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# How does nonlinear asymmetric dispersal affect the dynamics of a population and the coexistence of species in Two-patch source-sink heterogeneous environment?

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1 ARTICLE TEMPLATE

2 **How does nonlinear asymmetric dispersal affect the dynamics of a**  
3 **population and the coexistence of species in Two-patch source-sink**  
4 **heterogeneous environment?**

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7 **ARTICLE HISTORY**

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9 **ABSTRACT**

10 This paper analyze source-sink system with nonlinear asymmetric dispersal between  
11 two patches, where the populations grows logistically on source patch and decay log-  
12 gistically on sink patch. First, used the theory of a cooperative differential system,  
13 we prove the global stability of the model. Next, used the theory of singular pertur-  
14 bation and theorem of Tikhonov, in the case of perfect mixing,i.e. when the diffusion  
15 rate tends to infinity, we calculate the equilibrium of the model which is different  
16 from the carrying capacity of the source patch and we give a good approximations  
17 of the solutions in this case. Second, complete analysis on the model demonstrate  
18 a mechanism by which the nonlinear asymmetric dispersal can lead to either an in-  
19 creased total size of the species population in two patches, a decreased total size with  
20 persistence in the patches, or even extinction in both patches when the migration  
21 rate goes to infinity. We also compare numerically, for some particular parameters,  
22 the two total equilibrium populations for the both models, with linear and nonlinear  
23 asymmetric dispersion, we show numerically, that these two populations are differ-  
24 ent in general, and can be equal for certain values of migrations. Finally, we study  
25 the effect of the rapid growth of the population in source patch and the rapid death  
26 of the population in sink patch on the dynamics of the total equilibrium population  
27 and on the coexistence of the populations in the both patches.

28 **KEYWORDS**

29 Population Dynamics, Nonlinear diffusion, Migration rate, Source-sink, Logistic  
30 growth, Global stability, Slow-fast systems, Tikhonov's theorem.

31 **Mathematics Subject Classification:** 37N25 92D25 34D23 34D15

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52 **1. Introduction**

53 Population dynamics is a wide field of mathematics, which contains many problems,  
54 for example fragmentation of population and the effect of migration in the general  
55 dynamics of population. Bibliographies can be found in the work of Levin [27, 28] and  
56 Holt [25]. There are ecological situations that motivate the representation of space as  
57 a finite set of patches connected by migrations, for instance an archipelago with bird  
58 population and predators. It is an example of insular bio-geography. A reference work  
59 on mathematical models is the book of Levin et al. [28], whereas Hanski and Gaggiotti  
60 [23] give a more ecological account of the subject. The standard question in this type of  
61 biomathematical problems, is to study the effect of migration on the general population  
62 dynamics, and the consequences of fragmentation on the persistence or extinction of  
63 the population.

64 An ecological model is used to describe population changes in two habitats, both  
65 occupied by the same species. One habitat is of high quality and allows a population  
66 to increase, leading to a surplus. This is the source. The other habitat is of low quality,  
67 leading to a deficit that ordinarily would lead to the habitat being abandoned. This is  
68 the sink. The source-sink model was first proposed by biologist Crick [8]. In population  
69 ecology, the source-sink model is used to describe how variation in habitat quality may  
70 affect the population growth or decline of organisms.

71 In 2019, Wu et al. [34] studied the following two-patch source-sink model:

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

72 where  $x_1$  and  $x_2$  represent population densities of the species in patch 1 and 2, respec-  
73 tively. The parameters  $r_i > 0$  and  $K_i > 0$  are respectively the intrinsic growth rate  
74 and the carrying capacity of patch  $i$ . Parameter  $\epsilon$  represents the dispersal intensity  
75 while the parameter  $s$  reflects the dispersal asymmetry. The authors show that the

76 dispersal asymmetry can lead to either an increased total size of the population in two  
77 patches, a decreased total size with persistence in the patches, or even extinction in  
78 both patches. They show also that for a large growth rate of the species in the source  
79 and a fixed dispersal intensity: (i) If the asymmetry is small, the population would  
80 persist in both patches and reach a density higher than that without dispersal and  
81 the population approaches its maximal density at an appropriate asymmetry, (ii) If  
82 the asymmetry is intermediate, the population persists in both patches but reaches a  
83 density less than that without dispersal, (iii) If the asymmetry is large, the population  
84 goes to extinction in both patches.

85 Arino et al. [6] also studied a source-sink model of  $n$  patches, where the source patch  
86 follows a logistic growth rate, and the sink patch follows exponential decay and they  
87 proved the existence of a threshold number of source patches such that the population  
88 potentially becomes extinct below the threshold and persistent above the threshold.

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

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \Gamma_i(x), \quad i = 1, \dots, n, \quad (2)$$

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

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} (x_j - \theta_{ij} x_i), \quad i = 1, \dots, n, \quad (3)$$

93 where  $\epsilon_{ij}$  and  $\theta_{ij}$  are positive constants. Dispersal by linear diffusion implies that the  
94 species is able to move to all locations within its environment with equal probability.  
95 The mechanism for biased diffusion is given by:

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} x_i (x_j - \theta_{ij} x_i), \quad i = 1, \dots, n, \quad (4)$$

96 where  $\epsilon_{ij}$  and  $\theta_{ij}$  are positive constants. Note that, the term 'biased' means that the  
97 diffusion rate is a function of population density. The diffusion rate is regulated by  
98 population density, increasing for large populations and decreasing for small popula-  
99 tions. The third type of mechanism, is the directed diffusion which is formulated by  
100 Gurney and Nisbet [22], given by:

$$\Gamma_i(x) = \sum_{j=1, j \neq i}^n \epsilon_{ij} (x_j^2 - \theta_{ij} x_i^2), \quad i = 1, \dots, n, \quad (5)$$

101 where  $\epsilon_{ij}$  and  $\theta_{ij}$  are positive constants. Dispersal by directed diffusion implies that the  
102 individuals move from high population concentration to low ones, i.e., the movement  
103 is a function of species density. For more information on the biological interpretation  
104 and also the continuous version of those types of diffusion, we refer the readers to [1]  
105 and [22]. The objective of the work of Allen [2] is to study the effect of different types  
106 of the dispersion on the persistence and extinction of the species. The persistence and  
107 extinction behavior is completely determined in a two-patch model (2)(3) for  $n = 2$  (

108 see Theorem 1 in [2]). For model (2)(4), Allen [2, Theorem 2] showed that a population  
 109 modelled with biased diffusion is always persistent and in fact represents a strongly  
 110 persistent population. For more details on the results of persistence and extinction,  
 111 see Theorem 3 of [2] for  $n$ -patch model (2)(4) and Proposition 1 of [2] for 2-patch case;  
 112 Theorem 4 of [2] for the  $n$ -patch model (2)(5).

113 In [12], Elbetch et al. considered the following two-patch model coupled by nonlinear  
 114 terms of migration:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left( 1 - \frac{x_2}{K_2} \right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2). \end{cases} \quad (6)$$

115 For system (6), the authors given a complete classification of the model parameter  
 116 space as to whether nonlinear dispersal is beneficial or detrimental to the sum of two  
 117 carrying capacities. They studied also the model (6) in the case where one growth rate  
 118 is much larger than the second one. For general information on the effect of asymmetric  
 119 and nonlinear diffusion on the total population abundance for the  $n$ -patch model, the  
 120 reader is referred to [12].

121 Our aim of the present paper, is to study the effect of the nonlinear asymmetric  
 122 migration i.e. when the individuals move from high population concentration between  
 123 patches, on the total population and on the persistence/ extinction for two-patch  
 124 source-sink model ( Model (26)), and we compare our results with those obtained by  
 125 Wu et al. [34] for two-patch source-sink model with linear asymmetric dispersal (Model  
 126 (7)), and also the results of Arditi et al. [4, 5] for two-patch logistic model.

127 This paper is organized as follows: In Section 2, some proprieties of Two-patch  
 128 source-sink model with linear asymmetric dispersal (1) have been recalled as a function  
 129 of the two parameters  $\theta_1$  and  $\theta_2$ , Theorem 2.1 for the global dynamic, Theorem 2.2  
 130 for the effect of linear asymmetric dispersal on the dynamic of the total equilibrium  
 131 population in two patches, Proposition 2.1 give the perfect mixing formula and our first  
 132 result for this model is given in Theorem 2.3, which I studied the model in two time  
 133 scales different used Tykhonov's theorem [7, 29, 32, 33]. In Section 3, we introduce the  
 134 two-patch source-sink model coupled by nonlinear asymmetric terms of migration. In  
 135 Subsection 3.1, we prove their global stability in the interior of the positive cone. Next,  
 136 in Subsection 3.2, we study the behavior of the model in the case when the migration  
 137 rate goes to infinity using singular perturbation arguments and Tykhonov's theorem  
 138 [7, 29, 32, 33] ( see Theorems 3.1 and 3.2 ). In Subsection 3.3, we compare the total  
 139 equilibrium population with the carrying capacity of source patch for all parameter  
 140 space by using the same method as in the works of Arditi et al. [5] and Wu et al. [34]  
 141 ( see Theorem 3.3 and Corollary 3.2 ). In subsections 3.4 and 3.5, Two-patch model  
 142 with the growth (resp. death) rate much larger than the death (resp. growth) rate is  
 143 considered. In both last cases, we compare the total equilibrium population with the  
 144 capacity (see Theorems 3.4 and 3.6). In Section 4, some numerical examples which  
 145 illustrate, confirm and extend our results are given. Section 5 concludes the paper and  
 146 describes the future works suggestion. The rest of the paper contains appendices, which  
 147 in Appendix A, we demonstrate nonnegativeness and boundedness of the solutions, we  
 148 give also the detailed proof of the existence and stability of the equilibrium point of  
 149 (1). In Appendices B and C, we have calculated the derivatives of the total equilibrium  
 150 population of (7),  $T_1^*$ , and also of (26),  $T_2^*$  respectively, with respect of  $\epsilon$ .

151 **2. Some preliminary results for Two-patch source-sink model with linear**  
 152 **dispersion**

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

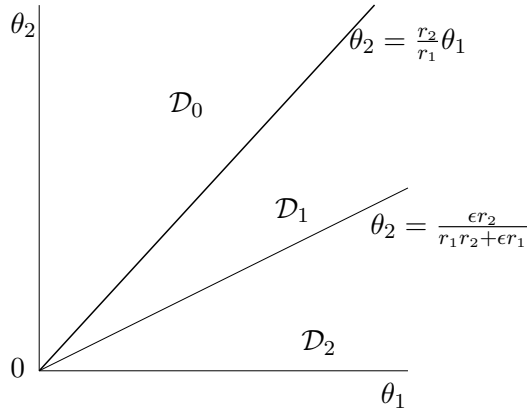
$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2 - \theta_1 x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1 - \theta_2 x_2), \end{cases} \quad (7)$$

154 where  $x_1$  and  $x_2$  represent population densities of the species in patch 1 and 2, re-  
 155 spectively. Patch 1 is assumed to be the source but patch 2 is the sink, i.e.  $r_1, r_2 > 0$ .  
 156 The parameters  $\alpha_i := r_i/K_i$  are the intraspecific competition degree. Parameter  $\epsilon$   
 157 represents the dispersal intensity. We denote  $\theta_2$  the migration rate from source patch  
 158 to the sink patch and  $\theta_1$  from sink patch to source patch, the dispersal is symmetric  
 159 if  $\theta_1 = \theta_2$ . This system is studied in [34]. We recall some essential results of [34] as  
 160 function of the parameters  $\theta_1$  and  $\theta_2$ . Note that, Wu et al. [34] studied the model (1)  
 161 as function of  $s = \theta_1/\theta_2$ . First of all, let's start by recalling the global dynamics of  
 162 System (7).

163 **2.1. Global dynamics**

164 We consider the following regions in the set of parameters  $\theta_1$  and  $\theta_2$ , denoted  $\mathcal{D}_0, \mathcal{D}_1$   
 165 and  $\mathcal{D}_2$  depicted in Figure 1 and defined by:

$$\begin{cases} \mathcal{D}_0 = \left\{ (\theta_1, \theta_2) : \theta_2 \geq \frac{r_2}{r_1} \theta_1 \right\}, \\ \mathcal{D}_1 = \left\{ (\theta_1, \theta_2) : \frac{r_2}{r_1} \theta_1 < \theta_2 < \frac{r_2 \epsilon}{r_1 r_2 + \epsilon r_1} \theta_1 \right\}, \\ \mathcal{D}_2 = \left\{ (\theta_1, \theta_2) : \theta_2 \geq \frac{a_2 \epsilon}{r_1 r_2 + \epsilon r_1} \theta_1 \right\}. \end{cases} \quad (8)$$



**Figure 1.** Global stability of Model (7). 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.

166

167 The global dynamic of System (7) is described as follows.

168 **Theorem 2.1** (Prop. 5.5 in [34]). Consider Model (7). Then, if  $(\theta_1, \theta_2) \in \mathcal{D}_0 \cup \mathcal{D}_1$ ,  
 169 System (7) admits unique equilibrium in  $\mathbb{R}^2 \setminus \{0\}$  denoted  $E_1^*(\epsilon)$ , which is globally  
 170 asymptotically stable (GAS), and if  $(\theta_1, \theta_2) \in \mathcal{D}_2$ , then the origin is GAS.

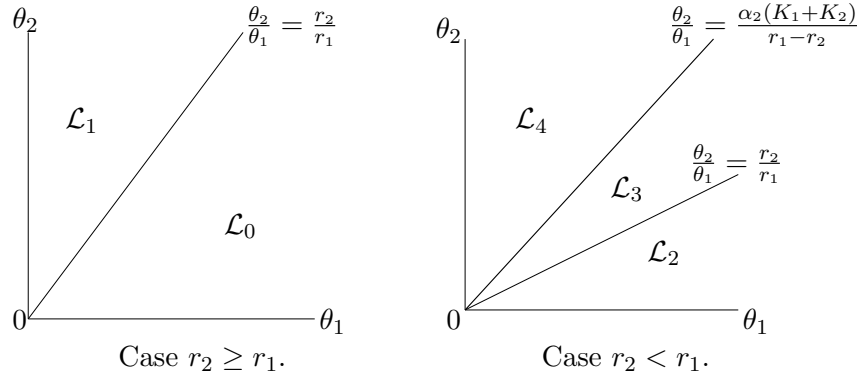
## 171 2.2. Total population abundance

In this section, we recall the comparison given in [34, Proposition 5.11], between the total equilibrium population

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

172 of (7) and carrying capacity  $K_1$ , by analyzing the stable positive equilibrium  $E_1^*(\epsilon)$ .  
 173 Note that, when there is no dispersal (i.e.,  $\epsilon = 0$ ), the total equilibrium population is  
 174  $T_1^*(0) = K_1$ . We consider the regions in the set of the parameters  $\theta_1$  and  $\theta_2$ , denoted  
 175  $\mathcal{L}_0, \mathcal{L}_1, \mathcal{L}_2, \mathcal{L}_3$  and  $\mathcal{L}_4$ , depicted in Figure 2 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \left\{ \begin{array}{l} \mathcal{L}_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \mathcal{L}_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{r_2}{r_1} \right\}. \end{array} \right. \\ \\ \text{If } r_2 < r_1 \text{ then } \left\{ \begin{array}{l} \mathcal{L}_2 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2}{r_1} \right\}, \\ \mathcal{L}_3 = \left\{ (\theta_1, \theta_2) : \frac{r_2}{r_1} < \frac{\theta_2}{\theta_1} < \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right\}, \\ \mathcal{L}_4 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \geq \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right\}. \end{array} \right. \end{array} \right. \quad (9)$$



**Figure 2.** Qualitative properties of source-sink model (7). In  $\mathcal{L}_0$  and  $\mathcal{L}_1$  the effect is detrimental with extinction in two patches for  $\mathcal{L}_0$  and persistence for  $\mathcal{L}_1$ . In  $\mathcal{L}_2$  and  $\mathcal{L}_3$ , the effect is beneficial for  $\epsilon < \epsilon_0$  and detrimental for  $\epsilon > \epsilon_0$  with persistence of the population in the region  $\mathcal{L}_2$  and extinction in the region  $\mathcal{L}_3$ . In  $\mathcal{L}_4$ , patchiness has a beneficial effect on the total equilibrium population.

176

177 **Theorem 2.2.** The total equilibrium population described by (7) satisfies the following  
 178 properties

179 (1) If  $r_2 \geq r_1$ , let  $\mathcal{L}_0$  and  $\mathcal{L}_1$  be defined by (9). Then we have:

180 • 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  $\epsilon^* =$   
 181  $\frac{\theta_2 r_1 r_2}{\theta_1 r_2 - \theta_2 r_1}$ , such that:

$$\begin{cases} 0 < T_1^*(\epsilon) \leq K_1 & \text{If } \epsilon < \epsilon^*, \\ T_1^*(\epsilon) = 0 & \text{If } \epsilon \geq \epsilon^*. \end{cases} \quad (10)$$

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

183 (2) If  $r_2 < r_1$ , let  $\mathcal{L}_2, \mathcal{L}_3$  and  $\mathcal{L}_4$  be defined by (9). Then we have:

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

$$\epsilon_0 = \frac{(r_1 - r_2)(K_1 + K_2)}{(\theta_2(r_1 - r_2) + \theta_1 \alpha_1(K_1 + K_2))(\alpha_1^{-1} + \alpha_2^{-1})}, \quad \text{with } \alpha_i = r_i/K_i. \quad (11)$$

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

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

$$\begin{cases} T_1^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^*, \\ 0 < T_1^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^*. \end{cases} \quad (12)$$

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

189 **Proof.** All the results were established by Wu et al. [34, Proposition 5.11]. Note that,  
 190 the explicit expression (11) of  $\epsilon_0$  was not given in [34].  $\square$

191 In biological terms, the results of the previous theorem for source-sink patch-model  
 192 shows that, the nonlinear asymmetry dispersal can lead to an increased total size of  
 193 the species in two patches, a decreased total size with persistence in the patches, and  
 194 even extinction in both patches. Comparing these results with that of [4, 5] for 1-source  
 195 1-source patch model, we deduce that the existence of a sink patch among the two  
 196 patches, can cause an extinction of the total population in the two patches.

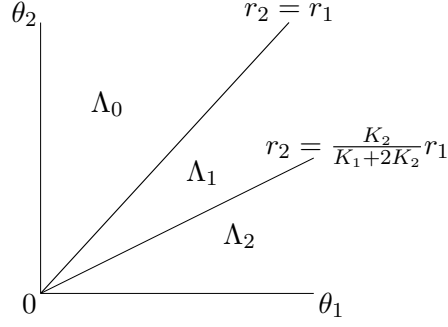
197 Let us explain the result of Theorem 2.2 in the particular case where the dispersion  
 198 is symmetric i.e.  $\frac{\theta_1}{\theta_2} = 1$ . Note that, this case is not initialized by Wu et al. [34]. We  
 199 consider the regions in the set of the parameters  $r_1$  and  $r_2$ , denoted  $\Lambda_0, \Lambda_1$  and  $\Lambda_2$ ,  
 200 depicted in Figure 3 and defined by:

$$\begin{cases} \Lambda_0 = \{(r_1, r_2) : r_2 \geq r_1\}, \\ \Lambda_1 = \{(r_1, r_2) : r_1 < r_2 < \frac{K_2}{K_1 + 2K_2} r_1\}, \\ \Lambda_2 = \{(r_1, r_2) : r_2 \geq \frac{K_2}{K_1 + 2K_2} r_1\}. \end{cases} \quad (13)$$

201 **Corollary 2.1.** Consider the model (7) with  $\theta_1 = \theta_2 = 1$ . Let  $\Lambda_0, \Lambda_1$  and  $\Lambda_2$  be defined  
 202 by (13). The total equilibrium population  $T_1^*$  of (7) satisfies the following properties

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

$$\begin{cases} 0 < T_1^*(\epsilon) \leq K_1 & \text{If } \epsilon < \epsilon^*, \\ T_1^*(\epsilon) = 0 & \text{If } \epsilon \geq \epsilon^*. \end{cases} \quad (14)$$



**Figure 3.** Qualitative properties of source-sink model (7) with  $\theta_1 = \theta_2 = 1$ . In  $\Lambda_0$ , the effect is detrimental with extinction in two patches. In  $\Lambda_1$ , the effect is beneficial for  $\epsilon < \epsilon^{**}$  and detrimental for  $\epsilon > \epsilon^{**}$  with persistence of the population. In  $\Lambda_2$ , patchiness has a beneficial effect on the total equilibrium population.

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

$$\begin{cases} T_1^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^{**}, \\ 0 < T_1^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^{**}. \end{cases} \quad (15)$$

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

207 (3) 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  
208  $T_1^*(\infty) = K_1$  for all  $\epsilon$ .

209 **Proof.** Consequence direct of the theorem 2.2. □

### 210 2.3. Perfect mixing

211 In the case of perfect mixing (i.e when  $\epsilon \rightarrow \infty$ ), we have the following result [34,  
212 Proposition 5.10]:

213 **Proposition 2.1.** *We have:*

$$T_1^*(\infty) := \lim_{\epsilon \rightarrow \infty} T_1^*(\epsilon) = \begin{cases} (\theta_1 + \theta_2) \frac{\theta_2 r_1 - \theta_1 r_2}{\theta_2^2 r_1 / K_1 + \theta_1^2 r_2 / K_2} & \text{if } \theta_1 / \theta_2 < r_1 / r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (16)$$

214 Or, as function of  $s = \frac{\theta_1}{\theta_2}$ , (16) becomes

$$T_1^*(\infty) = \begin{cases} (1 + s) \frac{r_1 - s r_2}{r_1 / K_1 + s^2 r_2 / K_2} & \text{if } s < r_1 / r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (17)$$

215 We can use the theory of singular perturbations and Tikhonov's theorem [7, 29, 32,  
216 33] to obtain a better understanding of the behaviour of the system (7) in the case  
217 of perfect mixing and we find again the formula (16). In the following theorem, we  
218 present our first result in this work.

219 **Theorem 2.3.** *Consider the system (7). Let  $(x_1(t, \epsilon), x_2(t, \epsilon))$  be the solution of the  
220 system (7) with initial condition  $(x_1^0, x_2^0)$  satisfying  $x_i^0 \geq 0$  for  $i = 1, 2$ . Let  $Z(t)$  be the*

221 *solution of the logistic equation*

$$\begin{cases} \frac{dX}{dt} = rX \left( 1 - \frac{X}{(\theta_1 + \theta_2)K} \right), \\ X(0) = x_1^0 + x_2^0, \end{cases} \quad (18)$$

222 *where*  $r = \frac{\theta_2 r_1 - \theta_1 r_2}{2}$  *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*

$$x_1(t, \epsilon) + x_2(t, \epsilon) = Z(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (19)$$

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

$$\begin{cases} x_1(t, \epsilon) = \frac{\theta_2}{\theta_1 + \theta_2} Z(t) + o_\epsilon(1), \\ x_2(t, \epsilon) = \frac{\theta_1}{\theta_1 + \theta_2} Z(t) + o_\epsilon(1) \end{cases} \quad \text{uniformly for } t \in [t_0, +\infty). \quad (20)$$

224 **Proof.** Let  $X(t, \epsilon) = x_1(t, \epsilon) + x_2(t, \epsilon)$ . We rewrite the system (7) using the variables  
225  $(X, x_1)$ . One obtains:

$$\begin{cases} \frac{dX}{dt} = r_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) - r_2 (X - x_1) \left( 1 + \frac{X - x_1}{K_2} \right), \\ \frac{dx_1}{dt} = r_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) + \epsilon (-(\theta_1 + \theta_2)x_1 + \theta_2 X). \end{cases} \quad (21)$$

When  $\epsilon \rightarrow \infty$ , (21) is a *slow-fast* system, with one *slow variable*,  $X$ , and one *fast variable*  $x_1$ . According to Tikhonov's theorem [7, 29, 32, 33] we consider the dynamics of the fast variable in the time scale  $\tau = \epsilon t$ . One obtains

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

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

$$\frac{dx_1}{d\tau} = -(\theta_1 + \theta_2)x_1 + \theta_2 X. \quad (22)$$

227 The *slow manifold* is formed by the equilibrium points of the fast equation (22), which  
228 given by:

$$x_1^* = \frac{\theta_2}{\theta_1 + \theta_2} X. \quad (23)$$

Since  $x_1^*$  is locally asymptotically stable (LAS) for the system (22), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (21) 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:

$$\frac{dX}{dt} = r_1 \frac{\theta_2}{\theta_1 + \theta_2} X \left( 1 - \frac{\theta_2}{\theta_1 + \theta_2} \frac{X}{K_1} \right) - r_2 \frac{\theta_1}{\theta_1 + \theta_2} X \left( 1 + \frac{\theta_1}{\theta_1 + \theta_2} \frac{X}{K_2} \right), \quad (24)$$

229 which gives the equation (18). If  $\theta_2 r_1 > \theta_1 r_2$ , (18) admits  $X^* = (\theta_1 + \theta_2)K$  as a  
 230 positive equilibrium point, which is LAS in the positive axis, and if  $\theta_2 r_1 \leq \theta_1 r_2$ , (18)  
 231 admits the origin as unique equilibrium point, which is LAS. The approximation given  
 232 by Tikhonov's theorem holds for all  $t \geq 0$  for the slow variable and for all  $t \geq t_0 > 0$   
 233 for the fast variable, where  $t_0$  is small as we want. Therefore, let  $Z(t)$  be the solution  
 234 of the reduced model (24) of initial condition  $Z(0) = X(0, \epsilon) = x_1^0 + x_2^0$ , then, when  
 235  $\epsilon \rightarrow \infty$ , we have the approximations (19) and (20).  $\square$

236 Wu et al. [34] proved that large dispersal intensity (i.e.,  $\epsilon \rightarrow \infty$ ), the intermediate  
 237 asymmetry  $\theta_1/\theta_2$  can lead to population density higher than that without dispersal,  
 238 and extremely small asymmetry is still favorable, while extremely large asymmetry  
 239 is unfavorable: (i) When the dispersal asymmetry is small, the species can approach  
 240 a density larger than that without dispersal, while it reaches its maximum value at  
 241 an intermediate asymmetry  $\frac{\theta_1}{\theta_2} = \frac{r_1 - r_2}{2\alpha_2(K_1 + K_2)}$ . (ii) When  $\theta_1/\theta_2$  is extremely large, the  
 242 species goes to extinction in both patches. Mathematically speaking, we can rewrite  
 243 the following result [34, Proposition 5.10]:

244 **Proposition 2.2.** [34, Proposition 5.10] Assume that  $\frac{\theta_1}{\theta_2} < \frac{r_1}{r_2}$ . Consider the total  
 245 equilibrium population for  $\epsilon \rightarrow \infty$  given by (16). We have:

$$T_1^*(+\infty) \begin{cases} > K_1 & \text{if } \frac{\theta_1}{\theta_2} < \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}, \\ = K_1 & \text{if } \frac{\theta_1}{\theta_2} = \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}, \\ < K_1 & \text{if } \frac{\theta_1}{\theta_2} > \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}. \end{cases} \quad (25)$$

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

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

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

### 247 3. Two-patch source-sink model with nonlinear dispersion

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

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left( -1 - \frac{x_2}{K_2} \right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (26)$$

251 where  $x_1$  and  $x_2$  represent population densities of the species in patch 1 and 2, re-  
 252 spectively. Patch 1 is assumed to be the source but patch 2 is the sink, i.e.  $r_1, r_2 > 0$ .  
 253 The parameters  $\alpha_i := r_i/K_i > 0$  are the intraspecific competition degree. Parameter  $\epsilon$   
 254 represents the dispersal intensity. We denote  $\theta_1$  the migration rate from source patch  
 255 1 to the sink patch 2 and  $\theta_2$  from sink patch 2 to source patch 1, the dispersal is  
 256 symmetric if  $\theta_1 = \theta_2$ .

$$\boxed{\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right)} \begin{array}{c} \xleftarrow{\epsilon \theta_2 x_2^2} \\ \xrightarrow{\epsilon \theta_1 x_1^2} \end{array} \boxed{\frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right)}$$

**Figure 4.** A Two-patch source-sink coupled system

### 257 3.1. Global stability

258 According to Appendix A, model (26) has always a unique positive equilibrium, again  
 259 denoted by  $E_2^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$  which given by the positive intersection between  
 260 the ellipse  $\mathbb{E}^1$  and the hyperbola  $\mathcal{H}_\epsilon$  ( see Fig. 5), i.e satisfies to

$$\begin{cases} r_1 x_1^{**}(\epsilon) \left(1 - \frac{x_1^{**}(\epsilon)}{K_1}\right) - r_2 x_2^{**}(\epsilon) \left(1 + \frac{x_2^{**}(\epsilon)}{K_2}\right) = 0, \\ x_2^{**}(\epsilon) = \sqrt{\frac{1}{\theta_2} \left(\theta_1 (x_1^{**})^2(\epsilon) - \frac{r_1}{\epsilon} x_1^{**}(\epsilon) \left(1 - \frac{x_1^{**}(\epsilon)}{K_1}\right)\right)} \end{cases} \quad (27)$$

261 Note that, the origin is always unstable. The equilibrium  $E_2^*$  is GAS in  $\mathbb{R}^2 \setminus \{0\}$  (see  
 262 Appendix A). Comparing these stability results with those of Wu et al. [34] for the  
 263 system (1), we conclude that the origin cannot be globally asymptotically stable as  
 264 in the case of linear diffusion. Biologically speaking, dispersal with high concentration  
 265 between patches ensures persistence in the two patches.

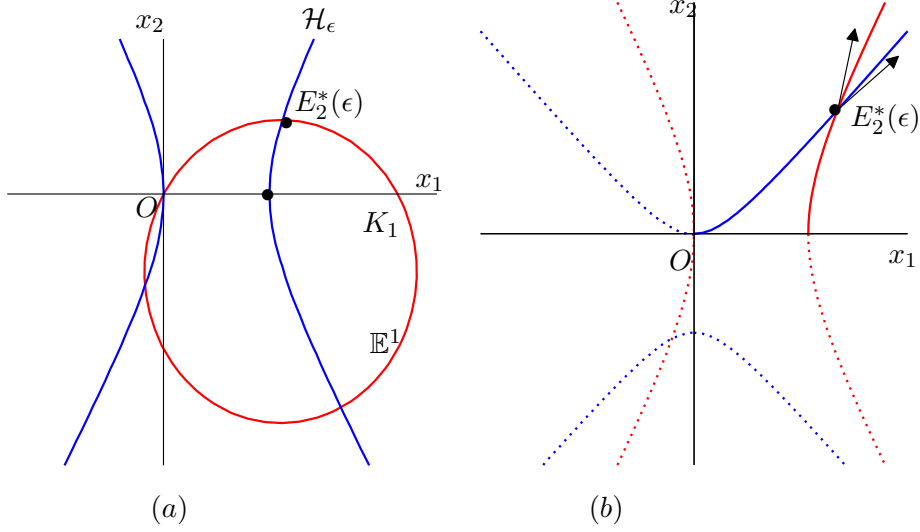
266 We thus define the total equilibrium population at the positive equilibrium under  
 267 dispersal rate , i.e.

$$T_2^*(\epsilon) = x_1^{**}(\epsilon) + x_2^{**}(\epsilon), \quad (28)$$

268 as the total realized asymptotic population abundance.

269 Our aim in this work is to study Two-patch source-sink model coupled by nonlinear  
 270 asymmetric migration terms ( same type of dispersion (5)) given by (26). In particular,  
 271 we are interested in studying the effect of nonlinear dispersion on the dynamics of  
 272 population and coexistence of species, more precisely, is it possible, depending on  
 273 the migration rate, that the total equilibrium population be larger than the carrying  
 274 capacity  $K_1$ ? Note that, this last question has been studied by many researches, see  
 275 [4, 5, 9, 10, 12, 14] for effect of linear diffusion on the total biomass with logistic growth,  
 276 [12] for nonlinear diffusion, [6, 13, 34] for Source-Sink patch model and [19, 20] for  
 277 susceptible-infected-susceptible (SIS) patch-model).

278 In the next section, we looked the system (26) when the migration rate goes to  
 279 infinity, in other words, when there is no restriction whatsoever on travel.



**Figure 5.** (a) The ellipse  $\mathbb{E}^1$  and  $\mathcal{H}_\epsilon$  for some parameters of the model. The equilibrium points are the intersection in the positive cone between  $\mathbb{E}^1$  and  $\mathcal{H}_\epsilon$ , this intersections contains the origin and a second positive point  $E_2^*(\epsilon)$ . (b) Possible configurations for the isoclines of the system (26) (in red for  $x_1$  and in blue for  $x_2$ ) for certain parameters. The equilibrium points are the intersection between these two isoclines: the origin and the positive equilibrium  $E_2^*(\epsilon)$ .

### 280 3.2. Fast dispersal

281 Let we denote by  $s := \frac{\theta_1}{\theta_2}$ , the dispersal asymmetry. In this case, we can rewritten the  
 282 model (26) as follow:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (x_2^2 - s x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (s x_1^2 - x_2^2). \end{cases} \quad (29)$$

283 Let  $X(t, \epsilon) = x_1(t, \epsilon) + x_2(t, \epsilon)$ . We rewrite the system (29) using the variables  $(X, x_1)$ .  
 284 One obtains:

$$\begin{cases} \frac{dX}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - r_2 (X - x_1) \left(1 + \frac{X - x_1}{K_2}\right), \\ \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon ((1 - s)x_1^2 - 2Xx_1 + X^2). \end{cases} \quad (30)$$

When  $\epsilon \rightarrow \infty$ , (30) is a *slow-fast* system, with one *slow variable*,  $X$ , and one *fast variable*  $x_1$ . According to Tikhonov's theorem [7, 29, 32, 33] we consider the dynamics of the fast variable in the time scale  $\tau = \epsilon t$ . One obtains

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

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

$$\frac{dx_1}{d\tau} = (1-s)x_1^2 - 2Xx_1 + X^2. \quad (31)$$

We propose to study the behavior of the model (29) distinguishing three following cases:

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

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

287 **Theorem 3.1.** Consider the system (29) with  $s = 1$ . Let  $(x_1(t, \epsilon), x_2(t, \epsilon))$  be the  
 288 solution of the system (29) with initial condition  $(x_1^0, x_2^0)$  satisfying  $x_i^0 \geq 0$  for  $i = 1, 2$ .  
 289 Let  $Z(t)$  be the solution of the logistic equation

$$\begin{cases} \frac{dX}{dt} = rX \left(1 - \frac{X}{2K}\right), \\ X(0) = x_1^0 + x_2^0, \end{cases} \quad (32)$$

290 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

$$x_1(t, \epsilon) + x_2(t, \epsilon) = Z(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (33)$$

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

$$\begin{cases} x_1(t, \epsilon) = \frac{1}{2}Z(t) + o_\epsilon(1), \\ x_2(t, \epsilon) = \frac{1}{2}Z(t) + o_\epsilon(1) \end{cases} \quad \text{uniformly for } t \in [t_0, +\infty). \quad (34)$$

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

$$x_{1,1}^{**} = 0 \quad \text{and} \quad x_{1,2}^{**} = \frac{1}{2}X. \quad (35)$$

Since  $x_{1,2}^{**} = \frac{1}{2}X$  is LAS for the system (31), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (30) are approximated by the solutions of the *reduced model* which is obtained by replacing  $x_{1,2}^{**} = \frac{1}{2}X$  into the dynamics of the slow variable, that is:

$$\frac{dX}{dt} = r_1 \frac{1}{2}X \left(1 - \frac{X}{2K_1}\right) - r_2 \frac{1}{2}X \left(1 + \frac{X}{2K_2}\right), \quad (36)$$

294 which gives the equation (32). If  $r_1 > r_2$ , (32) admits  $X^* = 2K$  as a positive equilib-  
 295 rium point, which is LAS in the positive axis, and if  $r_1 \leq r_2$ , (32) admits the origin  
 296 as unique equilibrium point, which is LAS. The approximation given by Tikhonov's  
 297 theorem holds for all  $t \geq 0$  for the slow variable and for all  $t \geq t_0 > 0$  for the fast vari-  
 298 able, where  $t_0$  is small as we want. Therefore, let  $Z(t)$  be the solution of the reduced

299 model (36) of initial condition  $Z(0) = X(0, \epsilon) = x_1^0 + x_2^0$ , then, when  $\epsilon \rightarrow \infty$ , we have  
 300 the approximations (33) and (34).  $\square$

301 Note that, in the case of perfect mixing, Approximation (33) shows that: if  $r_1 > r_2$   
 302 then the total population behaves like the unique logistic equation (32) and then, when  
 303  $t$  and  $\epsilon$  tend to  $\infty$ , the total population  $x_1(t, \epsilon) + x_2(t, \epsilon)$  tends toward  $2 \frac{r_1 - r_2}{\alpha_1 + \alpha_2}$  where  
 304  $\alpha_i = r_i / K_i$ . If  $r_1 \leq r_2$ , then Equation (32) has the origin as unique equilibrium, and  
 305 then, when  $t$  and  $\epsilon$  tend to  $\infty$ , the total population  $x_1(t, \epsilon) + x_2(t, \epsilon)$  tends toward 0.

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

307 **Theorem 3.2.** Consider the system (29). Assume that  $s \neq 1$ . Let  $(x_1(t, \epsilon), x_2(t, \epsilon))$   
 308 be the solution of the system (29) with initial condition  $(x_1^0, x_2^0)$  satisfying  $x_i^0 \geq 0$  for  
 309  $i = 1, 2$ . Let  $U(t)$  be the solution of the following equation

$$\frac{dX}{dt} = \begin{cases} RX \left( 1 - \frac{X}{(1 - \sqrt{s})K} \right) & \text{if } 0 < s < 1, \\ RX \left( 1 - \frac{X}{(1 + \sqrt{s})K} \right) & \text{if } s > 1, \end{cases} \quad (37)$$

310 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  
 311  $\epsilon \rightarrow \infty$ , we have

$$x_1(t, \epsilon) + x_2(t, \epsilon) = U(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (38)$$

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

$$(x_1(t, \epsilon), x_2(t, \epsilon)) = \begin{cases} \left( \frac{1}{1 + \sqrt{s}}U(t) + o_\epsilon(1), \frac{\sqrt{s}}{1 + \sqrt{s}}U(t) + o_\epsilon(1) \right) & \text{if } 0 < s < 1 \\ \left( \frac{1}{1 - \sqrt{s}}U(t) + o_\epsilon(1), \frac{\sqrt{s}}{1 - \sqrt{s}}U(t) + o_\epsilon(1) \right) & \text{if } s > 1, \end{cases} \quad (39)$$

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

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

$$x_{1,1}^{**} = \frac{\sqrt{s} - 1}{s - 1}X \quad \text{and} \quad x_{1,2}^{**} = -\frac{1 + \sqrt{s}}{s - 1}X. \quad (40)$$

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  $x_1 < x_{1,2}^{**}$  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 (31), the theorem of Tikhonov ensures that after a fast transition  
 toward the slow manifold, the solutions of (30) 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:

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

316 which gives the equation (37).

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 (31), the theorem of Tikhonov ensures that after a fast transition toward the slow manifold, the solutions of (30) 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:

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

317 which gives the equation (37). If  $r_1 > \sqrt{s}r_2$  (37) admits  $X^* = (1 + \sqrt{s})K$  if  $s > 1$   
318 and  $X^* = (1 - \sqrt{s})K$  if  $s < 1$  as a positive equilibrium point, which is LAS in the  
319 positive axis, and if  $r_1 \leq \sqrt{s}r_2$ , (37) admits the origin as unique equilibrium point,  
320 which is LAS. The approximation given by Tikhonov's theorem holds for all  $t \geq 0$  for  
321 the slow variable and for all  $t \geq t_0 > 0$  for the fast variable, where  $t_0$  is small as we  
322 want. Therefore, let  $U(t)$  be the solution of the reduced model (36) of initial condition  
323  $U(0) = X(0, \epsilon) = x_1^0 + x_2^0$ , then, when  $\epsilon \rightarrow \infty$ , we have the approximations (38) and  
324 (39).  $\square$

325 Note that, in the case of perfect mixing, Approximation (38) shows that: if  $r_1 > \sqrt{s}r_2$   
326 then the total population behaves like the unique equation (37) and then, when  $t$  and  
327  $\epsilon$  tend to  $\infty$ , 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  
328 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  
329 (37) has the origin as unique equilibrium, and then, when  $t$  and  $\epsilon$  tend to  $\infty$ , the total  
330 population  $T_2^*(t, \epsilon) = x_1(t, \epsilon) + x_2(t, \epsilon)$  tends toward 0.

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

333 **Corollary 3.1.** *We have:*

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } T_2^*(+\infty) = \begin{cases} (1 - \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 0 < s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \\ \text{If } r_2 < r_1 \text{ then } T_2^*(+\infty) = \begin{cases} (1 - \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 0 < s < 1, \\ (1 + \sqrt{s}) \frac{r_1 - \sqrt{s}r_2}{\frac{r_1}{K_1} + s\frac{r_2}{K_2}} & \text{if } 1 \leq s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \end{array} \right. \quad (41)$$

334 **3.3. Effect of nonlinear dispersal on total population**

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

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

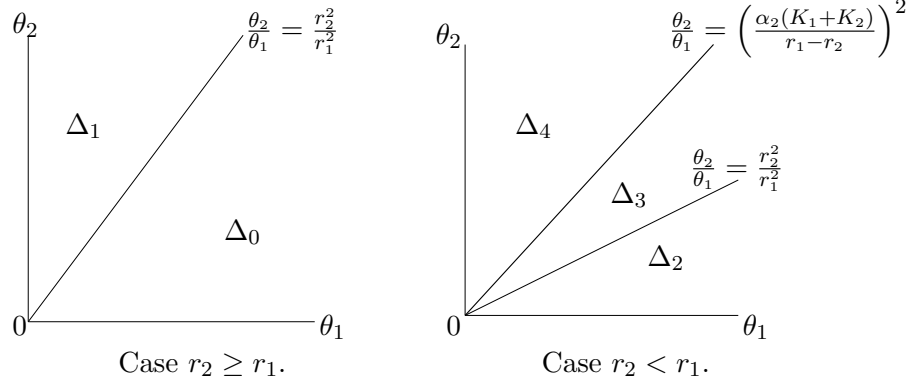
335 of (26) and carrying capacity  $K_1$ , by analyzing the stable positive equilibrium  $E_2^*(\epsilon)$ .  
 336 Note that, when there is no dispersal (i.e.,  $\epsilon = 0$ ), the total equilibrium population  
 337 is  $T_2^*(0) = K_1$ . We study the effect of nonlinear asymmetric dispersal on the total  
 338 equilibrium population for the two-patch source-sink system (26). Using the method  
 339 graphic of Arditi et al. [5] and of Wu et al. [34], we describe the position affects the  
 340 equilibrium  $E_2^*(\epsilon)$  when the migration rate varies from zero to infinity, we will give  
 341 the condition whether  $T_2^*$  is greater or smaller than the carrying capacity  $T_2^*(0) = K_1$ .  
 342 We prove there are only five cases as in the two-patch source-sink model with linear  
 343 diffusion can occur. We consider the regions in the set of the parameters  $\theta_1$  and  $\theta_2$ ,  
 344 denoted  $\Delta_0, \Delta_1, \Delta_2, \Delta_3$  and  $\Delta_4$ , depicted in Figure 6 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \begin{cases} \Delta_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2^2}{r_1^2} \right\}, \\ \Delta_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{r_2^2}{r_1^2} \right\}. \end{cases} \\ \text{If } r_2 < r_1 \text{ then } \begin{cases} \Delta_2 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \leq \frac{r_2^2}{r_1^2} \right\}, \\ \Delta_3 = \left\{ (\theta_1, \theta_2) : \frac{r_2^2}{r_1^2} < \frac{\theta_2}{\theta_1} < \left( \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2 \right\}, \\ \Delta_4 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} \geq \left( \frac{\alpha_2(K_1+K_2)}{r_1-r_2} \right)^2 \right\}. \end{cases} \end{array} \right. \quad (42)$$

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

348 **Theorem 3.3.** *The total equilibrium population  $T_2^*$  of (26) satisfies the following*  
 349 *properties*

350 (1) *If  $r_2 \geq r_1$ , let  $\Delta_0$  and  $\Delta_1$  be defined by (42). Then we have:*



**Figure 6.** Qualitative properties of source-sink model (26). In  $\Delta_0$  and  $\Delta_1$ , the effect is detrimental, with extinction in two patches for  $\Delta_0$ , and persistence for  $\Delta_1$ . In  $\Delta_2$  and  $\Delta_3$ , the effect is beneficial for  $\epsilon < \epsilon_0$  and detrimental for  $\epsilon > \epsilon_0$  with persistence of the population in the region  $\Delta_3$ , and extinction in the region  $\Delta_2$ . In  $\Delta_4$ , patchiness has a beneficial effect on the total equilibrium population.

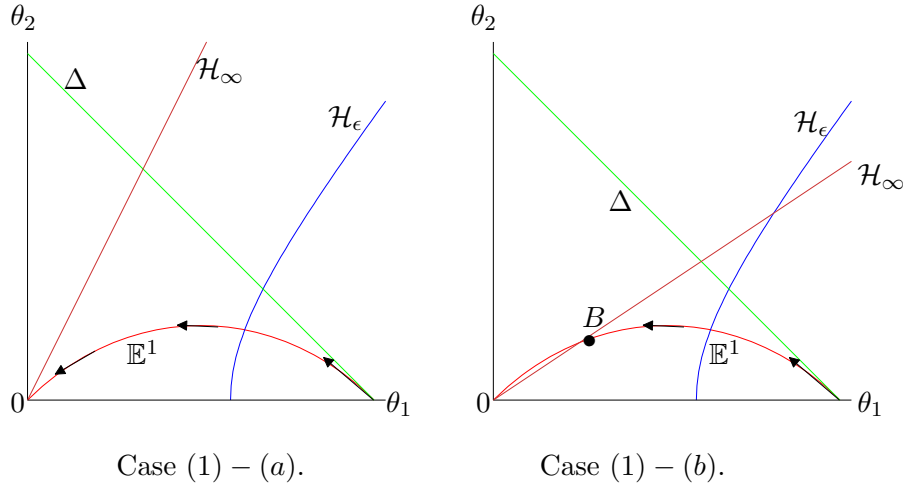
- 351 (a) if  $(\theta_1, \theta_2) \in \Delta_0$  then  $T_2^*(\epsilon) \leq K_1$  for all  $\epsilon \geq 0$ . Moreover,  $T_2^*(\epsilon) \rightarrow 0$  when  
352  $\epsilon \rightarrow +\infty$ .
- 353 (b) if  $(\theta_1, \theta_2) \in \Delta_1$  then  $0 < T_2^*(\epsilon) \leq K_1$  for all  $\epsilon \geq 0$ . Moreover,  $T_2^*(\epsilon) \rightarrow$   
354  $T_2^*(\infty) > 0$  when  $\epsilon \rightarrow +\infty$ .
- 355 (2) If  $r_2 < r_1$ , let  $\Delta_2, \Delta_3$  and  $\Delta_4$  be defined by (42). Then we have:
- 356 (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  
357  $T_2^*(\epsilon) < K_1$  for all  $\epsilon > \epsilon_0$ . Moreover,  $T_2^*(\epsilon) \rightarrow 0$  when  $\epsilon \rightarrow +\infty$ .
- 358 (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  
359  $T_2^*(\epsilon) < K_1$  for all  $\epsilon > \epsilon^\sharp$ . Moreover,  $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$  when  $\epsilon \rightarrow +\infty$ .
- 360 (c) if  $(\theta_1, \theta_2) \in \Delta_4$ , then  $T_2^*(\epsilon) \geq K_1$  for all  $\epsilon \geq 0$ . Moreover, if  $\frac{\theta_2}{\theta_1} =$   
361  $\left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2}\right)^2$ , then  $T_2^* \rightarrow T_2^*(\infty) = K_1$ .

362 **Proof.** Recall that, the equilibrium points of (26) are the non-negative intersec-  
363 tion between the ellipse  $\mathbb{E}^1$  and hyperbola  $\mathcal{H}_\epsilon$ . There are two equilibrium points.  
364 The first is the trivial point  $(0,0)$  and the second is a non trivial point noted  
365  $E^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$  whose position depend on migration rate  $\epsilon$  ( see Fig. 5-(a)).  
366 As our study is limited in the positive cone, then we are interested only in the positive  
367 branch of  $\mathcal{H}_\epsilon$ . The hyperbola  $\mathcal{H}_\epsilon$  ( shown in blue in Fig. 5-(a)) depend on the mi-  
368 gration rate  $\epsilon$ . It always passes through the origin and the point  $\mathcal{B} := \left(K_1, \sqrt{\frac{\theta_1}{\theta_2}} K_1\right)$ .  
369 Notice that, the hyperbola  $\mathcal{H}_\epsilon$  intersect the axis  $(Ox_1)$  at 0 and a second positive point  
370  $x_1 = \frac{r_1/\epsilon}{\theta_1 + \alpha_1/\epsilon}$  which always smaller than  $K_1$ .

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,

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

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



**Figure 7.** This illustrates the cases (1)-a and (1)-b in Theorem 3.3. Case (a) illustrate an example with  $(\theta_1, \theta_2) \in \Delta_0$  and the case (b) illustrate an example with  $(\theta_1, \theta_2) \in \Delta_1$ . The ellipse  $\mathbb{E}^1$  and the hyperbola  $\mathcal{H}_\epsilon$  are shown in red and blue respectively for some parameters of the model (26), the straight lines  $\Delta$  and  $\mathcal{H}_\infty$  are shown in green and orange respectively. As the migration intensity  $\epsilon$  increases from 0 to  $\infty$ , 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  $\epsilon \geq 0$ .

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

381 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  
 382  $\mathbb{E}^1$  is below the line  $\Delta$  in the first quadrant and  $T_2^*(\epsilon) < T_2^*(\infty)$ , as shown in Fig. 7. If  
 383 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  
 384 below the line  $\Delta$  in the first quadrant. Thus, there is  $\epsilon^*$ , such that, when  $0 < \epsilon \leq \epsilon^*$ ,  
 385 the equilibrium  $E_2^*(\epsilon)$  changes from point  $A$  to  $O$ . When  $\epsilon \geq \epsilon^*$ , we have  $E_2^*(\epsilon) \rightarrow O$   
 386 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  
 387  $\mathcal{H}_\infty$  has an intersection  $B$ . Then we have  $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$ , as shown in Fig. 7-(b).  
 388

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

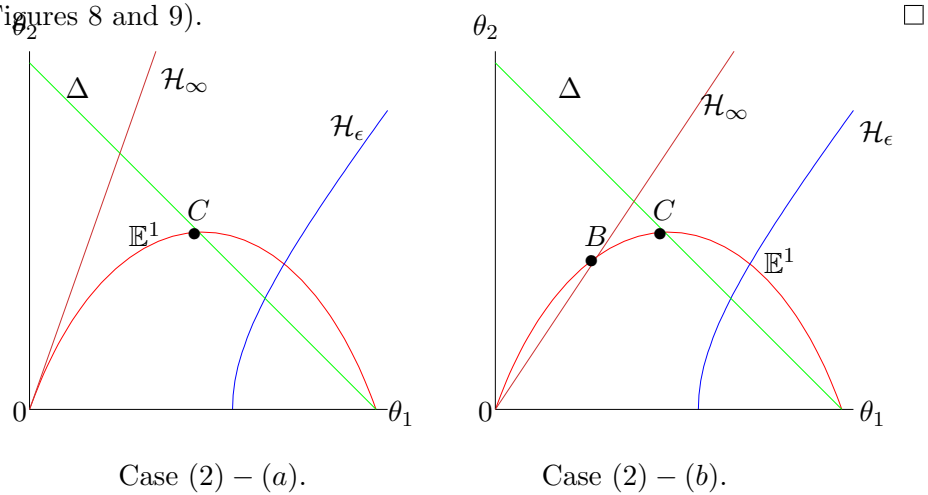
$$A = (K_1, 0), \text{ and } C = \left( \alpha_2 \frac{K_1 + K_2}{\alpha_1 + \alpha_2}, \frac{r_1 - r_2}{\alpha_1 + \alpha_2} \right).$$

We denote by  $\Sigma$  the straight line joint the origin and  $C$ . The slope of  $\Sigma$  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  $\Sigma$  whose slopes respectively are

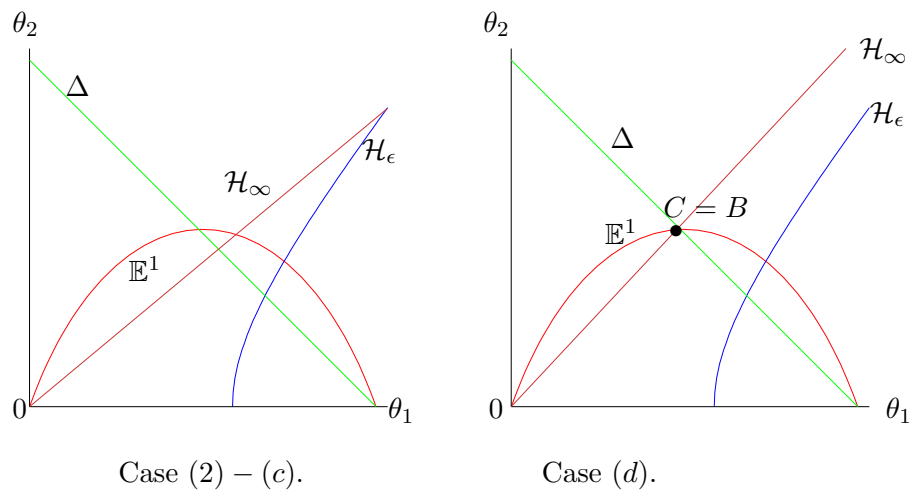
$$\frac{r_1}{r_2}, \quad \sqrt{\frac{\theta_1}{\theta_2}} \quad \text{and} \quad \frac{r_1 - r_2}{\alpha_2(K_1 + K_2)}.$$

389 By the method graphic of Arditi et al. [5] ( see also [34]), we conclude the complete

390 proof ( see Figures 8 and 9).



**Figure 8.** This illustrates the cases (2)-a and (2)-b in Theorem 3.3. As the migration intensity  $\epsilon$  increases from 0 to  $\infty$ , 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  $\Delta$ . The dispersal is favorable when  $E_2^*(\epsilon)$  is between  $A$  and  $C$ , and unfavorable when  $E_2^*(\epsilon)$  is between  $C$  and  $B$ .



**Figure 9.** This illustrates the case (2)-c in Theorem 3.3. As the migration intensity  $\epsilon$  increases from 0 to  $\infty$ , 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  $\epsilon$ , because it belongs to the ellipse and the limit point  $B$  is above  $\Delta$ . The figure (d) is a particular case of (2)-(c), where  $T_2^* \rightarrow K_1 = T_2^*(\infty)$  for  $\frac{\theta_2}{\theta_1} = \left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2}\right)^2$ .

391 Speaking biologically, the result of the previous theorem show that the nonlinear  
 392 asymmetric dispersal can lead to either an increased total size of the population in two  
 393 patches, a decreased total size with persistence in the patches, or even extinction in  
 394 both patches when the growth of migration goes to infinity. Let us explain the result  
 395 of Theorem 3.3 in the particular case where the dispersion is symmetric i.e.  $\frac{\theta_1}{\theta_2} = 1$ . In

396 this case, the system (26) becomes

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (x_2^2 - x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (x_1^2 - x_2^2), \end{cases} \quad (43)$$

397 **Corollary 3.2.** Consider the model (43). Let  $\Lambda_0, \Lambda_1$  and  $\Lambda_2$  be defined by (13). The  
398 total equilibrium population  $T_2^*$  of (43) satisfies the following properties

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

$$\begin{cases} T_2^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^{**}, \\ 0 < T_2^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^{**}. \end{cases} \quad (44)$$

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

- 402 (3) 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  
403  $T_2^*(\infty) = K_1$ .

404 **Proof.** Consequence direct of the theorem 3.3. □

405 Comparing the effects of linear and nonlinear asymmetric dispersion on the persis-  
406 tence and extinction of population, we remark that, the nonlinear symmetry between  
407 patches assure that: if the derivative of the total equilibrium population at  $\epsilon = 0$   
408 is negative, then the population goes to extinction in two patches. Comparing this  
409 situation with the nonlinear asymmetric case, we obtain that we can have the deriva-  
410 tive of the total equilibrium population at  $\epsilon = 0$  is negative without the population  
411 goes to extinction in two patches. The second conclusion, in the nonlinear symmetric  
412 case, when there is a  $\epsilon^*$  such that  $T_2^*(\epsilon^*) = K_1$ , then the population persistent in  
413 two patches unlike in the asymmetric case, i.e. we can have  $T_2^*(\epsilon^\#) = K_1$  for certain  
414 value of migration rate  $\epsilon^\#$ , but, the population goes to extinction in two patches. As  
415 conclusion, the nonlinear dispersal without the condition of symmetry, increases the  
416 probability of extinction of population in the patches.

417 In the remainder of this section, we study the effect of the rapid growth of the  
418 population in the source patch and rapid death of the population in the sink patch  
419 on the dynamics of the total equilibrium population and on the coexistence of the  
420 population in both patches. Note that, these situations were not examined in [4, 5, 34].  
421 Here, we study the total equilibrium population as a function of the migration rate  
422 in the case where the growth (resp. death) rate is much larger than the death (resp.  
423 growth) rate. In particular, we explicitly calculate the total equilibrium in the both  
424 situations, its derivative in the absence of the migration, its limit for large migration  
425 rate and we compare the total equilibrium population with the carrying capacity of  
426 the source patch. First, we start by the following situation:

#### 427 3.4. The death rate is much larger than the growth rate

428 In this part, we consider the two-patch model (26) and we assume that the death rate  
429  $r_2$  is much larger than the growth rate  $r_1$ . One can write the model in the following

430 way:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = \frac{r_2}{\eta} x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (45)$$

431 where  $\eta$  is assumed to be a small positive number. First, we have the following result:

432 **Theorem 3.4.** *Let  $(x_1(t, \eta), x_2(t, \eta))$  be the solution of System (45) with initial con-*  
 433 *dition  $(x_1^0, x_2^0)$  satisfying  $x_i^0 \geq 0$  for  $i = 1, 2$ . Let  $z(t)$  be the solution of the differential*  
 434 *equation*

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \epsilon \theta_1 x_1^2 =: \varphi(x_1), \quad (46)$$

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

$$x_1(t, \eta) = z(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (47)$$

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

$$x_2(t, \eta) = o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (48)$$

437 **Proof.** When  $\eta \rightarrow 0$ , System (45) is a slow-fast system, with one slow variable,  $x_1$ ,  
 438 and one fast variable,  $x_2$ . Tikhonov's theorem [7, 29, 32, 33] prompts us to consider  
 439 the dynamics of the fast variables in the time scale  $\tau = \frac{1}{\eta}t$ . One obtains

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon \eta (\theta_1 x_1^2 - \theta_2 x_2^2). \quad (49)$$

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

$$\frac{dx_2}{d\tau} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right). \quad (50)$$

441 The slow manifold is given by the equilibrium of System (50), i.e.  $x_2 = 0$ , which is LAS  
 442 in the positive axis. When  $\eta$  goes to zero, Tikhonov's theorem ensures that after a fast  
 443 transition toward the slow manifold, the solutions of (45) converge to the solutions of  
 444 the *reduced model* (46), obtained by replacing  $x_2 = 0$  into the dynamics of the slow  
 445 variable.

The differential equation (46) admits as a positive equilibrium

$$x_1^{**}(\epsilon, 0^+) := \frac{r_1 K_1}{r_1 + \epsilon \theta_1 K_1}. \quad (51)$$

446 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,  
 447 the equilibrium  $x_1^{**}(\epsilon, 0^+)$  is LAS in the positive axis, so, the approximation given by  
 448 Tikhonov's theorem holds for all  $t \geq 0$  for the slow variable and for all  $t \geq t_0 > 0$  for  
 449 the fast variable, where  $t_0$  is as small as we want. Therefore, let  $z(t)$  be the solution

450 of the reduced model (46) of initial condition  $z(0) = x_1^0$ , then, when  $\eta \rightarrow 0$ , we have  
 451 Approximations (47) and (48).  $\square$

452 We have the following result which gives the conditions for which patchiness is  
 453 beneficial or detrimental in System (45) when  $\epsilon$  goes to zero.

454 **Theorem 3.5.** *The total equilibrium population  $x_1^{**}(\epsilon, 0^+)$  of System (45) when  $\eta \rightarrow$   
 455  $0$ , given by (51) is decreasing. Moreover,  $0 < x_1^{**}(\epsilon, 0^+) < K_1$  for  $\epsilon$  and  $x_1^{**}(\epsilon, 0^+) \rightarrow 0$   
 456 as  $\epsilon \rightarrow \infty$ .*

457 **Proof.** The derivative of (51) is given by:

$$\frac{dx_1^{**}}{d\epsilon}(\epsilon, 0^+) = -\frac{r_1 K_1^2 \theta_1}{(r_1 + \epsilon \theta_1 K_1)^2}, \quad (52)$$

458 which is negative for all  $\epsilon$ .  $\square$

### 459 3.5. The growth rate is much larger than the death rate

460 In this part, we consider the two-patch model (26) and we assume that the growth  
 461 rate  $r_1$  is much larger than the death rate  $r_2$ . One can write the model in the following  
 462 way:

$$\begin{cases} \frac{dx_1}{dt} = \frac{r_1}{\eta} x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases} \quad (53)$$

463 where  $\eta$  is assumed to be a small positive number. We prove the following result:

464 **Theorem 3.6.** *Let  $(x_1(t, \eta), x_2(t, \eta))$  be the solution of System (53) with initial con-*  
 465 *dition  $(x_1^0, x_2^0)$  satisfying  $x_i^0 \geq 0$  for  $i = 1, 2$ . Let  $z(t)$  be the solution of the differential*  
 466 *equation*

$$\frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon (\theta_1 K_1^2 - \theta_2 x_2^2) =: \psi(x_2), \quad (54)$$

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

$$x_2(t, \eta) = z(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (55)$$

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

$$x_1(t, \eta) = K_1 + o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (56)$$

469 **Proof.** When  $\eta \rightarrow 0$ , System (53) is a *slow-fast* system, with one *slow variable*,  $x_2$ ,  
 470 and one *fast variable*,  $x_1$ . Tikhonov's theorem [7, 29, 32, 33] prompts us to consider  
 471 the dynamics of the fast variables in the time scale  $\tau = \frac{1}{\eta}t$ . One obtains

$$\frac{dx_1}{d\tau} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon \eta (-\theta_1 x_1^2 + \theta_2 x_2^2). \quad (57)$$

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

$$\frac{dx_1}{d\tau} = r_1 x_1 \left( 1 - \frac{x_1}{K_1} \right). \quad (58)$$

The slow manifold is given by the equilibrium of System (58), i.e.  $x_1 = K_1$ , which is LAS in the positive axis. When  $\eta$  goes to zero, Tikhonov's theorem ensures that after a fast transition toward the slow manifold, the solutions of (53) converge to the solutions of the *reduced model* (54), obtained by replacing  $x_1 = K_1$  into the dynamics of the slow variable.

The differential equation (54) admits as a positive equilibrium

$$x_2^{**}(\epsilon, 0^+) := 1/2 \frac{-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}}{r_2 + \epsilon K_2 \theta_2}. \quad (59)$$

473 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,  
 474 the equilibrium  $x_2^{**}(\epsilon, 0^+)$  is LAS in the positive axis, so, the approximation given by  
 475 Tikhonov's theorem holds for all  $t \geq 0$  for the slow variable and for all  $t \geq t_0 > 0$  for  
 476 the fast variable, where  $t_0$  is as small as we want. Therefore, let  $z(t)$  be the solution of  
 477 the reduced model (54) with initial condition  $z(0) = x_2^0$ , then, when  $\eta \rightarrow 0$ , we have  
 478 Approximations (55) and (56).  $\square$

479 As a corollary of the previous theorem, we have the following result which give the  
 480 limit of the total equilibrium population  $T_2^*(\epsilon, 0^+)$  of System (53) when  $\eta$  goes to zero:

**Corollary 3.3.** *We have:*

$$T_2^*(\epsilon, 0^+) := K_1 + 1/2 \frac{-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}}{r_2 + \epsilon K_2 \theta_2}. \quad (60)$$

481 In the following proposition, we calculate the derivative of  $T_2^*(\epsilon, 0^+)$  at  $\epsilon = 0$  and  
 482 the formula of perfect mixing (i.e. when  $\epsilon \rightarrow \infty$ ) of the total equilibrium population  
 483 defined by (60).

484 **Proposition 3.1.** *Consider the total equilibrium population (60). Then,*

$$\frac{dT_2^*}{d\epsilon}(0, 0^+) = \frac{\theta_1 K_1^2}{r_2}, \quad (61)$$

485 *and*

$$T_2^*(+\infty, 0^+) = (1 + \sqrt{s})K_1 = \frac{\sqrt{\theta_1} + \sqrt{\theta_2}}{\sqrt{\theta_2}} K_1. \quad (62)$$

**Proof.** The derivative of the total equilibrium population  $T_2^*(\epsilon, 0^+)$  defined by (60)

with respect to  $\epsilon$  is:

$$\begin{aligned} \frac{dT_2^*}{d\epsilon}(\epsilon, 0^+) &= -1/2 \frac{\left(-r_2 K_2 + \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}\right) K_2 \theta_2}{(r_2 + \epsilon K_2 \theta_2)^2} \\ &+ 1/4 \frac{4 K_2 \theta_1 K_1^2 r_2 + 8\epsilon K_2^2 \theta_1 K_1^2 \theta_2}{(r_2 + \epsilon K_2 \theta_2) \sqrt{r_2^2 K_2^2 + 4\epsilon K_2 \theta_1 K_1^2 r_2 + 4\epsilon^2 K_2^2 \theta_1 K_1^2 \theta_2}} \end{aligned} \quad (63)$$

486 In particular, the derivative of the total equilibrium population at  $\epsilon = 0$  is given by  
487 the formula (61).

488 By taking the limit of (60) when  $\epsilon \rightarrow \infty$ , we get that the total equilibrium population  
489  $T_2^*(\epsilon, 0^+)$  tends to (62).  $\square$

490 We have the following result which gives the conditions for which patchiness is  
491 beneficial or detrimental in model (53) when  $\eta$  goes to zero.

492 **Theorem 3.7.** Consider the total equilibrium population  $T_2^*(\epsilon, 0^+)$  given by (60).  
493 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  $\epsilon$ , 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

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

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

497 Biologically speaking, from Sections 3.4 and 3.5, we conclude that, the rapid increase  
498 in the population in the source patch results in persistence in the both patches with  
499 increased total size population, and the rapid decrease in the sink population results  
500 in extinction in both patches.

#### 501 4. Numerical simulations

502 In this section, we give some numerical examples which illustrates the results of  
503 Proposition 2.1, Corollary 3.1, and also the results of Theorem 3.3. First, we start  
504 by given some examples of the graphs of the functions  $s \mapsto \psi_1(s) := T_1^*(+\infty)$  and  
505  $s \mapsto \psi_2(s) := T_2^*(+\infty)$  defined by (17) and (41) respectively. In the figure 10, we plot  
506 the graphs of the functions  $\psi_1$  ( shown in red) and  $\psi_2$  ( shown in green), as a function  
507 of the dispersal asymmetry parameter  $s$  for some parameters of the model. Its clear  
508 that  $\psi_1, \psi_2 \rightarrow K_1$  when  $s \rightarrow 0$  and  $\psi_1, \psi_2 \rightarrow 0$  when  $s \rightarrow \infty$ . The derivative of  $\psi_1$  with

509 respect to  $s$  is given by:

$$\frac{d\psi_1}{ds}(s) = \begin{cases} -\frac{(-r_2\alpha_2 + \alpha_2 r_1) s^2 + (2\alpha_2 r_1 + 2r_2\alpha_1) s - r_1\alpha_1 + r_2\alpha_1}{(\alpha_1 + s^2\alpha_2)^2} & \text{if } s < r_1/r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (64)$$

510 We have  $\frac{d\psi_1}{ds}(s) = 0$  if and only if,  $s_1 = -\frac{\alpha_2 r_1 + r_2\alpha_1 + \sqrt{\alpha_2^2 r_1^2 + r_2^2 \alpha_1^2 + r_2^2 \alpha_2 \alpha_1 + \alpha_2 r_1^2 \alpha_1}}{\alpha_2(-r_2 + r_1)}$  or  
511  $s_2 = \frac{-\alpha_2 r_1 - r_2\alpha_1 + \sqrt{\alpha_2^2 r_1^2 + r_2^2 \alpha_1^2 + r_2^2 \alpha_2 \alpha_1 + \alpha_2 r_1^2 \alpha_1}}{\alpha_2(-r_2 + r_1)}$ . If  $r_1 \leq r_2$  then,  $s_2 < 0 < s_1$ , so, the  
512 derivative of  $\psi_1$  is negative for all  $s < r_1/r_2$ , since  $s_1 > r_1/r_2$  ( see figure 10-(a)). If  
513  $r_1 > r_2$ , then  $s_1 < 0 < s_2$ , therefore, the derivative of  $\psi_1$  is positive for all  $0 < s < s_2$   
514 and negative for  $s > s_2$  since  $s_2 < r_1/r_2$  ( see Fig. 10-(b), (c), (d)).

515 The derivative of  $\psi_2$  with respect to  $s$  is given by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \frac{d\psi_2}{ds}(s) = \begin{cases} -\frac{r_1 - r_2\sqrt{s}}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1-\sqrt{s})r_2}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1-\sqrt{s})(r_1 - r_2\sqrt{s})\alpha_2}{(\alpha_1 + s\alpha_2)^2} & \text{if } 0 < s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \\ \text{If } r_2 < r_1 \text{ then } \frac{d\psi_2}{ds}(s) = \begin{cases} -\frac{r_1 - r_2\sqrt{s}}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1-\sqrt{s})r_2}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1-\sqrt{s})(r_1 - r_2\sqrt{s})\alpha_2}{(\alpha_1 + s\alpha_2)^2} & \text{if } 0 < s < 1, \\ \frac{r_1 - r_2\sqrt{s}}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1+\sqrt{s})r_2}{2\sqrt{s}(\alpha_1 + s\alpha_2)} - \frac{(1+\sqrt{s})(r_1 - r_2\sqrt{s})\alpha_2}{(\alpha_1 + s\alpha_2)^2} & \text{if } 1 \leq s < \frac{r_1^2}{r_2^2}, \\ 0 & \text{if } s \geq \frac{r_1^2}{r_2^2}. \end{cases} \end{array} \right. \quad (65)$$

516 If  $r_2 \geq r_1$ , then the derivative of  $\psi_2$  is negative for all  $0 < s < \frac{r_1^2}{r_2^2}$  and zero for all

517  $s \geq \frac{r_1^2}{r_2^2}$  ( see Fig. (10)-(a)). If  $r_2 < r_1$ , then the derivative of  $\psi_2$  is negative for all

518  $0 < s < 1$  and zero for all  $s \geq \frac{r_1^2}{r_2^2}$ . For  $1 < s < \frac{r_1^2}{r_2^2}$ , the sign of  $\frac{d\psi_2}{ds}$  is difficult to study.

519 We give two examples where the derivative of  $\psi_2$  has a negative sign ( see Fig. (10)-(b)

520 and Fig. (10)-(c) ) and a non-constant sign for  $1 < s < \frac{r_1^2}{r_2^2}$  ( see Fig. (10)-(d)).

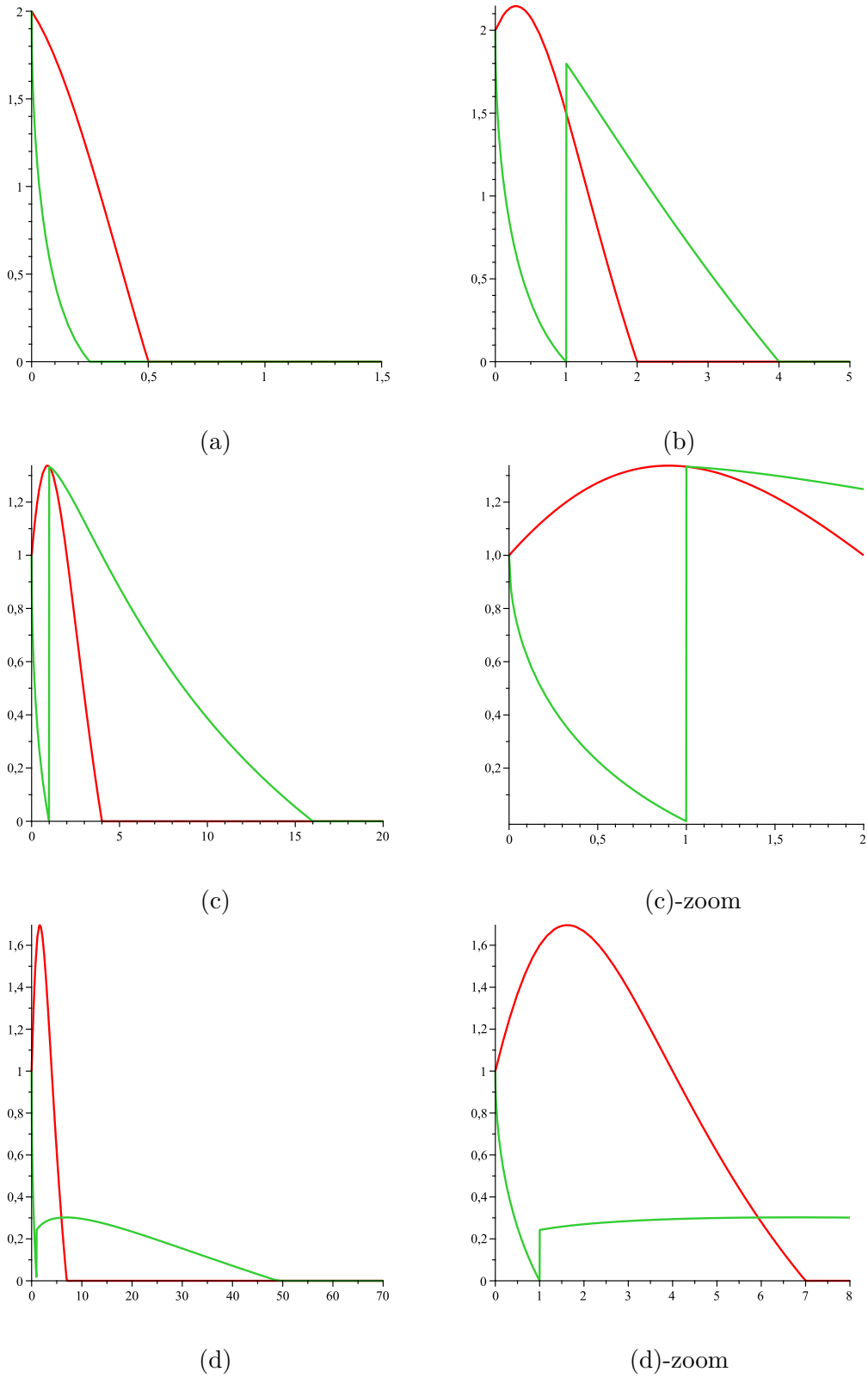
521 In Table 1, we give the space of parameters  $(r_1, r_2, K_1, K_2) \in \mathbb{R}_+^4$ .

**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

#### 522 4.1. Asymmetric dispersion

523 In this part, we plot in the figures 11, 12, 13, 14, 15 and 16, the curves of the total  
524 equilibrium populations  $\epsilon \mapsto T_1^*(\epsilon)$  and  $\epsilon \mapsto T_2^*(\epsilon)$  as a function of migration rate  $\epsilon$ ,

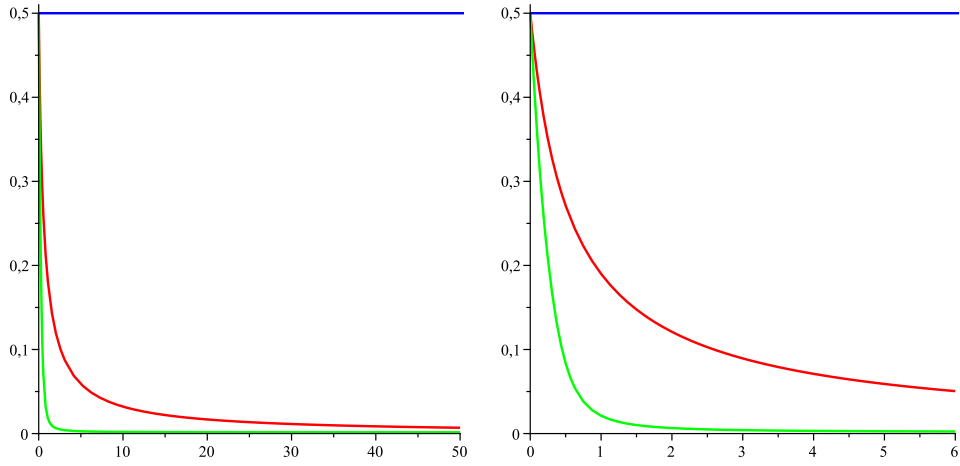


**Figure 10.** The graphs of  $\psi_1$  (red) and  $\psi_2$  (green) as function of  $s$  for the parametrers given in Table 1. The function  $\psi_1$  is continuous for all  $s$ . If  $r_2 < r_1$ , at symmetric case ( $s = 1$ ),  $\psi_2$  is discontinuous as shown in case (b), (c) and (d).

525 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  $\mathcal{L}_i$   
 526 and  $\Delta_i$  are given by (9) and (42) respectively, choosing in Table 2.

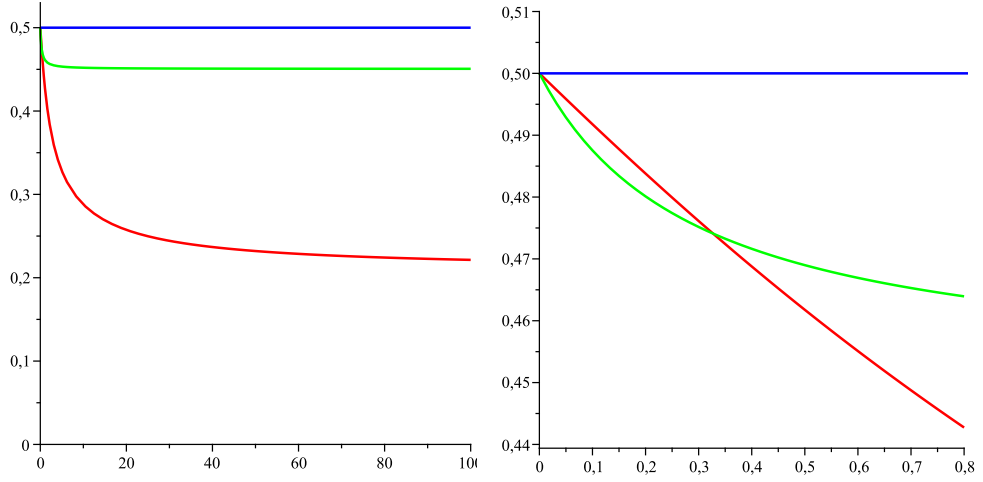
**Table 2.** Parameters values of the six cases used in Fig. 11, 12, 13, 14, 15 and 16. The derivatives  $\frac{dT_1^*}{d\epsilon}(0)$ ,  $\frac{dT_2^*}{d\epsilon}(0)$  and the perfect mixing abundances  $T_1^*(\infty)$  and  $T_2^*(\infty)$  are calculated with the expressions given in (B1), (C1), (16) and (41) respectively . .

Figure	$r_1$	$r_2$	$K_1$	$K_2$	$\theta_1$	$\theta_2$	$\frac{dT_1^*}{d\epsilon}(0)$	$T_1^*(\infty)$	$\frac{dT_2^*}{d\epsilon}(0)$	$T_2^*(\infty)$
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

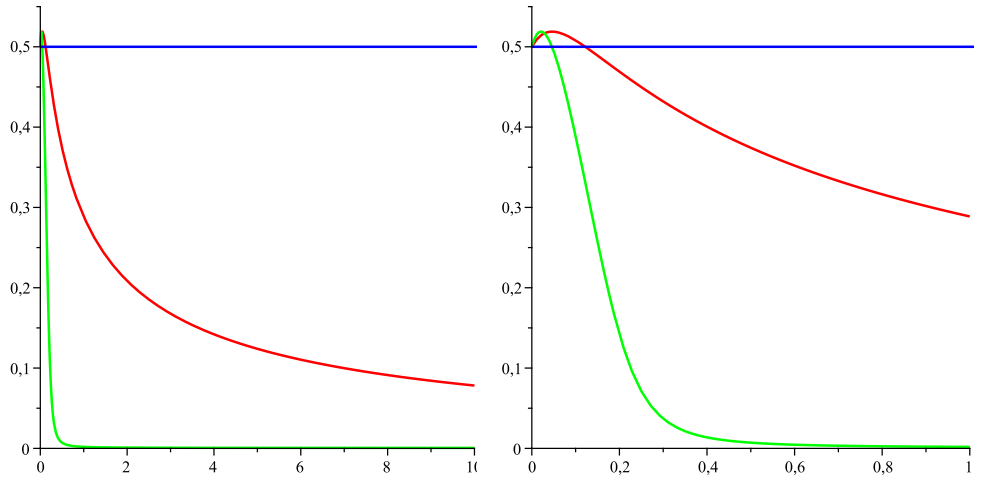


**Figure 11.** Total equilibrium population  $T_1^*$  (shown in green) and  $T_2^*$  (shown in red) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with  $(\theta_1, \theta_2) \in \Delta_0 \cap \mathcal{L}_0$ . The horizontal line shown in blue is  $K_1$ .

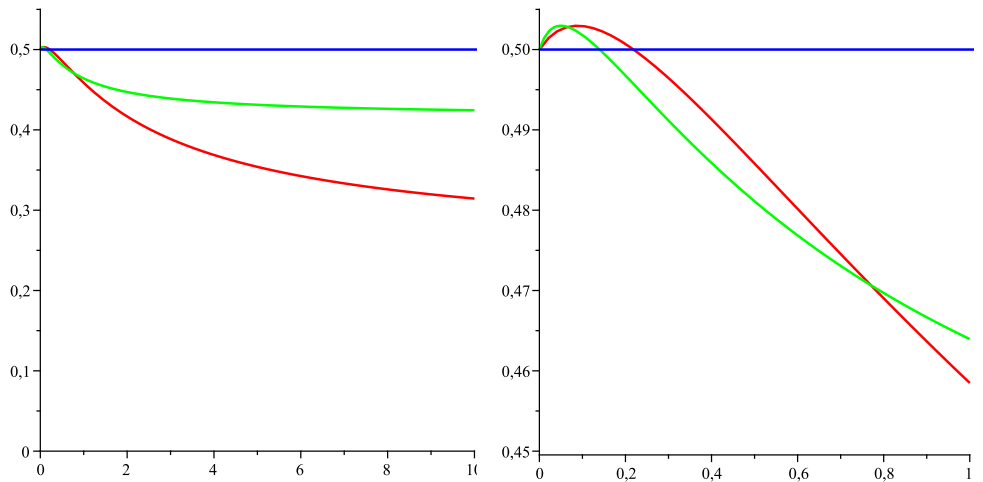
527 Depending on the values of the migration rate  $\epsilon$ , as shown in the figures (11), (12),  
 528 (13), (14), (15) and (16), in which we have the following examples of inequalities  
 529 between the total equilibrium populations  $T_1^*$ ,  $T_2^*$  and also the value  $K_1$  which is again  
 530 represented by the horizontal blue line.



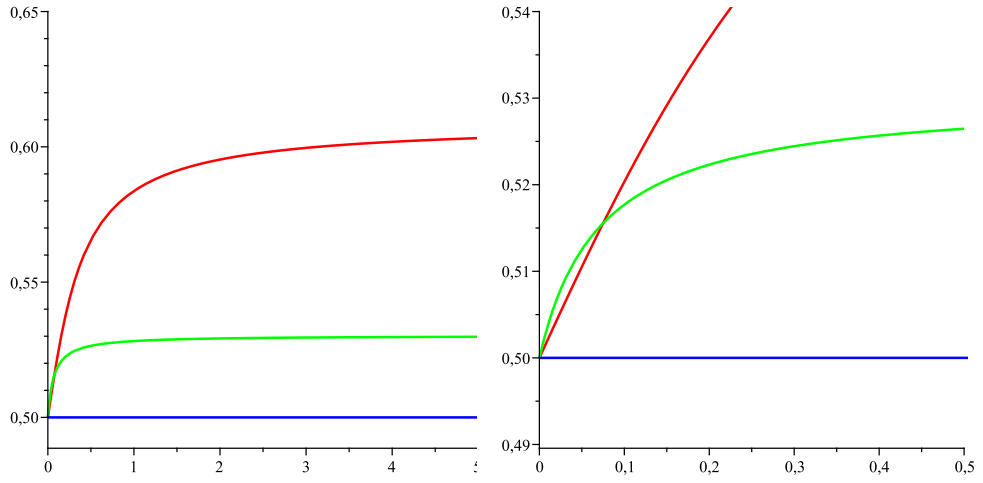
**Figure 12.** Total equilibrium population  $T_1^*$  (shown in green) and  $T_2^*$  (shown in red) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with  $(\theta_1, \theta_2) \in \mathcal{L}$



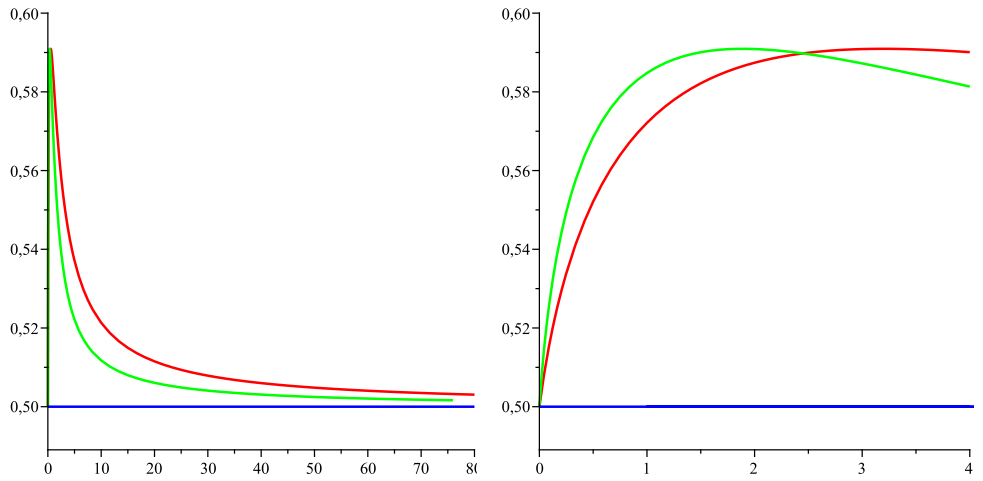
**Figure 13.** Total equilibrium population  $T_1^*$  (shown in green) and  $T_2^*$  (shown in red) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with  $(\theta_1, \theta_2) \in \Delta_2 \cap \mathcal{L}_2$ . 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) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with  $(\theta_1, \theta_2) \in \Delta_3 \cap \mathcal{L}_3$ . 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) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with  $(\theta_1, \theta_2) \in \Delta_4 \cap \mathcal{L}_4$ . The horizontal line shown in blue is  $K_1$ .



**Figure 16.** Total equilibrium population  $T_1^*$  (shown in green) and  $T_2^*$  (shown in red) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 1 with the condition  $\frac{\theta_2}{\theta_1} = \frac{\alpha_2(K_1+K_2)}{\tau_1-r_2} = \left(\frac{\alpha_2(K_1+K_2)}{\tau_1-r_2}\right)^2$ . The horizontal line shown in blue is  $K_1$ .

531 In the figure 11, that is plotted for the parameter values given in the first line of  
532 Table 2, the total equilibrium population  $T_1^*$  is smaller than  $T_2^*$ , and both smaller  
533 than  $K_1$ . In addition, there is a migration rate  $\epsilon_0 \simeq 0.84$  such that  $T_1^*(\epsilon) = 0$  for all  
534  $\epsilon \geq 0.84$ . The total equilibrium  $T_2^*$  goes to zero when migration rate goes to infinity.  
535 This example prove that, linear asymmetric dispersal can give extinction of population  
536 in both patches for small values of migration rate and this extinction is faster compared  
537 to the extinction for the nonlinear asymmetric dispersal, which product for the large  
538 migration rate.

539 In the figure 12, that is plotted for the parameter values given in the second line  
540 of Table 2. We have, the total equilibrium population  $T_1^*$  is smaller than  $T_2^*$  for all  
541  $0 \leq \epsilon \leq 0.82$ , and  $T_1^*$  is greater than  $T_2^*$  for all  $\epsilon \geq 0.82$ , and both smaller than  $K_1$ . For  
542  $\epsilon \simeq 0.82$ ,  $T_1^*(0.82) = T_2^*(0.82) \simeq 0.47$ . The difference between the case of the figure 11  
543 and 12, is that we have the persistence of the population in two patches for nonlinear  
544 symmetric and asymmetric dispersal.

545 In the figure 13, that is plotted for the parameter values given in the third line  
546 of Table 2. We have, the total equilibrium population  $T_1^*$  is greater than  $T_2^*$  for all  
547  $0 \leq \epsilon \leq 0.03$ , and  $T_1^*$  is smaller than  $T_2^*$  for all  $\epsilon \geq 0.03$ , for  $\epsilon \simeq 0.03$ ,  $T_1^*(0.03) =$   
548  $T_2^*(0.03) \simeq 0.52$ . There are two migration rates  $\epsilon_1 \simeq 0.05$  and  $\epsilon_2 \simeq 0.12$  such that  
549  $T_1^*(0.05) = T_2^*(0.12) = 0.5$ . The total equilibrium  $T_1^*(\epsilon) = 0$  for all  $\epsilon \geq 0.26$ .

550 In the figure 14, that is plotted for the parameter values given in the fourth line  
551 of Table 2. We have, the total equilibrium population  $T_1^*$  is greater than  $T_2^*$  for all  
552  $0 \leq \epsilon \leq 0.06$  and  $\epsilon \geq 0.77$ ,  $T_1^*$  is smaller than  $T_2^*$  for all  $0.06 \leq \epsilon \leq 0.77$ , for  $\epsilon \simeq 0.06$ ,  
553  $T_1^*(0.06) = T_2^*(0.06) \simeq 0.51$  and for  $\epsilon \simeq 0.77$ ,  $T_1^*(0.77) = T_2^*(0.77) \simeq 0.47$ . There are  
554 two migration rates  $\epsilon_1 \simeq 0.13$  and  $\epsilon_2 \simeq 0.22$  such that  $T_1^*(0.13) = T_2^*(0.22) = 0.5$ . The  
555 total equilibrium  $T_1^*$  and  $T_2^*$  tends to 0.42 and 0.29 respectively.

556 In the figure 15, that is plotted for the parameter values given in the five line of  
557 Table 2, the total equilibrium population  $T_1^*$  is greater than  $T_2^*$  for all  $0 \leq \epsilon \leq 0.08$ ,  
558  $T_1^*$  is smaller than  $T_2^*$  for all  $\epsilon \geq 0.08$ , and both greater than  $K_1$ . The figure 16 is an  
559 example which that  $T_1^*, T_2^* \rightarrow 0.5 = K_1$ .

#### 560 4.2. Symmetric dispersion

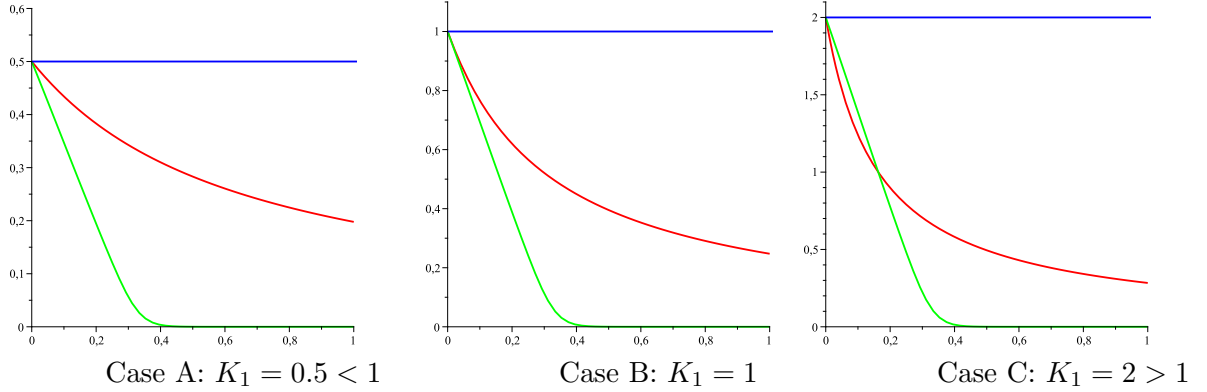
561 In this part, we consider the case of symmetric migration i.e. when  $\theta_1 = \theta_2 = 1$ .  
562 We plot the total equilibrium populations  $\epsilon \mapsto T_1^*(\epsilon)$  and  $\epsilon \mapsto T_2^*(\epsilon)$  as a function of  
563 migration rate  $\epsilon$ . We give some examples of the three cases given in Corollaries 2.1 and  
564 3.2. We plot in the figures 17, 18 and 19, the curves of the total equilibrium population  
565  $T_1^*, T_2^*$  and the line  $K_1$ , for the sets of parameters choosing in Table 3.

566 Depending on the values of the migration rate  $\epsilon$ , as shown in the figures (17),  
567 (18) and (19), in which we have the following three examples of inequalities and equality  
568 between the total equilibrium populations  $T_1^*, T_2^*$  and also the value  $K_1$  which is again  
569 represented by the horizontal blue line. We propose here to plot three figures, and  
570 each figure contain three cases corresponding to the three values of capacity:  $K_1 < 1$ ,  
571  $K_1 = 1$  and  $K_1 > 1$ . Note that,  $\frac{dT_1^*}{d\epsilon}(0) = \frac{dT_2^*}{d\epsilon}(0) \Leftrightarrow K_1 = 1$  or  $r_1 = r_2$ . As the two  
572 derivatives equals for  $K_1 = 1$ , we choose to plot the figures for values smaller than,  
573 equal to and greater than  $K_1 = 1$ .

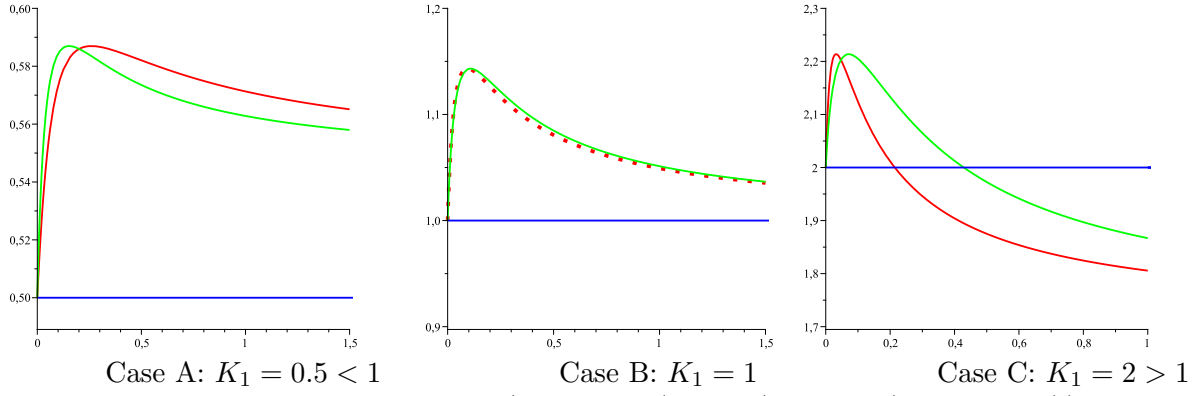
574 In the figure 17, that is plotted for the parameter values given in the three first lines  
575 of Table 3. In case A, for  $K_1 < 1$ , the total equilibrium population  $T_1^*$  is smaller than  
576  $T_2^*$ , and both smaller than  $K_1$ . In case B, for  $K_1 = 1$ , the total equilibrium population  
577  $T_1^*$  is smaller than  $T_2^*$ , moreover,  $T_1^*(\epsilon) \simeq T_2^*(\epsilon)$  for all  $\epsilon \in [0, 0.1]$ . In case C, for

**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 (B1), (C1), (16) and (41) respectively.

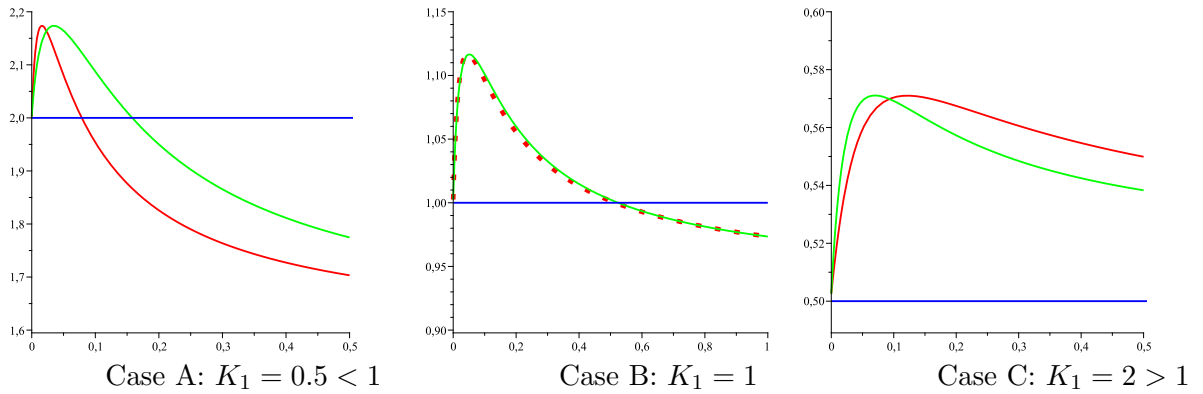
Figure	Case	$r_1$	$r_2$	$K_1$	$K_2$	$\frac{dT_1^*}{d\epsilon}(0)$	$T_1^*(\infty)$	$\frac{dT_2^*}{d\epsilon}(0)$	$T_2^*(\infty)$
Fig. 17	Case A	0.25	1	0.5	20	-1.5	0	-0.75	0.2
	Case B	0.25	1	1	20	-3	0	-3	0.24
	Case C	0.25	1	2	20	-6	0	-12	0.2
Fig. 18	Case A	0.25	1	0.5	20	3	0.56	1.5	0.57
	Case B	0.25	0.1	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



**Figure 17.** Total equilibrium population  $T_1^*$  (shown in green) and  $T_2^*$  (shown in red) of the system (7) and (26) respectively as a function of the migration rate  $\epsilon$  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 (7) and (26) respectively as a function of the migration rate  $\epsilon$  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 (7) and (26) respectively as a function of the migration rate  $\epsilon$  for the sets of the parameter values given in Table 3. The horizontal line shown in blue is  $K_1$ .

578  $K_1 > 1$ , there is a  $\epsilon_0 \simeq 0.16$ , such that, the total equilibrium population  $T_1^*$  is greater  
579 than  $T_2^*$  for  $0 \leq \epsilon \leq 0.16$ , and  $T_1^*$  is smaller than  $T_2^*$  for  $\epsilon \geq 0.16$ . For  $\epsilon \simeq 0.16$  we have  
580  $T_1^*(0.16) \simeq T_2^*(0.16) \simeq 1$ . The total equilibrium  $T_1^*$  equal to zero when migration rate  
581 greater than 0.4.

582 In the figure 18, that is plotted for the parameter values given in the three second  
583 lines of Table 3. In case A, for  $K_1 < 1$ , there is a  $\epsilon_0 \simeq 0.2$ , such that, the total  
584 equilibrium population  $T_1^*$  is greater than  $T_2^*$  for all  $0 \leq \epsilon \leq 0.2$ ,  $T_1^*$  is smaller than  $T_2^*$   
585 for all  $\epsilon \geq 0.2$  and both greater than  $K_1$ . For  $\epsilon \simeq 0.2$ , we have  $T_1^*(0.2) \simeq T_2^*(0.2) \simeq 0.59$ .  
586 In case B, for  $K_1 = 1$ , the total equilibrium population  $T_1^*$  is equal to  $T_2^*$ ,  $T_1^*(\epsilon) \simeq T_2^*(\epsilon)$   
587 for all  $\epsilon$  positive. In case C, for  $K_1 > 1$ , there is a  $\epsilon_0 \simeq 0.04$ , such that, the total  
588 equilibrium population  $T_1^*$  is smaller than  $T_2^*$  for  $0 \leq \epsilon \leq 0.2$ , and  $T_1^*$  is greater than  
589  $T_2^*$  for  $\epsilon \geq 0.2$ . For  $\epsilon \simeq 0.2$  we have  $T_1^*(0.2) \simeq T_2^*(0.2) \simeq 2.2$ . The same situations are  
590 product in the figure 19. Note that, according to these examples of figures, the passage  
591 for values of  $K_1$  lower than 1 to values higher than 1, the positions of the curves of  
592  $T_1^*$  and  $T_2^*$  change, and are same for the particular value of capacity  $K_1 = 1$ . In the  
593 case when  $\theta_1 = \theta_2 = 1$ , the total equilibrium population  $T_1^*$  satisfies:

$$T_1^*(\epsilon) = K_1 + \epsilon(x_2^*(\epsilon) - x_1^*(\epsilon)) \left( \frac{1}{\alpha_1 x_1^*(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^*(\epsilon)} \right), \quad (66)$$

594 and  $T_2^*$ :

$$T_2^*(\epsilon) = \frac{K_1}{1 - \epsilon(x_2^{**}(\epsilon) - x_1^{**}(\epsilon)) \left( \frac{1}{\alpha_1 x_1^{**}(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(\epsilon)} \right)}. \quad (67)$$

595 It is very difficult to prove analytically these numerical results, and I think, according to  
596 numerical simulations, for all symmetric migration, we only have these configurations,  
597 so we can give the following conjecture:

598 **Conjecture 4.1.** Consider the models (7) and (26) with  $\theta_1 = \theta_2 = 1$ . Let  $T_1^*$  and  
599  $T_2^*$  be the total equilibrium populations of (29) and (43) respectively. Let  $\Lambda_0, \Lambda_1$  and  
600  $\Lambda_2$  be defined by (13). The total equilibrium populations  $T_1^*$  and  $T_2^*$  satisfied to the  
601 following properties

- 602 (1) if  $(r_1, r_2) \in \Lambda_0$  then,  
603 (a) if  $K_1 < 1$ , then  $T_1^*(\epsilon) < T_2^*(\epsilon)$  for all  $\epsilon > 0$ .  
604 (b) if  $K_1 = 1$ , then, there is a  $\epsilon^* > 0$  such that,  $T_1^*(\epsilon) = T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
605 and  $T_1^*(\epsilon) < T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .  
606 (c) if  $K_1 > 1$ , then, there is a  $\epsilon^* > 0$  such that,  $T_1^*(\epsilon) \geq T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
607 and  $T_1^*(\epsilon) < T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .  
608 (2) if  $(r_1, r_2) \in \Lambda_1$  then,  
609 (a) if  $K_1 < 1$ , then, there is a  $\epsilon^* > 0$  such that  $T_1^*(\epsilon) \leq T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
610 and  $T_1^*(\epsilon) > T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .  
611 (b) if  $K_1 = 1$ , then,  $T_1^*(\epsilon) = T_2^*(\epsilon)$  for all  $\epsilon \geq 0$ .  
612 (c) if  $K_1 > 1$ , then, there is a  $\epsilon^* > 0$  such that  $T_1^*(\epsilon) \geq T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
613 and  $T_1^*(\epsilon) < T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .  
614 (3) if  $(r_1, r_2) \in \Lambda_2$ , then  
615 (a) if  $K_1 < 1$ , then, there is a  $\epsilon^* > 0$  such that  $T_1^*(\epsilon) \geq T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
616 and  $T_1^*(\epsilon) < T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .  
617 (b) if  $K_1 = 1$ , then,  $T_1^*(\epsilon) = T_2^*(\epsilon)$  for all  $\epsilon \geq 0$ .

618 (c) if  $K_1 > 1$ , then, there is a  $\epsilon^* > 0$  such that  $T_1^*(\epsilon) \leq T_2^*(\epsilon)$  for all  $0 \leq \epsilon \leq \epsilon^*$ ,  
619 and  $T_1^*(\epsilon) > T_2^*(\epsilon)$  for all  $\epsilon > \epsilon^*$ .

## 620 5. Conclusion

621 This work was aimed to find out whether the total equilibrium population of the two  
622 patches source-sink connected by nonlinear asymmetric migration can be greater than  
623 the carrying capacity of the source isolated patch, i.e. at equilibrium. The system has  
624 a unique positive equilibrium, which furthermore is globally asymptotically stable in  
625 the interior of the positive cone, and the origin as trivial equilibrium which is unstable,  
626 unlike in the symmetric case, which can be globally asymptotically stable ( see Prop.  
627 5.5 in [34] and Theorem 2.1).

628 In Section 3.2, we considered the particular case of perfect mixing, i.e. when the dif-  
629 fusion rate goes to infinity, that is, individuals may travel freely between two patches.  
630 We compute the total equilibrium population in that case, and by perturbation argu-  
631 ments, we proved that the dynamics in this ideal case provides a good approximation  
632 for the case when the diffusion rate is large. Rigorous analysis on the model demon-  
633 strate a mechanism by which the nonlinear dispersal asymmetry can lead to either an  
634 increased total size of the species in two patches, a decreased total size with persis-  
635 tence in the patches, or even extinction in both patches for large migration rates. In  
636 Subsections 3.3 and 3.4, we study the total equilibrium population of the source-sink  
637 patch model (26) as a function of the diffusion rate in the case where the growth  
638 (resp. death) rate is much larger than the death (resp. growth) rate. Some numerical  
639 simulations are given which we confirm and extend our results. We also compare our  
640 present results with the result of previous work [34] for linear asymmetry dispersal.  
641 Finally, comparison of the present results with those of Wu et al. [34] suggests that  
642 this nonlinear asymmetric dispersal mechanism has the same impact as in the case of  
643 linear asymmetric dispersal. However, comparing the conditions (9) and (42) shows  
644 that this nonlinear asymmetry dispersal can have a strong quantitative influence on  
645 the effect of dispersal. In the case symmetric  $\theta_1 = \theta_2$ , the conditions (9) and (42) are  
646 the same, and becomes (13).

647 Some questions remain open, for examples, how our results generalize to situa-  
648 tions with more than two patches i. e. the generalization of the present results to the  
649 three-patch source-sink model with nonlinear asymmetric migration. In particular, the  
650 global stability, the behavior of the model for large migration rate and the influence  
651 of nonlinear asymmetric dispersal on total population abundance. The mathematical  
652 extension to  $n$  patches ( $n > 2$ ) is probably very intricate and is a challenge for further  
653 work. I think this question is difficult and requires a lot of work and mathematical  
654 tools.

## 655 Appendix A. Equilibria and stability of (26)

656 In this section, our goal is to prove the global stability of the system (26). In the  
657 absence of migration, i.e. the case where  $\epsilon = 0$ , the system (26) admits  $(K_1, 0)$  as  
658 a non trivial equilibrium point, which furthermore is globally asymptotically stable  
659 (GAS) in the positive cone  $\mathbb{R}_+^2$ . The problem is whether the equilibrium continues to  
660 be positive and globally stable for any  $\epsilon > 0$  or not. We first prove the non negativity  
661 of the solutions of System (26). We have the following proposition:

662 **Proposition A.1.** *The positive cone  $\mathbb{R}_+^2$  is positively invariant for the system (26).*

663 **Proof.** Suppose that, at a given time  $t$ , one of the state variables of the system (26)  
664 is at a boundary of  $\mathbb{R}_+^2$ , meaning that at least one population is at 0. We suppose first  
665 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  
666  $x_2 = 0$ , 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  
667 boundary of  $\mathbb{R}_+^2$  either remains at the boundary or goes to the interior of  $\mathbb{R}_+^2$ . According  
668 to [31, Proposition B.7, page 267], no trajectory comes out of  $\mathbb{R}_+^2$ . Therefore,  $\mathbb{R}_+^2$  is  
669 positively invariant for (26).  $\square$

670 The equilibrium of the system (26) is the solutions of the following algebraic system:

$$\begin{cases} 0 = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(\theta_2 x_2^2 - \theta_1 x_1^2), \\ 0 = -r_2 x_2 \left(1 + \frac{x_2}{K_2}\right) + \epsilon(\theta_1 x_1^2 - \theta_2 x_2^2). \end{cases} \quad (\text{A1})$$

671 The sum of the two equations of (A1) shows that the equilibrium points are in a ellipse  
672 noted  $\mathbb{E}^1$ , which its equation is given by:

$$\mathbb{E}^1 : \quad \varphi(x_1, x_2) := r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - r_2 x_2 \left(1 + \frac{x_2}{K_2}\right) = 0. \quad (\text{A2})$$

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

Solving the first equation of system (A1) for  $x_2$  yields a hyperbola noted  $\mathcal{H}_\epsilon$  defined by

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

675 As our study is limited in the positive cone, then we are interested only in the  
676 positive branch of  $\mathcal{H}_\epsilon$ . The hyperbola  $\mathcal{H}_\epsilon$  ( shown in blue in Fig. 5-(a)) depend on the  
677 migration rate  $\epsilon$ . It always passes through the origin and the point  $\mathcal{B} := \left(K_1, \sqrt{\frac{\theta_1}{\theta_2} K_1}\right)$ .  
678 So, the equilibrium points are the non-negative intersection between the curves  $\mathbb{E}_2^1$   
679 and  $\mathcal{H}_\epsilon$ . There are two equilibrium points. The first is the trivial point  $(0, 0)$  and the  
680 second is a non trivial point noted  $E^*(\epsilon) := (x_1^{**}(\epsilon), x_2^{**}(\epsilon))$  whose position depend on  
681 migration rate  $\epsilon$  ( see Fig. 5-(a)).

**Remark A.1.** The isoclines of the system (26) are given by the two equations:

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

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

684 In the following, our aim is to show the global stability of the equilibrium  $E^*(\epsilon)$ .  
 685 For this, we need some results. First, for the non-negativity and boundedness of the  
 686 solutions of the system (26), we have the following result:

**Lemma A.1.** *For any non-negative initial condition, the solutions of the system (26) remain bounded, for all  $t \geq 0$ . Moreover, the set*

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

687 where  $\xi_1^* = \min\{r_1, r_2\}$  and  $\xi_2^* = r_1 K_1 + r_2 K_2$ , is positively invariant and is a global  
 688 attractor for the system (26).

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

$$\dot{X}_T(t) = r_1 x_1(t) \left(1 - \frac{x_1(t)}{K_1}\right) - r_2 x_2(t) \left(1 + \frac{x_2(t)}{K_2}\right). \quad (\text{A3})$$

691 For all  $r_i$  and  $K_i$ , we have the inequality:

$$r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) \leq r_1 (K_1 - x_1), \quad \text{and} \quad r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) \leq -r_2 x_2. \quad (\text{A4})$$

Substituting Equation (A4) into (A3), we get

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

692 which gives

$$X_T(t) \leq \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*}\right) e^{-\xi_1^* t} + \frac{\xi_2^*}{\xi_1^*}, \quad \text{for all } t \geq 0. \quad (\text{A5})$$

Hence,

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

693 Therefore, the solutions of System (26) are positively bounded and defined for all  
 694  $t \geq 0$ . From (A5), it can be deduced that the set  $\Sigma$  is positively invariant and it is a  
 695 global attractor for the system (26).  $\square$

696 Recall that, a matrix  $A = (a_{ij})$  is called cooperative if  $a_{ij} \geq 0$  for all  $i \neq j$ . Let we  
 697 consider the autonomous system:

$$\dot{x} = \Phi(x), \quad (\text{A6})$$

698 where  $\dot{x}$  denote the derivative of  $x$ ,  $\Phi = (\Phi_1, \dots, \Phi_n)$  is  $\mathcal{C}^1$  on a domain  $\mathbb{R}_+^n$ . System  
 699 (A6) is called cooperative if the Jacobian matrix of (A6) is a cooperative matrix for  
 700 all  $x \in \mathbb{R}_+^n$ .

701 Recall that, for general cooperative systems, we have the following result, which  
 702 guarantees that all solutions converge to equilibria/infinity without periodic oscilla-  
 703 tion (see page 28 Hofbauer and Sigmund [24]). The solutions of a two-dimensional  
 704 cooperative system converge either to an equilibrium or to infinity. We have the fol-  
 705 lowing result:

706 **Theorem A.1.** *The equilibrium  $E_2^*(\epsilon)$  of (26) is GAS in the positive cone  $\mathbb{R}_+^2 \setminus \{0\}$ .*

**Proof.** The two-dimensional system (26) is cooperative. Indeed, its Jacobian matrix  
 evaluate at  $E_2^*(\epsilon)$  is given by:

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

707 where  $\kappa_1 = r_1 - 2r_1\frac{x_1^{**}(\epsilon)}{K_1} - 2\epsilon\theta_1x_1^{**}(\epsilon)$ , and  $\kappa_2 = r_2 - 2r_2\frac{x_2^{**}(\epsilon)}{K_2} - 2\epsilon\theta_2x_2^{**}(\epsilon)$ . We  
 708 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  $0 < \frac{d\mathcal{H}_{\epsilon,2}}{dx_2}(x_1^{**}(\epsilon), x_2^{**}(\epsilon)) =$   
 709  $-\frac{1}{2\epsilon\theta_1\mathcal{H}_{\epsilon,2}(x_2^{**}(\epsilon))}\kappa_2$ . Therefore,  $\kappa_1 < 0$  and  $\kappa_2 < 0$ . This implies that  $\text{tr}(\mathbb{J}(E_2^*(\epsilon))) =$   
 710  $\kappa_1 + \kappa_2 < 0$ , where  $\text{tr}$  means the trace.

711 It's clear that, in the figures 5-(b), at the equilibrium  $E_2^*(\epsilon)$ , we have:

$$712 \frac{d\mathcal{H}_{\epsilon,1}}{dx_1}(E_2^*(\epsilon)) > \left(\frac{d\mathcal{H}_{\epsilon,2}}{dx_2}(E_2^*(\epsilon))\right)^{-1}, \text{ which gives } -\frac{\kappa_1}{2\epsilon\theta_2\mathcal{H}_{\epsilon,1}(x_1^{**}(\epsilon))} > -\frac{\kappa_2}{2\epsilon\theta_1\mathcal{H}_{\epsilon,2}(x_2^{**}(\epsilon))}.$$

713 Thus,  $\det \mathbb{J}(E_2^*(\epsilon)) = \kappa_1\kappa_2 - 4\epsilon^2\theta_1\theta_2x_1^{**}(\epsilon)x_2^{**}(\epsilon) > 0$ .

714 Hence by the Routh-Hurwitz criteria for stability, the real parts of the eigenvalues  
 715 value of the Jacobian matrix  $\mathbb{J}(E_2^*(\epsilon))$  are negative, proving that  $E_2^*(\epsilon)$  is asymptoti-  
 716 cally stable. Lemma A.1 imply that there cannot be any non-trivial closed paths lying  
 717 in the interior of the positive quadrant and hence the asymptotic stability must be  
 718 global.  $\square$

## 719 Appendix B. Derivative of the total equilibrium population $T_1^*$ at $\epsilon = 0$

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

$$\frac{dT_1^*}{d\epsilon}(0) = \theta_1K_1 \left( \frac{1}{r_2} - \frac{1}{r_1} \right). \quad (\text{B1})$$

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

723 **Proof.** The equilibrium point  $E_1^*(\epsilon)$  of (7) satisfies the system

$$\begin{cases} 0 = r_1x_1^*(\epsilon) \left( 1 - \frac{x_1^*(\epsilon)}{K_1} \right) + \epsilon(\theta_2x_2^*(\epsilon) - \theta_1x_1^*(\epsilon)), \\ 0 = r_2x_2^*(\epsilon) \left( -1 - \frac{x_2^*(\epsilon)}{K_2} \right) + \epsilon(\theta_1x_1^*(\epsilon) - \theta_2x_2^*(\epsilon)). \end{cases} \quad (\text{B2})$$

724 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,

725 one obtains

$$\begin{cases} x_1^*(\epsilon) = K_1 + \epsilon \frac{\theta_2 x_2^*(\epsilon) - \theta_1 x_1^*(\epsilon)}{\frac{r_1}{K_1} x_1^*(\epsilon)}, \\ x_2^*(\epsilon) = \epsilon \frac{\theta_1 x_1^*(\epsilon) - \theta_2 x_2^*(\epsilon)}{r_2 + \frac{r_2}{K_2} x_2^*(\epsilon)}. \end{cases} \quad (\text{B3})$$

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

$$T_1^*(\epsilon) = K_1 + \epsilon(\theta_2 x_2^*(\epsilon) - \theta_1 x_1^*(\epsilon)) \left( \frac{1}{\alpha_1 x_1^*(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^*(\epsilon)} \right). \quad (\text{B4})$$

727 By differentiating the equation (B4) at  $\epsilon = 0$ , we get:

$$\frac{dT_1^*}{d\epsilon}(0) = (\theta_2 x_2^*(0) - \theta_1 x_1^*(0)) \left( \frac{1}{\alpha_1 x_1^*(0)} - \frac{1}{r_2 + \alpha_2 x_2^*(0)} \right), \quad (\text{B5})$$

728 which gives (B1), since  $x_1^*(0) = K_1$  and  $x_2^*(0) = 0$ . □

729 Note that, the derivative (B1) is dependent on the parameters  $r_1, r_2, \theta_1$  and  $K_1$ . It  
730 is equal to zero if and only if both patches have the same growth rates and positive if  
731 and only if,  $r_1 < r_2$ .

### 732 Appendix C. Derivative of the total equilibrium population $T_2^*$ at $\epsilon = 0$

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

$$\frac{dT_2^*}{d\epsilon}(0) = \theta_1 K_1^2 \left( \frac{1}{r_2} - \frac{1}{r_1} \right). \quad (\text{C1})$$

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

736 **Proof.** The equilibrium point  $E_2^*(\epsilon)$  of (26) satisfies the system

$$\begin{cases} 0 = r_1 x_1^{**}(\epsilon) \left( 1 - \frac{x_1^{**}(\epsilon)}{K_1} \right) + \epsilon(\theta_2 (x_2^{**}(\epsilon))^2 - \theta_1 (x_1^{**}(\epsilon))^2), \\ 0 = r_2 x_2^{**}(\epsilon) \left( -1 - \frac{x_2^{**}(\epsilon)}{K_2} \right) + \epsilon(\theta_1 (x_1^{**}(\epsilon))^2 - \theta_2 (x_2^{**}(\epsilon))^2). \end{cases} \quad (\text{C2})$$

737 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,  
738 one obtains

$$\begin{cases} x_1^{**}(\epsilon) = K_1 + \epsilon \frac{\theta_2 (x_2^{**}(\epsilon))^2 - \theta_1 (x_1^{**}(\epsilon))^2}{\frac{r_1}{K_1} x_1^{**}(\epsilon)}, \\ x_2^{**}(\epsilon) = \epsilon \frac{\theta_1 (x_1^{**}(\epsilon))^2 - \theta_2 (x_2^{**}(\epsilon))^2}{r_2 + \frac{r_2}{K_2} x_2^{**}(\epsilon)}. \end{cases} \quad (\text{C3})$$

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

$$T_2^*(\epsilon) = K_1 + \epsilon(\sqrt{\theta_2}x_2^{**}(\epsilon) + \sqrt{\theta_1}x_1^{**}(\epsilon))(\sqrt{\theta_2}x_2^{**}(\epsilon) - \sqrt{\theta_1}x_1^{**}(\epsilon)) \left( \frac{1}{\alpha_1 x_1^{**}(\epsilon)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(\epsilon)} \right). \quad (C4)$$

740 By differentiating the equation (C4) at  $\epsilon = 0$ , we get:

$$\frac{dT_1^*}{d\epsilon}(0) = (\sqrt{\theta_2}x_2^{**}(0) + \sqrt{\theta_1}x_1^{**}(0))(\sqrt{\theta_2}x_2^{**}(0) - \sqrt{\theta_1}x_1^{**}(0)) \left( \frac{1}{\alpha_1 x_1^{**}(0)} - \frac{1}{r_2 + \alpha_2 x_2^{**}(0)} \right), \quad (C5)$$

741 which gives (C1), since  $x_1^{**}(0) = K_1$  and  $x_2^{**}(0) = 0$ .  $\square$

742 Note that, the derivative (C1) is dependent on the parameters  $r_1, r_2, \theta_1$  and  $K_1$ . It  
743 is equal to zero if and only if both patches have the same growth rates, and positive,  
744 if and only if,  $r_1 < r_2$ .

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