the dispersal is symmetric if $\theta_1 = \theta_2$. This system is studied in [32]. We recall some essential results of [32] as function of the parameters θ_1 and θ_2 . Note that, Wu et al. [32] studied the model (1.1) as function of $s = \theta_1/\theta_2$. First of all, let's start by recalling the global dynamics of System (2.1).

2.1. Global dynamics. We consider the following regions in the set of parameters θ_1 and θ_2 , denoted $\mathcal{D}_0, \mathcal{D}_1$ and $\mathcal{D}_2$ depicted in Figure 1 and defined by:

$$\begin{cases} \mathcal{D}_0 = \left\{ (\theta_1, \theta_2) : \theta_2 \geq \frac{r_2}{r_1} \theta_1 \right\}, \\ \mathcal{D}_1 = \left\{ (\theta_1, \theta_2) : \frac{r_2}{r_1} \theta_1 < \theta_2 < \frac{r_2 \epsilon}{r_1 r_2 + \epsilon r_1} \theta_1 \right\}, \\ \mathcal{D}_2 = \left\{ (\theta_1, \theta_2) : \theta_2 \geq \frac{a_2 \epsilon}{r_1 r_2 + \epsilon r_1} \theta_1 \right\}. \end{cases} \quad (2.2)$$

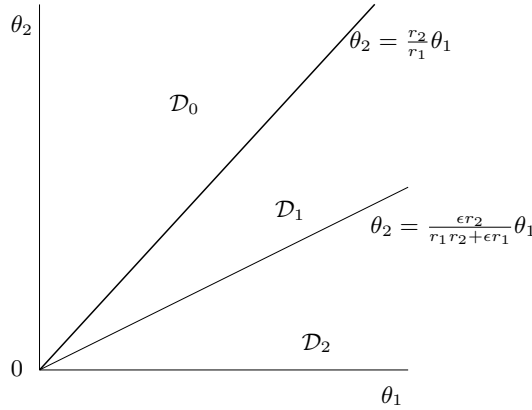


FIGURE 1. Global stability of Model (2.1). In $\mathcal{D}_0$ and $\mathcal{D}_1$ the system has unique equilibrium $E_1^*(\epsilon)$ which is GAS. In the region $\mathcal{D}_2$, the system has the origin as unique equilibrium which is GAS.

The global dynamic of System (2.1) is described as follows.

Theorem 2.1 (Prop. 5.5 in [32]). *Consider Model (2.1). Then, if $(\theta_1, \theta_2) \in \mathcal{D}_0 \cup \mathcal{D}_1$, System (2.1) admits unique equilibrium in $\mathbb{R}^2 \setminus \{0\}$ denoted by $E_1^*(\epsilon)$, which is globally asymptotically stable (GAS), and if $(\theta_1, \theta_2) \in \mathcal{D}_2$, then the origin is GAS.*

2.2. Total population abundance. In this section, we recall the comparison given in [32, Proposition 5.11], between the total equilibrium population

$$T_1^*(\epsilon) = x_1^*(\epsilon) + x_2^*(\epsilon), \quad E_1^*(\epsilon) = (x_1^*(\epsilon), x_2^*(\epsilon)),$$

of (2.1) and carrying capacity K_1 , by analyzing the stable positive equilibrium $E_1^*(\epsilon)$. Note that, when there is no dispersal (i.e., $\epsilon = 0$), the total equilibrium population is

$T_1^*(0) = K_1$. We consider the regions in the set of the parameters θ_1 and θ_2 , denoted $\mathcal{L}_0$, $\mathcal{L}_1$, $\mathcal{L}_2$, $\mathcal{L}_3$ and $\mathcal{L}_4$, depicted in Figure 2 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \left\{ \begin{array}{l} \mathcal{L}_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \mathcal{L}_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{r_2}{r_1} \right\}. \end{array} \right. \\ \\ \text{If } r_2 < r_1 \text{ then } \left\{ \begin{array}{l} \mathcal{L}_2 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \mathcal{L}_3 = \left\{ (\theta_1, \theta_2) : \frac{r_2}{r_1} < \frac{\theta_2}{\theta_1} < \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right\}, \\ \mathcal{L}_4 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \geq \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right\}. \end{array} \right. \end{array} \right. \quad (2.3)$$

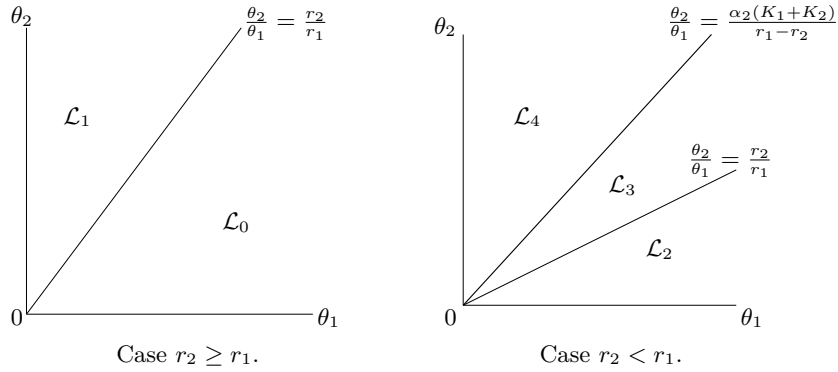


FIGURE 2. Regions $\mathcal{L}_0$, $\mathcal{L}_1$, $\mathcal{L}_2$, $\mathcal{L}_3$ and $\mathcal{L}_4$ defined by (2.3).

Theorem 2.2. *The total equilibrium population described by (2.1) satisfies the following properties*

- (i) *If $r_2 \geq r_1$, let $\mathcal{L}_0$ and $\mathcal{L}_1$ be defined by (2.3). Then we have:*
- if $(\theta_1, \theta_2) \in \mathcal{L}_0$ then $T_1^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$. More over, there is $\epsilon^* = \frac{\theta_2 r_1 r_2}{\theta_1 r_2 - \theta_2 r_1}$, such that:*

$$\begin{cases} 0 < T_1^*(\epsilon) \leq K_1 & \text{If } \epsilon < \epsilon^*, \\ T_1^*(\epsilon) = 0 & \text{If } \epsilon \geq \epsilon^*. \end{cases} \quad (2.4)$$

- if $(\theta_1, \theta_2) \in \mathcal{L}_1$ then $0 < T_1^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$.*

- (ii) *If $r_2 < r_1$, let $\mathcal{L}_2$, $\mathcal{L}_3$ and $\mathcal{L}_4$ be defined by (2.3). Then we have:*

- (a) *if $(\theta_1, \theta_2) \in \mathcal{L}_2$ then $T_1^*(\epsilon) > K_1$ for $\epsilon < \epsilon_0$, $T_1^*(\epsilon) = K_1$ for $\epsilon = \epsilon_0$ and $T_1^*(\epsilon) < K_1$ for all $\epsilon > \epsilon_0$, where*

$$\epsilon_0 = \frac{(r_1 - r_2)(K_1 + K_2)}{(\theta_2(r_1 - r_2) + \theta_1 \alpha_1(K_1 + K_2))(\alpha_1^{-1} + \alpha_2^{-1})}, \quad \text{with } \alpha_i = r_i/K_i. \quad (2.5)$$

Moreover, there is $\epsilon^ \geq \epsilon_0$ such that $T_1^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon^*$.*

- (b) *if $(\theta_1, \theta_2) \in \mathcal{L}_3$ then we have*

$$\begin{cases} T_1^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^*, \\ 0 < T_1^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^*. \end{cases} \quad (2.6)$$

- (c) *if $(\theta_1, \theta_2) \in \mathcal{L}_4$, then $T_1^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$.*

Proof. All the results were established by Wu et al. [32, Proposition 5.11]. Note that, the explicit expression (2.5) of ϵ_0 was not given in [32]. Indeed, the sum of the equilibrium equations of (2.1) show the equilibrium $(x_1^*(\epsilon), x_2^*(\epsilon))$ satisfied to:

$$r_1 x_1^*(\epsilon) \left(1 - \frac{x_1^*(\epsilon)}{K_1}\right) - r_2 x_2^*(\epsilon) \left(1 + \frac{x_2^*(\epsilon)}{K_2}\right) = 0. \quad (2.7)$$

On other hand, $T_1^*(\epsilon) = K_1$ implies that $x_1^*(\epsilon) + x_2^*(\epsilon) = K_1$. Combines this last equation and (2.7) we get

$$(x_1^*(\epsilon), x_2^*(\epsilon)) = \left(\frac{r_2 K_1 (K_2 + K_1)}{r_1 K_2 + r_2 K_1}, \frac{K_1 K_2 (r_1 - r_2)}{r_1 K_2 + r_2 K_1} \right). \quad (2.8)$$

We replace (2.8) in the equilibrium equations of (2.1) we obtain ϵ_0 given in (2.5). $\square$

In biological terms, the results of the previous theorem for source-sink patch-model shows that, the nonlinear asymmetry dispersal 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 [3, 4] for source-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.

Let us explain the result of Theorem 2.2 in the particular case where the dispersion is symmetric i.e. $\frac{\theta_1}{\theta_2} = 1$. We consider the regions in the set of the parameters r_1 and r_2 , denoted Λ_0 , Λ_1 and Λ_2 , depicted in Figure 3 and defined by:

$$\begin{cases} \Lambda_0 = \{(r_1, r_2) : r_2 \geq r_1\}, \\ \Lambda_1 = \{(r_1, r_2) : r_1 < r_2 < \frac{K_2}{K_1 + 2K_2} r_1\}, \\ \Lambda_2 = \{(r_1, r_2) : r_2 \geq \frac{K_2}{K_1 + 2K_2} r_1\}. \end{cases} \quad (2.9)$$

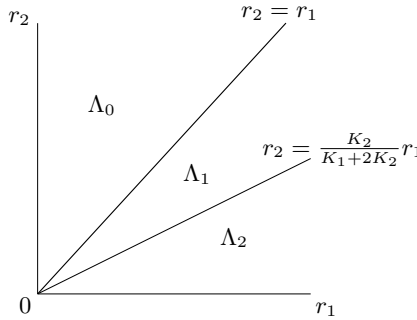


FIGURE 3. Regions Λ_0 , Λ_1 and Λ_2 defined by (2.9).

Corollary 2.1. Consider the model (2.1) with $\theta_1 = \theta_2 = 1$. Let Λ_0, Λ_1 and Λ_2 be defined by (2.9). The total equilibrium population T_1^* of (2.1) satisfies the following properties

- (i) if $(r_1, r_2) \in \Lambda_0$ then, $T_1^*(\epsilon) \leq K_1$ for all ϵ . More over, there is $\epsilon^* = \frac{r_1 r_2}{r_2 - r_1}$, such that:

$$\begin{cases} 0 < T_1^*(\epsilon) \leq K_1 & \text{If } \epsilon < \epsilon^*, \\ T_1^*(\epsilon) = 0 & \text{If } \epsilon \geq \epsilon^*. \end{cases} \quad (2.10)$$

- (ii) if $(r_1, r_2) \in \Lambda_1$ then, there is $\epsilon^{**} > 0$, such that

$$\begin{cases} T_1^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^{**}, \\ 0 < T_1^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^{**}. \end{cases} \quad (2.11)$$

Moreover, $T_1^*(\epsilon) \rightarrow T_1^*(\infty) > 0$ when $\epsilon \rightarrow \infty$.

- (iii) if $(r_1, r_2) \in \Lambda_2$, then $T_1^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$. Moreover, if $\frac{r_1}{r_2} = \frac{K_2}{K_1 + 2K_2}$, then $T_1^*(\infty) = K_1$ for all ϵ .

Proof. Direct consequence of the theorem 2.2. $\square$

2.3. Perfect mixing. In this part, we study the model (2.1) with asymmetric dispersal, in the case of perfect mixing (i.e when $\epsilon \rightarrow \infty$), we have the following result [32, Proof of Proposition 5.10]:

Proposition 2.2. *We have:*

$$T_1^*(\infty) := \lim_{\epsilon \rightarrow \infty} T_1^*(\epsilon) = \begin{cases} (\theta_1 + \theta_2) \frac{\theta_2 r_1 - \theta_1 r_2}{\theta_2^2 r_1 / K_1 + \theta_1^2 r_2 / K_2} & \text{if } \theta_1 / \theta_2 < r_1 / r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (2.12)$$

Or, as function of $s = \frac{\theta_1}{\theta_2}$, (2.12) becomes

$$T_1^*(\infty) = \begin{cases} (1 + s) \frac{r_1 - s r_2}{r_1 / K_1 + s^2 r_2 / K_2} & \text{if } s < r_1 / r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (2.13)$$

We can use the theory of singular perturbations and Tikhonov's theorem [26, 29, 31, 6] to obtain a better understanding of the behaviour of the system (2.1) in the case of perfect mixing and we find again the formula (2.12).

Theorem 2.3. *Consider the system (2.1). Let $(x_1(t, \epsilon), x_2(t, \epsilon))$ be the solution of the system (2.1) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $Z(t)$ be the solution of the logistic equation*

$$\begin{cases} \frac{dX}{dt} = rX \left(1 - \frac{X}{(\theta_1 + \theta_2)K} \right), \\ X(0) = x_1^0 + x_2^0, \end{cases} \quad (2.14)$$

where $r = \frac{\theta_2 r_1 - \theta_1 r_2}{\theta_2^2 \alpha_1 + \theta_1^2 \alpha_2}$ and $K = \frac{\theta_2 r_1 - \theta_1 r_2}{\theta_2^2 \alpha_1 + \theta_1^2 \alpha_2}$, with $\alpha_i = \frac{r_i}{K_i}$. Then, when $\epsilon \rightarrow \infty$, we have

$$x_1(t, \epsilon) + x_2(t, \epsilon) = Z(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (2.15)$$

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

$$\begin{cases} x_1(t, \epsilon) = \frac{\theta_2}{\theta_1 + \theta_2} Z(t) + o_\epsilon(1), \\ x_2(t, \epsilon) = \frac{\theta_1}{\theta_1 + \theta_2} Z(t) + o_\epsilon(1) \end{cases} \quad \text{uniformly for } t \in [t_0, +\infty). \quad (2.16)$$

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

$$\begin{cases} \frac{dX}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) - r_2 (X - x_1) \left(1 + \frac{X - x_1}{K_2} \right), \\ \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (-(\theta_1 + \theta_2)x_1 + \theta_2 X). \end{cases} \quad (2.17)$$

When $\epsilon \rightarrow \infty$, (2.17) is a *slow-fast* system, with one *slow variable*, X , and one *fast variable* x_1 . According to Tikhonov's theorem [26, 29, 31, 6] we consider the dynamics of the fast variable in the time scale $\tau = \epsilon t$. One obtains

$$\frac{dx_1}{d\tau} = \frac{1}{\epsilon} r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + -(\theta_1 + \theta_2)x_1 + \theta_2 X.$$

In the limit $\epsilon \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_1}{d\tau} = -(\theta_1 + \theta_2)x_1 + \theta_2 X. \quad (2.18)$$

The *slow manifold* is formed by the equilibrium points of the fast equation (2.18), which is given by:

$$x_1^* = \frac{\theta_2}{\theta_1 + \theta_2} X. \quad (2.19)$$

Since x_1^* is locally asymptotically stable (LAS) for the system (2.18), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (2.17) are approximated by the solutions of the *reduced model* which is obtained by replacing x_1^* into the dynamics of the slow variable, that is:

$$\frac{dX}{dt} = r_1 \frac{\theta_2}{\theta_1 + \theta_2} X \left(1 - \frac{\theta_2}{\theta_1 + \theta_2} \frac{X}{K_1} \right) - r_2 \frac{\theta_1}{\theta_1 + \theta_2} X \left(1 + \frac{\theta_1}{\theta_1 + \theta_2} \frac{X}{K_2} \right), \quad (2.20)$$

which gives the equation (2.14). If $\theta_2 r_1 > \theta_1 r_2$, (2.14) admits $X^* = (\theta_1 + \theta_2)K$ as a positive equilibrium point, which is LAS in the positive axis, and if $\theta_2 r_1 \leq \theta_1 r_2$, (2.14) admits the origin as unique equilibrium point, which is LAS. The approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is small as we want. Therefore, let $Z(t)$ be the solution of the reduced model (2.20) of initial condition $Z(0) = X(0, \epsilon) = x_1^0 + x_2^0$, then, when $\epsilon \rightarrow \infty$, we have the approximations (2.15) and (2.16). $\square$

Wu et al. [32] proved that large dispersal intensity (i.e., $\epsilon \rightarrow \infty$), the intermediate asymmetry θ_1/θ_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 $\frac{\theta_1}{\theta_2} = \frac{r_1 - r_2}{2\alpha_2(K_1 + K_2)}$. (ii) When θ_1/θ_2 is extremely large, the species goes to extinction in both patches. Mathematically speaking, we can rewrite the following result [32, Proposition 5.10]:

Proposition 2.3. [32, Proposition 5.10] *Assume that $\frac{\theta_1}{\theta_2} < \frac{r_1}{r_2}$. Consider the total equilibrium population $T_1^*(\epsilon)$ for $\epsilon \rightarrow \infty$ given by (2.12). We have:*

$$T_1^*(+\infty) \begin{cases} > K_1 & \text{if } \frac{\theta_1}{\theta_2} < \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}, \\ = K_1 & \text{if } \frac{\theta_1}{\theta_2} = \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}, \\ < K_1 & \text{if } \frac{\theta_1}{\theta_2} > \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}. \end{cases} \quad (2.21)$$

Moreover, $T_1^*(+\infty)$ reaches its maximum value

$$\theta_2^2 r_2 K_1 \frac{K_1 + K_2}{4(\theta_2^2 r_1 K_2 + \theta_1^2 r_2 K_1)} \left(\frac{r_1 - r_2}{\alpha_2(K_1 + K_2)} \right)^2$$

$$\text{at } \frac{\theta_1}{\theta_2} = \frac{r_1 - r_2}{2\alpha_2(K_1 + K_2)}.$$

3. TWO-PATCH SOURCE-SINK MODEL WITH NONLINEAR DISPERSION

In this section, we consider the two-patch system with source-sink dynamics coupled by nonlinear terms of migration (see Fig. 4), which can be written in the following form:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2} \right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (3.1)$$

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. $r_1, r_2 > 0$. The parameters $\alpha_i := r_i/K_i > 0$ are the intraspecific competition degree. Parameter ϵ represents the dispersal intensity. We denote θ_1 the migration rate from source patch 1 to the sink patch 2 and θ_2 from sink patch 2 to source patch 1, the dispersal is symmetric if $\theta_1 = \theta_2$.

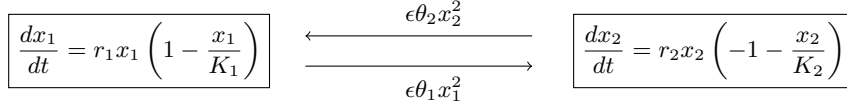


FIGURE 4. A Two-patch source-sink coupled system

3.1. Global stability. We have the following result:

Theorem 3.1. *The equilibrium $E_2^*(\epsilon)$ of (3.1) is GAS in the positive cone $\mathbb{R}_+^2 \setminus \{0\}$.*

Proof. The two-dimensional system (3.1) is cooperative. Indeed, the Jacobian matrix evaluated at the equilibrium point $E_2^*(\epsilon)$ is given by

$$\mathbb{J}(E_2^*(\epsilon)) = \begin{bmatrix} \kappa_1 & 2\epsilon\theta_2x_2^{**}(\epsilon) \\ 2\epsilon\theta_1x_1^{**}(\epsilon) & \kappa_2 \end{bmatrix},$$

where

$$\kappa_1 = r_1 - 2r_1 \frac{x_1^{**}(\epsilon)}{K_1} - 2\epsilon\theta_1x_1^{**}(\epsilon), \quad \kappa_2 = r_2 - 2r_2 \frac{x_2^{**}(\epsilon)}{K_2} - 2\epsilon\theta_2x_2^{**}(\epsilon).$$

We also have

$$0 < \frac{d\mathcal{H}_{\epsilon,1}}{dx_1}(x_1^{**}(\epsilon), x_2^{**}(\epsilon)) = -\frac{1}{2\epsilon\theta_2 \mathcal{H}_{\epsilon,1}(x_1^{**}(\epsilon))} \kappa_1,$$

and

$$0 < \frac{d\mathcal{H}_{\epsilon,2}}{dx_2}(x_1^{**}(\epsilon), x_2^{**}(\epsilon)) = -\frac{1}{2\epsilon\theta_1 \mathcal{H}_{\epsilon,2}(x_2^{**}(\epsilon))} \kappa_2.$$

Hence, necessarily $\kappa_1 < 0$ and $\kappa_2 < 0$. It follows that the trace satisfies

$$\text{tr}(\mathbb{J}(E_2^*(\epsilon))) = \kappa_1 + \kappa_2 < 0.$$

Moreover, from Figure 5-(b), we observe that at the equilibrium $E_2^*(\epsilon)$,

$$\frac{d\mathcal{H}_{\epsilon,1}}{dx_1}(E_2^*(\epsilon)) > \left(\frac{d\mathcal{H}_{\epsilon,2}}{dx_2}(E_2^*(\epsilon)) \right)^{-1},$$

which yields

$$-\frac{\kappa_1}{2\epsilon\theta_2 \mathcal{H}_{\epsilon,1}(x_1^{**}(\epsilon))} > -\frac{\kappa_2}{2\epsilon\theta_1 \mathcal{H}_{\epsilon,2}(x_2^{**}(\epsilon))}.$$

Therefore,

$$\det \mathbb{J}(E_2^*(\epsilon)) = \kappa_1 \kappa_2 - 4\epsilon^2 \theta_1 \theta_2 x_1^{**}(\epsilon) x_2^{**}(\epsilon) > 0.$$

By the Routh–Hurwitz criterion, the eigenvalues of $\mathbb{J}(E_2^*(\epsilon))$ have strictly negative real parts, which proves that $E_2^*(\epsilon)$ is locally asymptotically stable. Finally, Lemma A.3 implies that no non-trivial closed orbits exist in the interior of the positive quadrant, and thus the asymptotic stability of $E_2^*(\epsilon)$ is in fact global. $\square$

According to Theorem 3.1, model (3.1) has always a unique positive equilibrium, again denoted by $E_2^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$ which is given by the positive intersection between the ellipse $\mathbb{E}^1$ and the hyperbola $\mathcal{H}_\epsilon$ (see Fig. 5), i.e. satisfies to

$$\begin{cases} r_1 x_1^{**}(\epsilon) \left(1 - \frac{x_1^{**}(\epsilon)}{K_1} \right) - r_2 x_2^{**}(\epsilon) \left(1 + \frac{x_2^{**}(\epsilon)}{K_2} \right) = 0, \\ x_2^{**}(\epsilon) = \sqrt{\frac{1}{\theta_2} \left(\theta_1 (x_1^{**}(\epsilon))^2 - \frac{r_1}{\epsilon} x_1^{**}(\epsilon) \left(1 - \frac{x_1^{**}(\epsilon)}{K_1} \right) \right)} \end{cases} \quad (3.2)$$

where $\frac{r_1/\epsilon}{\theta_1 + r_1/\epsilon} < x_1^{**}(\epsilon) < K_1$. Note that, the origin is always unstable. The equilibrium E_2^* is GAS in $\mathbb{R}^2 \setminus \{0\}$. Comparing these stability results with those of Wu et al. [32] for the system (1.1), we conclude that the origin cannot be globally asymptotically stable as in the case of linear diffusion.

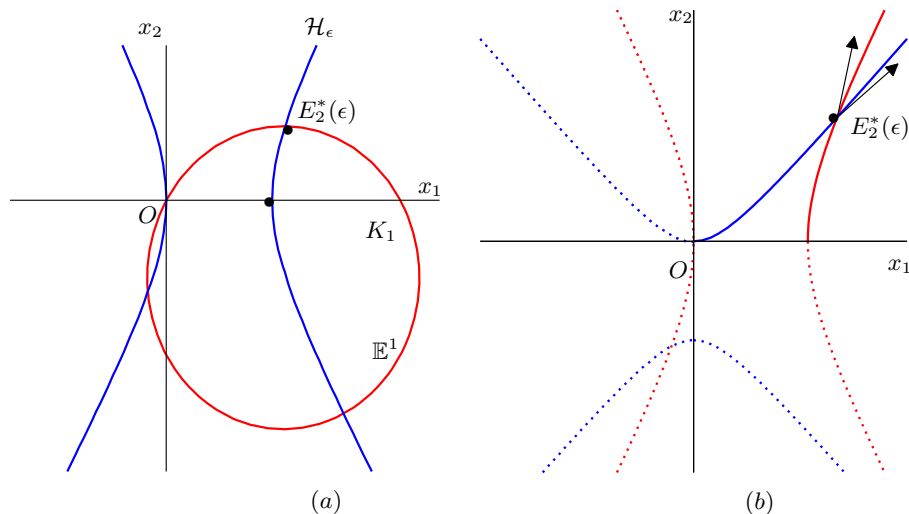


FIGURE 5. (a) The ellipse $\mathbb{E}^1$ and the curve $\mathcal{H}_\epsilon$ for selected parameter values of the model. The equilibrium points correspond to the intersections of $\mathbb{E}^1$ and $\mathcal{H}_\epsilon$ within the positive quadrant, which include the origin and a second positive equilibrium point $E_2^*(\epsilon)$. (b) Possible configurations of the isoclines of system (3.1), shown in red for x_1 and in blue for x_2 , for certain parameter sets. The equilibrium points are given by the intersections of these two isoclines, consisting of the origin and the positive equilibrium $E_2^*(\epsilon)$.

We thus define the total equilibrium population at the positive equilibrium under dispersal rate ϵ , i.e.

$$T_2^*(\epsilon) = x_1^{**}(\epsilon) + x_2^{**}(\epsilon), \quad (3.3)$$

as the total realized asymptotic population abundance.

In the next section, we consider the system (3.1) when the migration rate goes to infinity, in other words, when there is no restriction whatsoever on travel.

3.2. Fast dispersal. Let us denote by $s := \frac{\theta_1}{\theta_2}$, the dispersal asymmetry. In this case, we can rewrite the model (3.1) as follows:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (x_2^2 - s x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (s x_1^2 - x_2^2). \end{cases} \quad (3.4)$$

Let $X(t, \epsilon) = x_1(t, \epsilon) + x_2(t, \epsilon)$. We rewrite the system (3.4) using the variables (X, x_1) . One obtains:

$$\begin{cases} \frac{dX}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - r_2 (X - x_1) \left(1 + \frac{X - x_1}{K_2}\right), \\ \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon ((1 - s)x_1^2 - 2Xx_1 + X^2). \end{cases} \quad (3.5)$$

When $\epsilon \rightarrow \infty$, (3.5) is a *slow-fast* system, with one *slow variable*, X , and one *fast variable* x_1 . According to Tikhonov's theorem [26, 29, 31, 6] we consider the dynamics of the fast

variable in the time scale $\tau = \epsilon t$. One obtains

$$\frac{dx_1}{d\tau} = \frac{1}{\epsilon} r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + (1-s)x_1^2 - 2Xx_1 + X^2.$$

In the limit $\epsilon \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_1}{d\tau} = (1-s)x_1^2 - 2Xx_1 + X^2. \quad (3.6)$$

We will study the behavior of the model (3.4) distinguishing three following cases:

$$0 < s < 1, \quad s = 1, \quad \text{and} \quad s > 1.$$

First, let us start by the symmetric case ($s = 1$).

Theorem 3.2. *Consider the system (3.4) with $s = 1$. Let $(x_1(t, \epsilon), x_2(t, \epsilon))$ be the solution of the system (3.4) 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 logistic equation*

$$\begin{cases} \frac{dX}{dt} = rX \left(1 - \frac{X}{2K}\right), \\ X(0) = x_1^0 + x_2^0, \end{cases} \quad (3.7)$$

where $r = \frac{r_1 - r_2}{2}$ and $K = \frac{r_1 - r_2}{\alpha_1 + \alpha_2}$, with $\alpha_i = \frac{r_i}{K_i}$. Then, when $\epsilon \rightarrow \infty$, we have

$$x_1(t, \epsilon) + x_2(t, \epsilon) = Z(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.8)$$

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

$$\begin{cases} x_1(t, \epsilon) = \frac{1}{2}Z(t) + o_\epsilon(1), \\ x_2(t, \epsilon) = \frac{1}{2}Z(t) + o_\epsilon(1) \end{cases} \quad \text{uniformly for } t \in [t_0, +\infty). \quad (3.9)$$

Proof. The *slow manifold* is formed by the equilibrium points of the fast equation (3.6) with $s = 1$, which is given by:

$$x_1^{**} = \frac{1}{2}X. \quad (3.10)$$

Since $x_1^{**} = \frac{1}{2}X$ is LAS for the system (3.6), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (3.5) are approximated by the solutions of the *reduced model* which is obtained by replacing $x_1^{**} = \frac{1}{2}X$ into the dynamics of the slow variable, that is:

$$\frac{dX}{dt} = r_1 \frac{1}{2}X \left(1 - \frac{X}{2K_1}\right) - r_2 \frac{1}{2}X \left(1 + \frac{X}{2K_2}\right), \quad (3.11)$$

which gives the equation (3.7). If $r_1 > r_2$, (3.7) admits $X^* = 2K$ as a positive equilibrium point, which is LAS in the positive axis, and if $r_1 \leq r_2$, (3.7) admits the origin as unique equilibrium point, which is LAS. The approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is small as we want. Therefore, let $Z(t)$ be the solution of the reduced model (3.11) of initial condition $Z(0) = X(0, \epsilon) = x_1^0 + x_2^0$, then, when $\epsilon \rightarrow \infty$, we have the approximations (3.8) and (3.9). $\square$

Note that, in the case of perfect mixing, Approximation (3.8) shows that: if $r_1 > r_2$ then the total population behaves like the unique logistic equation (3.7) and then, when t and ϵ tend to ∞ , the total population $x_1(t, \epsilon) + x_2(t, \epsilon)$ tends toward $2 \frac{r_1 - r_2}{\alpha_1 + \alpha_2}$ where $\alpha_i = r_i/K_i$. If $r_1 \leq r_2$, then Equation (3.7) has the origin as unique equilibrium, and then, when t and ϵ tend to ∞ , the total population $x_1(t, \epsilon) + x_2(t, \epsilon)$ tends toward 0.

Next, we consider the asymmetric case $s \neq 1$:

Theorem 3.3. Consider the system (3.4). Assume that $s \neq 1$. Let $(x_1(t, \epsilon), x_2(t, \epsilon))$ be the solution of the system (3.4) with initial condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $U(t)$ be the solution of the following equation

$$\frac{dX}{dt} = \begin{cases} RX \left(1 - \frac{X}{(1 - \sqrt{s})K} \right) & \text{if } 0 < s < 1, \\ RX \left(1 - \frac{X}{(1 + \sqrt{s})K} \right) & \text{if } s > 1, \end{cases} \quad (3.12)$$

where $X(0) = x_1^0 + x_2^0$, $R = \frac{r_1 - \sqrt{s}r_2}{1 + \sqrt{s}}$ and $K = \frac{r_1 - \sqrt{s}r_2}{\alpha_1 + s\alpha_2}$ with $\alpha_i = \frac{r_i}{K_i}$. Then, when $\epsilon \rightarrow \infty$, we have

$$x_1(t, \epsilon) + x_2(t, \epsilon) = U(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.13)$$

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

$$(x_1(t, \epsilon), x_2(t, \epsilon)) = \begin{cases} \left(\frac{1}{1 - \sqrt{s}}U(t) + o_\epsilon(1), \frac{\sqrt{s}}{1 - \sqrt{s}}U(t) + o_\epsilon(1) \right) & \text{if } 0 < s < 1 \\ \left(\frac{1}{1 + \sqrt{s}}U(t) + o_\epsilon(1), \frac{\sqrt{s}}{1 + \sqrt{s}}U(t) + o_\epsilon(1) \right) & \text{if } s > 1, \end{cases} \quad (3.14)$$

uniformly for $t \in [t_0, +\infty)$.

Proof. The slow manifold is formed by the equilibrium points of the fast equation (3.6), which given by:

$$x_{1,1}^{**} = \frac{\sqrt{s} - 1}{s - 1}X \quad \text{and} \quad x_{1,2}^{**} = -\frac{1 + \sqrt{s}}{s - 1}X. \quad (3.15)$$

If $s > 1$, then $x_{1,1}^{**} > 0$ and $x_{1,2}^{**} < 0$. As $\frac{dx_1}{d\tau} > 0$ for all $x_{1,2}^{**} < x_1 < x_{1,1}^{**}$ and $\frac{dx_1}{d\tau} < 0$ for all $x_1 < x_{1,1}^{**}$ and $x_1 > x_{1,1}^{**}$ then $x_{1,1}^{**}$ is LAS and $x_{1,2}^{**}$ is unstable. Since $x_{1,1}^{**}$ is LAS for the system (3.6), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (3.5) are approximated by the solutions of the reduced model which is obtained by replacing $x_{1,1}^{**}$ into the dynamics of the slow variable, that is:

$$\begin{aligned} \frac{dX}{dt} &= r_1 \frac{\sqrt{s} - 1}{s - 1}X \left(1 - \frac{\frac{\sqrt{s} - 1}{s - 1}X}{K_1} \right) - r_2 \frac{s - \sqrt{s}}{s - 1}X \left(1 + \frac{\frac{s - \sqrt{s}}{s - 1}X}{K_2} \right) \\ &= RX \left(1 - \frac{X}{(1 + \sqrt{s})K} \right), \end{aligned}$$

which gives the equation (3.12).

If $s < 1$, then $0 < x_{1,1}^{**} < x_{1,2}^{**}$. As $\frac{dx_1}{d\tau} > 0$ for all $x_{1,1}^{**} < x_1 < x_{1,2}^{**}$ and $\frac{dx_1}{d\tau} < 0$ for all $x_1 < x_{1,1}^{**}$ and $x_1 > x_{1,2}^{**}$ then $x_{1,2}^{**}$ is LAS and $x_{1,1}^{**}$ is unstable. Since $x_{1,2}^{**}$ is LAS for the system (3.6), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (3.5) are approximated by the solutions of the reduced model which is obtained by replacing $x_{1,2}^{**}$ into the dynamics of the slow variable, that is:

$$\begin{aligned} \frac{dX}{dt} &= r_1 \frac{\sqrt{s} + 1}{1 - s}X \left(1 - \frac{\frac{\sqrt{s} + 1}{1 - s}X}{K_1} \right) - r_2 \frac{s + \sqrt{s}}{s - 1}X \left(1 + \frac{\frac{s + \sqrt{s}}{s - 1}X}{K_2} \right) \\ &= RX \left(1 - \frac{X}{(1 - \sqrt{s})K} \right), \end{aligned}$$

which gives the equation (3.12). If $r_1 > \sqrt{s}r_2$ (3.12) admits $X^* = (1 + \sqrt{s})K$ if $s > 1$ and $X^* = (1 - \sqrt{s})K$ if $s < 1$ as a positive equilibrium point, which is LAS in the positive axis, and if $r_1 \leq \sqrt{s}r_2$, (3.12) admits the origin as unique equilibrium point, which is LAS. The approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is small as we want. Therefore, let $U(t)$

be the solution of the reduced model (3.11) of initial condition $U(0) = X(0, \epsilon) = x_1^0 + x_2^0$, then, when $\epsilon \rightarrow \infty$, we have the approximations (3.13) and (3.14). $\square$

Note that, in the case of perfect mixing, Approximation (3.13) shows that: if $r_1 > \sqrt{s}r_2$ then the total population behaves like the unique equation (3.12) and then, when t and ϵ tend to ∞ , the total population $T_2^*(t, \epsilon)$ tends toward $(1 + \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\alpha_1 + s\alpha_2}$ if $s > 1$ and tends toward $(1 - \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\alpha_1 + s\alpha_2}$ if $s < 1$ where $\alpha_i = r_i/K_i$. If $r_1 \leq \sqrt{s}r_2$, then Equation (3.12) has the origin as unique equilibrium, and then, when t and ϵ tend to ∞ , the total population $T_2^*(t, \epsilon) = x_1(t, \epsilon) + x_2(t, \epsilon)$ tends toward 0.

As a corollary of the previous theorems we obtain the following result which describes the total equilibrium population when $\epsilon \rightarrow \infty$ for all possible value of s :

Corollary 3.1. *We have:*

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } T_2^*(+\infty) = \begin{cases} (1 - \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 0 < s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \\ \text{If } r_2 < r_1 \text{ then } T_2^*(+\infty) = \begin{cases} (1 - \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 0 < s < 1, \\ (1 + \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 1 \leq s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \end{array} \right. \quad (3.16)$$

3.3. Effect of nonlinear dispersal on total population. Our aim in this section is to study Two-patch source-sink model coupled by nonlinear asymmetric migration terms (same type of dispersion (1.5)) given by (3.1). In particular, we are interested in studying the effect of nonlinear dispersion on the dynamics of population, more precisely, we are looking the following question: is it possible, depending on the migration rate, that the total equilibrium population be larger than the carrying capacity K_1 ? Note that, this last question has been studied by many researches, see [3, 4, 8, 9, 10, 11, 13, 14, 15, 16] for effect of linear diffusion on the total biomass with logistic growth, [11] for nonlinear diffusion, [5, 12, 32] for Source-Sink patch model and [17, 18] for susceptible-infected-susceptible (SIS) patch-model).

Our aim is to compare the total equilibrium population

$$T_2^*(\epsilon) = x_1^{**}(\epsilon) + x_2^{**}(\epsilon), \quad E_2^*(\epsilon) = (x_1^{**}(\epsilon), x_2^{**}(\epsilon)),$$

of (3.1) and carrying capacity K_1 , by analyzing the stable positive equilibrium $E_2^*(\epsilon)$. Note that, when there is no dispersal (i.e., $\epsilon = 0$), the total equilibrium population is $T_2^*(0) = K_1$. We study the effect of nonlinear asymmetric dispersal on the total equilibrium population for the two-patch source-sink system (3.1). Using the graphical method of Arditi et al. [4] and of Wu et al. [32]. We describe the positional effects of the equilibrium $E_2^*(\epsilon)$ as the migration rate ϵ varies from 0 to $+\infty$. We will give the condition whether T_2^* is greater or smaller than the carrying capacity $T_2^*(0) = K_1$. We prove there are only five cases as in the two-patch source-sink model with linear diffusion can occur. We consider the regions in the set of the parameters θ_1 and θ_2 , denoted $\Delta_0, \Delta_1, \Delta_2, \Delta_3$ and Δ_4 , depicted in Figure 6 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \left\{ \begin{array}{l} \Delta_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2^2}{r_1^2} \right\}, \\ \Delta_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{r_2^2}{r_1^2} \right\}. \end{array} \right. \\ \\ \text{If } r_2 < r_1 \text{ then } \left\{ \begin{array}{l} \Delta_2 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2^2}{r_1^2} \right\}, \\ \Delta_3 = \left\{ (\theta_1, \theta_2) : \frac{r_2^2}{r_1^2} < \frac{\theta_2}{\theta_1} < \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2 \right\}, \\ \Delta_4 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \geq \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2 \right\}. \end{array} \right. \end{array} \right. \quad (3.17)$$

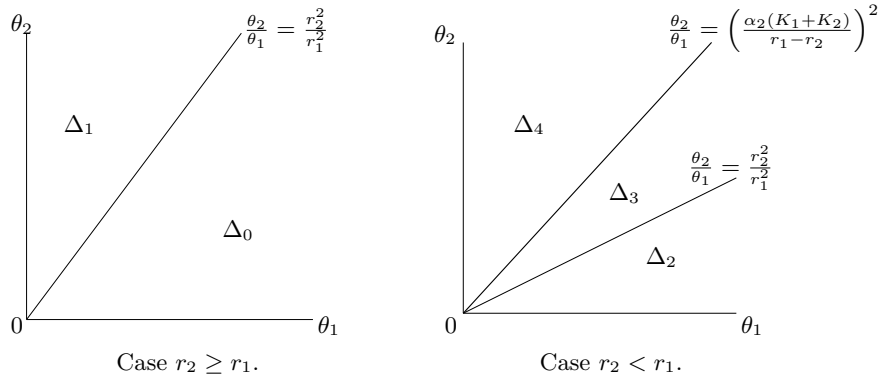


FIGURE 6. Regions Δ_0 , Δ_1 , Δ_2 , Δ_3 and Δ_4 defined by (3.17).

We have the following results which gives the conditions under which fragmentation and nonlinear asymmetrical migration can lead to a total equilibrium population greater or smaller than the sum of the carrying capacities:

Theorem 3.4. *The total equilibrium population T_2^* of (3.1) satisfies the following properties*

- (i) If $r_2 \geq r_1$, let Δ_0 and Δ_1 be defined by (3.17). Then we have:
 - (a) if $(\theta_1, \theta_2) \in \Delta_0$ then $T_2^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$. Moreover, $T_2^*(\epsilon) \rightarrow 0$ when $\epsilon \rightarrow +\infty$.
 - (b) if $(\theta_1, \theta_2) \in \Delta_1$ then $0 < T_2^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$. Moreover, $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$ when $\epsilon \rightarrow +\infty$.
- (ii) If $r_2 < r_1$, let Δ_2, Δ_3 and Δ_4 be defined by (3.17). Then we have:
 - (a) if $(\theta_1, \theta_2) \in \Delta_2$ then, there is $\epsilon_0 > 0$, such that: $T_2^*(\epsilon) > K_1$ for $\epsilon < \epsilon_0$ and $T_2^*(\epsilon) < K_1$ for all $\epsilon > \epsilon_0$. Moreover, $T_2^*(\epsilon) \rightarrow 0$ when $\epsilon \rightarrow +\infty$.
 - (b) if $(\theta_1, \theta_2) \in \Delta_3$ then, there is $\epsilon^\sharp > 0$, such that: $T_2^*(\epsilon) > K_1$ for $\epsilon < \epsilon^\sharp$ and $T_2^*(\epsilon) < K_1$ for all $\epsilon > \epsilon^\sharp$. Moreover, $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$ when $\epsilon \rightarrow +\infty$.
 - (c) if $(\theta_1, \theta_2) \in \Delta_4$, then $T_2^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$. Moreover, if $\frac{\theta_2}{\theta_1} = \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2$, then $T_2^* \rightarrow T_2^*(\infty) = K_1$.

Proof. Recall that, the equilibrium points of (3.1) are the non-negative intersection between the ellipse $\mathbb{E}^1$ and hyperbola $\mathcal{H}_\epsilon$. There are two equilibrium points. The first is the trivial point $O := (0, 0)$ and the second is a non trivial point noted $E^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$ whose position depend on migration rate ϵ (see Fig. 5-(a)). As our study is limited in the positive cone, then we are interested only in the positive branch of $\mathcal{H}_\epsilon$. The hyperbola $\mathcal{H}_\epsilon$

(shown in blue in Fig. 5-(a)) depend on the migration rate ϵ . It always passes through the origin and the point $\mathcal{B} := (K_1, \sqrt{\frac{\theta_1}{\theta_2}} K_1)$.

When $\epsilon \rightarrow 0$, the left branch of hyperbola $\mathcal{H}_\epsilon$ tend to the vertical line $x_1 = 0$ and the right branch into the vertical line $\mathcal{H}_0 : x_1 = K_1$. Moreover, $\mathbb{E}^1 \cap \mathcal{H}_0 = \{(K_1, 0)\}$. In the case when $\epsilon \rightarrow \infty$, the hyperbola $\mathcal{H}_\epsilon$ tend to the oblique line $\mathcal{H}_\infty : x_2 = \sqrt{\frac{\theta_1}{\theta_2}} x_1$. Moreover,

$$\mathbb{E}^1 \cap \mathcal{H}_\infty = \left\{ (0, 0), \left(\sqrt{\theta_2} \frac{\sqrt{\theta_2} r_1 - \sqrt{\theta_1} r_2}{\theta_2 r_1 / K_1 + \theta_1 r_2 / K_2}, \sqrt{\theta_1} \frac{\sqrt{\theta_2} r_1 - \sqrt{\theta_1} r_2}{\theta_2 r_1 / K_1 + \theta_1 r_2 / K_2} \right) \right\}.$$

The tangent space of the ellipse $\mathbb{E}^1$ at $O = (0, 0)$ and $A = (K_1, 0)$ is $T_O \mathbb{E}^1 : x_2 = \frac{r_1}{r_2} x_1$, and $T_A \mathbb{E}^1 : x_2 = -\frac{r_1}{r_2} x_1$ respectively.

To facilitate comparison between the total equilibrium population $T_2^*(\epsilon)$ and $T_2^*(0) = K_1$, we define a straight line $\Delta : x_1 + x_2 = K_1$. If the intersection of the ellipse $\mathbb{E}^1$ and the hyperbola $\mathcal{H}_\epsilon$, i.e., the equilibrium $(x_1^*(\epsilon), x_2^*(\epsilon))$, is on or below the line Δ , then $T_2^*(\epsilon) \leq T_2^*(0)$, whereas if the intersection is above the line Δ , then $T_2^*(\epsilon) \geq T_2^*(0)$. We see very simply that dispersal is favorable to $T_2^*(\epsilon)$ if $E_2^*(\epsilon)$ is above Δ , unfavorable if below Δ . The equilibrium point $E_2^*(\epsilon)$ is always in ellipse, then, for $\epsilon = 0$, the equilibrium point states at A , and when ϵ increases, $E_2^*(\epsilon)$ describes an arc of the ellipse and ends at point $E^*(\infty)$.

Suppose $r_1 \leq r_2$. Then the slope of $T_O \mathbb{E}^1$, $-\frac{r_1}{r_2} \geq -1$, which means that the ellipse $\mathbb{E}^1$ is below the line Δ in the first quadrant and $T_2^*(\epsilon) < T_2^*(\infty)$, as shown in Fig. 7. If the slope of $\mathcal{H}_\infty$, $\sqrt{\frac{\theta_1}{\theta_2}}$, is bigger than the slope of $T_O \mathbb{E}^1$, i.e. $\sqrt{\frac{\theta_1}{\theta_2}} \geq \frac{r_1}{r_2}$, the ellipse is below the line Δ in the first quadrant. Thus, there is ϵ^* , such that, when $0 < \epsilon \leq \epsilon^*$, the equilibrium $E_2^*(\epsilon)$ changes from point A to O . When $\epsilon \geq \epsilon^*$, we have $E_2^*(\epsilon) \rightarrow O$ and $T_2^*(\epsilon) \rightarrow 0$ when $\epsilon \rightarrow \infty$ (see Fig. 7-(a)). If $\sqrt{\frac{\theta_1}{\theta_2}} < \frac{r_1}{r_2}$, the ellipse and the line $\mathcal{H}_\infty$ has an intersection B . Then we have $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$, as shown in Fig. 7-(b).

In the case when $r_1 > r_2$, direct calculation finds that the ellipse $\mathbb{E}^1$ and the line Δ have two intersections:

$$A = (K_1, 0), \text{ and } C = \left(\alpha_2 \frac{K_1 + K_2}{\alpha_1 + \alpha_2}, \frac{r_1 - r_2}{\alpha_1 + \alpha_2} \right).$$

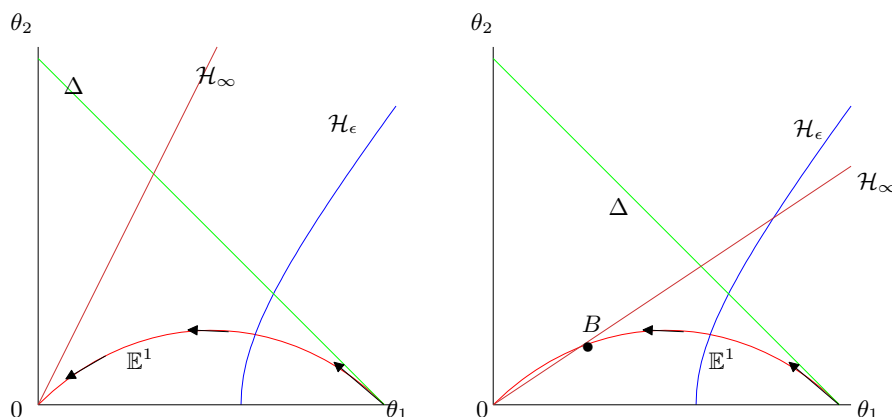
We denote by Σ the straight line joint the origin and C . The slope of Σ is equal to $\frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}$. We distinguish three cases relative position of the points $O, B = E_2^*(\infty)$, and C , or equivalently, the three lines $T_O \mathbb{E}^1$, $\mathcal{H}_\infty$ and Σ whose slopes respectively are

$$\frac{r_1}{r_2}, \quad \sqrt{\frac{\theta_1}{\theta_2}} \quad \text{and} \quad \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}.$$

By using the graphical method of Arditi et al. [4] (see also [32]), and by discussing the relative positions of the three lines $T_O \mathbb{E}^1$, $\mathcal{H}_\infty$, and Σ , we complete the proof. (see Figures 8 and 9).

□

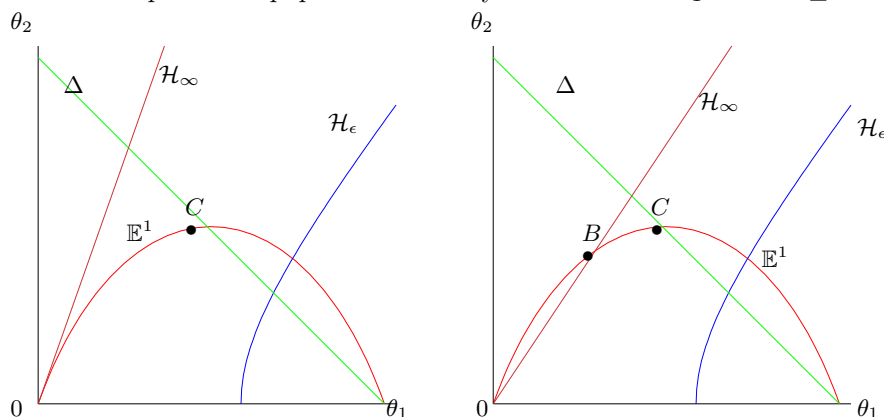
Speaking biologically, the result of the previous theorem show that the nonlinear asymmetric dispersal can lead to either an increased total size of the population in two patches, a decreased total size with persistence in the patches, or even extinction in both patches when the growth of migration goes to infinity. Let us explain the result of Theorem 3.4 in the particular case where the dispersion is symmetric i.e. $\frac{\theta_1}{\theta_2} = 1$. In this case, the system



Case (1) – (a).

Case (1) – (b).

FIGURE 7. This illustrates the cases (1)-a and (1)-b in Theorem 3.4. Case (a) $(\theta_1, \theta_2) \in \Delta_0$ and the case (b) $(\theta_1, \theta_2) \in \Delta_1$. The ellipse $\mathbb{E}^1$ and the hyperbola $\mathcal{H}_\epsilon$ are shown in red and blue respectively for some parameters of the model (3.1), the straight lines Δ and $\mathcal{H}_\infty$ are shown in green and orange respectively. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the ellipse from $A = (K_1, 0)$ to O in the case (1)-a, from A to B in the case (1)-b. The total equilibrium population is always smaller than K_1 for all $\epsilon \geq 0$.



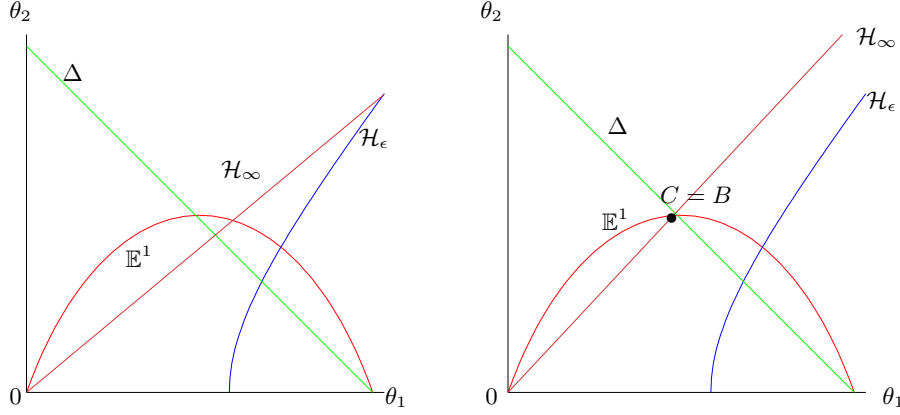
Case (2) – (a).

Case (2) – (b).

FIGURE 8. This illustrates the cases (2)-a and (2)-b in Theorem 3.4. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the ellipse from $A = (K_1, 0)$ to O in the case (a) from A to B in the case (b), passing through the point C which is the other point of intersection between the ellipse and the line Δ . The dispersal is favorable when $E_2^*(\epsilon)$ is between A and C , and unfavorable when $E_2^*(\epsilon)$ is between C and B .

(3.1) becomes

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (x_2^2 - x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (x_1^2 - x_2^2), \end{cases} \quad (3.18)$$



Case (2) – (c).

Case (d).

FIGURE 9. This illustrates the case (2)-c in Theorem 3.4. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the ellipse from $A = (K_1, 0)$ to B . The total equilibrium point is always greater than K_1 for all ϵ , because it belongs to the ellipse and the limit point B is above Δ . The figure (d) is a particular case of (2)-(c), where $T_2^* \rightarrow K_1 = T_2^*(\infty)$ for $\frac{\theta_2}{\theta_1} = \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2}\right)^2$.

Corollary 3.2. Consider the model (3.18). Let Λ_0, Λ_1 and Λ_2 be defined by (2.9). The total equilibrium population T_2^* of (3.18) satisfies the following properties

- (i) if $(r_1, r_2) \in \Lambda_0$ then, $T_2^*(\epsilon) \leq K_1$ for all ϵ . Moreover, $T_2^*(\epsilon) \rightarrow 0$ when $\epsilon \rightarrow \infty$.
- (ii) if $(r_1, r_2) \in \Lambda_1$ then, there is $\epsilon^{**} > 0$, such that

$$\begin{cases} T_2^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^{**}, \\ 0 < T_2^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^{**}. \end{cases} \quad (3.19)$$

Moreover, $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$ when $\epsilon \rightarrow \infty$.

- (iii) if $(r_1, r_2) \in \Lambda_2$, then $T_2^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$. Moreover, if $\frac{r_1}{r_2} = \frac{K_2}{K_1+2K_2}$, then $T_2^*(\infty) = K_1$.

Proof. Consequence direct of the theorem 3.4. □

Comparing the effects of linear and nonlinear asymmetric dispersal on the persistence or extinction of the population, we observe the following phenomena. In the **nonlinear symmetric case**, the symmetry between patches ensures that if the derivative of the total equilibrium population at $\epsilon = 0$ is negative, then the population goes to extinction in both patches. By contrast, in the **nonlinear asymmetric case**, it is possible that the derivative of the total equilibrium population at $\epsilon = 0$ is negative without leading to extinction in both patches.

A second difference concerns the threshold phenomenon. In the nonlinear symmetric case, if there exists a migration rate ϵ^* such that $T_2^*(\epsilon^*) = K_1$, then the population persists in both patches. However, in the nonlinear asymmetric case, one may also have $T_2^*(\epsilon^\sharp) = K_1$ for some value of the migration rate $\epsilon^\sharp$, but the population nevertheless goes extinct in both patches. Hence, we conclude that nonlinear dispersal without the condition of symmetry increases the probability of extinction of the population across the two patches.

In the remainder of this section, we investigate the effect of rapid growth in the source patch and rapid death in the sink patch on the dynamics of the total equilibrium population and on the coexistence of populations in both patches. These particular situations were

not analyzed in [3, 4, 32]. Here, we study the total equilibrium population as a function of the migration rate in the case where the growth rate (resp. death rate) is much larger than the corresponding death rate (resp. growth rate). In particular, we explicitly compute the total equilibrium population in both scenarios, determine its derivative at the absence of migration, evaluate its limit as the migration rate tends to infinity, and compare the total equilibrium population with the carrying capacity of the source patch. We begin with the following situation:

3.4. The death rate is much larger than the growth rate. In this part, we consider the two-patch model (3.1) and we assume that the death rate r_2 is much larger than the growth rate r_1 . One can write the model in the following way:

$$\begin{cases} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} &= \frac{r_2}{\eta} x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (3.20)$$

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

Theorem 3.5. *Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of System (3.20) 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*

$$\frac{dz}{dt} = r_1 z \left(1 - \frac{z}{K_1}\right) - \epsilon \theta_1 z^2 =: \varphi(z), \quad (3.21)$$

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

$$x_1(t, \eta) = z(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.22)$$

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

$$x_2(t, \eta) = o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (3.23)$$

Proof. When $\eta \rightarrow 0$, System (3.20) is a slow-fast system, with one slow variable, x_1 , and one fast variable, x_2 . Tikhonov's theorem [26, 29, 31, 6] prompts us to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{\eta}t$. One obtains

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon \eta (\theta_1 x_1^2 - \theta_2 x_2^2). \quad (3.24)$$

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

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right). \quad (3.25)$$

The slow manifold is given by the equilibrium of System (3.25), i.e. $x_2 = 0$, which is LAS in the positive axis. When η goes to zero, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (3.20) converge to the solutions of the *reduced model* (3.21), obtained by replacing $x_2 = 0$ into the dynamics of the slow variable.

The differential equation (3.21) admits a positive equilibrium

$$x_1^{**}(\epsilon, 0^+) := \frac{r_1 K_1}{r_1 + \epsilon \theta_1 K_1}. \quad (3.26)$$

As $\varphi(x_1) > 0$ for all $0 \leq x_1 < x_1^{**}(\epsilon, 0^+)$ and $\varphi(x_1) < 0$ for all $x_1 > x_1^{**}(\epsilon, 0^+)$ then, the equilibrium $x_1^{**}(\epsilon, 0^+)$ is LAS 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 (3.21) of initial condition $z(0) = x_1^0$, then, when $\eta \rightarrow 0$, we have Approximations (3.22) and (3.23). $\square$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in System (3.20) when ϵ goes to zero.

Theorem 3.6. *The total equilibrium population $x_1^{**}(\epsilon, 0^+)$ of System (3.20) when $\eta \rightarrow 0$, given by (3.26) is decreasing. Moreover, $0 < x_1^{**}(\epsilon, 0^+) < K_1$ for ϵ and $x_1^{**}(\epsilon, 0^+) \rightarrow 0$ as $\epsilon \rightarrow \infty$.*

Proof. The derivative of (3.26) is given by:

$$\frac{dx_1^{**}}{d\epsilon}(\epsilon, 0^+) = -\frac{r_1 K_1^2 \theta_1}{(r_1 + \epsilon \theta_1 K_1)^2}, \quad (3.27)$$

which is negative for all ϵ . $\square$

3.5. The growth rate is much larger than the death rate. In this part, we consider the two-patch model (3.1) and we assume that the growth rate r_1 is much larger than the death rate r_2 . One can write the model in the following way:

$$\begin{cases} \frac{dx_1}{dt} = \frac{r_1}{\eta} x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (3.28)$$

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

Theorem 3.7. *Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of System (3.28) 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*

$$\frac{dz}{dt} = r_2 z \left(-1 - \frac{z}{K_2}\right) + \epsilon (\theta_1 K_1^2 - \theta_2 z^2) =: \psi(z), \quad (3.29)$$

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

$$x_2(t, \eta) = z(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (3.30)$$

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

$$x_1(t, \eta) = K_1 + o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (3.31)$$

Proof. When $\eta \rightarrow 0$, System (3.28) is a *slow-fast* system, with one *slow* variable, x_2 , and one *fast* variable, x_1 . Tikhonov's theorem [26, 29, 31, 6] prompts us to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{\eta}t$. One obtains

$$\frac{dx_1}{d\tau} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon \eta (-\theta_1 x_1^2 + \theta_2 x_2^2). \quad (3.32)$$

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

$$\frac{dx_1}{d\tau} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right). \quad (3.33)$$

The slow manifold is given by the equilibrium of System (3.33), i.e. $x_1 = K_1$, which is LAS in the positive axis. When η goes to zero, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (3.28) converge to the solutions of the *reduced model* (3.29), obtained by replacing $x_1 = K_1$ into the dynamics of the slow variable.

The differential equation (3.29) admits as a positive equilibrium

$$x_2^{**}(\epsilon, 0^+) := 1/2 \frac{-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}}{r_2 + \epsilon K_2 \theta_2}. \quad (3.34)$$

As $\psi(x_2) > 0$ for all $0 \leq x_2 < x_2^{**}(\epsilon, 0^+)$ and $\psi(x_2) < 0$ for all $x_2 > x_2^{**}(\epsilon, 0^+)$ then, the equilibrium $x_2^{**}(\epsilon, 0^+)$ is LAS 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 (3.29) with initial condition $z(0) = x_2^0$, then, when $\eta \rightarrow 0$, we have Approximations (3.30) and (3.31). $\square$

As a corollary of the previous theorem, we have the following result which give the limit of the total equilibrium population $T_2^*(\epsilon, 0^+)$ of System (3.28) when η goes to zero:

Corollary 3.3. *We have:*

$$T_2^*(\epsilon, 0^+) := K_1 + 1/2 \frac{-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}}{r_2 + \epsilon K_2 \theta_2}. \quad (3.35)$$

In the following proposition, we calculate the derivative of $T_2^*(\epsilon, 0^+)$ at $\epsilon = 0$ and the formula of perfect mixing (i.e. when $\epsilon \rightarrow \infty$) of the total equilibrium population defined by (3.35).

Proposition 3.4. *Consider the total equilibrium population (3.35). Then,*

$$\frac{dT_2^*}{d\epsilon}(0, 0^+) = \frac{\theta_1 K_1^2}{r_2}, \quad (3.36)$$

and

$$T_2^*(+\infty, 0^+) = (1 + \sqrt{s})K_1 = \frac{\sqrt{\theta_1} + \sqrt{\theta_2}}{\sqrt{\theta_2}} K_1. \quad (3.37)$$

Proof. The derivative of the total equilibrium population $T_2^*(\epsilon, 0^+)$ defined by (3.35) with respect to ϵ is:

$$\begin{aligned} \frac{dT_2^*}{d\epsilon}(\epsilon, 0^+) &= -1/2 \frac{\left(-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}\right) K_2 \theta_2}{(r_2 + \epsilon K_2 \theta_2)^2} \\ &\quad + 1/4 \frac{4 K_2 \theta_1 K_1^2 r_2 + 8\epsilon K_2^2 \theta_1 K_1^2 \theta_2}{(r_2 + \epsilon K_2 \theta_2) \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}} \end{aligned} \quad (3.38)$$

In particular, the derivative of the total equilibrium population at $\epsilon = 0$ is given by the formula (3.36).

By taking the limit of (3.35) when $\epsilon \rightarrow \infty$, we get that the total equilibrium population $T_2^*(\epsilon, 0^+)$ tends to (3.37). $\square$

We have the following result which gives the conditions for which patchiness is beneficial or detrimental in model (3.28) when η goes to zero.

Theorem 3.8. *Consider the total equilibrium population $T_2^*(\epsilon, 0^+)$ given by (3.35). Then, $T_2^*(\epsilon, 0^+) \geq K_1$, for all $\epsilon \geq 0$.*

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

$$\begin{aligned} T_2^*(\epsilon, 0^+) = K_1 &\iff 1/2 \frac{-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}}{r_2 + \epsilon K_2 \theta_2} = 0 \\ &\iff \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2} = r_2 K_2 \\ &\iff 4\epsilon K_2 \theta_1 K_1^2 (r_2 + \epsilon K_2 \theta_2) = 0 \\ &\iff \epsilon = 0. \end{aligned}$$

Therefore, since $\frac{dT_2^*}{d\epsilon}(0, 0^+) > 0$, the curve of the total equilibrium population intersects the straight line $\epsilon \mapsto K_1$ in a unique point which is $(0, K_1)$. Therefore, $T_2^*(\epsilon, 0^+) \geq K_1$, for all $\epsilon \geq 0$. $\square$

4. NUMERICAL SIMULATIONS

In this section, we present several numerical examples that illustrate the results of Proposition 2.2, Corollary 3.1, and Theorem 3.4. We begin by examining the functions

$$s \mapsto \psi_1(s) := T_1^*(+\infty), \quad s \mapsto \psi_2(s) := T_2^*(+\infty),$$

defined in (2.13) and (3.16), respectively. Figure 10 displays the graphs of ψ_1 (in red) and ψ_2 (in green) as functions of the dispersal asymmetry parameter s , for a selection of parameter values specified in Table 1.

TABLE 1. Parameters values of the four cases used in Fig. 10. .

Figure	r_1	r_2	K_1	K_2
10-a	1	2	2	3
10-b	2	1	2	3
10-c	4	1	1	2
10-d	7	1	1	2

4.1. **Asymmetric dispersion.** In this part, we plot in the figures 11, 12, 13, 14, 15 and 16, the curves of the total equilibrium populations $\epsilon \mapsto T_1^*(\epsilon)$ and $\epsilon \mapsto T_2^*(\epsilon)$ as a function of migration rate ϵ , and the line K_1 , for the sets of parameters $(\theta_1, \theta_2) \in \Delta_i \cap \mathcal{L}_i$ for $i = 0, \dots, 4$, where $\mathcal{L}_i$ and Δ_i are given by (2.3) and (3.17) respectively, choosing in Table 2. The intersection between $\mathcal{L}_i$ and Δ_i is defined as follows:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \left\{ \begin{array}{l} \Delta_0 \cap \mathcal{L}_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \Delta_1 \cap \mathcal{L}_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{r_2}{r_1} \right\}. \end{array} \right. \\ \\ \text{If } r_2 < r_1 \text{ then } \left\{ \begin{array}{l} \Delta_2 \cap \mathcal{L}_2 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \Delta_3 \cap \mathcal{L}_3 = \left\{ (\theta_1, \theta_2) : \frac{r_2}{r_1} < \frac{\theta_2}{\theta_1} < \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2 \right\}, \\ \Delta_4 \cap \mathcal{L}_4 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \geq \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right\}. \end{array} \right. \end{array} \right. \quad (4.1)$$

TABLE 2. Parameters values of the six cases used in Fig. 11, 12, 13, 14, 15 and 16. The derivatives $\frac{dT_1^*}{d\epsilon}(0)$, $\frac{dT_2^*}{d\epsilon}(0)$ and the perfect mixing abundances $T_1^*(\infty)$ and $T_2^*(\infty)$ are calculated with the expressions given in (B.1), (C.1), (2.12) and (3.16) respectively

Figure	r_1	r_2	K_1	K_2	θ_1	θ_2	$\frac{dT_1^*}{d\epsilon}(0)$	$T_1^*(\infty)$	$\frac{dT_2^*}{d\epsilon}(0)$	$T_2^*(\infty)$
Fig. 11	1	3	0.5	1.5	5	11	-1.76	0	-0.83	0
Fig. 12	1	3	0.5	1.5	0.5	11	-1.67	0.45	-0.83	0.22
Fig. 13	1.5	1	0.5	5	12	4	2.00	0	0.99	0
Fig. 14	1.5	1	0.5	0.083	1	4	0.16	0.42	0.08	0.29
Fig. 15	7	1	0.5	6	1	14	0.42	0.58	0.21	0.6
Fig. 16	12	2	0.5	0.125	2	2	0.41	0.5	0.20	0.5

Depending on the values of the migration rate ϵ , the numerical simulations reported in Figures 11–16 illustrate several possible inequalities between the total equilibrium populations T_1^* , T_2^* , and the carrying capacity K_1 , represented by the horizontal blue line.

Figure 11. For the parameter values given in the first row of Table 2, we observe that $T_1^* < T_2^* < K_1$. In addition, there exists a migration rate $\epsilon_0 \simeq 0.84$ such that $T_1^*(\epsilon) = 0$ for all $\epsilon \geq 0.84$. Meanwhile, $T_2^*(\epsilon) \rightarrow 0$ as $\epsilon \rightarrow \infty$. This example shows that linear asymmetric dispersal can lead to extinction in both patches for relatively small values of the migration rate. Moreover, this extinction occurs more rapidly than in the case of nonlinear asymmetric dispersal, where extinction only appears for large values of ϵ .

Figure 12. For the parameter values given in the second row of Table 2, $T_1^* < T_2^*$ for $0 \leq \epsilon \leq 0.82$, while $T_1^* > T_2^*$ for $\epsilon \geq 0.82$, with both remaining below K_1 . At $\epsilon \simeq 0.82$, the two equilibria coincide, $T_1^*(0.82) = T_2^*(0.82) \simeq 0.47$. Compared to Figure 11, this case illustrates the persistence of the population in both patches under nonlinear symmetric and asymmetric dispersal.

Figure 13. For the parameter values given in the third row of Table 2, $T_1^* > T_2^*$ for $0 \leq \epsilon \leq 0.03$, whereas $T_1^* < T_2^*$ for $\epsilon \geq 0.03$. At $\epsilon \simeq 0.03$, we have $T_1^*(0.03) = T_2^*(0.03) \simeq 0.52$. Moreover, there exist two migration rates $\epsilon_1 \simeq 0.05$ and $\epsilon_2 \simeq 0.12$ such that $T_1^*(0.05) = T_2^*(0.12) = 0.5$. Finally, extinction occurs for $T_1^*(\epsilon) = 0$ whenever $\epsilon \geq 0.26$.

Figure 14. For the parameter values given in the fourth row of Table 2, $T_1^* > T_2^*$ for $0 \leq \epsilon \leq 0.06$ and $\epsilon \geq 0.77$, while $T_1^* < T_2^*$ for $0.06 \leq \epsilon \leq 0.77$. At $\epsilon \simeq 0.06$, we have $T_1^*(0.06) = T_2^*(0.06) \simeq 0.51$, and at $\epsilon \simeq 0.77$, we obtain $T_1^*(0.77) = T_2^*(0.77) \simeq 0.47$. Furthermore, there exist two migration rates $\epsilon_1 \simeq 0.13$ and $\epsilon_2 \simeq 0.22$ such that $T_1^*(0.13) = T_2^*(0.22) = 0.5$. As $\epsilon \rightarrow \infty$, the equilibria tend to the limits $T_1^* \rightarrow 0.42$ and $T_2^* \rightarrow 0.29$.

Figure 15. For the parameter values given in the fifth row of Table 2, $T_1^* > T_2^*$ for $0 \leq \epsilon \leq 0.08$, while $T_1^* < T_2^*$ for $\epsilon \geq 0.08$. In both cases, the equilibria remain strictly greater than K_1 .

Figure 16. Finally, for the parameter values given in the sixth row of Table 2, we obtain the convergence $T_1^*, T_2^* \rightarrow 0.5 = K_1$.

4.2. Symmetric dispersion. In this part, we consider the case of symmetric migration, i.e., when $\theta_1 = \theta_2 = 1$. We plot the total equilibrium populations $\epsilon \mapsto T_1^*(\epsilon)$ and $\epsilon \mapsto T_2^*(\epsilon)$ as functions of the migration rate ϵ . Several examples are provided to illustrate the three cases described in Corollaries 2.1 and 3.2. Figures 17, 18, and 19 display the curves of the total equilibrium populations T_1^* and T_2^* , together with the line K_1 , for the parameter sets given in Table 3.

TABLE 3. Parameters values of the three case used in Fig. 17, 18 and 19. The derivatives $\frac{dT_1^*}{d\epsilon}(0)$ and $\frac{dT_2^*}{d\epsilon}(0)$ and the perfect mixing abundances $T_1^*(\infty)$ and $T_2^*(\infty)$ are calculated with the expressions given in (B.1), (C.1), (2.12) and (3.16) respectively.

Figure	Case	r_1	r_2	K_1	K_2	$\frac{dT_1^*}{d\epsilon}(0)$	$T_1^*(\infty)$	$\frac{dT_2^*}{d\epsilon}(0)$	$T_2^*(\infty)$
Fig. 17	Case A	0.25	1	0.5	20	-1.5	0	-0.75	0.2
	Case B	0.25	1	1	20	-3	0	-3	0.24
	Case C	0.25	1	2	20	-6	0	-12	0.2
Fig. 18	Case A	0.25	1	0.5	20	3	0.56	1.5	0.57
	Case B	0.25	0.1	1	2	6	1.04	6	1.04
	Case C	0.25	0.1	2	2	12	1.82	24	1.79
Fig. 19	Case A	0.14	0.06	0.5	20	18	1.72	36	1.71
	Case B	0.14	0.06	1	2	9	0.97	9	0.97
	Case C	0.25	0.1	2	2	4.5	0.49	2.25	0.55

Depending on the values of the migration rate ϵ , and as illustrated in Figures 17, 18, and 19, we obtain three representative examples describing the inequalities and equalities between the total equilibrium populations T_1^* , T_2^* , and the value K_1 , represented by the horizontal blue line. Each figure contains three cases corresponding to the three possible regimes of the carrying capacity: $K_1 < 1$, $K_1 = 1$, and $K_1 > 1$. Note that

$$\frac{dT_1^*}{d\epsilon}(0) = \frac{dT_2^*}{d\epsilon}(0) \Leftrightarrow K_1 = 1 \text{ or } r_1 = r_2,$$

which motivates the analysis of these three regimes.

Figure 17 (first three rows of Table 3):

- $K_1 < 1$: $T_1^* < T_2^* < K_1$.
- $K_1 = 1$: $T_1^* < T_2^*$, with $T_1^* \simeq T_2^*$ for small ϵ .
- $K_1 > 1$: there exists $\epsilon_0 \simeq 0.16$ such that $T_1^* > T_2^*$ for $\epsilon < \epsilon_0$, and $T_1^* < T_2^*$ for $\epsilon > \epsilon_0$. Moreover, $T_1^*(0.16) \simeq T_2^*(0.16) \simeq 1$, and T_1^* vanishes for $\epsilon > 0.4$.

Figure 18 (second three rows of Table 3):

- $K_1 < 1$: there exists $\epsilon_0 \simeq 0.2$ such that $T_1^* > T_2^*$ for $\epsilon < 0.2$, and $T_1^* < T_2^*$ for $\epsilon > 0.2$.
- $K_1 = 1$: $T_1^* = T_2^*$ for all $\epsilon > 0$.
- $K_1 > 1$: there exists $\epsilon_0 \simeq 0.04$ such that $T_1^* < T_2^*$ for $\epsilon < 0.2$, and $T_1^* > T_2^*$ for $\epsilon > 0.2$, with $T_1^*(0.2) \simeq T_2^*(0.2) \simeq 2.2$.

Figure 19: shows the same qualitative behaviors as Figure 18, confirming the robustness of these patterns.

Hence, when K_1 crosses the threshold value 1, the relative positions of the curves T_1^* and T_2^* switch, while they coincide exactly for $K_1 = 1$.

When $\theta_1 = \theta_2 = 1$, the total equilibrium populations satisfy

$$T_1^*(\epsilon) = K_1 + \epsilon(x_2^*(\epsilon) - x_1^*(\epsilon)) \left(\frac{1}{\alpha_1 x_1^*(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^*(\epsilon)} \right), \quad (4.2)$$

and

$$T_2^*(\epsilon) = \frac{K_1}{1 - \epsilon(x_2^{**}(\epsilon) - x_1^{**}(\epsilon)) \left(\frac{1}{\alpha_1 x_1^{**}(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(\epsilon)} \right)}. \quad (4.3)$$

Although proving these behaviors analytically is very difficult, numerical simulations strongly suggest that only the above configurations occur under symmetric migration. This motivates the following conjecture.

Conjecture 4.1. *Consider the models (2.1) and (3.1) with $\theta_1 = \theta_2 = 1$. Let T_1^* and T_2^* be the total equilibrium populations of (3.4) and (3.18) respectively. Let Λ_0, Λ_1 and Λ_2 be defined by (2.9). Then T_1^* and T_2^* satisfy the following properties:*

- (i) *If $(r_1, r_2) \in \Lambda_0$:*
 - (a) *If $K_1 < 1$, then $T_1^*(\epsilon) < T_2^*(\epsilon)$ for all $\epsilon > 0$.*
 - (b) *If $K_1 = 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) = T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) < T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.*
 - (c) *If $K_1 > 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) \geq T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) < T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.*
- (ii) *If $(r_1, r_2) \in \Lambda_1$:*
 - (a) *If $K_1 < 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) \leq T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) > T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.*
 - (b) *If $K_1 = 1$, then $T_1^*(\epsilon) = T_2^*(\epsilon)$ for all $\epsilon \geq 0$.*
 - (c) *If $K_1 > 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) \geq T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) < T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.*
- (iii) *If $(r_1, r_2) \in \Lambda_2$:*
 - (a) *If $K_1 < 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) \geq T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) < T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.*
 - (b) *If $K_1 = 1$, then $T_1^*(\epsilon) = T_2^*(\epsilon)$ for all $\epsilon \geq 0$.*

- (c) If $K_1 > 1$, then there exists $\epsilon^* > 0$ such that $T_1^*(\epsilon) \leq T_2^*(\epsilon)$ for all $0 \leq \epsilon \leq \epsilon^*$, and $T_1^*(\epsilon) > T_2^*(\epsilon)$ for all $\epsilon > \epsilon^*$.

Conjecture 4.1 highlights a rich interplay between the diffusion rate ϵ , the carrying capacity K_1 , and the regions $\Lambda_0, \Lambda_1, \Lambda_2$ of the parameter plane (r_1, r_2) . The main phenomenon described is the possible *switch of dominance* between the total equilibrium populations $T_1^*(\epsilon)$ and $T_2^*(\epsilon)$ as ϵ varies.

- The role of the parameter K_1 is critical: the threshold case $K_1 = 1$ yields exact coincidence $T_1^*(\epsilon) = T_2^*(\epsilon)$ for all $\epsilon \geq 0$ in Λ_1 and Λ_2 , and a finite interval of equality in Λ_0 . Thus, $K_1 = 1$ acts as a bifurcation value separating the cases where the inequality between T_1^* and T_2^* is strict.
- For $K_1 \neq 1$, the conjecture predicts the existence of a *critical diffusion rate* $\epsilon^* > 0$ at which the ordering of $T_1^*(\epsilon)$ and $T_2^*(\epsilon)$ reverses. This suggests that diffusion may induce a transition from one system configuration to another, reminiscent of *threshold phenomena* commonly observed in patch-structured population models.
- The partition into $\Lambda_0, \Lambda_1, \Lambda_2$ reflects how the relative growth rates (r_1, r_2) influence the sign and monotonicity properties of the equilibrium comparison. In particular, Λ_0 exhibits a more constrained behaviour where T_1^* eventually falls below T_2^* for sufficiently large ϵ , while Λ_1 and Λ_2 allow for more symmetric switching dynamics.

Therefore, Conjecture 4.1 encapsulates a fundamental structural property of the two-patch models (2.1) and (3.1): the total biomass at equilibrium is not monotone with respect to diffusion, but undergoes parameter-dependent reversals, governed by the key threshold $K_1 = 1$ and by the location of (r_1, r_2) in the regions Λ_i .

5. CONCLUSION

This work aims at find out whether the total equilibrium population of the two patches source-sink connected by nonlinear asymmetric migration can be greater than the carrying capacity of the source isolated patch, i.e. at equilibrium. The system has a unique positive equilibrium, which furthermore is globally asymptotically stable in the interior of the positive cone, and the origin as trivial equilibrium which is unstable, unlike in the symmetric case, which can be globally asymptotically stable (see Prop. 5.5 in [32] and Theorem 2.1).

In Section 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 two patches. We compute the total equilibrium population in that case, 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. Rigorous analysis on the model demonstrate a mechanism by which the nonlinear dispersal asymmetry can lead to either an increased total size of the species in two patches, a decreased total size with persistence in the patches, or even extinction in both patches for large migration rates. In Subsections 3.3 and 3.4, we study the total equilibrium population of the source-sink patch model (3.1) 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 numerical simulations are given which we confirm and extend our results. We also compare our present results with the result of previous work [32] for linear asymmetry dispersal. Finally, comparison of the present results with those of Wu et al. [32] suggests that this nonlinear asymmetric dispersal mechanism has the same impact as in the case of linear asymmetric dispersal. However, comparing the conditions (2.3) and (3.17) shows that this nonlinear asymmetry dispersal can have a strong quantitative influence on the effect of dispersal. In the case symmetric $\theta_1 = \theta_2$, the conditions (2.3) and (3.17) are the same, and becomes (2.9).

Several questions remain open for future investigation. For instance, it would be of particular interest to examine how our results extend to systems with more than two

patches, such as the three-patch source-sink model with nonlinear and asymmetric migration. In this context, fundamental issues remain unresolved, including the characterization of global stability, the qualitative behavior of the system under large migration rates, and the impact of nonlinear asymmetric dispersal on the total population abundance. Extending the present analysis to a general n -patch framework ($n > 2$) appears to be highly nontrivial, both from a biological and a mathematical perspective. Such a generalization represents a significant challenge and a promising direction for future research.

APPENDIX A. EQUILIBRIA AND STABILITY OF (3.1)

In this section, our goal is to prove the global stability of the system (3.1). In the absence of migration, i.e. the case where $\epsilon = 0$, the system (3.1) admits $(K_1, 0)$ as a non trivial equilibrium point, which furthermore is globally asymptotically stable (GAS) in the positive cone $\mathbb{R}_+^2$. The problem is whether the equilibrium continues to be positive and globally stable for any $\epsilon > 0$ or not. We first prove the non negativity of the solutions of System (3.1). We have the following proposition:

Proposition A.1. *The positive cone $\mathbb{R}_+^2$ is positively invariant for the system (3.1).*

Proof. Suppose that, at a given time t , one of the state variables of the system (3.1) is at a boundary of $\mathbb{R}_+^2$, meaning that at least one population is at 0. We suppose first that $x_1 = 0$, and $x_2 \geq 0$, then the dynamics of x_1 is given by $\frac{dx_1}{dt} = \theta_2 x_2^2 \geq 0$, and, if $x_2 = 0$, and $x_1 \geq 0$, then we have $\frac{dx_2}{dt} = \theta_1 x_1^2 \geq 0$. So each trajectory initiated at a boundary of $\mathbb{R}_+^2$ either remains at the boundary or goes to the interior of $\mathbb{R}_+^2$. According to [28, Proposition B.7, page 267], no trajectory comes out of $\mathbb{R}_+^2$. Therefore, $\mathbb{R}_+^2$ is positively invariant for (3.1). $\square$

The equilibrium of the system (3.1) is the solutions of the following algebraic system:

$$\begin{cases} 0 = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(\theta_2 x_2^2 - \theta_1 x_1^2), \\ 0 = -r_2 x_2 \left(1 + \frac{x_2}{K_2}\right) + \epsilon(\theta_1 x_1^2 - \theta_2 x_2^2). \end{cases} \quad (\text{A.1})$$

The sum of the two equations of (A.1) shows that the equilibrium points are in a ellipse noted $\mathbb{E}^1$, whose equation is given by:

$$\mathbb{E}^1 : \quad r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - r_2 x_2 \left(1 + \frac{x_2}{K_2}\right) = 0. \quad (\text{A.2})$$

The ellipse $\mathbb{E}^1$ passes through the points $(0, 0)$, $(K_1, 0)$, $(0, -K_2)$ and $\mathcal{A} := (K_1, -K_2)$. Note that, it is independent of migration rate ϵ and θ_i (shown in red in Fig. 5-(a)).

Solving the first equation of system (A.1) for x_2 yields a hyperbola noted $\mathcal{H}_\epsilon$ defined by

$$\mathcal{H}_\epsilon : \quad h_\epsilon(x_1) := \sqrt{\frac{1}{\theta_2} \left(\theta_1 x_1^2 - \frac{r_1}{\epsilon} x_1 \left(1 - \frac{x_1}{K_1}\right) \right)}.$$

As our study is limited to the positive cone, then we are interested only in the positive branch of $\mathcal{H}_\epsilon$. The hyperbola $\mathcal{H}_\epsilon$ (shown in blue in Fig. 5-(a)) depends on the migration rate ϵ . It always passes through the origin and the point $\mathcal{B} := \left(K_1, \sqrt{\frac{\theta_1}{\theta_2}} K_1\right)$. So, the equilibrium points are the non-negative intersection between the curves $\mathbb{E}^1$ and $\mathcal{H}_\epsilon$. We have $h_\epsilon(x_1) = 0$ implies $x_1 = \frac{r_1/\epsilon}{\theta_1 + r_1/\epsilon} < K_1$. Thus, the hyperbola $\mathcal{H}_\epsilon$ intersect the axis $[Ox_1]$ at 0 and at a second positive point which always smaller than K_1 . Hence, there are two equilibrium points. The first is the trivial point $(0, 0)$ and the second is a non trivial point noted $E^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$ whose position depend on migration rate ϵ (see Fig. 5-(a)).

Remark A.2. The isoclines of the system (3.1) are given by the two equations:

$$\begin{cases} \mathcal{H}_{\epsilon,1}(x_1) = \sqrt{-\frac{r_1}{\epsilon\theta_2}x_1\left(1 - \frac{x_1}{K_1}\right) + \frac{\theta_1}{\theta_2}x_1^2}, \text{ with } x_1^{**}(\epsilon) > \frac{r_1/\epsilon}{\theta_1+r_1/\epsilon}, \\ \mathcal{H}_{\epsilon,2}(x_2) = \sqrt{\frac{r_2}{\epsilon\theta_1}x_2\left(1 + \frac{x_2}{K_2}\right) + \frac{\theta_2}{\theta_1}x_2^2} \text{ with } x_2^{**}(\epsilon) > 0. \end{cases}$$

The equilibrium points are the intersection between these two isoclines: the origin and the positive equilibrium $E_2^*(\epsilon)$ (see Fig. 5-(b)).

In the following, our aim is to show the global stability of the equilibrium $E^*(\epsilon)$. For this, we need some results. Recall that, a matrix $A = (a_{ij})$ is called cooperative if $a_{ij} \geq 0$ for all $i \neq j$. Let us consider the autonomous system:

$$\dot{x} = \Phi(x), \quad (\text{A.3})$$

where $\dot{x}$ denote the derivative of x with respect to time t , $\Phi = (\Phi_1, \dots, \Phi_n)$ is $\mathcal{C}^1$ on a domain $\mathbb{R}_+^n$. System (A.5) is called cooperative if the Jacobian matrix of (A.5) is a cooperative matrix for all $x \in \mathbb{R}_+^n$.

Recall that, for general two-dimensional cooperative differential system, we have the following result, which guarantees that all solutions converge to equilibria/infinity without periodic oscillation (see page 28 Hofbauer and Sigmund [21]). The solutions of a two-dimensional cooperative system converge either to an equilibrium or to infinity.

First, for the non-negativity and boundedness of the solutions of the system (3.1), we have the following result:

Lemma A.3. *For any non-negative initial condition, the solutions of the system (3.1) remain bounded, for all $t \geq 0$. Moreover, the set*

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

where $\xi_1^* = \min\{r_1, r_2\}$ and $\xi_2^* = r_1K_1 + r_2K_2$, is positively invariant and is a global attractor for the system (3.1).

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

$$\dot{X}_T(t) = r_1x_1(t)\left(1 - \frac{x_1(t)}{K_1}\right) - r_2x_2(t)\left(1 + \frac{x_2(t)}{K_2}\right). \quad (\text{A.4})$$

For all r_i and K_i , we have the inequality:

$$r_1x_1\left(1 - \frac{x_1}{K_1}\right) \leq r_1(K_1 - x_1), \quad \text{and} \quad r_2x_2\left(-1 - \frac{x_2}{K_2}\right) \leq -r_2x_2. \quad (\text{A.5})$$

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

$$\dot{X}_T(t) \leq -\xi_1^*X_T(t) + \xi_2^* \quad \text{for all } t \geq 0,$$

which gives

$$X_T(t) \leq \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*}\right)e^{-\xi_1^*t} + \frac{\xi_2^*}{\xi_1^*}, \quad \text{for all } t \geq 0. \quad (\text{A.6})$$

Hence,

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

Therefore, the solutions of System (3.1) are positively bounded and defined for all $t \geq 0$. From (A.6), it can be deduced that the set Σ is positively invariant and it is a global attractor for the system (3.1). $\square$

APPENDIX B. DERIVATIVE OF THE TOTAL EQUILIBRIUM POPULATION T_1^* AT $\epsilon = 0$

Proposition B.1. *The derivative of the total equilibrium population T_1^* at $\epsilon = 0$ is given by:*

$$\frac{dT_1^*}{d\epsilon}(0) = \theta_1 K_1 \left(\frac{1}{r_2} - \frac{1}{r_1} \right). \quad (\text{B.1})$$

In particular, $\frac{dT_1^*}{d\epsilon}(0) = 0$ if and only if, $r_1 = r_2$.

Proof. The equilibrium point $E_1^*(\epsilon)$ of (2.1) satisfies the system

$$\begin{cases} 0 = r_1 x_1^*(\epsilon) \left(1 - \frac{x_1^*(\epsilon)}{K_1} \right) + \epsilon(\theta_2 x_2^*(\epsilon) - \theta_1 x_1^*(\epsilon)), \\ 0 = r_2 x_2^*(\epsilon) \left(-1 - \frac{x_2^*(\epsilon)}{K_2} \right) + \epsilon(\theta_1 x_1^*(\epsilon) - \theta_2 x_2^*(\epsilon)). \end{cases} \quad (\text{B.2})$$

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

$$\begin{cases} x_1^*(\epsilon) = K_1 + \epsilon \frac{\theta_2 x_2^*(\epsilon) - \theta_1 x_1^*(\epsilon)}{\frac{r_1}{K_1} x_1^*(\epsilon)}, \\ x_2^*(\epsilon) = \epsilon \frac{\theta_1 x_1^*(\epsilon) - \theta_2 x_2^*(\epsilon)}{r_2 + \frac{r_2}{K_2} x_2^*(\epsilon)}. \end{cases} \quad (\text{B.3})$$

Hence, the total equilibrium population T_1^* is given by

$$T_1^*(\epsilon) = K_1 + \epsilon(\theta_2 x_2^*(\epsilon) - \theta_1 x_1^*(\epsilon)) \left(\frac{1}{\alpha_1 x_1^*(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^*(\epsilon)} \right), \quad (\text{B.4})$$

where $\alpha_i = r_i/K_i$. By differentiating the equation (B.4) at $\epsilon = 0$, we get:

$$\frac{dT_1^*}{d\epsilon}(0) = (\theta_2 x_2^*(0) - \theta_1 x_1^*(0)) \left(\frac{1}{\alpha_1 x_1^*(0)} - \frac{1}{r_2 + \alpha_2 x_2^*(0)} \right), \quad (\text{B.5})$$

which gives (B.1), since $x_1^*(0) = K_1$ and $x_2^*(0) = 0$. $\square$

Note that, the derivative (B.1) is dependent on the parameters r_1, r_2, θ_1 and K_1 . It is equal to zero if and only if both patches have the same growth rates and positive if and only if, $r_1 < r_2$.

APPENDIX C. DERIVATIVE OF THE TOTAL EQUILIBRIUM POPULATION T_2^* AT $\epsilon = 0$

Proposition C.1. *The derivative of the total equilibrium population T_2^* at $\epsilon = 0$ is given by:*

$$\frac{dT_2^*}{d\epsilon}(0) = \theta_1 K_1^2 \left(\frac{1}{r_2} - \frac{1}{r_1} \right). \quad (\text{C.1})$$

In particular, $\frac{dT_2^*}{d\epsilon}(0) = 0$ if and only if, $r_1 = r_2$.

Proof. The equilibrium point $E_2^*(\epsilon)$ of (3.1) satisfies the system

$$\begin{cases} 0 = r_1 x_1^{**}(\epsilon) \left(1 - \frac{x_1^{**}(\epsilon)}{K_1} \right) + \epsilon(\theta_2 (x_2^{**}(\epsilon))^2 - \theta_1 (x_1^{**}(\epsilon))^2), \\ 0 = r_2 x_2^{**}(\epsilon) \left(-1 - \frac{x_2^{**}(\epsilon)}{K_2} \right) + \epsilon(\theta_1 (x_1^{**}(\epsilon))^2 - \theta_2 (x_2^{**}(\epsilon))^2). \end{cases} \quad (\text{C.2})$$

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

$$\begin{cases} x_1^{**}(\epsilon) = K_1 + \epsilon \frac{\theta_2 (x_2^{**}(\epsilon))^2 - \theta_1 (x_1^{**}(\epsilon))^2}{\frac{r_1}{K_1} x_1^{**}(\epsilon)}, \\ x_2^{**}(\epsilon) = \epsilon \frac{\theta_1 (x_1^{**}(\epsilon))^2 - \theta_2 (x_2^{**}(\epsilon))^2}{r_2 + \frac{r_2}{K_2} x_2^{**}(\epsilon)}. \end{cases} \quad (\text{C.3})$$

Hence, the total equilibrium population T_2^* is given by

$$T_2^*(\epsilon) = K_1 + \epsilon(\sqrt{\theta_2}x_2^{**}(\epsilon) + \sqrt{\theta_1}x_1^{**}(\epsilon))(\sqrt{\theta_2}x_2^{**}(\epsilon) - \sqrt{\theta_1}x_1^{**}(\epsilon)) \left(\frac{1}{\alpha_1 x_1^{**}(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(\epsilon)} \right). \quad (\text{C.4})$$

By differentiating the equation (C.4) at $\epsilon = 0$, we get:

$$\frac{dT_1^*}{d\epsilon}(0) = (\sqrt{\theta_2}x_2^{**}(0) + \sqrt{\theta_1}x_1^{**}(0))(\sqrt{\theta_2}x_2^{**}(0) - \sqrt{\theta_1}x_1^{**}(0)) \left(\frac{1}{\alpha_1 x_1^{**}(0)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(0)} \right), \quad (\text{C.5})$$

which gives (C.1), since $x_1^{**}(0) = K_1$ and $x_2^{**}(0) = 0$. $\square$

Note that, the derivative (C.1) is dependent on the parameters r_1, r_2, θ_1 and K_1 . It is equal to zero if and only if both patches have the same growth rates, and positive, if and only if, $r_1 < r_2$.

REFERENCES

- [1] L. J. S. Allen, *Persistence and extinction in Lotka–Volterra reaction-diffusion equations*, Math. Biosci. **65** (1983), 1–12.
- [2] L. J. S. Allen, *Persistence and extinction in single-species reaction-diffusion models*, Bull. Math. Biol. **45** (1983), 209–227.
- [3] R. Arditi, C. Lobry and T. Sari, *Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation*, Theor. Popul. Biol. **106** (2015), 45–59.
- [4] R. Arditi, C. Lobry and T. Sari, *Asymmetric dispersal in the multi-patch logistic equation*, Theor. Popul. Biol. **120** (2018), 11–15.
- [5] J. Arino, N. Bajeux and S. Kirkland, *Number of Source Patches Required for Population Persistence in a Source-Sink Metapopulation with Explicit Movement*, Bull. Math. Biol. **81** (2019), 1916–1942.
- [6] J. Banasiak, *A Note on the Tikhonov Theorem on an Infinite Interval*, Vietnam J. Math. **49** (2021), 69–86.
- [7] F. Crick, *Diffusion in Embryogenesis*, Nature **225** (1970), 420–422.
- [8] B. Elbetch, T. Benzekri, D. Massart and T. Sari, *The multi-patch logistic equation*, Discrete Contin. Dyn. Syst. Ser. B **26** (2020), 6405–6424.
- [9] B. Elbetch, T. Benzekri, D. Massart and T. Sari, *The multi-patch logistic equation with asymmetric migration*, Rev. Integr. Temas Mat. **40** (2022), 25–57.
- [10] B. Elbetch, *Effect of dispersal in Two-patch environment with Richards growth on population dynamics*, J. Innov. Appl. Math. Comput. Sci. **2** (2022), 41–68.
- [11] B. Elbetch and A. Moussaoui, *Nonlinear diffusion in the multi-patch logistic model*, J. Math. Biol. **87** (2023), Article 1.
- [12] B. Elbetch, *Effect of dispersal in single-species discrete diffusion systems with source-sink patches*, Math. Applicanda **51** (2023), 51–97.
- [13] B. Elbetch, *Effects of rapid population growth on total biomass in multi-patch environment*, Differ. Equ. Appl. **15** (2023), 323–359.
- [14] B. Elbetch, *Generalized logistic equation on Networks*, C. R. Math. **361** (2023), 911–934.
- [15] B. Elbetch, *On the effect of density-dependent dispersal on the global dynamics of population*, Ann. Math. Sci. Appl. **9** (2024), 341–364.
- [16] H. I. Freedman, B. Rai and P. Waltman, *Mathematical Models of Population Interactions with Dispersal II: Differential Survival in a Change of Habitat*, J. Math. Anal. Appl. **115** (1986), 140–154.
- [17] H. Guo, M. Y. Li and Z. Shuai, *Global stability of the endemic equilibrium of multigroup SIR epidemic models*, Can. Appl. Math. Q. **14** (2006), 259–284.
- [18] D. Gao and S. Ruan, *A Multipatch Malaria Model with Logistic Growth Populations*, SIAM J. Appl. Math. **72** (2012), 819–841.

- [19] W. S. C. Gurney and R. M. Nisbet, *The regulation of inhomogeneous populations*, J. Theor. Biol. **52** (1975), 441–457.
- [20] I. Hanski and O. E. Gaggiotti (Eds.), *Ecology, Genetics and Evolution of Metapopulations*, Academic Press, 2004.
- [21] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, 1998.
- [22] R. D. Holt, *Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution*, Theor. Popul. Biol. **28** (1985), 181–208.
- [23] S. A. Levin, *Dispersion and Population Interactions*, Am. Nat. **108**(960) (1974), 2076–228.
- [24] S. A. Levin, *Spatial patterning and the structure of ecological communities*, In: *Some Mathematical Questions in Biology VII*, Lectures on Mathematics in the Life Sciences, Vol. 8, Amer. Math. Soc., Providence, RI, 1976, pp. 1–35.
- [25] S. A. Levin, T. M. Powell and J. W. Steele (Eds.), *Patch Dynamics*, Lecture Notes in Biomathematics, Vol. 96, Springer, Berlin, 1993.
- [26] C. Lobry, T. Sari and S. Touhami, *On Tykhonov's theorem for convergence of solutions of slow and fast systems*, Electron. J. Differ. Equ. **19** (1998), 1–22.
- [27] Z. Lu and Y. Takeuchi, *Global asymptotic behavior in single-species discrete diffusion systems*, J. Math. Biol. **32** (1993), 67–77.
- [28] H. L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge Studies in Mathematical Biology, Vol. 13, Cambridge University Press, Cambridge, 1995.
- [29] A. N. Tikhonov, *Systems of differential equations containing small parameters in the derivatives*, Mat. Sb. (N.S.) **31** (1952), 575–586.
- [30] Y. Takeuchi, *Cooperative systems theory and global stability of diffusion models*, Acta Appl. Math. **14** (1989), 49–57.
- [31] W. R. Wasow, *Asymptotic Expansions for Ordinary Differential Equations*, Robert E. Krieger Publishing Company, Huntington, NY, 1976.
- [32] H. Wu, Y. Wang, Y. Li and D. L. DeAngelis, *Dispersal asymmetry in a two-patch system with source-sink populations*, Theor. Popul. Biol. **131** (2020), 54–65.

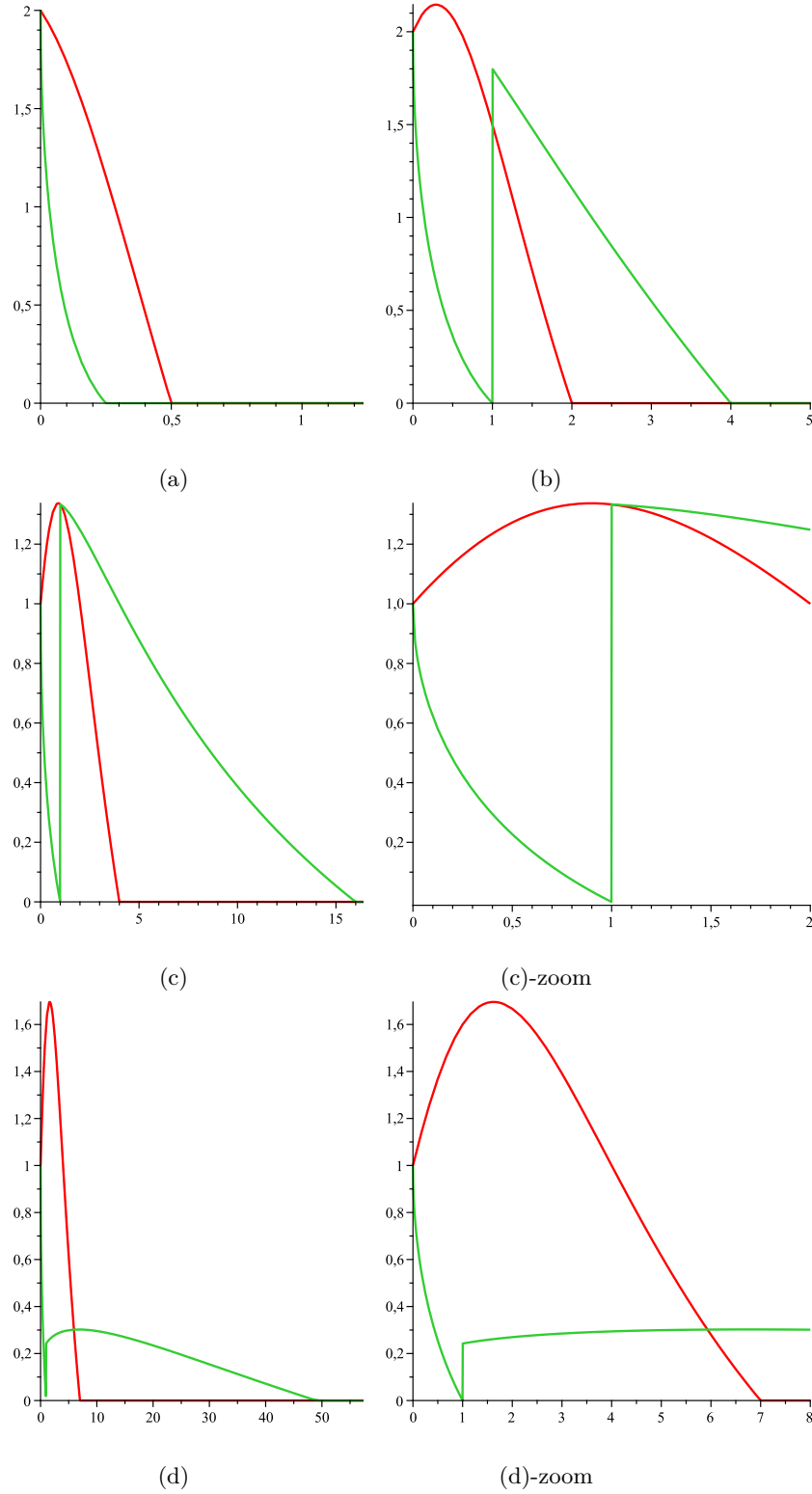


FIGURE 10. The graphs of the functions $s \mapsto \psi_1(s) := T_1^*(+\infty)$ (red) and $s \mapsto \psi_2(s) := T_2^*(+\infty)$ (green) defined by (2.13) and (3.16) respectively as function of s for the parameters given in Table 1. The function ψ_1 is continuous for all s . If $r_2 < r_1$, at symmetric case ($s = 1$), ψ_2 is discontinuous as shown in case (b), (c) and (d).

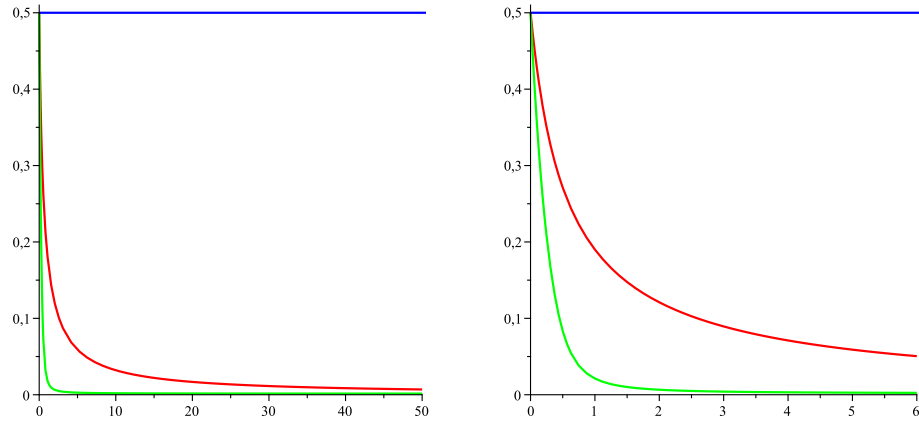


FIGURE 11. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) of the system (2.1) and (3.1) respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with $(\theta_1, \theta_2) \in \Delta_0 \cap \mathcal{L}_0$ where $\Delta_0 \cap \mathcal{L}_0$ is given in (4.1). The horizontal line shown in blue is K_1 .

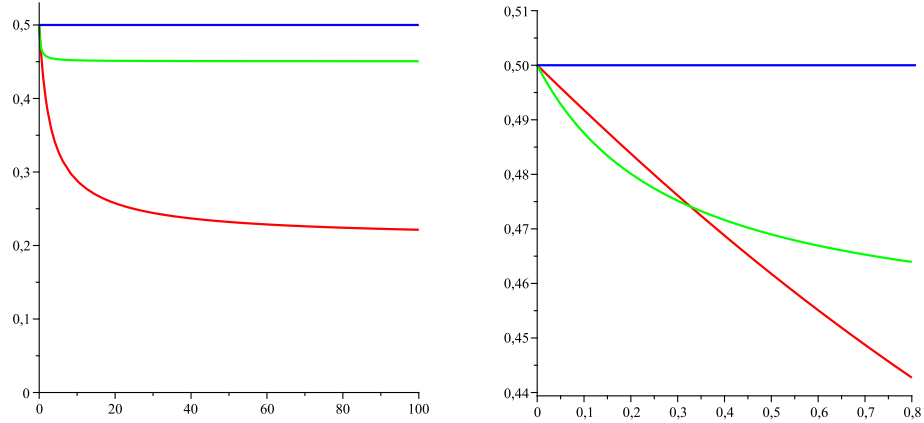


FIGURE 12. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) for linear and nonlinear dispersal respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with $(\theta_1, \theta_2) \in \Delta_1 \cap \mathcal{L}_1$ where $\Delta_1 \cap \mathcal{L}_1$ is given in (4.1). The horizontal line shown in blue is K_1 .

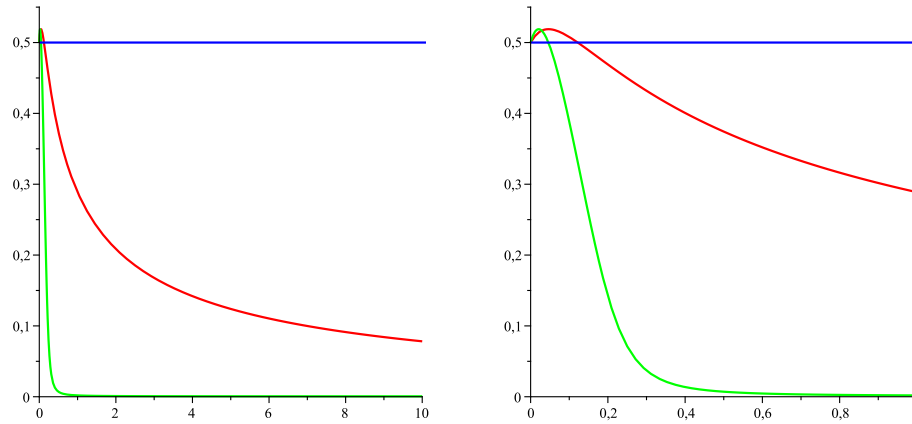


FIGURE 13. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) for linear and nonlinear dispersal respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with $(\theta_1, \theta_2) \in \Delta_2 \cap \mathcal{L}_2$ where $\Delta_2 \cap \mathcal{L}_2$ is given in (4.1). The horizontal line shown in blue is K_1 .

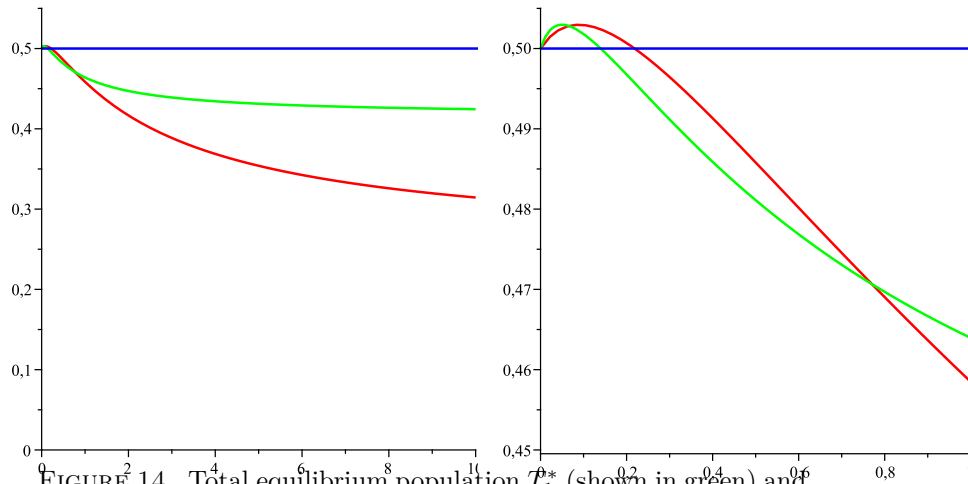


FIGURE 14. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) for linear and nonlinear dispersal respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with $(\theta_1, \theta_2) \in \Delta_3 \cap \mathcal{L}_3$ where $\Delta_3 \cap \mathcal{L}_3$ is given in (4.1). The horizontal line shown in blue is K_1 .

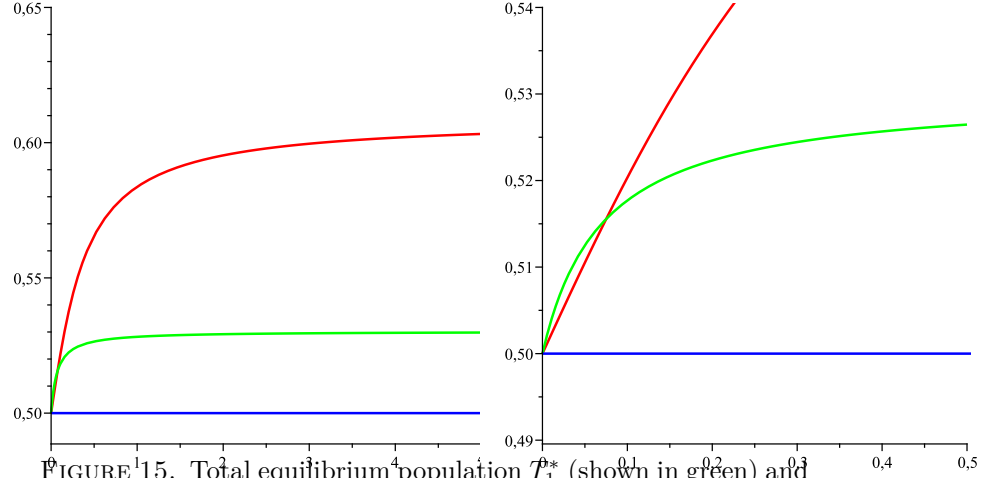


FIGURE 15. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) for linear and nonlinear dispersal respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with $(\theta_1, \theta_2) \in \Delta_4 \cap \mathcal{L}_4$ where $\Delta_4 \cap \mathcal{L}_4$ is

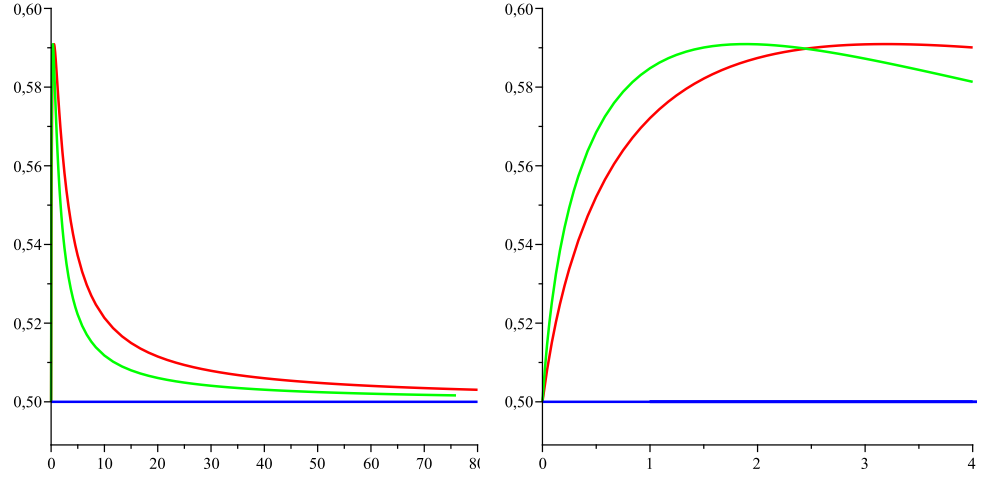


FIGURE 16. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) for linear and nonlinear dispersal respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 1 with the condition $\frac{\theta_2}{\theta_1} = \frac{\alpha_2(K_1+K_2)}{r_1-r_2} = \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2}\right)^2$. The horizontal line shown in blue is K_1 .

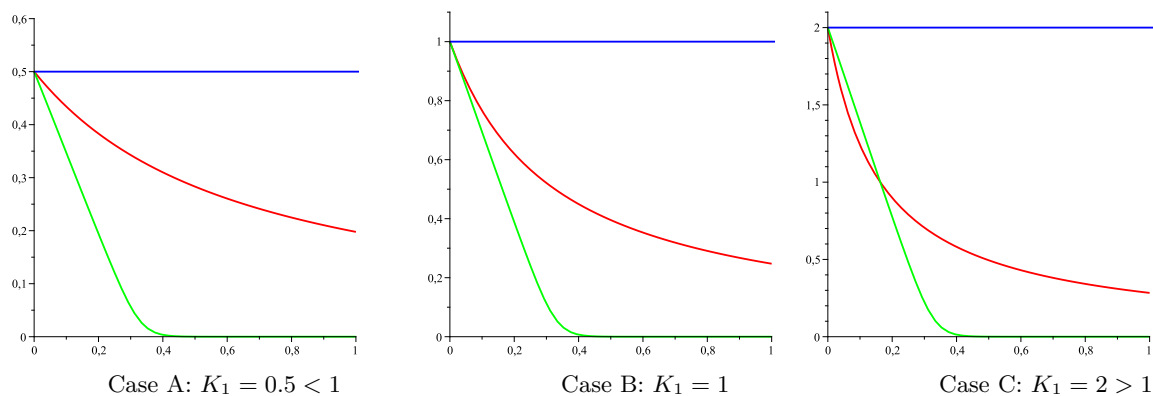


FIGURE 17. Total equilibrium population T_1^* (shown in green) and T_2^* (shown in red) of the system (2.1) and (3.1) respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 3. The horizontal line shown in blue is K_1 .

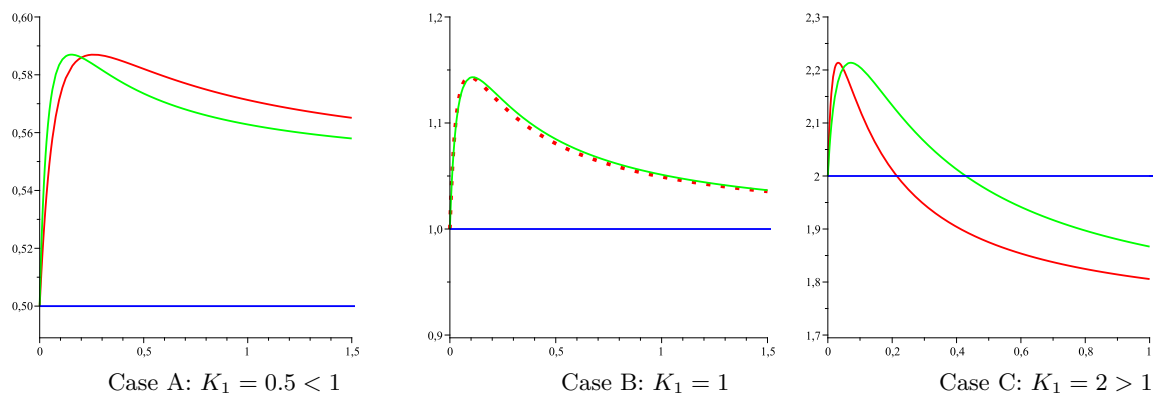


FIGURE 18. Total equilibrium populations T_1^* (shown in green) and T_2^* (shown in red) of the system (2.1) and (3.1) respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 3. The horizontal line shown in blue is K_1 .

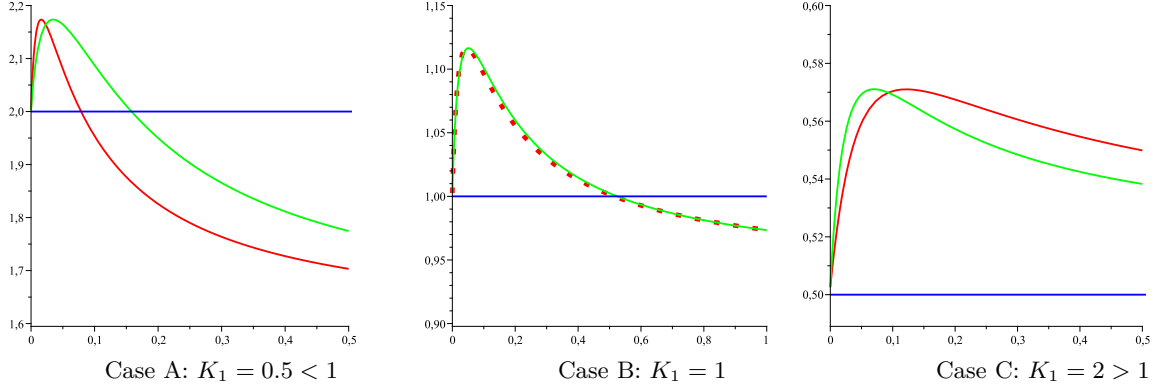


FIGURE 19. Total equilibrium populations T_1^* (shown in green) and T_2^* (shown in red) of the system (2.1) and (3.1) respectively as a function of the migration rate ϵ for the sets of the parameter values given in Table 3. The horizontal line shown in blue is K_1 .