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Generalized Coupled Source-Sink Models

Bilel Elbetch

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2 **Generalized Coupled Source-Sink Models**

3 Bilel Elbetch

4 Department of Mathematics, University Dr. Moulay Tahar, Saida, Algeria.

5 **ARTICLE HISTORY**

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7 **ABSTRACT**

8 In this paper, we consider a general single species model in a heterogeneous envi-
 9 ronment of n patches ($n \geq 2$), which each patch is either a source or a sink. First,
 10 we study the dynamics of the model when the matrix of migration is irreducible
 11 and reducible. We show that, there is a threshold number of source patches such
 12 that the population potentially becomes extinct below the threshold and established
 13 above the threshold. Next, used the theory of singular perturbation and theorem of
 14 Tikhonov, in the case of perfect mixing, i.e. when the diffusion rate tends to infinity,
 15 we calculate implicitly the equilibrium of the model, which in general is different
 16 from the sum of the s carrying capacities of source patches. We give also a good
 17 approximations of the solutions in this case. Second, we give some properties of the
 18 total equilibrium population and we compute its derivative at no dispersal. In some
 19 particular cases, we determine the conditions under which fragmentation and mi-
 20 gration can lead to a total equilibrium population which might be equal or smaller
 21 than the sum of the s carrying capacities. The following both cases: death rates are
 22 much larger than the growth rates and growth rates are much larger than the death
 23 rates are considered. Finally, we study an example of two-patch source-sink model
 24 where the first patch follows a logistic law and the second a Richard's law, we give
 25 a complete classification of the model parameter space as to whether dispersal is
 26 beneficial or detrimental to the carrying capacity.

27 **KEYWORDS**

28 Population Dynamics, Migration rate, Source-sink model, generalized Logistic
29 growth, Global stability, Slow-fast systems, Tikhonov's theorem.

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

31 **Contents**

32	1 Introduction	2
33	2 Mathematical model and assumptions	6
34	3 Global stability	9
35	4 Fast diffusion rate	12
36	4.1 Properties of the migration matrix Γ	12
37	4.2 Two time scale dynamics	13

38	5 Total equilibrium population	17
39	5.1 Derivative of T_n^* at no dispersal	17
40	5.2 Homogeneous source-sink system	19
41	5.3 Heterogeneous source-sink system	20
42	5.4 Two blocks of identical source and sink patches	21
43	6 The growth and death rates with two different scales	24
44	6.1 Death rates are much larger than the growth rates	24
45	6.2 Growth rates are much larger than the death rates	25
46	7 Example of Two-patch Source-sink model	26
47	7.1 Effect of dispersal on total equilibrium population	28
48	7.2 Two-patch model where one growth rate is much larger than the second	
49	one	33
50	7.2.1 Case where $r_2 \rightarrow \infty$	33
51	7.2.2 Case where $r_1 \rightarrow \infty$	35
52	8 Conclusion	36
53	A Background concepts and preliminaries results	37

54 **1. Introduction**

55 Many complex systems in sciences and engineering can be modeled by coupled systems
56 of differential equations on networks. A network can be mathematically treated as a
57 weighted digraph (directed graph), consisting of a set of n vertices and a set of directed
58 arcs. In 1977, Freedman and Waltman [23] consider a two-patch model with a single
59 species in logistic population growth as follows:

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

60 where x_i represents the population density in patch i , the parameter r_i is the intrinsic
61 growth rate, K_i is carrying capacity and ϵ is the dispersal rate. Freedman and Waltman
62 show that under certain conditions, the total population abundance can be larger than
63 the total carrying capacities $K_1 + K_2$. Holt [34] generalized these results to a source-
64 sink system. In 2015, Arditi et al. [1] gave a full mathematical analysis of the model
65 (1) of Freedman and Waltman with symmetric dispersal.

66 In 2018, Arditi et al. [2] extended the model (1) by considering asymmetric dispersal,
67 i.e. the model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \epsilon(\gamma_{21} x_1 - \gamma_{12} x_2), \end{cases} \quad (2)$$

where $\epsilon\gamma_{12}$ and $\epsilon\gamma_{21}$ with $\gamma_{ij} > 0, i \neq j$ and $\epsilon \geq 0$, are the migration terms which describe the flows of individuals from the patch 2 to the patch 1, and from the patch

1 to the patch 2 respectively. These flows can for example depend on the distance between the patches. By noting that the positive equilibrium $(x_1^*(\epsilon), x_2^*(\epsilon))$ of model (2) is the unique positive solution to

$$\begin{cases} r_1 x_1^*(\epsilon) \left(1 - \frac{x_1^*(\epsilon)}{K_1}\right) + r_2 x_2^*(\epsilon) \left(1 - \frac{x_2^*(\epsilon)}{K_2}\right) = 0, \\ x_2^*(\epsilon) = \frac{1}{\gamma_{12}} \left(\gamma_{21} x_1^*(\epsilon) - \frac{r_1}{\epsilon} x_1^*(\epsilon) \left(1 - \frac{x_1^*(\epsilon)}{K_1}\right) \right), \end{cases}$$

68 i.e., the intersection of an ellipse and a parabola, they used a graphical method to
69 completely the analyze of the model (2) in order to determine when dispersal is either
70 favorable or unfavorable to the total population abundance

71 In [14], I suggested to study the two-patch coupled model where each patches follows
72 a Richard's law, i.e, the model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \left(\frac{x_1}{K_1}\right)^\mu\right) + \epsilon(\gamma_{12} x_2 - \gamma_{21} x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \left(\frac{x_2}{K_2}\right)^\mu\right) + \epsilon(\gamma_{21} x_1 - \gamma_{12} x_2), \end{cases} \quad (3)$$

73 where x_1 and x_2 represent population densities of the species in patch 1 and 2, re-
74 spectively. The parameters K_i and r_i represents the carrying capacity and the growth
75 rate respectively. Parameter ϵ represents the dispersal rate and μ is a positive param-
76 eter. γ_{12} denote the migration rate from patch 2 to the patch 1 and γ_{21} from patch
77 1 to patch 2. For this model, I interested in the effect of this choice, which generalize
78 the logistic, on the dynamic of the total population in two patches. I have given a
79 complete classification of the model parameters regarding when the dispersion causes
80 a total biomass smaller or greater than the sum of the carrying capacities. I used for
81 this classification, the geometric method of Arditi et al. [2].

82 In 2019, Wu et al. [49] studied the following two-patch source-sink model:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(x_2 - s x_1), \\ \frac{dx_2}{dt} = r_2 x_2 \left(-1 - \frac{x_2}{K_2}\right) + \epsilon(s x_1 - x_2), \end{cases} \quad (4)$$

83 where x_1 and x_2 represent population densities of the species in patch 1 and 2, respec-
84 tively. Parameter ϵ represents the dispersal intensity while the parameter s reflects
85 the dispersal asymmetry. The authors show that the dispersal asymmetry can lead to
86 either an increased total size of the population in two patches, a decreased total size
87 with persistence in the patches, or even extinction in both patches. They show also
88 that for a large growth rate of the species in the source and a fixed dispersal intensity:

- 89 • If the asymmetry is small, the population would persist in both patches and reach
90 a density higher than that without dispersal and the population approaches its
91 maximal density at an appropriate asymmetry.
- 92 • If the asymmetry is intermediate, the population persists in both patches but
93 reaches a density less than that without dispersal.
- 94 • If the asymmetry is large, the population goes to extinction in both patches.

95 Arino et al. [3] also studied a source-sink model of n patches, where the source

96 patch follows a logistic growth rate, and the sink patch follows exponential decay, i.e
 97 the model

$$\begin{cases} \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \epsilon \sum_{j=1}^n \gamma_{ij} x_j, & i = 1, \dots, s, \\ \frac{dx_i}{dt} = -r_i x_i + \epsilon \sum_{j=1}^n \gamma_{ij} x_j, & i = s + 1, \dots, n, \end{cases} \quad (5)$$

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

$$\gamma_{ii} = - \sum_{j=1, j \neq i}^n \gamma_{ji}. \quad (6)$$

101 For system (5), the authors proved the existence of a threshold number of source
 102 patches such that the population potentially becomes extinct below the threshold and
 103 persistent above the threshold.

104 In 2021, Elbetch et al. [13] have considered the model of multi-patch logistic growth,
 105 coupled by asymmetric linear migration terms

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n, \quad (7)$$

where n is the number of patches in the system. The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity of patch i . The term on the right hand side of the system (7) describes the effect of the linear migration between the patches, where ϵ is the migration rate and $\Gamma := (\gamma_{ij})$ is the matrix representing the migrations between the patches. Note that, the system (7) is studied also by Elbetch et al. [12] and Takeuchi [46] in the case when the matrix Γ is symmetric. We recall that, when the matrix of migration Γ is irreducible, System (7) admits a unique positive equilibrium which is globally asymptotically stable, see [3, Theorem 1] [4, Theorem 2.2] or [12, Theorem 6.1], when $\epsilon \rightarrow \infty$, this equilibrium tend to

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

106 where $\alpha_i = \frac{r_i}{K_i}$ and $(\delta_1, \dots, \delta_n)^T$ the vector which generate the vector space $\ker \Gamma$ (for
 107 more properties of the vector space $\ker \Gamma$, see subsection 4.1).

108 In [12, 13], Elbetch et al. have answered in some particular cases of the model (7)
 109 to the following important question: Is it possible, depending on the migration rate,
 110 that the total equilibrium population be larger than the sum of the carrying capacities
 111 $\sum_i K_i$? This question is of ecological importance since the answer gives the conditions
 112 under which the linear dispersal is either beneficial or detrimental to total equilibrium
 113 population. Note that, this question has been studied by many researches, see [1, 2, 9–
 114 13, 15, 17, 21–24] for logistic model, [3, 16, 18, 49] for source-sink models, [28–30]
 115 for susceptible-infected-susceptible (SIS) patch-model and [5, 6, 35] for populations

116 with time-varying growth rates living in sinks and also some details of the dispersal-
117 induced growth (DIG) phenomenon (i.e. it is possible for populations in a set of
118 patches, with dispersal among them, to persist and grow despite the fact that all these
119 patches are sinks). They proved that, if all the patches do not differ with respect to the
120 intrinsic growth rate (i.e., $r_1 = \dots = r_n$), then the effect of linear migration is always
121 detrimental. In the case when $(K_1, \dots, K_n)^T \in \ker \Gamma$ (if the matrix Γ is symmetric,
122 the condition $(K_1, \dots, K_n)^T \in \ker \Gamma$ means that the patches do not differ with respect
123 to the carrying capacity), linear migration has no effect on the total equilibrium
124 population. An example when the effect of linear migration is always beneficial, is in
125 the case when Γ is symmetric and all the patches do not differ with respect to the
126 parameter $\alpha = r/K$ quantifying intraspecific competition (i.e., $\alpha_1 = \dots, \alpha_n$) (see also
127 [13, Prop. 4.2]).

128 With the aim to generalize the results obtained in [12, 13] for a multi-patch lo-
129 gistic model, to a multi-patch model with generalized growth rate, recently, Elbetch
130 [20] have considered the model of multi-patch generalized logistic growth, coupled by
131 asymmetric linear migration terms:

$$\frac{dx_i}{dt} = x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n, \quad (8)$$

132 where $\varphi_i(x_i)$ represents the specific growth rate of the population in the i -th patch
133 and satisfied to the following conditions: $\varphi_i(0) > 0$, $\frac{d\varphi_i}{dx_i}(x_i) < 0$, there exist $K_i > 0$
134 such that $\varphi_i(K_i) = 0$ and $x_i \varphi_i(x_i) \rightarrow -\infty$ as $x_i \rightarrow +\infty$ for all $i = 1, \dots, n$. When the
135 matrix of migration $\Gamma = (\gamma_{ij})_{n \times n}$ is irreducible, System (8) admits a unique positive
136 equilibrium which is GAS, see [20, Theorem 6]. When $\epsilon \rightarrow \infty$, this equilibrium tend
137 to $\lambda_0(\delta_1, \dots, \delta_n)$, where λ_0 is the unique solution in the positive axis of the following
138 equation $\sum_i \delta_i \varphi_i(\delta_i x) = 0$, see Theorem 7 in [20]. For this last model, Elbetch [20]
139 have shown that, if the n patches do not differ with respect to $K_i \frac{d\varphi_i}{dx_i}(K_i)$ then the total
140 equilibrium population on the n connected patches is always less than or equal to the
141 sum of carrying capacity of the isolated patches. In the general case when $K_i \frac{d\varphi_i}{dx_i}(K_i)$
142 are different, He determined some conditions for which the total population size of the
143 n connected patches at equilibrium may be greater than the sum of carrying capacities
144 of n isolated patches.

145 For general information of the effects of patchiness and migration in both continuous
146 and discrete cases, and the results beyond the logistic model, the reader is referred to
147 the work of Levin [37, 38], DeAngelis et al. [9, 10] and Freedman et al. [22].

148 Our aim in this work is to study the model of n patches with generalized source-
149 sink dynamics, coupled by migration terms. In particular, we are interested in studying
150 the effect of dispersion and the specific growth and death rates on the dynamics of
151 population. Thus we generalize some results of [20] for n-source, 0-sink generalized
152 logistic patch model to s-source, (n-s)-sink patch model and also we extend the results
153 proved by Elbetch et al. [12, 13] for n-source, 0-sink patch logistic model to s-source,
154 (n - s)-sink patch model and also we extend the results proved by Wu et al. [49] for
155 1-source, 1-sink patch model.

156 This paper is organized as follows: The introduction consists of giving an overview
157 of the different models of two and n patches, as well as of the two-patch source-sink
158 models of a single population and also for n patches. In Section 2, we introduce the
159 mathematical model and we give some definitions and notations. Next, in Section
160 3, We prove that there exists a threshold number of source patches such that the

161 population becomes extinct below the threshold and persist above the threshold for
162 the model (9). In Section 4, we study the behavior of the system (9) in the case when
163 the migration rate goes to infinity by using perturbation arguments and Tikhonov's
164 theorem [36, 47, 48]. In Section 5, we compare the total equilibrium population with the
165 sum of the s carrying capacities for some parameter space. In Section 6, the following
166 both cases: death rates are much larger than the growth rates and growth rates are
167 much larger than the death rates are considered. In Section 7, using the method graphic
168 of Arditi et al. [2] and of [49], we give a complete analysis of two-patch source-sink case,
169 where the first patch follows a logistic law and the second Richards law. Two-patch
170 model where one growth rate is much larger than the second one is also examined. In
171 Appendix A, we give some background concepts and preliminaries results which are
172 used in the analysis of the global stability of our different models. We ends with a
173 conclusion in the section 8.

174 In the following, we shall use for convenience the abbreviation LAS for Locally
175 Asymptotically Stable and GAS for Globally Asymptotically Stable equilibria.

176 2. Mathematical model and assumptions

177 Let us consider the growth of single specie which can disperse among of n patches,
178 with s source and $n - s$ sink patches, described by:

$$\begin{cases} \frac{dx_i}{dt} = x_i\varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), & i = 1, \dots, s, \\ \frac{dx_i}{dt} = -x_i\varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j - \gamma_{ji}x_i), & i = s + 1, \dots, n, \end{cases} \quad (9)$$

179 where x_i represents the population density of the species in the i -th patch and $\varphi_i(x_i)$
180 represents the specific growth rate of the population in the i -th patch for $i \leq s$ and
181 specific death rate for $i \leq s + 1$, see figure 2 for an example when $n = 3$. Since the
182 specific growth and death rates may depend on each patch environment, the function
183 $\varphi_i(x_i)$ is supposed to be different in each patch. The second term of the right hand
184 side in (9) describes the diffusion effect between source and sink patches where ϵ is
185 the migration rate and $\gamma_{ij} \geq 0$, for all $i \neq j$ is the term of asymmetrical migration
186 which describes the flows of individuals from the patch j to the patch i . These flows
187 can for example depend on the distance between the patches. We list the following
188 hypotheses, the first three of which are standard in single species models (see [22, 46]):

189 **H1.** All solutions of the initial value problem (9) exist, are unique and are continuable
190 for all positive time.

191 **H2.** Source patch: $\varphi_i(0) > 0$, $\frac{d\varphi_i}{dx_i}(x_i) < 0$, there exist $K_i > 0$ such that $\varphi_i(K_i) = 0$
192 and $x_i\varphi_i(x_i) \rightarrow -\infty$ as $x_i \rightarrow +\infty$ for all $i = 1, \dots, s$.

193 **H3.** Sink patch: $\varphi_i(0) > 0$, $\frac{d\varphi_i}{dx_i}(x_i) > 0$, and $x_i\varphi_i(x_i) \rightarrow +\infty$ as $x_i \rightarrow +\infty$ for all
194 $i = s + 1, \dots, n$.

195 **H4.** The matrix $\Gamma := (\gamma_{ij})$ where γ_{ii} given by (6), is irreducible.

196 In term of graph theory, given a network represented by digraph \mathcal{G} with n vertices,
197 $n \geq 2$, a coupled generalized source-sink system can be built on \mathcal{G} by assigning each
198 vertex its own internal dynamics and then coupling these vertex dynamics based on
199 directed arcs in \mathcal{G} (see Figure 1).

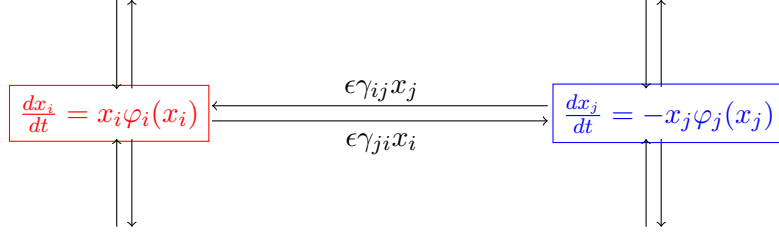


Figure 1. A coupled generalized source-sink system on a network. Under the irreducibility of the matrix Γ , a patch (source or sink) among the n patches can connect, only source patches, or, only sink patches, or, mixture of source and sink patches, see figure 2.

200 System (9) can be written:

$$\begin{cases} \frac{dx_i}{dt} = x_i \varphi_i(x_i) + \epsilon \sum_{j=1}^n \gamma_{ij} x_j, & i = 1, \dots, s, \\ \frac{dx_i}{dt} = -x_i \varphi_i(x_i) + \epsilon \sum_{j=1}^n \gamma_{ij} x_j, & i = s+1, \dots, n, \end{cases} \quad (10)$$

201 where the term γ_{ii} accounts for the flux out of patch i and takes the form (6). The
202 system (9) can also be written in matrix form as follows:

$$\begin{cases} \dot{X}_s = \text{diag}(\varphi_1(x_1), \dots, \varphi_s(x_s)) X_s + \epsilon (\Gamma_{ss} X_s + \Gamma_{sp} X_p), \\ \dot{X}_p = \text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p + \epsilon (\Gamma_{ps} X_s + \Gamma_{pp} X_p), \end{cases} \quad (11)$$

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

$$\Gamma = \begin{bmatrix} \Gamma_{ss} & \Gamma_{sp} \\ \Gamma_{ps} & \Gamma_{pp} \end{bmatrix}. \quad (12)$$

206 Assumption H1 is a just mathematical one. The first part in H2 ensures the expo-
207 nential growth of the population for its small density. The second in H2 means the
208 limited resources and K_i given in H2 is a carrying capacity of the source patch. Note
209 that $\varphi(x) = r(1 - x/K)$ for logistic growth and it satisfies all the above assumption
210 H2. In H2, for $i \leq s$, all patches are source since $\varphi_i(0) > 0$, and in H3, for $i \geq s+1$,
211 all patches are sink since $-\varphi_i(0) < 0$. We remark that growth and death functions
212 of patches can be very different; that is, system (9) allows patch-specific population
213 dynamics. To model this specification using continuous space model, one needs to deal
214 with partial differential equations with spatially varying coefficients, which are par-
215 ticularly challenging in stability analysis. General growth model $\dot{x} = x\varphi(x)$ which φ
216 satisfies to H2, has been used by many ecologists. For example, Richard's model [42],
217 see also Gilpin and Ayala 1973 [33], $\dot{x} = rx \left(1 - \left(\frac{x}{K}\right)^\mu\right)$, Gompertz's model (see Swann
218 and Vincent 1977 [44]), $\dot{x} = -r \log\left(\frac{x}{K}\right)$, Schoener 1973 [43], $\dot{x} = rx \left(\frac{I}{x} - C - bx\right)$ and
219 Pianka 1972 [41], $\dot{x} = x \left(b + \frac{a-x}{1+cx}\right)$, where r, K, μ, a, I, C, b and c are positive con-
220 stants. Note that, last model exhibits an Alee effect, which occurs in a population with
221 difficulties in reproducing at low densities. That is, the growth rate of the members in

222 the population is enhanced up to a certain density by aggregation and beyond its den-
 223 sity the rate decreases as the density increases by the limited resources. The function
 224 φ in Pianka's model has a maximum at $x_m = (-1 + \sqrt{1 + ca})/c > 0$ and the solution
 225 converges to $x^* > 0$ as $t \rightarrow \infty$, where $\varphi(x^*) = 0$. Further, φ can be approximated by
 226 the function $b + ax$ for small $x > 0$, by $b + a/c - x/c$ for large $x > 0$ and verify the
 227 Allee effect.

228 In hypothesis H4, The matrix Γ being irreducible means that the set of the source
 229 and sink patches cannot be partitioned into two nonempty disjoint subsets, I and J ,
 230 such that there is no migrations between a patch in subset I and a patch in subset J , i.e
 231 the irreducibility of matrix Γ implies that every patch in the model (9) is connected
 232 by migration term, i.e. the species can reach any i -th patch from any j -patch. For
 233 Two-patch model, the matrix Γ is irreducible if and only if γ_{12} and γ_{21} are positives.
 234 If $n = 3$, we have four cases possible as in figure 2, and when Γ is irreducible, we have
 235 five cases, see figure 3.

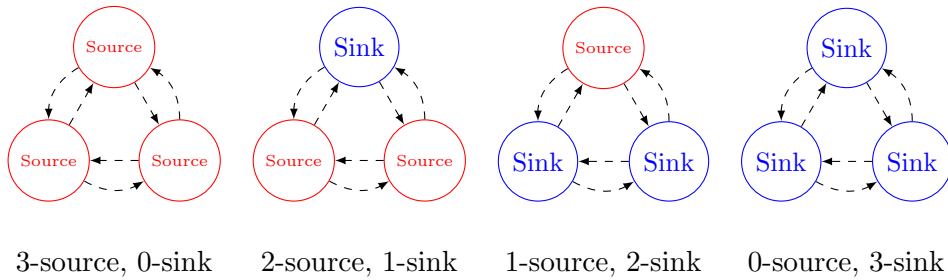


Figure 2. The possible cases modulo permutation of the three patches, for $n = 3$ and $s \in \{0, 1, 2, 3\}$. Source patches are in red and sink patches are in blue. Under the irreducibility hypothesis on the matrix Γ , there are five possible cases, modulo permutation of the three patches, which patches can connect, see figure 3.

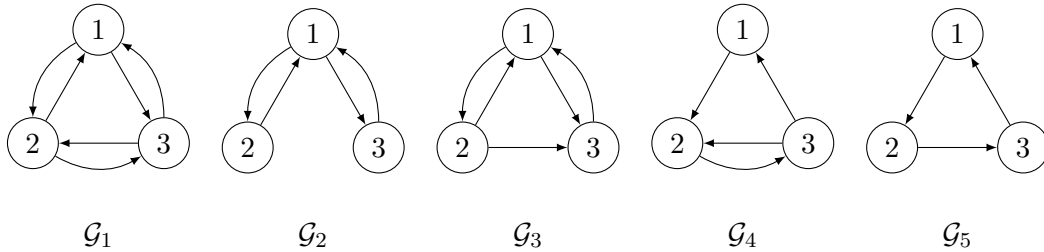


Figure 3. The assumption that the matrix Γ is irreducible, implies that the species can reach any i -th patch from any j -patch. For Three-patch model, under the irreducibility hypothesis on the matrix Γ , there are five possible cases, modulo permutation of the three patches. The two graphs \mathcal{G}_1 and \mathcal{G}_2 for which the migration matrix may be symmetric, if $\gamma_{ij} = \gamma_{ji}$. For the remaining cases, the graphs $\mathcal{G}_3, \mathcal{G}_4$ and \mathcal{G}_5 , cannot be symmetrical.

The model (9) studied in [49] for two patches, i.e $(n, s) = (2, 1)$, $\varphi_1(x_1) = r_1 - \frac{r_1}{K_1}x_1$ and $\varphi_2(x_2) = r_2 + \frac{r_2}{K_2}x_2$. The same model studied in [3] for n patches where the source population flow at the growth rate: $\dot{x}_i = r_i x_i (1 - x_i/K_i)$ for all $1 \leq i \leq s$, and the sink population flow at the death rate: $\dot{x}_i = -r_i x_i$ for all $s + 1 \leq i \leq n$. Recently, Elbetch [20] studied the model (9) for $s = n$. Note that, (9) studied in [1, 2, 7, 9, 22, 23, 34] for two source patches, $s = 0$ sink patch and logistic growth rate, i.e.

$$\varphi_i(x_i) = r_i - \frac{r_i}{K_i}x_i, \quad i = 1, 2.$$

236 Model (9) is studied in [10, 11, 50] for n source patches, 0 sink patches and a logistic
 237 growth rate, where the matrix Γ take the following form:

$$\gamma_{1n} = \gamma_{n1} = \gamma_{i,i-1} = \gamma_{i-1,i} = 1 \text{ for } 2 \leq i \leq n \text{ and } \gamma_{ij} = 0 \text{ otherwise.} \quad (13)$$

238 We have the following result:

239 **Proposition 2.1.** *The domain $\Omega = \{(x_1, \dots, x_n) \in \mathbb{R}^n / x_i \geq 0, i = 1, \dots, n\}$ is posi-*
 240 *tively invariant for the system (9).*

241 **Proof.** Assume that $x_i = 0$ and $x_j \geq 0$ for all $j \neq i$. We have

$$\frac{dx_i}{dt} = \epsilon \sum_{j=1, j \neq i} \gamma_{ij} x_j \geq 0, \quad i = 1, \dots, n.$$

242 Hence, on the boundary of Ω , the vector field associated to (9) either is tangent to Ω ,
 243 or points inward Ω . According to [45, Proposition B.7, page 267], no trajectory comes
 244 out of Ω .

245 Therefore, Ω is positively invariant for the system (9). □

246 3. Global stability

In this part, our goal is to study the dynamics of the system (9). Note that, in the
 absence of migration, i.e. the case where $\epsilon = 0$, the equations (9) are uncoupled:

$$\begin{cases} \frac{dx_i}{dt} = x_i \varphi_i(x_i) & i = 1, \dots, s, \\ \frac{dx_i}{dt} = -x_i \varphi_i(x_i) & i = s + 1, \dots, n, \end{cases}$$

and according to the hypotheses H2 and H3, the system (9) admits
 $(K_1, \dots, K_s, 0, \dots, 0)$ as a non trivial equilibrium point, which furthermore is GAS
 in the positive cone, indeed, consider the following Liapunov function:

$$V(x_1, \dots, x_n) = \sum_{i=1}^s \left\{ x_i - K_i - K_i \log \left(\frac{x_i}{K_i} \right) \right\} + \sum_{i=s+1}^n x_i.$$

247 System (9) admits origin as trivial equilibrium which is unstable and a boundary
 248 equilibrium occur where one or more of the $K_i, i \leq s$ are replaced by zero. The problem
 249 is whether or not, the equilibrium continues to exist and GAS for any $\epsilon > 0$. Here,
 250 we obtain a complete global asymptotic behavior of solutions which depends on the
 251 maximal eigenvalue of Jacobian of (9) evaluated at the origin 0. The Jacobian matrix
 252 of the system (9) evaluated at $x = 0$ is given by:

$$\mathbb{J}_s(0) = \text{diag}(\varphi_1(0), \dots, \varphi_s(0), -\varphi_{s+1}(0), \dots, -\varphi_n(0)) + \epsilon \Gamma, \quad (14)$$

253 which is the same as the matrix obtained by Arino et al. [3, Equation 7] for the model
 254 (5) (just replace $\varphi_i(0)$ by r_i). The matrix $\mathbb{J}_s(0)$ is cooperative (see Appendix A). We
 255 have the following result:

256 **Lemma 3.1.** Consider the matrix $\mathbb{J}_s(0)$. Then, if $s = 0$, $S(\mathbb{J}_0(0)) < 0$, and if $s = n$,
 257 $S(\mathbb{J}_n(0)) > 0$, where S denote the stability modulus defined by (A1) .

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

$$\mathbb{J}_0(0) = \text{diag}(-\varphi_1(0), \dots, -\varphi_n(0)) + \epsilon\Gamma. \quad (15)$$

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

$$\mathbb{J}_0(0)^T u = (-\varphi_1(0), \dots, -\varphi_n(0))^T \leq \lambda u, \quad \text{where } \lambda = \max\{-\varphi_1(0), \dots, -\varphi_n(0)\} < 0.$$

Therefore, since $\mathbb{J}_0(0)$ is a cooperative matrix, according to Lemma A.2, we have

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

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

$$\mathbb{J}_n(0) = \text{diag}(\varphi_1(0), \dots, \varphi_n(0)) + \epsilon\Gamma. \quad (16)$$

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

$$\mathbb{J}_n(0)^T u = (\varphi_1(0), \dots, \varphi_n(0))^T \geq \lambda u, \quad \text{where } \lambda = \min\{\varphi_1(0), \dots, \varphi_n(0)\} > 0.$$

Therefore, since $\mathbb{J}_n(0)$ is a cooperative matrix, according to Lemma A.2, we have

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

260 This completes the proof of the lemma. □

261 We have also the following result:

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

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

266 The dynamics of the system (9) in the case where Γ is reducible, is given as follow:

267 **Theorem 3.1.** Consider the system (9). Assume that Γ is reducible. Then, there
 268 exists a unique interval $\mathcal{I} \subset]0, n[\subset \mathbb{R}$, such that:

- 269 • If $s < \min \mathcal{I}$, then the origin is LAS, and
- 270 • if $s > \max \mathcal{I}$, then the origin is unstable.

271 **Proof.** Since $S(\mathbb{J}_0(0)) < 0$, and $S(\mathbb{J}_n(0)) > 0$ by Lemma 3.1. Moreover, the function
 272 $s \mapsto S(\mathbb{J}_s(0))$ is non-decreasing by Lemma 3.2 and continues with respect s (See [27,
 273 Theorem 2.4.9.2]). So by the intermediate value theorem, there exists an interval \mathcal{I} ,
 274 possibly reduced to a single point, such that $S(\mathbb{J}_s(0)) = 0$ for all $s \in \mathcal{I}$. Criteria for
 275 local asymptotic stability and instability of equilibria gives the completes proof of the
 276 theorem. □

277 Our goal in the remainder of this section is to study the dynamics of the model (9)
 278 in the case when the matrix Γ is irreducible. First, according to hypothesis H1, the
 279 solutions of (9) exist for all $t \geq 0$ and remain non negative for non negative initial
 280 conditions. Thus, the positive cone \mathbb{R}_+^n is invariant under the flow of the system (9).
 281 To establish the boundedness of solutions, we have the following result:

282 **Proposition 3.1.** *For any non negative initial condition, the solutions of the system*
 283 *(9) remain non negative and positively bounded.*

284 **Proof.** To show that all solutions are bounded, we consider the quantity defined by
 285 $X_T = \sum_{i=1}^n x_i$. So, we have

$$\dot{X}_T = \sum_{i=1}^s x_i \varphi_i(x_i) - \sum_{i=s+1}^n x_i \varphi_i(x_i). \quad (17)$$

286 According to hypotheses H2 and H3, for sufficiently large x_i for $i = 1, \dots, n$, we have
 287 $\dot{X}_T < 0$, so $X_T(t) \leq X_T(0)$. Therefore, the solutions of system (9) are positively
 288 bounded and defined for all $t \geq 0$. \square

289 We have the result:

290 **Theorem 3.2.** *Consider the system (9). Assume that the matrix Γ is irreducible,*
 291 *then, there exists a unique point $\mathcal{I}^* \in]0, n[$, such that:*

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

Proof. If the matrix Γ is irreducible, then the interval \mathcal{I} reduced to a single point \mathcal{I}^* ,
 such that: if $s < \mathcal{I}^*$, then $S(\mathbb{J}_s(0)) < 0$, and if $s > \mathcal{I}^*$, then $S(\mathbb{J}_s(0)) > 0$. According to
 [39, Theorem 1], if $S(\mathbb{J}_s(0)) < 0$, the origin is GAS. If $S(\mathbb{J}_s(0)) > 0$, then, the model (9)
 is persistent for any $\epsilon > 0$, that is, any solution $x(t)$ satisfies $\lim_{t \rightarrow \infty} \inf x_i(t) > 0$, for
 all i , and furthermore, since all the solutions to (9) are bounded, there exists a positive
 equilibrium point. We note $(x_1^*(\epsilon), \dots, x_n^*(\epsilon))$ an equilibrium of (9). Now, define the
 map:

$$\Upsilon_i :]0, +\infty[\rightarrow \mathbb{R}, \quad \Upsilon_i(\xi) = \Psi_i(\xi E^*(\epsilon)),$$

where $\Psi = (\Psi_1, \dots, \Psi_n)$ denote the vector field associated to (9). We have,

$$\Upsilon_i(\xi) = \begin{cases} \xi x_i^*(\epsilon) \{ \varphi_i(\xi x_i^*(\epsilon)) - \varphi_i(x_i^*(\epsilon)) \}, & i = 1, \dots, s. \\ \xi x_i^*(\epsilon) \{ \varphi_i(x_i^*(\epsilon)) - \varphi_i(\xi x_i^*(\epsilon)) \}, & i = s + 1, \dots, n. \end{cases}$$

By hypotheses H2 and H3, $\frac{d\varphi_i}{dx_i}(x_i) < 0$ for all $i \leq s$, and $\frac{d\varphi_i}{dx_i}(x_i) > 0$ for all $i \geq s + 1$
 respectively, we deduce that:

$$\Upsilon_i(\xi) \begin{cases} > 0 & \text{for } 0 < \xi < 1, \\ < 0 & \text{for } \xi > 1, \end{cases}$$

295 Therefore, according to Theorem A.1, we conclude the proof of theorem. \square

296 As a corollary of the previous theorem we obtain the following result which proven
 297 in [20, Theorem 6.1]:

298 **Corollary 3.1.** *If $s = n$, the model (9) has a unique equilibrium point in the interior*
 299 *of the positive cone, which is GAS.*

Remark 3.1. As it is initialized by Arino [3, Prop. 8] for the system (5), in the irreducible case, we can express the result of Theorem 3.2 using a basic reproduction number \mathcal{R}_0 defined by

$$\mathcal{R}_0 = \rho \left(\left[\Gamma_{ss} + \Gamma_{sp} \{ \text{diag}(-\varphi_{s+1}, \dots, -\varphi_n(0)) - \Gamma_{pp} \}^{-1} \Gamma_{ps} \right]^{-1} \text{diag}(\varphi_1(0), \dots, \varphi_s(0)) \right),$$

300 where the matrices $\Gamma_{ss}, \Gamma_{pp}, \Gamma_{sp}, \Gamma_{ps}$ describe the flux within and between source and
 301 sink patches given by (12).

302 In all of this work, the globally asymptotically stable positive equilibrium of the
 303 system (9) is denoted by $E_n^*(\epsilon) = (x_1^*(\epsilon), \dots, x_n^*(\epsilon))$, and by $T_n^*(\epsilon)$ the total equilibrium
 304 population

$$T_n^*(\epsilon) = \sum_{i=1}^n x_i^*(\epsilon). \quad (18)$$

305 4. Fast diffusion rate

306 The goal in the next is to give the behavior of the model (9) when the growth of
 307 diffusion tend to infinity (i.e $\epsilon \rightarrow \infty$).

308 4.1. Properties of the migration matrix Γ

309 Note that the matrix Γ combines the connection matrix deduced from the graph of
 310 patches, and a description of the intensity of the connections. The connection matrix
 311 of the graph is thus easily reconstructed from Γ by setting diagonal entries in Γ to
 312 zero, and nonzero off diagonal entries to 1. We recall that, if Γ is irreducible, then 0
 313 is a simple eigenvalue of Γ and all non-zero eigenvalues of Γ have negative real part.
 314 Moreover, the kernel of the matrix Γ is generated by a positive vector (see Lemma 2
 315 in [3]). In all of this paper, we denote by $\delta := (\delta_1, \dots, \delta_n)^T$ this positive vector. For the
 316 existence, uniqueness, and positivity of δ see Lemma 1 of Cosner et al. [7], Lemma
 317 4.1 and Lemma 1 of Elbetch et al. [12, 13]. Note that, if the matrix Γ is symmetric,
 318 then $\ker \Gamma$ is generated by $\delta = (1, \dots, 1)^T$. On the other hand, it is shown in Guo et al.
 319 [31, Lemma 2.1] and Gao and Dong [30, Lemma 3.1] that the vector $(\Gamma_{11}^*, \dots, \Gamma_{nn}^*)^T$
 320 is a right eigenvector of Γ associated with the zero eigenvalue. Here, Γ_{ii}^* is the cofactor
 321 of the i -th diagonal entry of Γ , and $\text{sgn}(\Gamma_{ii}^*) = (-1)^{n-1}$. As in our work, the matrix
 322 Γ is assumed to be irreducible, then $(-1)^{n-1}(\Gamma_{11}^*, \dots, \Gamma_{nn}^*)^T$ is strictly positive, i.e
 323 $\delta_i = (-1)^{n-1} \Gamma_{ii}^* > 0$ for all i . Therefore, we have explicit formula for the components
 324 of the vector δ , as functions of the coefficients of Γ , at our disposal. For two patches

325 we have $\delta = (\gamma_{12}, \gamma_{21})^T$, and for three patches we have $\delta = (\delta_1, \delta_2, \delta_3)^T$, where

$$\begin{cases} \delta_1 = \gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{23} + \gamma_{32}\gamma_{13}, \\ \delta_2 = \gamma_{21}\gamma_{13} + \gamma_{21}\gamma_{23} + \gamma_{31}\gamma_{23}, \\ \delta_3 = \gamma_{21}\gamma_{32} + \gamma_{31}\gamma_{12} + \gamma_{31}\gamma_{32}. \end{cases} \quad (19)$$

326 In Lemma 2.1 of Guo et al [31] gives explicit formulas of the components of the vector
327 δ , with respect of the coefficients of γ as follow:

$$\delta_k = \sum_{T \in \mathcal{T}_k} \prod_{(i,j) \in E(T)} \gamma_{ij}, \quad k = 1, \dots, n, \quad (20)$$

328 where \mathcal{T}_k is the set of all directed trees of n vertices rooted at the k -th vertex, and
329 $E(T)$ denotes the set of arcs in a directed tree T .

330 4.2. Two time scale dynamics

331 In this part, we use the theory of singular perturbations to obtain a better under-
332 standing of the behavior of the system (9) in the case of perfect mixing. We have the
333 following result:

334 **Theorem 4.1.** *Let $(x_1(t, \epsilon), \dots, x_n(t, \epsilon))$ be the solution of the system (9) with initial*
335 *condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1 \dots n$. Let $Y(t)$ be the solution of the*
336 *equation*

$$\left(\sum_{i=1}^n \delta_i \right) \frac{dX}{dt} = X \left(\sum_{i=1}^s \delta_i \varphi_i \left(\frac{\delta_i}{\sum_{i=1}^n \delta_i} X \right) - \sum_{i=s+1}^n \delta_i \varphi_i \left(\frac{\delta_i}{\sum_{i=1}^n \delta_i} X \right) \right), \quad (21)$$

337 with initial condition $X_0 = \sum_{i=1}^n x_i^0$. Then, when $\epsilon \rightarrow \infty$, we have

$$\sum_{i=1}^n x_i(t, \epsilon) = Y(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (22)$$

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

$$x_i(t, \epsilon) = \frac{\delta_i}{\sum_{i=1}^n \delta_i} Y(t) + o_\epsilon(1), \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \quad (23)$$

339 **Proof.** Let $X(t, \epsilon) = \sum_{i=1}^n x_i(t, \epsilon)$. We rewrite the system (9) using the variables

340 (X, x_1, \dots, x_{n-1}) . One obtains:

$$\begin{cases} \frac{dX}{dt} = \sum_{i=1}^s x_i \varphi_i(x_i) - \sum_{i=s+1}^n x_i \varphi_i(x_i), \\ \frac{dx_i}{dt} = x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = 1, \dots, s. \\ \frac{dx_i}{dt} = -x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = s+1, \dots, n-1. \end{cases} \quad (24)$$

341 This system is actually a system in the variables (X, x_1, \dots, x_{n-1}) , since, whenever
342 x_n appears in the right hand side of (24), it should be replaced by

$$x_n = X - \sum_{i=1}^{n-1} x_i. \quad (25)$$

343 When $\epsilon \rightarrow \infty$, (24) is a *slow-fast* system, with one *slow variable*, X , and $n-1$ *fast*
344 *variables*, x_i for $i = 1 \dots n-1$. According to Tikhonov's theorem [36, 47, 48] we
345 consider the dynamics of the fast variables in the time scale $\tau = \epsilon t$. One obtains

$$\begin{cases} \frac{dx_i}{d\tau} = \frac{1}{\epsilon} x_i \varphi_i(x_i) + \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = 1 \dots s. \\ \frac{dx_i}{d\tau} = -\frac{1}{\epsilon} x_i \varphi_i(x_i) + \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = s+1 \dots n-1. \end{cases} \quad (26)$$

346 where x_n is given by (25). In the limit $\epsilon \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_i}{d\tau} = \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), \quad i = 1, \dots, n-1. \quad (27)$$

347 This is an $n-1$ dimensional linear system differential. According to Lemma 3.9 of
348 Elbetch et al. [13], the slow manifold of system (24), which is the equilibrium point of
349 the fast dynamics (27), is unique and is given by:

$$x_i = \frac{\delta_i}{\sum_{i=1}^n \delta_i} X, \quad i = 1, \dots, n-1. \quad (28)$$

350 As this manifold is GAS, the theorem of Tikhonov ensures that after a fast transition
351 toward the slow manifold, the solutions of (24) are approximated by the solutions of
352 the *reduced model* which is obtained by replacing (28) into the dynamics of the slow
353 variable, which gives the equation (21).

Let we denote Ω the function

$$\Omega(X) := \sum_{i=1}^s \delta_i \varphi_i \left(\frac{\delta_i}{\sum_{i=1}^n \delta_i} X \right) - \sum_{i=s+1}^n \delta_i \varphi_i \left(\frac{\delta_i}{\sum_{i=1}^n \delta_i} X \right).$$

We have $\Omega(0) = \sum_{i=1}^s \delta_i \varphi_i(0) - \sum_{i=s+1}^n \delta_i \varphi_i(0)$, $\frac{d\Omega}{dX} < 0$ and $\Omega \rightarrow -\infty$ when $X \rightarrow +\infty$.

So by the intermediate value theorem, if $\Omega(0) > 0$, then there exists unique point $X^* > 0$ such that $\Omega(X^*) = 0$. Else, $\Omega(X) \leq 0$ for all X . Therefore, if $\sum_{i=1}^s \delta_i \varphi_i(0) >$

$\sum_{i=s+1}^n \delta_i \varphi_i(0)$, then (21) admits

$$X^* = \left(\sum_{i=1}^n \delta_i \right) \lambda_0$$

354 as a positive equilibrium point, which is GAS in the positive axis, where $\lambda_0 > 0$ is the
355 unique solution in the positive axis of the following equation:

$$\sum_{i=1}^s \delta_i \varphi_i(\delta_i x) - \sum_{i=s+1}^n \delta_i \varphi_i(\delta_i x) = 0. \quad (29)$$

356 If $\sum_{i=1}^s \delta_i \varphi_i(0) \leq \sum_{i=s+1}^n \delta_i \varphi_i(0)$, then (21) admits the origin as unique equilibrium point,

357 which is GAS. The approximation given by Tikhonov's theorem holds for all $t \geq 0$ for
358 the slow variable and for all $t \geq t_0 > 0$ for the fast variables, where t_0 is as small as we
359 want. Therefore, let $Y(t)$ be the solution of the reduced model (21) of initial condition

360 $Y(0) = X(0, \epsilon) = \sum_{i=1}^n x_i^0$, then, when $\epsilon \rightarrow \infty$, we have the approximations (22) and

361 (23). □

362 Approximation (23) shows that, with the exception of a thin initial boundary layer,
363 where the density population $x_i(t, \epsilon)$ quickly jumps from its initial condition x_i^0 to the
364 average $\delta_i X_0 / \sum_{i=1}^n \delta_i$, each patch of the n-patch source-sink model behaves like the
365 following equation:

$$\left(\sum_{i=1}^n \delta_i \right) \frac{du}{dt} = u \left(\sum_{i=1}^s \delta_i \varphi_i(u) - \sum_{i=s+1}^n \delta_i \varphi_i(u) \right). \quad (30)$$

366 Hence, when t and ϵ tend to ∞ , the density population $x_i(t, \epsilon)$ tends toward $K =$
367 $\delta_i \lambda_0$, if $\sum_{i=1}^s \delta_i \varphi_i(0) > \sum_{i=s+1}^n \delta_i \varphi_i(0)$, and $x_i(t, \epsilon)$ tends toward 0 if $\sum_{i=1}^s \delta_i \varphi_i(0) \leq$
368 $\sum_{i=s+1}^n \delta_i \varphi_i(0)$.

369 According to the previous theorem, we obtain the limit $E^*(\infty)$ of $E^*(\epsilon)$ when $\epsilon \rightarrow$
370 ∞ :

371 **Corollary 4.1.** *We have:*

$$\lim_{\epsilon \rightarrow +\infty} E^*(\epsilon) = \begin{cases} \lambda_0(\delta_1, \dots, \delta_n), & \text{if } \sum_{i=1}^s \delta_i \varphi_i(0) > \sum_{i=s+1}^n \delta_i \varphi_i(0), \\ 0 & \text{otherwise,} \end{cases} \quad (31)$$

372 where $(\delta_1, \dots, \delta_n)$ the vector which generate the kernel of Γ . Moreover, if the matrix

373 Γ is symmetric, then:

$$\lim_{\epsilon \rightarrow +\infty} E^*(\epsilon) = \begin{cases} \lambda_0(1, \dots, 1), & \text{if } \sum_{i=1}^s \varphi_i(0) > \sum_{i=s+1}^n \varphi_i(0), \\ 0 & \text{otherwise.} \end{cases} \quad (32)$$

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

376 **Corollary 4.2.** *We have*

$$T_n^*(+\infty) = \begin{cases} (\sum_{i=1}^n \delta_i) \lambda_0 & \text{if } \sum_{i=1}^s \delta_i \varphi_i(0) > \sum_{i=s+1}^n \delta_i \varphi_i(0), \\ 0, & \text{otherwise.} \end{cases} \quad (33)$$

377 *Moreover, if the matrix Γ is symmetric, then:*

$$T_n^*(+\infty) = \begin{cases} n\lambda_0, & \text{if } \sum_{i=1}^s \varphi_i(0) > \sum_{i=s+1}^n \varphi_i(0), \\ 0, & \text{otherwise.} \end{cases} \quad (34)$$

378 **Proof.** The sum of the n components of the point $E^*(\infty)$ immediately gives Formula
379 (33). \square

In the case $n = 2$ and $s = 1$, one has $\delta_1 = \gamma_{12}$ and $\delta_2 = \gamma_{21}$. Therefore (33) becomes

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

which is the formula given by Wu et al. [49, Equation 5.8]. In the case $n = s = 2$,
Formula (33) becomes

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

380 which is the formula given by Arditi et al. [2, Equation 7].

In the case of the multi-patch logistic model with asymmetric migration, i.e. the
model (9) with $s = n$, Formula (33) becomes

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

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

382 When the movement pattern of individuals among n patches is symmetric, the
383 previous theorem becomes:

384 **Theorem 4.2.** *Assume that the matrix Γ is symmetric. Let $(x_1(t, \epsilon), \dots, x_n(t, \epsilon))$ be*
385 *the solution of the system (9) with initial condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for*
386 *$i = 1 \dots n$. Let $Y(t)$ be the solution of the equation*

$$\frac{dX}{dt} = \frac{1}{n} X \left(\sum_{i=1}^s \varphi_i \left(\frac{1}{n} X \right) - \sum_{i=s+1}^n \varphi_i \left(\frac{1}{n} X \right) \right), \quad (35)$$

387 with initial condition $X_0 = \sum_{i=1}^n x_i^0$. Then, when $\epsilon \rightarrow \infty$, we have

$$\sum_{i=1}^n x_i(t, \epsilon) = Y(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (36)$$

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

$$x_i(t, \epsilon) = \frac{1}{n} Y(t) + o_\epsilon(1), \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \quad (37)$$

389 **Proof.** If the matrix Γ is symmetric, then $\delta = (1, \dots, 1)^T$. □

390 As a corollary of the previous theorem we obtain the following result which describes
391 the total equilibrium population for perfect mixing when the dispersal is symmetric.
392 We can state this result as follows:

393 **Corollary 4.3.** *If $\sum_{i=1}^s \varphi_i(0) > \sum_{i=s+1}^n \varphi_i(0)$ then, the total equilibrium population
394 for perfect mixing $T_n^*(+\infty)$ satisfied:*

$$\sum_{i=1}^s \varphi_i \left(\frac{T_n^*(+\infty)}{n} \right) = \sum_{i=s+1}^n \varphi_i \left(\frac{T_n^*(+\infty)}{n} \right). \quad (38)$$

395 **Proof.** If the matrix Γ is symmetric, then $\delta = (1, \dots, 1)^T$. The equation (21) prove
396 that $T_n^*(+\infty)$ is satisfied by Equation (38). □

397 5. Total equilibrium population

398 In this section, our aim is to compare the total equilibrium population T_n^* with the
399 sum of carrying capacities of source patches $T_n^*(0) = K_1 + \dots + K_s$, when the rate of
400 migration ϵ varies from zero to infinity. First, we compute the derivative of T_n^* at no
401 dispersal.

402 5.1. Derivative of T_n^* at no dispersal

Proposition 5.1. *The derivative of the total equilibrium population T_n^* at $\epsilon = 0$ is given by:*

$$\begin{aligned} \frac{dT_n^*}{d\epsilon}(0) &= - \sum_{i=1}^s \left(\frac{1}{K_i \frac{d\varphi_i}{dx_i}(K_i)} \sum_{j=1, j \neq i}^s (\gamma_{ij} K_j - \gamma_{ji} K_i) \right) + \sum_{i=s+1}^n \left(\frac{1}{\varphi_i(0)} \sum_{j=1, j \neq i}^s (\gamma_{ij} K_j - \gamma_{ji} K_i) \right) \\ &= \left(-\frac{1}{K_1 \frac{d\varphi_1}{dx_1}(K_1)}, \dots, -\frac{1}{K_s \frac{d\varphi_s}{dx_s}(K_s)}, \frac{1}{\varphi_{s+1}(0)}, \dots, \frac{1}{\varphi_n(0)} \right) \Gamma(K_1, \dots, K_s, 0, \dots, 0)^T. \end{aligned} \quad (39)$$

403 **Proof.** The equilibrium point $E_n^*(\epsilon)$ is the solution of the algebraic system:

$$\begin{cases} x_i^*(\epsilon)\varphi_i(x_i^*(\epsilon)) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)) = 0, & i = 1, \dots, s, \\ -x_i^*(\epsilon)\varphi_i(x_i^*(\epsilon)) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)) = 0, & i = s+1, \dots, n. \end{cases} \quad (40)$$

The derivative of the first equation in (40) with respect to ϵ give:

$$\begin{aligned} & \varphi_i(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) + x_i^*(\epsilon) \frac{d\varphi_i}{dx_i^*}(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) + \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)) \\ & + \epsilon \sum_{j=1, j \neq i}^n \left(\gamma_{ij} \frac{dx_j^*}{d\epsilon}(x_i^*(\epsilon)) - \gamma_{ji} \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) \right) = 0, \quad i = 1, \dots, s, \end{aligned}$$

and, the derivative of the second equation in (40) with respect to ϵ give:

$$\begin{aligned} & -\varphi_i(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) - x_i^*(\epsilon) \frac{d\varphi_i}{dx_i^*}(x_i^*(\epsilon)) \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) + \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(\epsilon) - \gamma_{ji}x_i^*(\epsilon)) \\ & + \epsilon \sum_{j=1, j \neq i}^n \left(\gamma_{ij} \frac{dx_j^*}{d\epsilon}(x_i^*(\epsilon)) - \gamma_{ji} \frac{dx_i^*}{d\epsilon}(x_i^*(\epsilon)) \right) = 0, \quad i = s+1, \dots, n. \end{aligned}$$

For $\epsilon = 0$, we obtain

$$\begin{cases} \varphi_i(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) + x_i^*(0) \frac{d\varphi_i}{dx_i^*}(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) + \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(0) - \gamma_{ji}x_i^*(0)) = 0, & i = 1, \dots, s, \\ -\varphi_i(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) - x_i^*(0) \frac{d\varphi_i}{dx_i^*}(x_i^*(0)) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) + \sum_{j=1, j \neq i}^n (\gamma_{ij}x_j^*(0) - \gamma_{ji}x_i^*(0)) = 0, & i = s+1, \dots, n. \end{cases}$$

Since $x_i^*(0) = K_i$ for all $i \leq s$ and $x_i^*(0) = 0$ for all $i \geq s+1$ then $\varphi_i(K_i) = 0$, and

$$\begin{cases} K_i \frac{d\varphi_i}{dx_i^*}(K_i) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) + \sum_{j=1, j \neq i}^s (\gamma_{ij}K_j - \gamma_{ji}K_i) = 0, & i = 1, \dots, s, \\ -\varphi_i(0) \frac{dx_i^*}{d\epsilon}(x_i^*(0)) + \sum_{j=1, j \neq i}^s (\gamma_{ij}K_j - \gamma_{ji}K_i) = 0, & i = s+1, \dots, n. \end{cases}$$

404 By summing the previous equations for $i = 1, \dots, n$ we obtain the formula of the
405 derivative (39). □

406 The formula (39) is an extension of the one obtained by Arditi et al. [1, 2] for two-
407 patch logistic model, the results of Elbetch [14] for two-patch Richard model, Elbetch
408 et al. [13, Equation 28] for multi-patch logistic model and also the result of Elbetch
409 [20, Equation 44] for multi-patch generalized logistic model.

In the rest of this section, we show that the total equilibrium population, $T_n^*(\epsilon)$, is generally different from the sum of the carrying capacities, $T_n^*(0)$, of the source patches. Depending on the kernel of the matrix Γ , the intrinsic growth and death functions, $T_n^*(\epsilon)$ can either be smaller than, or equal to the sum of the carrying capacities of the source patches. If the equilibrium $E^*(\epsilon)$ exist, then it is a solution of the algebraic

system:

$$\begin{cases} 0 = x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = 1, \dots, s, \\ 0 = -x_i \varphi_i(x_i) + \epsilon \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j - \gamma_{ji} x_i), & i = s+1, \dots, n. \end{cases}$$

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

$$\sum_{i=1}^s x_i \varphi_i(x_i) - \sum_{i=s+1}^n x_i \varphi_i(x_i) = 0. \quad (41)$$

411 Therefore $E_n^*(\epsilon)$ belongs to the locus of points described by the equation (41) consists
412 of the origin together with a connected $(n-1)$ -dimension surface denoted by:

$$\mathbb{S} := \left\{ x \in \mathbb{R}_+^n : \Theta(x) := \sum_{i=1}^s x_i \varphi_i(x_i) - \sum_{i=s+1}^n x_i \varphi_i(x_i) = 0 \right\}, \quad (42)$$

413 which passes through all boundary equilibria together with the equilibrium
414 $(K_1, \dots, K_s, 0, \dots, 0)$. Note that this surface is independent of the migration terms
415 ϵ and γ_{ij} . In all of the rest, we assume that \mathbb{S} is compact and convex. Let us start by
416 the following situation:

417 5.2. Homogeneous source-sink system

418 **Proposition 5.2.** Consider System (9). If $-K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = -K_s \frac{d\varphi_s}{dx_s}(K_s) =$
419 $\varphi_{s+1}(0) = \dots = \varphi_n(0)$, then $T_n^*(\epsilon) \leq \sum_{i=1}^s K_i$ for all $\epsilon \geq 0$, and $\frac{dT_n^*}{d\epsilon}(0) = 0$. Moreover,

- 420 • If $\sum_{i=1}^s \delta_i \varphi_i(0) \leq \sum_{i=s+1}^n \delta_i \varphi_i(0)$, then there is $\epsilon^* > 0$ such that, $T_n^*(\epsilon) > 0$ for
421 $\epsilon < \epsilon^*$, and $T_n^*(\epsilon) = 0$, for $\epsilon \geq \epsilon^*$.
- 422 • If $\sum_{i=1}^s \delta_i \varphi_i(0) > \sum_{i=s+1}^n \delta_i \varphi_i(0)$, then $T_n^*(\epsilon) > 0$ for all $\epsilon \geq 0$.

423 **Proof.** The equation of the tangent space to the surface \mathbb{S} , defined by (42), at point
424 $\mathcal{A}_s = (K_1, \dots, K_s, 0, \dots, 0)$ is given by

$$\sum_{i=1}^s (x_i - K_i) \frac{\partial \Theta}{\partial x_i}(\mathcal{A}_s) + \sum_{i=s+1}^n x_i \frac{\partial \Theta}{\partial x_i}(\mathcal{A}_s) = 0, \quad (43)$$

425 where Θ is given by Equation (42). Since $\frac{\partial \Theta}{\partial x_i}(\mathcal{A}_s) = -K_i \frac{d\varphi_i}{dx_i}(K_i)$ for all $i = 1, \dots, s$
426 and $\frac{\partial \Theta}{\partial x_i}(\mathcal{A}_s) = \varphi_i(0)$ for all $i = s+1, \dots, n$, Equation (43) can be written as follows:

$$\sum_{i=1}^s -K_i \frac{d\varphi_i}{dx_i}(K_i)(x_i - K_i) + \sum_{i=s+1}^n \varphi_i(0)x_i = 0. \quad (44)$$

If we take $-K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = -K_s \frac{d\varphi_s}{dx_s}(K_s) = \varphi_{s+1}(0) = \dots = \varphi_n(0)$, in Equation

(44), we get that the equation of the tangent plane to surface \mathbb{S} at the point \mathcal{A}_s is

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

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

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

427 Now, according to the formula of perfect mixing (33), we can see immediately that
 428 $T_n^*(+\infty) = 0$ if and only if $\sum_{i=1}^s \delta_i \varphi_i(0) = \sum_{i=s+1}^n \delta_i \varphi_i(0)$.

If $-K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = -K_s \frac{d\varphi_s}{dx_s}(K_s) = \varphi_{s+1}(0) = \dots = \varphi_n(0) =: r$, then the formula of the derivative (39) at $\epsilon = 0$ becomes

$$\frac{dT_n^*}{d\epsilon}(0) = \frac{1}{r} (1, \dots, 1) \Gamma(K_1, \dots, K_s, 0, \dots, 0)^T = 0.$$

429 This completes the proof of the proposition. □

430 Note that, the result of the previous proposition is also obtained by Arditi et al.
 431 [1, 2] for two-patch logistic model and by Elbetch et al. [12, 13] for n-patch model
 432 with logistic dynamic $\varphi_i(x_i) = r_i - r_i/K_i x_i$. They proved that, if the growth rates r_i
 433 are equal in all patches, then the total equilibrium population is always smaller than
 434 the sum of the carrying capacities. In the case when $s = n$, the previous proposition
 435 becomes: if $K_1 \frac{d\varphi_1}{dx_1}(K_1) = \dots = K_n \frac{d\varphi_n}{dx_n}(K_n)$, then $0 < T_n^*(\epsilon) \leq \sum_i K_i$, which is [20,
 436 Prop. 13].

437 5.3. Heterogeneous source-sink system

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

445 **Proposition 5.3.** *The equilibrium $E^*(\epsilon)$ does not depend on ϵ if and only if, $s = n$
 446 and $(K_1, \dots, K_n) \in \ker \Gamma$. In this case $E^*(\epsilon) = (K_1, \dots, K_n)$ for all $\epsilon > 0$.*

447 **Proof.** The equilibrium $E^*(\epsilon) := (X_s^*(\epsilon); X_p^*(\epsilon))$, where $X_s^*(\epsilon) = (x_1^*(\epsilon), \dots, x_s^*(\epsilon))$
 448 and $X_p^*(\epsilon) = (x_{s+1}^*(\epsilon), \dots, x_n^*(\epsilon))$, is the unique positive solution of the system (9), i.e:

$$\begin{cases} 0 = \text{diag}(\varphi_1(x_1^*(\epsilon)), \dots, \varphi_s(x_s^*(\epsilon))) X_s^*(\epsilon) + \epsilon (\Gamma_{ss} X_s^*(\epsilon) + \Gamma_{sp} X_p^*(\epsilon)), \\ 0 = -\text{diag}(\varphi_1(x_1^*(\epsilon)), \dots, \varphi_s(x_s^*(\epsilon))) X_s^*(\epsilon) + \epsilon (\Gamma_{ps} X_s^*(\epsilon) + \Gamma_{pp} X_p^*(\epsilon)). \end{cases} \quad (45)$$

449 Suppose that the equilibrium $E^*(\epsilon)$ does not depend on ϵ . The derivative of (45) with

450 respect to ϵ gives:

$$\begin{cases} 0 = \Gamma_{ss}X_s^*(\epsilon) + \Gamma_{sp}X_p^*(\epsilon) \\ 0 = \Gamma_{ps}X_s^*(\epsilon) + \Gamma_{pp}X_p^*(\epsilon) \end{cases} \Leftrightarrow \begin{bmatrix} \Gamma_{ss} & \Gamma_{sp} \\ \Gamma_{ps} & \Gamma_{pp} \end{bmatrix} \begin{bmatrix} X_s^*(\epsilon) \\ X_p^*(\epsilon) \end{bmatrix} = 0 \Leftrightarrow \Gamma E^*(\epsilon) = 0. \quad (46)$$

451 Replacing Equation (46) in (45), we get $E^*(\epsilon) = (K_1, \dots, K_s, 0, \dots, 0)$. From Equation
 452 (46), we conclude that $(K_1, \dots, K_s, 0, \dots, 0) \in \ker \Gamma$. Since the vector space $\ker \Gamma$ is
 453 generated by a positive vector, then $(K_1, \dots, K_s, 0, \dots, 0) \in \ker \Gamma$ is hold if and only
 454 if, $s = n$.

455 Now, suppose that $s = n$ and $(K_1, \dots, K_n) \in \ker \Gamma$, then (K_1, \dots, K_n) satisfies
 456 Equation (45), for all $\epsilon \geq 0$. So, $E^*(\epsilon) = (K_1, \dots, K_n)$, for all $\epsilon \geq 0$, which proves that
 457 the total equilibrium population is independent of the migration rate ϵ . \square

458 When all the patches are sources and the vector of the carrying capacities lies in
 459 the vector space $\ker \Gamma$, we obtain the results proved by Elbetch et al. [12, Prop. 3.2
 460], [13, Prop. 4.5] and [20, Prop. 15].

461 **5.4. Two blocks of identical source and sink patches**

462 We consider the model of source-sink patches (9) and we assume that we have one
 463 block of identical source patches and one block of identical sink patches. We denote
 464 by $I_{so} = \{1, \dots, s\}$ and $I_{si} = \{s + 1, \dots, n\}$ for the block of the source patches and
 465 sink patches respectively such that $I_{so} \cup I_{si} = \{1, \dots, n\}$. The source patches being
 466 identical means that they have the same growth functions φ_i . Therefore, we have

$$\varphi_1 = \dots = \varphi_s =: \varphi_{so}. \quad (47)$$

467 The same for the sink patches, we suppose that:

$$\varphi_{s+1} = \dots = \varphi_n =: \varphi_{si}. \quad (48)$$

468 First, we give some definitions:

Definition 5.1. Let the flux

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

- 469 • For $i \in I_{so}$, $\Gamma_{iI_{si}}$ is the flux from block I_{si} to patch i , i.e. the sum of the migration
 470 rates γ_{ij} from patches $j \in I_{si}$ to patch i .
- 471 • For $j \in I_{si}$, $\Gamma_{jI_{so}}$ is the flux from block I_{so} to patch j , i.e. the sum of the migration
 472 rates γ_{ji} from patches $i \in I_{so}$ to patch j .
- 473 • $\Gamma_{I_{so}I_{si}}$ is the flux from block I_{si} to block I_{so} , i.e. the sum of the migration rates
 474 γ_{ij} from patches $j \in I_{si}$, to patches $i \in I_{so}$.
- 475 • $\Gamma_{I_{si}I_{so}}$ is the flux from block I_{so} to block I_{si} , i.e. the sum of the migration rates
 476 γ_{ji} from patches $i \in I_{so}$, to patches $j \in I_{si}$.

For each patch i we denote by \mathcal{T}_i the sum of all migration rates γ_{ji} from patch i to
 another patch $j \neq i$ (i.e. the outgoing flux of patch i) minus the sum of the migration

rates γ_{ik} from patch k to patch i , where k belongs to the same block as i . Hence, we have:

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

477 We make the following assumption on the migration rates

$$\begin{aligned} \Gamma_{1I_{si}} = \dots = \Gamma_{sI_{si}}, \quad \Gamma_{(s+1)I_{so}} = \dots = \Gamma_{nI_{so}} \\ \mathcal{T}_1 = \dots = \mathcal{T}_s, \quad \mathcal{T}_{s+1} = \dots = \mathcal{T}_n \end{aligned} \quad (49)$$

478 If Conditions (49) are satisfied, then, according to [13, Lemma 4.6], for all $i \in I_{so}$ and
479 $j \in I_{si}$ one has

$$\Gamma_{iI_{si}} = \Gamma_{I_{so}I_{si}}/s, \quad \Gamma_{jI_{so}} = \Gamma_{I_{si}I_{so}}/\bar{s}, \quad \mathcal{T}_i = \Gamma_{I_{si}I_{so}}/s, \quad \mathcal{T}_j = \Gamma_{I_{so}I_{si}}/\bar{s}. \quad (50)$$

480 where $\bar{s} = n - s$, $\Gamma_{I_{so}I_{si}}$ and $\Gamma_{I_{si}I_{so}}$ are defined in Definition 5.1. We have the following
481 result

Theorem 5.1. *Assume that Conditions (47),(48) and (49) are satisfied. If System (9) admits unique equilibrium point in the interior of the positive cone, then is of the form*

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

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

$$\begin{cases} \frac{dx_{so}}{dt} = sx_{so}\varphi_{so}(x_{so}) + \epsilon(\Gamma_{I_{so}I_{si}}x_{si} - \Gamma_{I_{si}I_{so}}x_{so}), \\ \frac{dx_{si}}{dt} = -\bar{s}x_{si}\varphi_{si}(x_{si}) + \epsilon(\Gamma_{I_{si}I_{so}}x_{so} - \Gamma_{I_{so}I_{si}}x_{si}), \end{cases} \quad (51)$$

483 with specific growth rate $sx_{so}\varphi_{so}(x_{so})$ and death rate $\bar{s}x_{si}\varphi_{si}(x_{si})$, migration rates
484 $\Gamma_{I_{si}I_{so}}$ from source to the sink patch and $\Gamma_{I_{so}I_{si}}$ from the sink to the source patch.

485 **Proof.** Assume that Conditions (47) and (48) are satisfied. Then, if the interior equi-
486 librium point of (9) exist, it is the unique positive solution of the set of algebraic
487 equations

$$\begin{cases} x_i\varphi_{so}(x_i) + \epsilon \sum_{k=1, k \neq i}^n (\gamma_{ik}x_k - \gamma_{ki}x_i) = 0, & i = 1, \dots, s, \\ -x_i\varphi_{si}(x_i) + \epsilon \sum_{k=1, k \neq i}^n (\gamma_{ik}x_k - \gamma_{ki}x_i) = 0, & i = s+1, \dots, n. \end{cases} \quad (52)$$

488 We consider the following set of algebraic equations obtained from (52) by replacing

489 $x_i = x_{so}$ for $i = 1, \dots, s$ and $x_i = x_{si}$ for $i = s + 1, \dots, n$:

$$\begin{cases} x_{so}\varphi_{so}(x_{so}) + \epsilon \sum_{k=1, k \neq i}^n (\gamma_{ik}x_{si} - \gamma_{ki}x_{so}) = 0, & i = 1, \dots, s, \\ -x_{si}\varphi_{si}(x_{si}) + \epsilon \sum_{k=1, k \neq i}^n (\gamma_{ik}x_{so} - \gamma_{ki}x_{si}) = 0, & i = s + 1, \dots, n. \end{cases} \quad (53)$$

490 Now, using Condition (49), together with (50), we see that System (53) is equivalent
491 to the set of two algebraic equations:

$$\begin{cases} x_{so}\varphi_{so}(x_{so}) + \epsilon \left(\frac{\Gamma_{I_{so}I_{si}}}{s} x_{si} - \frac{\Gamma_{I_{si}I_{so}}}{s} x_{so} \right) = 0, \\ -x_{si}\varphi_{si}(x_{si}) + \epsilon \left(\frac{\Gamma_{I_{si}I_{so}}}{\bar{s}} x_{so} - \frac{\Gamma_{I_{so}I_{si}}}{\bar{s}} x_{si} \right) = 0. \end{cases} \quad (54)$$

492 Therefore, if $x_{so} = x_{so}^*$, $x_{si} = x_{si}^*$ is a positive solution of (54) then $x_i = x_{so}^*$ for
493 $i = 1, \dots, s$ and $x_i = x_{si}^*$ for $i = s + 1, \dots, n$ is a positive solution of (52). \square

494 As a corollary of the previous theorem:

Corollary 5.1. *Assume that Conditions (47), (48) and (49) are satisfied. Then, the total equilibrium population*

$$T_n^*(\epsilon) = sx_{so}^*(\epsilon) + \bar{s}x_{si}^*(\epsilon)$$

495 of (9) behaves like the total equilibrium population of the following Two-patch source-
496 sink model

$$\begin{cases} \frac{dy_{so}}{dt} = y_{so}\varphi_{so}\left(\frac{y_{so}}{s}\right) + \epsilon(\gamma_2 y_{si} - \gamma_1 y_{so}), \\ \frac{dy_{si}}{dt} = -y_{si}\varphi_{si}\left(\frac{y_{si}}{\bar{s}}\right) + \epsilon(\gamma_1 y_{so} - \gamma_2 y_{si}). \end{cases} \quad (55)$$

497 with migration rates $\gamma_1 = \frac{\Gamma_{I_{si}I_{so}}}{s}$, $\gamma_2 = \frac{\Gamma_{I_{so}I_{si}}}{\bar{s}}$.

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

$$\begin{cases} 0 = sx_{so}\varphi_{so}(x_{so}) + \epsilon(\Gamma_{I_{so}I_{si}}x_{si} - \Gamma_{I_{si}I_{so}}x_{so}), \\ 0 = -\bar{s}x_{si}\varphi_{si}(x_{si}) + \epsilon(\Gamma_{I_{si}I_{so}}x_{so} - \Gamma_{I_{so}I_{si}}x_{si}), \end{cases} \quad (56)$$

499 Therefore $(y_{so}^* = sx_{so}^*, y_{si}^* = \bar{s}x_{si}^*)$ is the solution of the set of equations

$$\begin{cases} y_{so}\varphi_{so}\left(\frac{y_{so}}{s}\right) + \epsilon(\gamma_2 y_{si} - \gamma_1 y_{so}) = 0, \\ -y_{si}\varphi_{si}\left(\frac{y_{si}}{\bar{s}}\right) + \epsilon(\gamma_1 y_{so} - \gamma_2 y_{si}) = 0, \end{cases} \quad (57)$$

500 obtained from (56) by using the change of variables $y_{so} = sx_{so}$, $y_{si} = \bar{s}x_{si}$. \square

501 **6. The growth and death rates with two different scales**

502 Recently, in [19], Elbetch is interested in some biological situations that can be found
 503 in the nature, that is, the case where several sub-populations grow with different speed.
 504 Mathematically speaking, he studied the system (8) under the hypothesis that some
 505 growth rates tend to infinity (i.e $r_i \rightarrow \infty$ for some i). In two following sections, we
 506 consider the model (9) and we assume that the death rates (resp. growth rates) are
 507 much larger than growth rates (resp. death rates).

508 **6.1. Death rates are much larger than the growth rates**

509 In this part, we consider the multi-patch source-sink model (9) and we assume that
 510 the death rates of the sink patches are much larger than the growth rates of the source
 511 patches. Under this assumption, one can write the model in the matrix form as follow:

$$\begin{cases} \dot{X}_s = \text{diag}(\varphi_1(x_1), \dots, \varphi_s(x_s)) X_s + \epsilon (\Gamma_{ss} X_s + \Gamma_{sp} X_p), \\ \dot{X}_p = \frac{1}{\eta} \text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p + \epsilon (\Gamma_{ps} X_s + \Gamma_{pp} X_p), \end{cases} \quad (58)$$

512 where η is assumed to be a small positive number and the point denotes the derivative
 513 with respect to t . We have the following result:

514 **Theorem 6.1.** *Let $(x_1(t, \eta), \dots, x_n(t, \eta))$ be the solution of System (58) with initial*
 515 *condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1, \dots, n$. Let $u(t) = (u_1(t), \dots, u_s(t))$*
 516 *be the solution of the following differential system*

$$\dot{X}_s = \text{diag}(\varphi_1(x_1), \dots, \varphi_s(x_s)) X_s + \epsilon \Gamma_{ss}, \quad (59)$$

517 *with initial condition $u(0) = (x_1^0, \dots, x_s^0)$, $X_s = (x_1, \dots, x_s)^T$ and Γ_{ss} is the sub matrix*
 518 *of Γ defined by (12). Then, when $\eta \rightarrow 0$, we have*

$$x_i(t, \eta) = u_i(t) + o_\eta(1), \quad i = 1, \dots, s \quad \text{uniformly for } t \in [0, T], \quad (60)$$

519 *and*

$$x_i(t, \eta) = o_\eta(1), \quad i = s + 1, \dots, n, \quad (61)$$

520 *uniformly for $t \in [t_0, T]$, where $0 < t_0 < T$ are arbitrary but fixed and independent of*
 521 *η . If the solution $u_s(t)$ of the reduced problem converges to an asymptotically stable*
 522 *equilibrium, then we can put $T = +\infty$ in Approximations (60) and (61).*

523 **Proof.** When $\eta \rightarrow 0$, System (58) is a *slow-fast* system, with x_1, \dots, x_s are slow
 524 variables, and x_{s+1}, \dots, x_n fast variables. Tikhonov's theorem [36, 47, 48] prompts us
 525 to consider the dynamics of the fast variables in the time scale $\tau = \frac{1}{\eta}t$. One obtains

$$\dot{X}_p = \text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p + \epsilon \eta (\Gamma_{ps} X_s + \Gamma_{pp} X_p), \quad (62)$$

526 where the point denotes the derivative of X_p with respect to τ . In the limit $\eta \rightarrow 0$, we
 527 find the fast dynamics

$$\dot{X}_p = \text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p. \quad (63)$$

528 The slow manifold is given by the equilibrium of System (63), i.e $X_p^* = 0$, which is LAS
529 in the positive axis. When η goes to zero, Tikhonov's theorem ensures that after a fast
530 transition toward the slow manifold, the solutions of (58) converge to the solutions of
531 the *reduced model* (59), obtained by replacing $X_p = 0$ into the dynamics of the slow
532 variable. Approximations (60) and (61) follow from Tikhonov's Theorem. Recall that
533 when the reduced problem (59) has an asymptotically stable equilibrium, then these
534 approximations hold for all $t > 0$ and not only on a compact interval $[0, T]$. Recall
535 also that there is a boundary layer for the fast variables, that is Approximations (61)
536 hold only for $t > t_0$ where $t_0 > 0$ can be arbitrarily small but fixed. \square

537 6.2. Growth rates are much larger than the death rates

538 In this part, we consider the multi-patch source-sink model (9) and we assume that
539 the growth rates of the source patches are much larger than the death rates of the
540 sink patches. Under this assumption, one can write the model in the matrix form as
541 follow:

$$\begin{cases} \dot{X}_s = \frac{1}{\eta} \text{diag}(\varphi_1(x_1), \dots, \varphi_s(x_s)) X_s + \epsilon (\Gamma_{ss} X_s + \Gamma_{sp} X_p), \\ \dot{X}_p = \text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p + \epsilon (\Gamma_{ps} X_s + \Gamma_{pp} X_p), \end{cases} \quad (64)$$

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

543 **Theorem 6.2.** *Let $(x_1(t, \eta), \dots, x_n(t, \eta))$ be the solution of System (58) with initial*
544 *condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1, \dots, n$.*
545 *Let $u(t) = (u_{s+1}(t), \dots, u_n(t))$ be the solution of the differential system*

$$\dot{X}_p = -\text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) X_p + \epsilon (\Gamma_{ps} \mathcal{K}_s + \Gamma_{pp} X_p), \quad (65)$$

546 *with initial condition $(x_{s+1}^0, \dots, x_n^0)$, $X_p = (x_{s+1}, \dots, x_n)^T$, $\mathcal{K}_s = (K_1, \dots, K_s)^T$, Γ_{pp}*
547 *and Γ_{ps} are the sub matrices of Γ defined by (12). Then, when $\eta \rightarrow 0$, we have*

$$x_i(t, \eta) = K_i + o_\eta(1), \quad i = 1, \dots, s \quad \text{uniformly for } t \in [0, T], \quad (66)$$

548 *and*

$$x_i(t, \eta) = u_i(t) + o_\eta(1), \quad i = s + 1, \dots, n, \quad (67)$$

549 *uniformly for $t \in [t_0, T]$, where $0 < t_0 < T$ are arbitrary but fixed and independent of*
550 *η . If the solution $u_p(t)$ of the reduced problem converges to an asymptotically stable*
551 *equilibrium, then we can put $T = +\infty$ in Approximations (66) and (67).*

552 **Proof.** The proof is the same as Theorem 6.1. \square

553 Our next goal is to prove the global stability of the reduced model (65) under the
554 hypothesis that the two matrices Γ_{pp} and Γ are irreducible. First, we start by the
555 following lemma:

556 **Lemma 6.1.** *Assume that the matrix Γ is irreducible. The reduced model (65) does*
557 *not have the origin as equilibrium.*

558 **Proof.** We suppose that the origin is an equilibrium of (65), then $\Gamma_{ps}\mathcal{K}_s = 0$, which
 559 is equivalent to $\Gamma_{ps} = 0$. So, we obtain a contradiction since Γ is irreducible. \square

560 **Theorem 6.3.** Assume that the two matrices Γ_{pp} and Γ are irreducible. The reduced
 561 model (65) has unique equilibrium point in the interior of the positive cone $\mathbb{R}_+^{n-s} \setminus \{0\}$
 562 which is GAS.

Proof. To show the global stability of the reduced model (65) in this case, we use
 the result of Hirsch [26] recalled in Theorem A.2. The Jacobian matrix of the reduced
 model (65) is given by

$$G(X_p) := -\text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) + \epsilon\Gamma_{pp},$$

563 which is irreducible because Γ_{pp} is also. Moreover, if $G(X_p) \leq G(Y_p)$
 564 then $-\text{diag}(\varphi_{s+1}(x_{s+1}), \dots, \varphi_n(x_n)) \leq -\text{diag}(\varphi_{s+1}(y_{s+1}), \dots, \varphi_n(y_n))$ which gives
 565 $\varphi_k(x_k) \geq \varphi_k(y_k)$ for all $k \geq s+1$. Since the function φ_i is increasing, then $x_k \geq y_k$, i.e
 566 $X_p \geq Y_p$. All solutions are bounded and the reduced model (65) does not admits the
 567 origin as equilibrium by Lemma 6.1. Hence, the reduced model (65) is globally stable
 568 according to Hirsch [26]. \square

569 7. Example of Two-patch Source-sink model

570 In this section, we concentrate on the following two-patch source-sink model:

$$\begin{cases} \frac{dx_1}{dt} = r_1x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon(\gamma_{12}x_2 - \gamma_{21}x_1), \\ \frac{dx_2}{dt} = -r_2x_2 \left(1 + \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon(\gamma_{21}x_1 - \gamma_{12}x_2), \end{cases} \quad (68)$$

571 where the first patch is assumed to follow a logistic law and the second a Richard law
 572 (see Fig. 4).

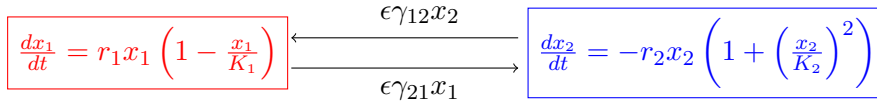


Figure 4. A Two-patch source-sink coupled system

The total equilibrium population of the model (68) in the perfect mixing case (i.e
 $\epsilon \rightarrow \infty$) equal $(\gamma_{12} + \gamma_{21}) \lambda_0$ where

$$\lambda_0 = \frac{\left(-\gamma_{12}^2 r_1 K_2 + \sqrt{\gamma_{12}^4 r_1^2 K_2^2 + 4 \gamma_{21}^3 r_2 K_1^2 \gamma_{12} r_1 - 4 \gamma_{21}^4 r_2^2 K_1^2}\right) K_2}{2 \gamma_{21}^3 r_2 K_1},$$

is the unique solution of the following equation:

$$\gamma_{12} r_1 \left(1 - \frac{\gamma_{12} x}{K_1}\right) - \gamma_{21} r_2 \left(1 + \left(\frac{\gamma_{21} x}{K_2}\right)^2\right) = 0 \Leftrightarrow -\frac{\gamma_{21}^3 r_2}{K_2^2} x^2 - \frac{\gamma_{12}^2 r_1}{K_1} x + \gamma_{12} r_1 - \gamma_{21} r_2 = 0.$$

573 Therefore, $T_2^*(+\infty)$ is given by the following formula:

$$T_2^*(+\infty) = \begin{cases} (\gamma_{12} + \gamma_{21}) \frac{(-\gamma_{12}^2 r_1 K_2 + \sqrt{\gamma_{12}^4 r_1^2 K_2^2 + 4\gamma_{21}^3 r_2 K_1^2 \gamma_{12} r_1 - 4\gamma_{21}^4 r_2^2 K_1^2}) K_2}{2\gamma_{21}^3 r_2 K_1} & \text{if } \gamma_{12} r_1 > \gamma_{21} r_2, \\ 0 & \text{otherwise,} \end{cases} \quad (69)$$

574 and the derivative of the total equilibrium population $T_2^*(\epsilon)$ at $\epsilon = 0$ becomes

$$\frac{dT_2^*}{d\epsilon}(0) = (\gamma_{12} K_2 - \gamma_{21} K_1) \left(\frac{1}{r_1} - \frac{1}{r_2} \right). \quad (70)$$

575 The equilibrium of the system (68) is the solutions of the following algebraic system:

$$\begin{cases} 0 = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) + \epsilon (\gamma_{12} x_2 - \gamma_{21} x_1), \\ 0 = -r_2 x_2 \left(1 + \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon (\gamma_{21} x_1 - \gamma_{12} x_2). \end{cases} \quad (71)$$

576 The sum of two equations of (71) shows that the equilibrium points are in curve noted
577 \mathbb{F} , where its equation is given by:

$$\mathbb{F} : r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) - r_2 x_2 \left(1 + \left(\frac{x_2}{K_2} \right)^2 \right) = 0. \quad (72)$$

The curve \mathbb{F} passes through the points $(0, 0)$ and $\mathcal{A} := (K_1, 0)$. Note that, it is independent of migration rate ϵ and γ_{ij} (shown in red in Fig. 5).

Solving the first equation of system (71) for x_2 yields a parabola noted \mathcal{P}_ϵ defined by

$$\mathcal{P}_\epsilon : p_\epsilon(x_1) := \frac{1}{\gamma_{12}} x_1 \left(\gamma_{21} - \frac{r_1}{\epsilon} \left(1 - \frac{x_1}{K_1} \right) \right).$$

578 As our study is limited in the positive cone, then we are interested only in the positive
579 branch of \mathcal{P}_ϵ . The parabola \mathcal{P}_ϵ (shown in blue in Fig. 5) depend on the migration rate
580 ϵ . It always passes through the origin and the point $\mathcal{B} := \left(K_1, \frac{\gamma_{21}}{\gamma_{12}} K_1 \right)$. Notice that,
581 the parabola \mathcal{P}_ϵ intersect the axis (Ox_1) at 0 and a second point $x_1 = -\frac{(\gamma_{21}\epsilon - r_1)K_1}{r_1}$ if
582 $\gamma_{21}\epsilon - r_1 < 0$, which always smaller than K_1 . So, the equilibrium points are the non
583 negative intersection between the curve \mathbb{F} and \mathcal{P}_ϵ . So, we have at most two equilibrium,
584 the origin as unique equilibrium, or, the trivial point $(0, 0)$ and the second is a non
585 trivial point $E_2^*(\epsilon) = (x_1^*(\epsilon), x_2^*(\epsilon))$ whose position depend on migration rate ϵ (see
586 Fig. 5).

When $\epsilon \rightarrow 0$, the left branch of parabola \mathcal{P}_ϵ tend to the vertical line $x_1 = 0$ and the right branch into the vertical line $\mathcal{P}_0 : x_1 = K_1$. Moreover, $\mathbb{F} \cap \mathcal{P}_0 = \{(K_1, 0)\}$. In the case when $\epsilon \rightarrow \infty$, the parabola \mathcal{P}_ϵ tend to the oblique line $\mathcal{P}_\infty : x_2 = \frac{\gamma_{21}}{\gamma_{12}} x_1$. Moreover,

$$\mathbb{F} \cap \mathcal{P}_\infty = \begin{cases} \{(0, 0), (\gamma_{12}\lambda_0, \gamma_{21}\lambda_0)\} & \text{if } r_1\gamma_{12} > \gamma_{21}r_2, \\ \{(0, 0)\} & \text{if } r_1\gamma_{12} \leq \gamma_{21}r_2. \end{cases}$$

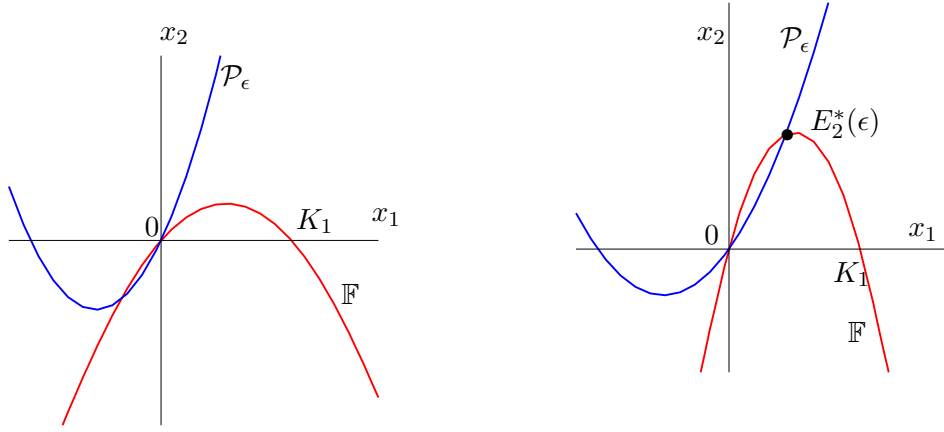


Figure 5. Some examples of the curve \mathbb{F} and the Parabola \mathcal{P}_ϵ . The equilibrium points are the intersection in the positive cone between \mathbb{F} and \mathcal{P}_ϵ , this intersections contains the origin or the origin and a second positive point $E_2^*(\epsilon)$.

587 **7.1. Effect of dispersal on total equilibrium population**

588 For two-patch source-sink model (4), it was shown by Wu et al. [49] that only three
 589 situations can occur: the case where the total equilibrium population is always greater
 590 than the carrying capacity of source patch, the case where it is always smaller with
 591 persistence or even extinction in both patches, and a third case, where the effect of
 592 migration is beneficial for lower values of the migration coefficient ϵ and detrimental for
 593 the higher values, with persistence or even extinction in both patches. More precisely,
 594 it was shown in [49] that, the following trichotomy holds

- 595 • If $T_2^*(+\infty) > K_1$ then $T_2^*(\epsilon) > K_1$ for all $\epsilon > 0$.
- 596 • If $\frac{dT_2^*}{d\epsilon}(0) > 0$ and $T_2^*(+\infty) < K_1$, then there exists $\epsilon_0 > 0$ such that $T_2^*(\epsilon) > K_1$
 597 for $0 < \epsilon < \epsilon_0$, $T_2^*(\epsilon) < K_1$ for $\epsilon > \epsilon_0$ and $T_2^*(\epsilon_0) = K_1$. Moreover, there exists
 598 $\epsilon^\# > \epsilon_0$ such that $T_2^*(\epsilon) > 0$ for all $\epsilon < \epsilon^\#$ and $T_2^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon^\#$.
- 599 • If $\frac{dT_2^*}{d\epsilon}(0) < 0$, then $T_2^*(\epsilon) < K_1$ for all $\epsilon > 0$. Moreover, there exists $\epsilon^\# > 0$ such
 600 that $T_2^*(\epsilon) > 0$ for all $\epsilon < \epsilon^\#$ and $T_2^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon^\#$.

601 Therefore, the condition $T_2^*(\epsilon) = K_1$ holds only for $\epsilon = 0$ and at most for one positive
 602 value ϵ_0 . The value ϵ_0 exists if and only if $\frac{dT_2^*}{d\epsilon}(0) > 0$ and $T_2^*(+\infty) < K_1$.

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

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

of (68) and carrying capacity of the source patch K_1 , by analyzing the stable positive equilibrium $E_2^*(\epsilon)$. Note that, when there is no dispersal (i.e., $\epsilon = 0$), the total equilibrium population is $T_2^*(0) = K_1$. We study the effect of asymmetric dispersal on the total equilibrium population for the two-patch source-sink system (68). Using the method graphic of Arditi et al. [2] and of Wu et al. [49], we describe the position affects the equilibrium $E_2^*(\epsilon)$ when the migration rate varies from zero to infinity, we will give the condition whether T_2^* is greater or smaller than the carrying capacity $T_2^*(0) = K_1$. We prove there are only three cases as in the two-patch source-sink model with linear

diffusion can occur. Denote

$$\xi = \frac{-r_1 K_2^2 - 2r_2 K_1^2 + \sqrt{r_1^2 K_2^4 + 4r_1 K_2^2 r_2 K_1^2 - 4r_2^2 K_1^2 K_2^2}}{2r_2 K_1}.$$

603 We consider the regions in the set of the parameters γ_{21} and γ_{12} , denoted $\Delta_0, \Delta_1, \Delta_2,$
604 Δ_3 and Δ_4 , depicted in Figure 6 and defined by:

$$\left\{ \begin{array}{l} \text{If } r_2 \geq r_1 \text{ then } \left\{ \begin{array}{l} \Delta_0 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} \leq \frac{r_2}{r_1} \right\}, \\ \Delta_1 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} > \frac{r_2}{r_1} \right\}. \end{array} \right. \\ \\ \text{If } r_2 < r_1 \text{ then } \left\{ \begin{array}{l} \Delta_2 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} \leq \frac{r_2}{r_1} \right\}, \\ \Delta_3 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{r_2}{r_1} < \frac{\gamma_{12}}{\gamma_{21}} < \frac{\xi}{K_1 - \xi} \right\}, \\ \Delta_4 = \left\{ (\gamma_{21}, \gamma_{12}) : \frac{\gamma_{12}}{\gamma_{21}} \geq \frac{\xi}{K_1 - \xi} \right\}. \end{array} \right. \end{array} \right. \quad (73)$$

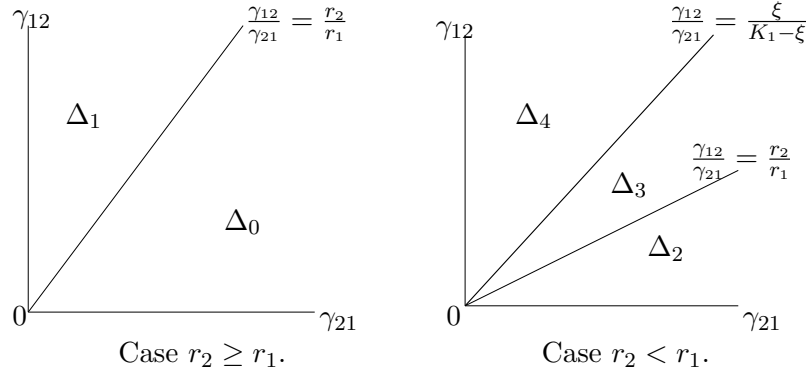


Figure 6. Qualitative properties of source-sink model (68). In Δ_0 and Δ_1 , the effect is detrimental, with extinction in two patches for Δ_0 , and persistence for Δ_1 . In Δ_2 and Δ_3 , the effect is beneficial for $\epsilon < \epsilon_0$ and detrimental for $\epsilon > \epsilon_0$ with persistence of the population in the region Δ_3 , and extinction in the region Δ_2 . In Δ_4 , patchiness has a beneficial effect on the total equilibrium population.

605 We have the following results which gives the conditions under which fragmentation
606 and asymmetrical migration can lead to a total equilibrium population greater or
607 smaller than the carrying capacity K_1 of the source patch:

608 **Theorem 7.1.** *The total equilibrium population T_2^* of (68) satisfies the following*
609 *properties*

- 610 (1) *If $r_2 \geq r_1$, let Δ_0 and Δ_1 be defined by (73). Then we have:*
611 (a) *if $(\gamma_{21}, \gamma_{12}) \in \Delta_0$ then $T_2^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$. Moreover, there is $\epsilon_0 > 0$*
612 *such that $T_2^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon_0$.*
613 (b) *if $(\gamma_{21}, \gamma_{12}) \in \Delta_1$ then $0 < T_2^*(\epsilon) \leq K_1$ for all $\epsilon \geq 0$. Moreover, $T_2^*(\epsilon) \rightarrow$*
614 *$T_2^*(\infty) > 0$ when $\epsilon \rightarrow +\infty$.*
615 (2) *If $r_2 < r_1$, let Δ_2, Δ_3 and Δ_4 be defined by (73). Then we have:*
616 (a) *if $(\gamma_{21}, \gamma_{12}) \in \Delta_2$ then, there is $\epsilon^* > 0$, such that: $T_2^*(\epsilon) > K_1$ for $\epsilon < \epsilon^*$ and*

617 $T_2^*(\epsilon) < K_1$ for all $\epsilon > \epsilon^*$. Moreover, there is $\epsilon_0 > \epsilon^*$ such that $T_2^*(\epsilon) = 0$
618 for all $\epsilon \geq \epsilon_0$.
619 (b) if $(\gamma_{21}, \gamma_{12}) \in \Delta_3$ then, there is $\epsilon^\natural > 0$, such that: $T_2^*(\epsilon) > K_1$ for $\epsilon < \epsilon^\natural$ and
620 $T_2^*(\epsilon) < K_1$ for all $\epsilon > \epsilon^\natural$. Moreover, $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$ when $\epsilon \rightarrow +\infty$.
621 (c) if $(\gamma_{21}, \gamma_{12}) \in \Delta_4$, then $T_2^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$. Moreover, if $\frac{\gamma_{12}}{\gamma_{21}} =$
622 $\left(\frac{\alpha_2(K_1+K_2)}{r_1-r_2}\right)^2$, then $T_2^* \rightarrow T_2^*(\infty) = K_1$.

623 **Proof.** Recall that, the equilibrium points of (68) are the non-negative intersection
624 between the curve \mathbb{F} and parabola \mathcal{P}_ϵ . There are most two equilibrium points. The
625 first is the trivial point $(0, 0)$ and the second is a non trivial point noted $E^*(\epsilon) :=$
626 $(x_1^*(\epsilon), x_2^*(\epsilon))$ whose position depend on migration rate ϵ (see Fig. 8). As our study is
627 limited in the positive cone, then we are interested only in the positive branch of \mathcal{P}_ϵ .

628 The tangent space of the curve \mathbb{F} at O and $A = (K_1, 0)$ is $T_O\mathbb{F} : x_2 = \frac{r_1}{r_2}x_1$, and
629 $T_A\mathbb{F} : x_2 = -\frac{r_1}{r_2}x_1 + \frac{r_1}{r_2}K_1$ respectively.

630 To facilitate comparison between the total equilibrium population $T_2^*(\epsilon)$ and
631 $T_2^*(0) = K_1$, we define a straight line $\Delta : x_1 + x_2 = K_1$. If the intersection of the
632 curve \mathbb{F} and the parabola \mathcal{P}_ϵ , i.e., the equilibrium $(x_1^*(\epsilon), x_2^*(\epsilon))$, is on or below the
633 line Δ , then $T_2^*(\epsilon) \leq T_2^*(0)$, whereas if the intersection is above the line Δ , then
634 $T_2^*(\epsilon) \geq T_2^*(0)$. We see very simply that dispersal is favorable to $T_2^*(\epsilon)$ if $E_2^*(\epsilon)$ is above
635 Δ , unfavorable if below Δ . The equilibrium point $E_2^*(\epsilon)$ is always in ellipse, then, for
636 $\epsilon = 0$, the equilibrium point states at A , and when ϵ increases, $E_2^*(\epsilon)$ describes an arc
637 of the curve and ends at point $E^*(\infty)$.

638 Suppose $r_1 \leq r_2$. Then the slope of $T_A\mathbb{F}$, $-\frac{r_1}{r_2} \geq -1$, which means that the curve
639 \mathbb{F} is below the line Δ in the first quadrant and $T_2^*(\epsilon) < T_2^*(\infty)$, as shown in Fig. 7.
640 If the slope of \mathcal{P}_∞ , $\frac{\gamma_{21}}{\gamma_{12}}$, is bigger than the slope of $T_O\mathbb{F}$, i.e. $\frac{\gamma_{21}}{\gamma_{12}} \geq \frac{r_1}{r_2}$, the curve is
641 below the line Δ in the first quadrant. Thus, there is ϵ_0 , such that, when $0 < \epsilon \leq \epsilon_0$,
642 the equilibrium $E_2^*(\epsilon)$ changes from point A to O . When $\epsilon \geq \epsilon_0$, we have $E_2^*(\epsilon) = O$
643 and $T_2^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon_0$ (see Fig. 7-(a)). If $\frac{\gamma_{21}}{\gamma_{12}} < \frac{r_1}{r_2}$, the curve and the line \mathcal{P}_∞
644 has an intersection B . Then we have $T_2^*(\epsilon) \rightarrow T_2^*(\infty) > 0$, as shown in Fig. 7-(b).

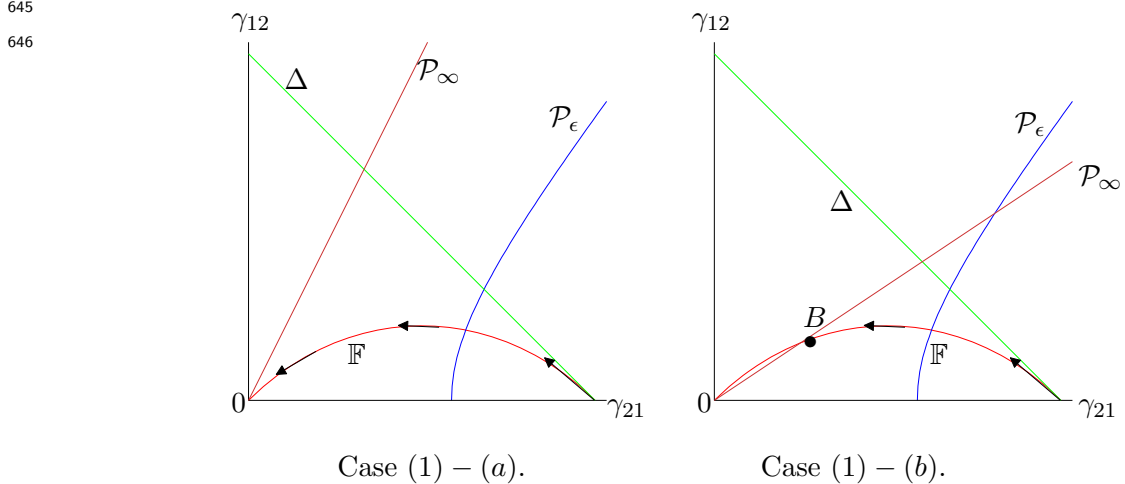


Figure 7. This illustrates the cases (1)-a and (1)-b in Theorem 7.1. Case (a) illustrate an example with $(\gamma_{21}, \gamma_{12}) \in \Delta_0$ and the case (b) illustrate an example with $(\gamma_{21}, \gamma_{12}) \in \Delta_1$. The curve \mathbb{F} and the parabola \mathcal{P}_ϵ are shown in red and blue respectively for some parameters of the model (68), the straight lines Δ and \mathcal{P}_∞ are shown in green and orange respectively. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the ellipse from $A = (K_1, 0)$ to O in the case (1)-a, from A to B in the case (1)-b. The total equilibrium population is always smaller than K_1 for all $\epsilon \geq 0$.

In the case when $r_1 > r_2$, direct calculation finds that the curve \mathbb{F} and the line Δ have two intersections: $A = (K_1, 0)$, and $C = (\xi, K_1 - \xi)$. We denote by Σ the straight line joint the origin and C . The slope of Σ is equal to $\frac{K_1 - \xi}{\xi}$. We distinguish three cases relative position of the points $O, B = E_2^*(\infty)$, and C , or equivalently, the three lines $T_O\mathbb{E}^1, \mathcal{P}_\infty$ and Σ whose slopes respectively are

$$\frac{r_1}{r_2}, \quad \frac{\gamma_{21}}{\gamma_{12}} \quad \text{and} \quad \frac{K_1 - \xi}{\xi}.$$

647 By the method graphic of Arditi et al. [2] (see also of [49]), we conclude the complete
 648 proof (see Figures 8 and 9). □

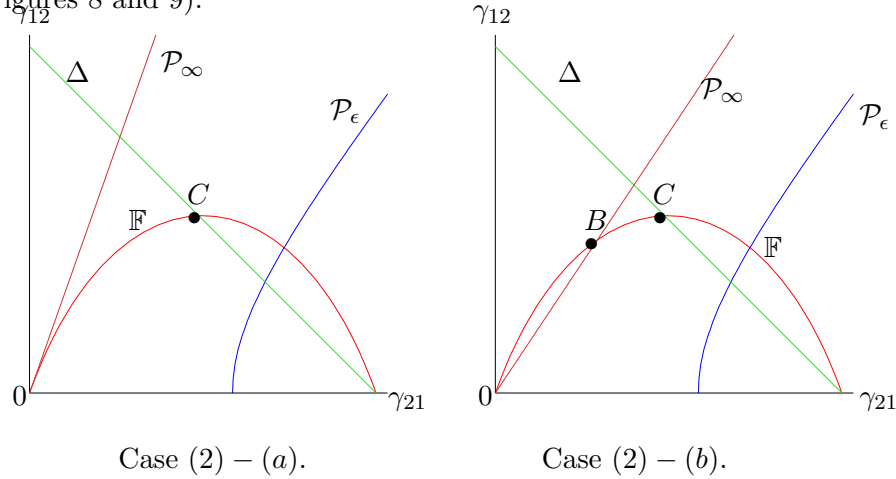


Figure 8. This illustrates the cases (2)-a and (2)-b in Theorem 7.1. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the ellipse from $A = (K_1, 0)$ to O in the case (a) from A to B in the case (b), passing through the point C which is the other point of intersection between the curve \mathbb{F} and the line Δ . The dispersal is favorable when $E_2^*(\epsilon)$ is between A and C , and unfavorable when $E_2^*(\epsilon)$ is between C and B .

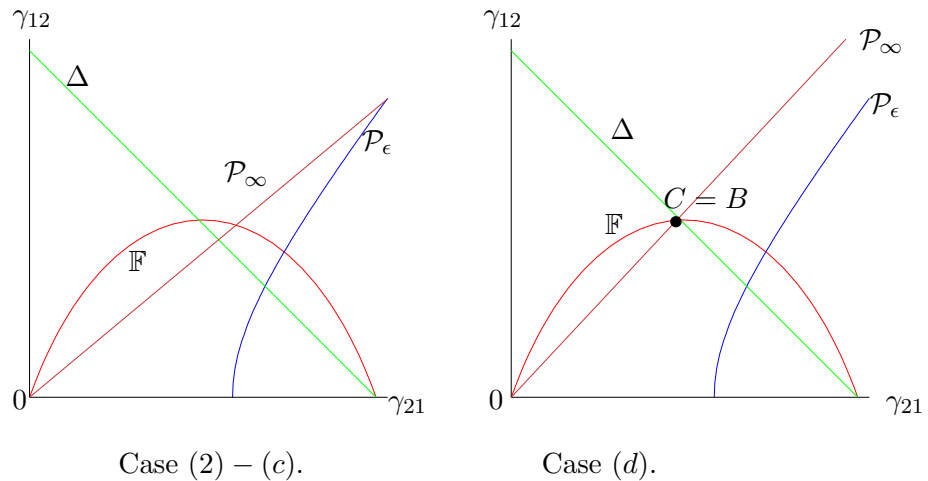


Figure 9. This illustrates the case (2)-c in Theorem 7.1. As the migration intensity ϵ increases from 0 to ∞ , the equilibrium point $E_2^*(\epsilon)$ moves counterclockwise along the curve \mathbb{F} from $A = (K_1, 0)$ to B . The total equilibrium point is always greater than K_1 for all ϵ , because it belongs to the ellipse and the limit point B is above Δ . The figure (d) is a particular case of (2)-(c), where $T_2^* \rightarrow K_1 = T_2^*(\infty)$ for $\frac{\gamma_{12}}{\gamma_{21}} = \frac{\xi}{K_1 - \xi}$.

649 Speaking biologically, the result of the previous theorem show that the asymmetric
650 dispersal can lead to either an increased total size of the population in two patches, a
651 decreased total size with persistence in the patches, or even extinction in both patches
652 when the growth of migration goes to infinity. Let us explain the result of Theorem
653 7.1 in the particular case where the dispersion is symmetric i.e. $\frac{\gamma_{21}}{\gamma_{12}} = 1$. In this case,
654 the system (68) becomes

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (x_2 - x_1), \\ \frac{dx_2}{dt} = -r_2 x_2 \left(1 + \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon (x_1 - x_2), \end{cases} \quad (74)$$

655 We consider the regions in the set of the parameters r_1 and r_2 , denoted Λ_0 , Λ_1 and
656 Λ_2 , depicted in Figure 10 and defined by:

$$\begin{cases} \Lambda_0 = \{(r_1, r_2) : r_2 \geq r_1\}, \\ \Lambda_1 = \{(r_1, r_2) : r_1 < r_2 < \frac{2K_2^2}{K_1^2 + 4K_2^2} r_1\}, \\ \Lambda_2 = \{(r_1, r_2) : r_2 \geq \frac{2K_2^2}{K_1^2 + 4K_2^2} r_1\}. \end{cases} \quad (75)$$

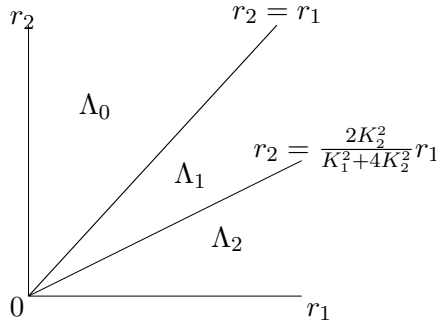


Figure 10. Qualitative properties of source-sink model (74) with $\gamma_{12} = \gamma_{21} = 1$. In Λ_0 , the effect is detrimental with extinction in two patches. In Λ_1 , the effect is beneficial for $\epsilon < \epsilon^{**}$ and detrimental for $\epsilon > \epsilon^{**}$ with persistence of the population. In Λ_2 , patchiness has a beneficial effect on the total equilibrium population.

657 **Corollary 7.1.** Consider the model (74). Let Λ_0, Λ_1 and Λ_2 be defined by (75). The
658 total equilibrium population T_2^* of (74) satisfies the following properties

- 659 (1) if $(r_1, r_2) \in \Lambda_0$ then, $T_2^*(\epsilon) \leq K_1$ for all ϵ . Moreover, there is $\epsilon_0 > 0$ such that
660 $T_2^*(\epsilon) = 0$ for all $\epsilon \geq \epsilon_0$.
661 (2) if $(r_1, r_2) \in \Lambda_1$ then, there is $\epsilon^* > 0$, such that

$$\begin{cases} T_2^*(\epsilon) \geq K_1 & \text{If } \epsilon \leq \epsilon^*, \\ 0 < T_2^*(\epsilon) < K_1 & \text{If } \epsilon > \epsilon^*. \end{cases} \quad (76)$$

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

663 (3) if $(r_1, r_2) \in \Lambda_2$, then $T_2^*(\epsilon) \geq K_1$ for all $\epsilon \geq 0$. Moreover, if $\frac{r_1}{r_2} = \frac{2K_2^2}{K_1^2 + 4K_2^2}$, then
 664 $T_2^*(\infty) = K_1$.

665 **Proof.** Consequence direct of the theorem 7.1. □

666 **7.2. Two-patch model where one growth rate is much larger than the**
 667 **second one**

668 Recently, in [19], Elbetch is interested in some biological situations that can be found
 669 in the nature, that is, the case where several sub-populations grow with different
 670 speed. Mathematically speaking, he studied the system (7) under the hypothesis that
 671 some growth rates tend to infinity (i.e $r_i \rightarrow \infty$ for some i). In the preceding two
 672 subsections, we consider the two-patch model (68) and we assume that the death rate
 673 r_2 (resp. growth rate r_1) is much larger than growth rate r_1 (resp. death rate r_2).

674 **7.2.1. Case where $r_2 \rightarrow \infty$**

675 In this part, we assume that the death rate r_2 is much larger than the growth rate r_1 .
 676 For simplicity we denote $\gamma_2 := \gamma_{12} > 0$ the migration rate from sink to source patch
 677 and $\gamma_1 := \gamma_{21} > 0$ from source to sink patch. The model (68) is written:

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = -\frac{r_2}{\eta} x_2 \left(1 + \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon (\gamma_1 x_1 - \gamma_2 x_2), \end{cases} \quad (77)$$

678 where η is assumed to be a small positive number. Denote $E_2^*(\epsilon, \eta) = (x_1^*(\epsilon, \eta), x_2^*(\epsilon, \eta))$
 679 the positive equilibrium of (77), and $T_2^*(\epsilon, \eta)$, the total equilibrium population. We
 680 recall that the derivative of $T_2^*(\epsilon, \eta)$ with respect to ϵ at $\epsilon = 0$ is written as follow:

$$\frac{dT_2^*}{d\epsilon}(0, \eta) = \gamma_1 K_1 \left(\frac{\eta}{r_2} - \frac{1}{r_1}\right). \quad (78)$$

681 The total equilibrium population of the model (77) for perfect mixing (i.e $\epsilon \rightarrow \infty$) is
 682 given by the following formula:

$$T_2^*(+\infty, \eta) = \begin{cases} (\gamma_1 + \gamma_2) \frac{(-\eta\gamma_2^2 r_1 K_2 + \sqrt{\eta^2 \gamma_2^4 r_1^2 K_2^2 + 4\eta\gamma_1^3 r_2 K_1^2 \gamma_2 r_1 - 4\gamma_1^4 r_2^2 K_1^2}) K_2}{2\gamma_1^3 r_2 K_1} & \text{if } \gamma_2 r_1 \eta > \gamma_1 r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (79)$$

683 First, we have the result:

684 **Theorem 7.2.** Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of the system (77) with initial
 685 condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $u(t)$ be the solution of the differ-
 686 ential equation

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \epsilon \gamma_1 x_1 =: \varphi(x_1), \quad (80)$$

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

$$x_1(t, \eta) = u(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (81)$$

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

$$x_2(t, \eta) = o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (82)$$

689 **Proof.** When $\eta \rightarrow 0$, the system (77) is a *slow-fast* system, with one *slow variable*,
 690 x_1 , and one *fast variable*, x_2 . Tikhonov's theorem [36, 47, 48] prompts us to consider
 691 the dynamics of the fast variables in the time scale $\tau = \frac{1}{\eta}t$. One obtains

$$\frac{dx_2}{d\tau} = -r_2x_2 \left(1 + \left(\frac{x_2}{K_2} \right)^2 \right) + \epsilon\eta(\gamma_1x_1 - \gamma_2x_2). \quad (83)$$

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

$$\frac{dx_2}{d\tau} = -r_2x_2 \left(1 + \left(\frac{x_2}{K_2} \right)^2 \right). \quad (84)$$

693 The slow manifold is given by the positive equilibrium of the system (84), i.e $x_2 = 0$,
 694 which is GAS in the positive axis. When η goes to zero, Tikhonov's theorem ensures
 695 that after a fast transition toward the slow manifold, the solutions of (77) converge
 696 to the solutions of the *reduced model* (80), obtained by replacing $x_2 = 0$ into the
 697 dynamics of the slow variable.

The differential equation (80) admits 0 as unique equilibrium if $r_1 \leq \epsilon\gamma_1$ which is GAS, else, (80) admits 0 which is unstable, and a positive equilibrium

$$x_1^*(\epsilon, 0^+) := \frac{r_1 - \epsilon\gamma_1}{\alpha_1}, \quad (85)$$

698 where $\alpha_1 = \frac{r_1}{K_1}$. As $\varphi(x_1) > 0$ for all $0 \leq x_1 < x_1^*(\epsilon, 0^+)$ and $\varphi(x_1) < 0$ for all
 699 $x_1 > x_1^*(\epsilon, 0^+)$ then, the equilibrium $x_1^*(\epsilon, 0^+)$ is GAS in the positive axis, so, the
 700 approximation given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable
 701 and for all $t \geq t_0 > 0$ for the fast variable, where t_0 is as small as we want. Therefore,
 702 let $u(t)$ be the solution of the reduced model (80) of initial condition $u(0) = x_1^0$, then,
 703 when $\eta \rightarrow 0$, we have the approximations (81) and (82). \square

704 As a corollary of the previous theorem, we have the following result which give the
 705 limit of the total equilibrium population $T_2^*(\epsilon, \eta)$ of the model (77) when η goes to
 706 zero:

Corollary 7.2. *We have:*

$$T_2^*(\epsilon, 0^+) := \lim_{\eta \rightarrow 0} T_2^*(\epsilon, \eta) = \lim_{\eta \rightarrow 0} (x_1^*(\epsilon, \eta) + x_2^*(\epsilon, \eta)) = \begin{cases} \frac{r_1 - \epsilon\gamma_1}{\alpha_1}, & \text{if } \epsilon < r_1/\gamma_1, \\ 0, & \text{otherwise} \end{cases} \quad (86)$$

707 Moreover, $0 < T_2^*(\epsilon, 0^+) < K_1$ for all $\epsilon < r_1/\gamma_1$, and $T_2^*(\epsilon, 0^+) = 0$, for $\epsilon \geq r_1/\gamma_1$.

708 **Proof.** According to the equations (81), (82) and (85), when η goes to zero, the
709 equilibrium $E_2^*(\epsilon, \eta)$ of the model (77) is converge to $E_2^*(\epsilon, 0^+) := (x_1^*(\epsilon, 0^+), 0)$, where
710 $x_1^*(\epsilon, 0^+)$ is given in (85). The sum of the coordinates of $E_2^*(\epsilon, 0^+)$ gives the formula
711 (86). \square

712 *7.2.2. Case where $r_1 \rightarrow \infty$*

713 In this part, we assume that r_1 is much larger than r_2 . The model (68) is written:

$$\begin{cases} \frac{dx_1}{dt} = \frac{r_1}{\eta} x_1 \left(1 - \frac{x_1}{K_1}\right) + \epsilon (\gamma_2 x_2 - \gamma_1 x_1), \\ \frac{dx_2}{dt} = -r_2 x_2 \left(1 + \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon (\gamma_1 x_1 - \gamma_2 x_2), \end{cases} \quad (87)$$

714 where η is assumed to be a small positive number. We recall that the derivative of
715 $T_2^*(\epsilon, \eta)$ with respect to ϵ at $\epsilon = 0$ is written as follow:

$$\frac{dT_2^*}{d\epsilon}(0, \eta) = \gamma_1 K_1 \left(\frac{1}{r_2} - \frac{\eta}{r_1}\right). \quad (88)$$

716 The total equilibrium population of the model (77) for perfect mixing (i.e $\epsilon \rightarrow \infty$) is
717 given by the following formula:

$$T_2^*(+\infty, \eta) = \begin{cases} (\gamma_1 + \gamma_2) \frac{(-\gamma_2^2 r_1 K_2 + \sqrt{\gamma_2^4 r_1^2 K_2^2 + 4\eta \gamma_1^3 r_2 K_1^2 \gamma_2 r_1 - 4\eta^2 \gamma_1^4 r_2^2 K_1^2}) K_2}{2\eta \gamma_1^3 r_2 K_1} & \text{if } \gamma_2 r_1 > \eta \gamma_1 r_2, \\ 0 & \text{otherwise.} \end{cases} \quad (89)$$

718 We have the result:

719 **Theorem 7.3.** Let $(x_1(t, \eta), x_2(t, \eta))$ be the solution of the system (87) with initial
720 condition (x_1^0, x_2^0) satisfying $x_i^0 \geq 0$ for $i = 1, 2$. Let $u(t)$ be the solution of the differ-
721 ential equation

$$\frac{dx_2}{dt} = -r_2 x_2 \left(1 + \left(\frac{x_2}{K_2}\right)^2\right) + \epsilon (\gamma_1 K_1 - \gamma_2 x_2) =: \varphi(x_1), \quad (90)$$

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

$$x_2(t, \eta) = u(t) + o_\eta(1), \quad \text{uniformly for } t \in [0, +\infty) \quad (91)$$

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

$$x_1(t, \eta) = K_1 + o_\eta(1), \quad \text{uniformly for } t \in [t_0, +\infty). \quad (92)$$

724 **Proof.** The proof is the same as in Theorem 7.2. Denote $\sigma_1 = \frac{r_2}{K_2^2}$, $\sigma_2 = r_2 + \epsilon \gamma_2$ and
725 $\sigma_3 = \epsilon \gamma_1 K_1$, the equation (90) becomes $\varphi(x_2) = -\sigma_1 x_2^3 - \sigma_2 x_2 + \sigma_3$. This last equation

726 admits unique positive solution given by

$$x_2^*(\epsilon, 0^+) = 1/6 \sqrt[3]{\left(108 \sigma_3 + 12 \sqrt{3} \sqrt{\frac{4 \sigma_2^3 + 27 \sigma_3^2 \sigma_1}{\sigma_1}}\right) \sigma_1^2 \sigma_1^{-1} - 2 \sigma_2} \frac{1}{\sqrt[3]{\left(108 \sigma_3 + 12 \sqrt{3} \sqrt{\frac{4 \sigma_2^3 + 27 \sigma_3^2 \sigma_1}{\sigma_1}}\right) \sigma_1^2}}. \quad (93)$$

727 As $\varphi(x_2) > 0$ for all $0 \leq x_2 < x_2^*(\epsilon, 0^+)$ and $\varphi(x_2) < 0$ for all $x_2 > x_2^*(\epsilon, 0^+)$ then,
 728 the equilibrium $x_2^*(\epsilon, 0^+)$ is GAS in the positive axis, so, the approximation given by
 729 Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for
 730 the fast variable, where t_0 is as small as we want. Therefore, let $u(t)$ be the solution
 731 of the reduced model (90) of initial condition $u(0) = x_2^0$, then, when $\epsilon \rightarrow 0$, we have
 732 the approximations (91) and (92). \square

733 The result of the previous theorem prove that $T_2^*(\epsilon, 0^+) \geq K_1$ for all ϵ .

734 8. Conclusion

735 The aim of this paper is to generalize, to a generalized source-sink multi-patch model,
 736 the results of Elbetch [20] for generalized multi-patch logistic model i.e. n-source 0-
 737 sink patch model, the results obtained in [12, 13] for a multi-patch logistic model and
 738 also the results obtained in [49] for a two-patch source-sink. The diffusion between
 739 source and sink patches is modeled by a cooperative matrix. When this last matrix is
 740 irreducible, two cases can produce for our system, either the origin is GAS, or there
 741 is a positive equilibrium, which furthermore is GAS (see Theorem 3.2). This is an
 742 extension of Elbetch's result [20, Theorem 6]. The extension is based on developed
 743 cooperative system theory and proprieties of cooperative matrix.

744 In Section 4, we consider the particular case of perfect mixing, when the migration
 745 rate goes to infinity. As in [12, 13] and [20], we implicitly compute the total equilibrium
 746 population as a function of the number of the source patches in that case, and, by
 747 perturbation arguments and Tikhonov's theorem [36, 47, 48], we prove that the dy-
 748 namics in this ideal case provides a good approximation to the case when the migration
 749 rate is large. Our results generalize those of [1, 2] for tow-patch logistic model, [49]
 750 for tow-patch source-sink model, [12] for n-patch logistic model with dispersal sym-
 751 metric between patches, [13] for many patches with movement between patches not
 752 necessarily symmetric, [16] for multi-patch source-sink model and [20] for generalized
 753 multi-patch logistic model.

754 In Section 5, we considered the total equilibrium population in the n patches. As
 755 shown in Proposition 5.2, diffusion could make total equilibrium population small
 756 than the sum of carrying capacities of the source patches and also the extinction
 757 in all patches. We give also sufficient and necessary conditions for which the total
 758 equilibrium population not to depend on the diffusion rate. More precisely, we show
 759 that, the only situation where the total equilibrium population is independent with
 760 respect to dispersal, is when all the patches are sources and the vector of the carrying
 761 capacities lies in the vector space $\ker \Gamma$. That is, if there is at least one sink patch, or
 762 we have n source patches and the vector of the carrying capacities does not belong to
 763 the vector space $\ker \Gamma$, then the total equilibrium population depends on the dispersion
 764 (See Proposition 5.3).

765 In Sections 6.1 and 6.2, we consider the model (9) and we assume that the death
 766 rates (resp. growth rates) is much larger than growth rates (resp. death rates). First,

767 for both cases, by perturbation arguments and Tikhonov's theorem [36, 47, 48], we
 768 construct the reduced models, and for the second case, under certain condition, we
 769 prove its global stability by using Hirsch's theorem A.2. Next, we compare the total
 770 equilibrium population of the source-sink patch model (9) with carrying capacities of
 771 the source patches.

772 In Section 7, Two-patch source-sink model where the first patch is assumed to follow
 773 a logistic law and the second a Richard law is studied. As in [49], we have shown that,
 774 the dispersal asymmetry can lead to either an increased total size of the population in
 775 two patches, a decreased total size with persistence in the patches, or even extinction in
 776 both patches. Next, the growth rate in the second (resp. first) patch is supposed to be
 777 much larger than that in the first (resp. second) one. We have given then the conditions
 778 for which patchiness is beneficial or detrimental for the population in models (77) and
 779 (87) when $\eta \rightarrow 0$. In this configuration where the population of one of the patches
 780 has a fast growing compared to the other patch, the critical value of migration rate
 781 ϵ_0 , which that the total equilibrium equal the some of carrying capacities, does not
 782 intervene.

Finally, comparisons the present results with previous works [1, 2, 12, 13, 16, 20, 49]
 indicate that, in general, the generalized growth rate mechanism has an effect on the
 dynamics of the total equilibrium population in the multi-patch source-sink model.
 Some important questions remain open: Is there a way to make connections between
 the source and sink patches ($n \geq 3$) that increases the total equilibrium population?
 Mathematically speaking, are there conditions on the parameters of the model in
 which:

$$\sum_{i=1}^n x_i^*(\epsilon) > \sum_{i=1}^s K_i$$

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

787 Appendix A. Background concepts and preliminaries results

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

791 **Definition A.1.** The kernel of a matrix A is defined by $\ker A = \{v \in \mathbb{R}^n; Av = 0\}$.

Definition A.2. A matrix $A = (a_{ij})$ is called reducible, if there is a matrix of per-
 mutation $P = (p_{ij})$ (i.e $p_{ij} = 0$ or $p_{ij} = 1$) such that:

$$P^T A P = \begin{bmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{bmatrix},$$

792 where A_{11} and A_{22} are two square sub-matrices of A . We say that A is irreducible if
 793 A is non-reducible.

794 **Definition A.3.** A matrix $A = (a_{ij})$ is called cooperative if $a_{ij} \geq 0$ for all $i \neq j$.

795 **Definition A.4.** The stability modulus of a matrix A is given by

$$S(A) = \max \{ \operatorname{Re}(\lambda) : \lambda \text{ is an eigenvalue of } A \}, \quad (\text{A1})$$

796 and the spectral radius of A is

$$\rho(A) = \max \{ |\lambda| : \lambda \text{ is an eigenvalue of } A \}. \quad (\text{A2})$$

797 We have the following result [40, Lemma 8]:

798 **Lemma A.1.** *Let A be a non negative matrix. Let $u \in \mathbb{R}_+^n$ be a non-zero vector and*
 799 *$\lambda \in \mathbb{R}_+$ be a real number. If $Au \geq \lambda u$ then $\rho(A) \geq \lambda$. If for a strictly positive vector u*
 800 *we have $Au \leq \lambda u$ then $\rho(A) \leq \lambda$.*

801 **Proof.** If $Au \geq \lambda u$ then, since A is non negative, $A^k u \geq \lambda^k u$ for all k . Therefore
 802 $\|A^k\| \geq \lambda^k$ for any matricial norm. Using the Gelfand formula $\rho(A) = \lim_{k \rightarrow \infty} \|A^k\|^{\frac{1}{k}}$,
 803 we obtain that $\rho(A) \geq \lambda$. The second statement is a simple consequence of the repre-
 804 sentation (2) in [40]. \square

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

806 **Lemma A.2.** *Let A be a cooperative matrix. Let $u \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$. If $Au \geq \lambda u$ then*
 807 *$S(A) \geq \lambda$. If for a strictly positive vector u we have $Au \leq \lambda u$ then $S(A) \leq \lambda$.*

Proof. Let A be a cooperative matrix, there exists $h > 0$ such that $A + hI$, where
 I is the identity matrix, is non negative. Let u and λ be such that $Au \geq \lambda u$. Since
 $S(A + hI)u \geq (\lambda + h)u$, using Lemma A.1, we deduce that $\rho(A + hI) \geq \lambda + h$. According
to the Perron-Frobenius Theorem [32, Theorem 3, page 66], we have

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

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

810 Let we consider the autonomous system:

$$\dot{x} = \Psi(x), \quad (\text{A3})$$

811 where \dot{x} denote the derivative of x , $\Psi = (\Psi_1, \dots, \Psi_n)$ is \mathcal{C}^1 on a domain \mathbb{R}_+^n .

812 **Definition A.5.** Consider System (A3). Let $x(t, x_0)$ is a trajectory, and x_0 is the
 813 initial point. The set \mathcal{O} of \mathbb{R}^n is said to be positively invariant if $x_0 \in \mathcal{O}$ implies that
 814 $x(t, x_0) \in \mathcal{O}$ for all $t \geq 0$. In other words, once a trajectory of the system enters \mathcal{O} , it
 815 will never leave it again.

816 **Definition A.6.** System (A3) is called cooperative if the Jacobian matrix $\mathbb{J}\Psi(x)$ is a
 817 cooperative matrix for all $x \in \mathbb{R}_+^n$.

818 To prove the global stability of the system cooperative (A3), generally, the following
 819 result is used:

820 **Theorem A.1.** [24, 25] If system (A3) possesses a positive equilibrium point x^* sat-
 821 isfying

$$\Psi_i(\xi x^*) \begin{cases} > 0 & \text{for } \xi \in]0, 1[, \\ < 0 & \text{for } \xi > 1, \end{cases} \quad (\text{A4})$$

822 then x^* is globally stable.

823 We have also the following result of Hirsch [26]:

824 **Theorem A.2.** If the cooperative system (A3) has the following proprieties:

- 825 • $\mathbb{J}\Psi(x)$ is irreducible for any $x \geq 0$,
- 826 • $\mathbb{J}\Psi(x) \leq \mathbb{J}\Psi(y)$ for any $x \geq y \geq 0$, and
- 827 • all solutions are bounded,

828 then either the origin is globally stable or there exists a unique positive equilibrium
 829 point and all the trajectories in $\mathbb{R}_+^n \setminus \{0\}$ tend to it.

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