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1 **NONLINEAR DIFFUSION IN THE MULTI-PATCH LOGISTIC**
2 **MODEL** *

3 BILEL ELBETCH †AND ALI MOUSSAOUI* ‡

4 **Abstract.** In this work, we study a multi-patch model, where the patches are coupled by
5 nonlinear asymmetrical migration terms, and each patch follows a logistic law. First, using the
6 theory of a cooperative differential system, we prove the global stability of the model. Next, in the
7 case of perfect mixing, i.e when the migration rate tends to infinity, the total population follows a
8 logistic law with a carrying capacity which in general is different from the sum of the n carrying
9 capacities, and depends on the migration terms. Second, we determine, in some particular cases,
10 the conditions under which fragmentation and nonlinear asymmetrical migration can lead to a total
11 equilibrium population greater or smaller than the sum of the carrying capacities. Finally, for the
12 two-patch model, we give a complete classification of the model parameter space as to whether
13 nonlinear dispersal is beneficial or detrimental to the sum of two carrying capacities.

14 **Key words.** Population Dynamics, Logistic equation, Nonlinear diffusion, Slow-fast systems;
15 Tikhonov's theorem, Perfect mixing.

16 **AMS subject classifications.** 37N25, 92D25, 34D23, 34D15.

17 **1. Introduction.** There are many factors affecting the growth and the general
18 dynamics of population. One such important factor is the dispersal amounts and in
19 random ways. These dispersal can cause disturbances to the various ecosystems as
20 well as to the persistence or extinction of organisms. Bibliographies can be found in
21 the work of Levin [27, 28], Holt [25], Allen [1, 2, 3], and Gurney and Nisbet[24].

22 In [1], Allen considered the n -patch general model given by the following equa-
23 tions:

24 (1.1)
$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \Upsilon_i(x), \quad i = 1, \dots, n,$$

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

28 (1.2)
$$\Upsilon_i(x) = \sum_{j=1, j \neq i}^n \beta_{ij} (x_j - \gamma_{ij} x_i), \quad , i = 1, \dots, n,$$

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

32 (1.3)
$$\Upsilon_i(x) = \sum_{j=1, j \neq i}^n \beta_{ij} x_i (x_j - \gamma_{ij} x_i), \quad , i = 1, \dots, n,$$

33 where β_{ij} and γ_{ij} are positive constants. Note that, the term 'biased' means that the
34 diffusion rate is a function of population density. The diffusion rate is regulated by

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35 population density, increasing for large populations and decreasing for small popula-
 36 tions. The third type of mechanism, is the directed diffusion which is formulated by
 37 Gurney and Nisbet [24], given by:

$$38 \quad (1.4) \quad \Upsilon_i(x) = \sum_{j=1, j \neq i}^n \beta_{ij} (x_j^2 - \gamma_{ij} x_i^2), \quad i = 1, \dots, n,$$

39 where β_{ij} and γ_{ij} are positive constants. Dispersal by directed diffusion implies that
 40 the individuals move from high population concentration to low ones, i.e., the move-
 41 ment is a function of species density. For more information on the biological interpre-
 42 tation and also the continuous version of those types of diffusion, we refer the readers
 43 to [1] and [24].

44 The objective of the work of Allen [1] is to study the effect of different types
 45 of the dispersion on the persistence and extinction of the species. The persistence
 46 and extinction behavior is completely determined in a two-patch model (1.1)(1.2) for
 47 $n = 2$ (see Theorem 1 in [1]). For model (1.1)(1.3), Allen [1, Theorem 2] showed that
 48 a population modelled with biased diffusion is always persistent and in fact represents
 49 a strongly persistent population. For more details on the results of persistence and
 50 extinction, see Theorem 3 of [1] for n -patch model (1.1)(1.3) and Proposition 1 of [1]
 51 for 2-patch case; Theorem 4 of [1] for the n -patch model (1.1)(1.4).

52 Lu and Takeuchi [29] have also considered the multi-patch logistic model with
 53 nonlinear diffusion terms, i.e the system (1.1)(1.4). They obtained the sufficient and
 54 necessary conditions for the system to be globally stable (see Theorem 3 in [29]).

55 DeAngelis and Zhang [12], DeAngelis et al. [13] and Zhang et al. [35] have
 56 considered the model (1.1) with

$$57 \quad (1.5) \quad \Upsilon_i(x) = \sum_{j=1, j \neq i}^n (x_{i-1} - 2x_i + x_{i+1}), \quad i = 1, \dots, n,$$

58 where we denote $x_0 = x_n$ and $x_{n+1} = x_1$, allowing the patches to join in a circle so
 59 that the same relationships hold between x_i, x_{i-1} and x_{i+1} for all values of i . An
 60 interesting result of (1.1)(1.5) is that in the case $r_i = K_i$, for $i = 1, \dots, n$, the total
 61 population at steady state satisfies

$$62 \quad (1.6) \quad \sum_{i=1}^n x_i^* > \sum_{i=1}^n K_i.$$

63 Our aim in this work is to study the model of n patches coupled by nonlinear
 64 migration terms (same type of dispersion (1.4)). In particular, we are interested
 65 in studying the effect of nonlinear dispersion on the dynamics of population, and to
 66 compare some results for the nonlinear dispersion with those obtained for the linear
 67 dispersion in [14, 15] for the model (1.7). In 2021, Elbetch et al. [15] have considered
 68 the model of multi-patch logistic growth, coupled by asymmetric linear migration
 69 terms

$$70 \quad (1.7) \quad \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n (\theta_{ij} x_j - \theta_{ji} x_i), \quad i = 1, \dots, n,$$

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 (1.7) describes the effect of the linear migration between the patches, where β is the migration rate and $\Theta := (\theta_{ij})$ is the matrix representing the migrations between the patches. Note that, the system (1.7) is studied also by Elbetch *et al.* [14] and Takeuchi [31] in the case when the matrix Θ is symmetric. We recall that, when the matrix of migration Θ is irreducible, System (1.7) admits a unique positive equilibrium which is globally asymptotically stable (GAS), see [7, Theorem 2.2], [6, Theorem 1] or [14, Theorem 6.1], when $\beta \rightarrow \infty$, this equilibrium tend to

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

71 where $\alpha_i = \frac{r_i}{K_i}$ and $(\delta_1, \dots, \delta_n)^T$ the vector which generate the vector space $\ker \Theta$ (
72 see Section 3).

73 In [14, 15], Elbetch *et al.* have answered in some particular cases of the model
74 (1.7) to the following important question: Is it possible, depending on the migration
75 rate, that the total equilibrium population be larger than the sum of the capacities
76 $\sum_i K_i$? This question is of ecological importance since the answer gives the conditions
77 under which the linear dispersal is either beneficial or detrimental to total equilibrium
78 population. Note that, this question has been studied by many researches (see
79 [4, 5, 8, 10, 11, 12, 13, 14, 15, 17, 18, 19, 22, 34, 35] and [20, 21] and on susceptible-
80 infected-susceptible (SIS) patch-model). They proved that, if all the patches do not
81 differ with respect to the intrinsic growth rate (i.e., $r_1 = \dots = r_n$), then the effect
82 of linear migration is always detrimental. In the case when $(K_1, \dots, K_n)^T \in \ker \Theta$
83 (if the matrix Θ is symmetric, the condition $(K_1, \dots, K_n)^T \in \ker \Gamma$ means that the
84 patches do not differ with respect to the carrying capacity), linear migration has
85 no effect on the total equilibrium population. An example when the effect of linear
86 migration is always beneficial, is in the case when Θ is symmetric and all the patches
87 do not differ with respect to the the parameter $\alpha = r/K$ quantifying intraspecific
88 competition (i.e., $\alpha_1 = \dots, \alpha_n$) (see also [15, Prop. 4.2]).

89 This paper is organized as follows: in Section 2, we introduce the mathematical
90 model and we give some definitions and notations. Next, in Section 3, we study the
91 asymptotic behavior of the stability modulus of the matrix A given by (2.7), and we
92 prove that the stability modulus of A is strictly decreasing as function of the migration
93 rate and it is always negative. This result is used in Section 4 to prove the global
94 stability of the model (2.1). In Section 5, we study the behavior of the system (2.1) in
95 the case when the migration rate goes to infinity by direct method and also by using
96 perturbation arguments. In Section 6, we compare the total equilibrium population
97 with the sum of the n carrying capacities for some parameter space, and by using
98 the same method as Arditi *et al.* [5], we give a complete analysis of two-patch case
99 in Section 7. In Section 8, two-patch model where one growth rate is much larger
100 than the second one is considered, we compare the total equilibrium population with
101 the sum of two capacities in this case. We perform some numerical simulations to
102 illustrate our results in this paper and give a brief concluding remark.

103 **2. The mathematical model.** We consider the model of multi-patch logistic
104 growth, coupled by nonlinear migration terms given by:

105 (2.1)
$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n,$$

106 where x_i is the population in patch i , the parameters r_i and K_i are respectively the
107 intrinsic growth rate and the carrying capacity patch i , n is the number of the patches

108 in the system. The parameter β represents the dispersal rate of the population; $\theta_{ij} \geq 0$
 109 denotes the flux between patches j and i , for $j \neq i$. Note that if $\theta_{ij} > 0$ there is a
 110 flux of migration between patches j and i and if $\theta_{ij} = 0$ there is no migration. The
 111 system (2.1) of differential equations can be written:

$$112 \quad (2.2) \quad \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1}^n \theta_{ij} x_j^2, \quad i = 1, \dots, n,$$

113 where

$$114 \quad (2.3) \quad \theta_{ii} = - \sum_{j=1, j \neq i}^n \theta_{ji}, \quad i = 1, \dots, n$$

115 denotes the outgoing flux of patch i . We denote by Θ the following matrix

$$116 \quad (2.4) \quad \Theta = \begin{pmatrix} -\sum_{k \neq 1} \theta_{k1} & \theta_{12} & \dots & \theta_{1n} \\ \theta_{21} & -\sum_{k \neq 2} \theta_{k2} & \dots & \theta_{2n} \\ \cdot & \dots & \ddots & \vdots \\ \theta_{n1} & \dots & \theta_{n, n-1} & -\sum_{k \neq n} \theta_{kn} \end{pmatrix}.$$

117 We call Θ the movement matrix of the system (2.1). Its columns sum to 0 since the
 118 diagonal elements θ_{ii} are defined by (2.3). The matrix

$$119 \quad (2.5) \quad \Theta_0 := \Theta - \text{diag}(\theta_{11}, \dots, \theta_{nn})$$

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

124 The system (2.1) can be also rewritten in matrix form as follow:

$$125 \quad (2.6) \quad \frac{dx}{dt} = \text{diag}(r_1, \dots, r_n)x + Ax^2,$$

126 where $x = (x_1, \dots, x_n)^T$, $x^2 := (x_1^2, \dots, x_n^2)^T$ and A the matrix defined by

$$127 \quad (2.7) \quad A := \beta\Theta - \text{diag}(\alpha_1, \dots, \alpha_n).$$

128 where $\alpha_i = \frac{r_i}{K_i}$. First, we start by giving some definitions.

DEFINITION 2.1. A matrix $M = (m_{ij})$ is called cooperative if $m_{ij} \geq 0$ for all $i \neq j$.

Recall that the differential system

$$\frac{dx}{dt} = F(x),$$

129 is said to be cooperative, if its jacobian matrix is cooperative, i.e., for all $i \neq j$;
 130 $(\partial F_i / \partial x_j) \geq 0$, for all x positive.

131 DEFINITION 2.2. The stability modulus of a matrix M is given by

$$132 \quad (2.8) \quad s(M) = \max \{ \text{Re}(\lambda) : \lambda \text{ is an eigenvalue of } M \}.$$

133 Note that, the matrix A is a non linear part of the system (2.1) and it is a cooperative
 134 matrix.

135 **3. Asymptotic behavior of the stability modulus of the matrix A .** Using
136 some results proven by Gao and Dong [22] on SIS patch-model. we give in this section
137 some proprieties of the stability modulus of the matrix A defined by (2.7), which is
138 a non linear part of the differential system (2.1). First for all, we recall that, if Θ is
139 irreducible, then 0 is a simple eigenvalue of Θ and all non-zero eigenvalues of Θ have
140 negative real part. Moreover, the kernel of the matrix Θ is generated by a positive
141 vector (see Lemma 2 in [6]). In all of this paper, we denote by $\delta := (\delta_1, \dots, \delta_n)^T$
142 this positive vector. For the existence, uniqueness, and positivity of δ see Lemma
143 1 of Cosner et al. [9], Lemma 4.1 and Lemma 1 of Elbetch et al. [14, 15]. Note
144 that, if the matrix Θ is symmetric, then $\ker \Theta$ is generated by $\delta = (1, \dots, 1)^T$. On
145 the other hand, it is shown in Guo et al. [23, Lemma 2.1] and Gao and Dong [22,
146 Lemma 3.1] that the vector $(\Theta_{11}^*, \dots, \Theta_{nn}^*)^T$ is a right eigenvector of Θ associated
147 with the zero eigenvalue. Here, Θ_{ii}^* is the cofactor of the i -th diagonal entry of Θ ,
148 and $\text{sgn}(\Theta_{ii}^*) = (-1)^{n-1}$. As in our work, the matrix Θ is assumed to be irreducible,
149 then $(-1)^{n-1}(\Theta_{11}^*, \dots, \Theta_{nn}^*)^T$ is strictly positive, i.e $\delta_i = (-1)^{n-1}\Theta_{ii}^* > 0$ for all i .
150 Therefore, we have explicit formula for the components of the vector δ , as functions
151 of the coefficients of Θ , at our disposal. For two patches we have $\delta = (\theta_{12}, \theta_{21})^T$, and
152 for three patches we have $\delta = (\delta_1, \delta_2, \delta_3)^T$, where

$$153 \quad (3.1) \quad \begin{cases} \delta_1 = \theta_{12}\theta_{13} + \theta_{12}\theta_{23} + \theta_{32}\theta_{13}, \\ \delta_2 = \theta_{21}\theta_{13} + \theta_{21}\theta_{23} + \theta_{31}\theta_{23}, \\ \delta_3 = \theta_{21}\theta_{32} + \theta_{31}\theta_{12} + \theta_{31}\theta_{32}. \end{cases}$$

154 In Lemma 2.1 of Guo et al. [23] gives explicit formulas of the components of the
155 vector δ , with respect of the coefficients of Θ as follow:

$$156 \quad (3.2) \quad \delta_k = \sum_{T \in \mathcal{T}_k} \prod_{(i,j) \in E(T)} \theta_{ij}, \quad k = 1, \dots, n,$$

157 where \mathcal{T}_k is the set of all directed trees of n vertices rooted at the k -th vertex, and
158 $E(T)$ denotes the set of arcs in a directed tree T .

159 **PROPOSITION 3.1.** *The stability modulus $\lambda^*(\beta) := s(A)$, with*

160 $A = \beta\Theta - \text{diag}\{\alpha_1, \dots, \alpha_n\}$ *satisfies*

- 161 1. λ^* *is strictly decreasing in* $\beta \in [0, +\infty[$.
- 162 2. $\lambda^* \rightarrow -\max\{\alpha_1, \dots, \alpha_n\}$ *as* $\beta \rightarrow 0$.
- 163 3. $\lambda^* \rightarrow \lambda_\infty^* := -\sum_{i=1}^n \alpha_i \delta_i / \sum_{i=1}^n \delta_i$ *as* $\beta \rightarrow \infty$. *In addition, if the matrix Θ is*
164 *symmetric, then* $\lambda_\infty^* = -\frac{1}{n} \sum_{i=1}^n \alpha_i$.

Proof. The proof is derived from Corollary 3.5 in Gao and Dong [22]. Indeed,
it was shown by Gao and Dong [22] for a SIS patch model that, the function $\beta \rightarrow$
 $s(F - D + \beta\Theta)$ is strictly decreasing in $\beta \in [0, \infty[$ where F and D be a two positive
diagonal matrix. Therefore, for $F = \mathbb{I}$ and $D = \text{diag}(\alpha_1, \dots, \alpha_n)$, we get

$$0 > \frac{d}{d\beta} s(\mathbb{I} - \text{diag}(\alpha_1, \dots, \alpha_n) + \beta\Theta) = \frac{d}{d\beta} (1 + s(-\text{diag}(\alpha_1, \dots, \alpha_n) + \beta\Theta)) = \frac{d\lambda^*}{d\beta}(\beta).$$

165 It is clear that limit λ^* tend to $-\max\{\alpha_1, \dots, \alpha_n\}$ as $\beta \rightarrow 0$.

166 When $\beta \rightarrow \infty$, by Corollary 3.5 in Gao and Dong [22] for the choice $F - D =$
167 $-\text{diag}(\alpha_1, \dots, \alpha_n)$ we obtain the limit λ_∞^* of λ^* . In particular, if Θ is symmetric, one
168 has $\delta_i = 1$ for all i . \square

169 As corollary of the previous proposition, we have the result:

170 **COROLLARY 3.2.** *Consider the matrix A defined by (2.7), then $s(A) < 0$.*

171 **4. Global dynamics.** In this section, our goal is to study the dynamics of
 172 the system (2.1). Note that, in the absence of migration, i.e the case where $\beta =$
 173 0, the system (2.1) admits (K_1, \dots, K_n) as a non trivial equilibrium point, which
 174 furthermore is GAS, and the origin as trivial equilibrium which is unstable. The
 175 problem is whether or not, the equilibrium continues to be exist and GAS for any
 176 $\beta > 0$. First, we prove the following result:

177 **PROPOSITION 4.1.** *The positive cone \mathbb{R}_+^n is positively invariant for the system*
 178 *(2.1).*

Proof. Suppose that, at a given time t , one of the state variables of the system
 (2.1) is at a boundary of \mathbb{R}_+^n , meaning that at least one population is at 0. We suppose
 that $x_i = 0$, and $x_j \geq 0$ for all $j \neq i$, then the dynamics of x_i is given by

$$\frac{dx_i}{dt} = \beta \sum_{j \neq i} \theta_{ij} x_j^2 \geq 0.$$

179 So each trajectory initiated at a boundary of \mathbb{R}_+^n either remains at the boundary or
 180 goes to the interior of \mathbb{R}_+^n . According to [30, Proposition B.7, page 267], no trajectory
 181 comes out of \mathbb{R}_+^n . Therefore, \mathbb{R}_+^n is positively invariant for (2.1). \square

182 To establish the boundedness of solutions of (2.1), we have the following result:

183 **PROPOSITION 4.2.** *For any non negative initial condition, the solutions of the*
 184 *system (2.1) remain non negative and positively bounded. Moreover, the set*

$$185 \quad (4.1) \quad \Lambda = \left\{ (x_1, \dots, x_n) \in \mathbb{R}^n : 0 \leq \sum_{i=1}^n x_i \leq \frac{\xi_2^*}{\xi_1^*} \right\}$$

186 *is positively invariant and is a global attractor for (2.1), where $\xi_1^* = \min_{1 \leq i \leq n} r_i$ and*
 187 *$\xi_2^* = \sum_{i=1}^n r_i K_i$.*

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

$$190 \quad (4.2) \quad \dot{X}_T(t) = \sum_{i=1}^n r_i x_i(t) \left(1 - \frac{x_i(t)}{K_i} \right).$$

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

$$192 \quad (4.3) \quad r_i x_i \left(1 - \frac{x_i}{K_i} \right) \leq r_i (K_i - x_i).$$

193 Substituting Equation (4.3) into (4.2), we get

$$194 \quad (4.4) \quad \dot{X}_T(t) \leq -\xi_1^* X_T(t) + \xi_2^* \quad \text{for all } t \geq 0,$$

195 which gives

$$196 \quad (4.5) \quad X_T(t) \leq \left(X_T(0) - \frac{\xi_2^*}{\xi_1^*} \right) e^{-\xi_1^* t} + \frac{\xi_2^*}{\xi_1^*}, \quad \text{for all } t \geq 0.$$

197 Hence,

$$198 \quad (4.6) \quad X_T(t) \leq \max \left(X_T(0), \frac{\xi_2^*}{\xi_1^*} \right), \quad \text{for all } t \geq 0.$$

199 Therefore, the solutions of system (2.1) are positively bounded and defined for all
 200 $t \geq 0$. From (4.5) it can be deduced that the set Λ is positively invariant and it is a
 201 global attractor for the system (2.1). \square

202 **THEOREM 4.3.** *Assume that the matrix $\Theta = (\theta_{ij})_{n \times n}$ (or equivalently, the con-*
 203 *nectivity matrix Θ_0) is irreducible. The model (2.1) has a unique positive equilibrium*
 204 *point which is GAS in the positive cone $\mathbb{R}_+^n \setminus \{0\}$.*

205 *Proof.* Consider the system (2.1). According to a result of Lu and Takeuchi [29,
 206 Theorem 3] for the nonlinear diffusion system with logistic growth rate functions, the
 207 system (2.1) possesses a globally stable positive equilibrium if the matrix A given by
 208 (2.7) is stable, (i.e., there exists a positive diagonal matrix C such that $CA + A^T C$
 209 is negative definite), which equivalent $s(A) < 0$ by Lemma 3 of [29]. According to
 210 Corollary 3.2, the model (2.1) has a unique positive equilibrium point which is GAS
 211 in the positive cone $\mathbb{R}_+^n \setminus \{0\}$. \square

212 **REMARK 1.** *The matrix Θ being irreducible means that the set of patches cannot*
 213 *be partitioned into two nonempty disjoint subsets, I and J , such that there is no*
 214 *migrations between a patch in subset I and a patch in subset J . The matrix Θ is*
 215 *assumed to be irreducible throughout the rest of the paper. Therefore species can reach*
 216 *any patch from any patch either directly or through other patches.*

217 In all of this work, the GAS equilibrium of the system (2.1), whose existence is shown
 218 in Theorem 4.3, is denoted by $E_n^*(\beta) = (x_1^*(\beta), \dots, x_n^*(\beta))$, and by $T_n^*(\beta)$ the total
 219 equilibrium population

$$220 \quad (4.7) \quad T_n^*(\beta) = \sum_{i=1}^n x_i^*(\beta).$$

221 **5. Large diffusion rate.** In this section our aim is to study the behavior of
 222 $E_n^*(\beta)$ and $T_n^*(\beta)$, defined by (4.7), for large migration rate, i.e when $\beta \rightarrow \infty$.

223 **5.1. The fast dispersal limit.** We have the following result:

224 **THEOREM 5.1.** *We have:*

$$225 \quad (5.1) \quad \lim_{\beta \rightarrow +\infty} E_n^*(\beta) = \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \delta_i \alpha_i} (\sqrt{\delta_1}, \dots, \sqrt{\delta_n})$$

226 where $\alpha_i = r_i/K_i$. Moreover, if the matrix Θ is symmetric, then the equilibrium
 227 $E_n^*(\beta)$ converges to an element of $\ker \Theta$

$$228 \quad (5.2) \quad \lim_{\beta \rightarrow +\infty} E_n^*(\beta) = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i} (1, \dots, 1).$$

229 *Proof.* The equilibrium E_n^* is a solution of the algebraic system:

$$230 \quad (5.3) \quad 0 = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n.$$

231 The sum of these equations shows that $E_n^*(\beta)$ satisfies the following equation

$$232 \quad (5.4) \quad \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) = 0.$$

233 Therefore $E_n^*(\beta)$ belongs to the ellipsoid:

$$234 \quad (5.5) \quad \mathbb{E}^{n-1} := \left\{ x \in \mathbb{R}^n : \Upsilon(x) := \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) = 0 \right\}.$$

235 Note that, this ellipsoid is independent of the migration terms β and θ_{ij} . The ellipsoid
236 \mathbb{E}^{n-1} passes through the points O , and $\mathcal{A} = (K_1, \dots, K_n)$.

237 So, the equilibrium E_n^* is the solution in the positive cone, of the equation $F_\beta = 0$,
238 where

$$239 \quad (5.6) \quad F_\beta(x) := \left(F_1^\beta(x), \dots, F_{n-1}^\beta(x), \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) \right),$$

240 with

$$241 \quad (5.7) \quad F_i^\beta(x) = \frac{1}{\beta} r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \sum_{j=1, j \neq i}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n-1.$$

242 On the other hand, the limit equations (obtained when $\beta \rightarrow \infty$) are given by:

$$243 \quad (5.8) \quad F_\infty(x) := \left(F_1^\infty(x), \dots, F_{n-1}^\infty(x), \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) \right),$$

244 with

$$245 \quad (5.9) \quad F_i^\infty(x) = \sum_{j=1, j \neq i}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n-1.$$

246 According to Lemma B.1 of [15], the system (5.9) admits unique solution given by:

247 $x_i = \sqrt{\frac{\delta_i}{\delta_n}} x_n$ for all $i = 1, \dots, n-1$. So, the solutions of the equation $F_\infty(x) = 0$ is
248 given by the solutions of the following system:

$$249 \quad (5.10) \quad \begin{cases} x_i = \sqrt{\frac{\delta_i}{\delta_n}} x_n, & i = 1, \dots, n-1. \\ \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right) = 0, \end{cases}$$

which admits $x_n = 0$ and $x_n = \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \delta_i \alpha_i} \sqrt{\delta_n}$ as solutions. So, the equation $F_\infty = 0$
admits two solutions, 0 and

$$E_n^*(\infty) := \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \delta_i \alpha_i} (\sqrt{\delta_1}, \dots, \sqrt{\delta_n}).$$

250 The ellipsoid \mathbb{E}^{n-1} is compact, so the equilibrium $E_n^*(\beta)$ has at least one limit
251 point in the ellipsoid, when β goes to infinity. By the same reason as in [15, Proof of
252 Theorem 3.3], we prove the convergence of $E_n^*(\beta)$ to $E_n^*(\infty)$.

253 If the matrix Θ is symmetric, one has $\delta_i = 1$, for all i . □

254 As a corollary of the previous theorem we obtain the following result which describes
255 the total equilibrium population for large growth rate:

256 COROLLARY 5.2. *We have*

$$257 \quad (5.11) \quad T_n^*(+\infty) = \left(\sum_{i=1}^n \sqrt{\delta_i} \right) \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \delta_i \alpha_i}.$$

258 *Moreover, if the matrix Θ is symmetric, then:*

$$259 \quad (5.12) \quad T_n^*(+\infty) = n \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i}.$$

260 *Proof.* The sum of the n components of the point $E_n^*(\infty)$ immediately gives the
261 equation (5.11). \square

262 We remark that, the total equilibrium population for large migration rate (5.12) is
263 equal the total equilibrium population for large migration rate of the multi-patch
264 logistic model with linear diffusion obtained in [14, Equation 24]. This result show
265 that, if the movement between the n patches is symmetric, the nonlinear diffusion has
266 no influence on the total equilibrium population for large migration rate.

267 **5.2. Two time scale dynamics.** We can use the theory of singular perturba-
268 tions to obtain a better understanding of the behavior of the system in the case of
269 perfect mixing. We have the following result:

270 **THEOREM 5.3.** *Let $(x_1(t, \beta), \dots, x_n(t, \beta))$ be the solution of the system (2.1) with*
271 *initial condition (x_1^0, \dots, x_n^0) satisfying $x_i^0 \geq 0$ for $i = 1, \dots, n$. Let $Y(t)$ be the*
272 *solution of the equation*

$$273 \quad (5.13) \quad \frac{dX}{dt} = rX \left(1 - \frac{X}{\left(\sum_{i=1}^n \sqrt{\delta_i} \right) K} \right),$$

274 *where*

$$275 \quad (5.14) \quad r = \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \sqrt{\delta_i}}, \quad K = \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum_{i=1}^n \delta_i \alpha_i} \quad \text{and} \quad \alpha_i = r_i / K_i.$$

276 *Then, when $\beta \rightarrow \infty$, we have*

$$277 \quad (5.15) \quad \sum_{i=1}^n x_i(t, \beta) = Y(t) + o_\beta(1) \quad \text{uniformly for } t \in [0, +\infty)$$

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

$$279 \quad (5.16) \quad x_i(t, \beta) = \frac{\sqrt{\delta_i}}{\sum_{i=1}^n \sqrt{\delta_i}} Y(t) + o_\beta(1) \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty).$$

280 *Proof.* Let $X(t, \beta) = \sum_{i=1}^n x_i(t, \beta)$. We rewrite the system (2.1) using the vari-
281 ables (X, x_1, \dots, x_{n-1}) , and get:

$$282 \quad (5.17) \quad \begin{cases} \frac{dX}{dt} = \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i} \right), \\ \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + \beta \sum_{j=1, j \neq i}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n-1. \end{cases}$$

283 This system is actually a system in the variables (X, x_1, \dots, x_{n-1}) , since, whenever
 284 x_n appears in the right hand side of (5.17), it should be replaced by

$$285 \quad (5.18) \quad x_n = X - \sum_{i=1}^{n-1} x_i.$$

286 When $\beta \rightarrow \infty$, (5.17) is a *slow-fast* system, with one *slow variable*, X , and $n-1$ *fast*
 287 *variables*, x_i for $i = 1 \dots n-1$. As suggested by Tikhonov's theorem [26, 32, 33], we
 288 consider the dynamics of the fast variables in the time scale $\tau = \beta t$. We get

$$289 \quad (5.19) \quad \frac{dx_i}{d\tau} = \frac{1}{\beta} r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \sum_{j=1, j \neq i}^n (\theta_{ij} x_j^2 - \theta_{ji} x_i^2), \quad i = 1, \dots, n-1.$$

where x_n is given by (5.18). In the limit $\beta \rightarrow \infty$, we find the *fast dynamics*

$$\frac{dx_i}{d\tau} = \sum_{j=1, j \neq i}^n (\gamma_{ij} x_j^2 - \gamma_{ji} x_i^2), \quad i = 1, \dots, n-1.$$

This is an $(n-1)$ -dimensional non linear differential system. According to [15, Lemma
 B.1], we can deduced that, this system admits unique equilibrium GAS given by

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

290 Thus, the slow manifold of System (5.17) is given by

$$291 \quad (5.20) \quad x_i = \frac{\sqrt{\delta_i}}{\sum_{i=1}^n \sqrt{\delta_i}} X, \quad i = 1, \dots, n-1.$$

As this manifold is GAS, Tikhonov's theorem ensures that after a fast transition
 toward the slow manifold, the solutions of (5.17) are approximated by the solutions
 of the *reduced model*, which is obtained by replacing (5.20) into the dynamics of the
 slow variable, that is:

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

where r and K are defined in (5.14). Therefore, the reduced model is (5.13). The
 system (5.13) admits

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

292 as a positive equilibrium point, which is GAS in the positive axis, the approximation
 293 given by Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq$
 294 $t_0 > 0$ for the fast variables, where t_0 is as small as we want. Therefore, letting $Y(t)$
 295 be the solution of the reduced model (5.13) with initial condition $Y(0) = X(0, \beta) =$
 296 $\sum_{i=1}^n x_i^0$, then, when $\beta \rightarrow \infty$, we have the approximations (5.15) and (5.16). \square

Note that, in the case of perfect mixing, the approximation (5.15) shows that, the total population behaves like the unique logistic equation (5.13) and then, when t and β tend to ∞ , the total population $\sum x_i(t, \beta)$ tends toward

$$\left(\sum_{i=1}^n \sqrt{\delta_i} \right) K = \left(\sum_{i=1}^n \sqrt{\delta_i} \right) \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum \delta_i \alpha_i}$$

as stated in Theorem 5.1. The approximation (5.16) shows that, with the exception of a thin initial boundary layer, where the density population $x_i(t, \beta)$ quickly jumps from its initial condition x_i^0 to the average $\sqrt{\delta_i} X_0 / \sum_{i=1}^n \sqrt{\delta_i}$, each patch of the model behaves like the single logistic equation

$$\frac{du}{dt} = ru \left(1 - \frac{u}{\sqrt{\delta_i} K} \right), \quad i = 1, \dots, n.$$

where r and K are given in (5.14). Hence, when t and β tend to ∞ , the density population $x_i(t, \beta)$ tends toward $K = \sqrt{\delta_i} \frac{\sum_{i=1}^n \sqrt{\delta_i} r_i}{\sum \delta_i \alpha_i}$ as stated in Theorem 5.1.

As a corollary of the previous theorem we obtain the following result which describes the behavior of the system (2.1) for perfect mixing and nonlinear symmetrical dispersal:

COROLLARY 5.4. *Assume that the matrix Θ is symmetric. Let $(x_1(t, \beta), \dots, x_n(t, \beta))$ be the solution of the system (2.1) with initial 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 equation*

$$(5.21) \quad \frac{dX}{dt} = rX \left(1 - \frac{X}{nK} \right),$$

where

$$(5.22) \quad r = \frac{\sum_{i=1}^n r_i}{n}, \quad K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i} \quad \text{and} \quad \alpha_i = r_i / K_i.$$

Then, when $\beta \rightarrow \infty$, we have

$$(5.23) \quad \sum_{i=1}^n x_i(t, \beta) = Y(t) + o_\beta(1) \quad \text{uniformly for } t \in [0, +\infty)$$

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

$$(5.24) \quad x_i(t, \beta) = \frac{Y(t)}{n} + o_\beta(1) \quad i = 1, \dots, n, \quad \text{uniformly for } t \in [t_0, +\infty).$$

Proof. If Θ is symmetric, one has $\delta_i = 1$ for all i . Therefore, the formulas (5.13), (5.14), and the approximations (5.15), (5.16) for $\delta_i = 1$, give the proof of the corollary. \square

5.3. Comparison of $T_n^*(+\infty)$ with $\sum_i K_i$. According to Formula (5.11), it is clear that the total equilibrium population at $\beta = 0$ and at $\beta = +\infty$ are different in general.

In the remainder of this section, we give some conditions, in the space of parameters r_i, K_i, α_i and δ_i , for limit of the total equilibrium population when $\beta \rightarrow \infty$ to be greater or smaller than the sum of the carrying capacities. We show that all three cases are possible, i.e $T_n^*(+\infty)$ can be greater than, smaller than, or equal to $T_n^*(0)$. First, we start by giving some particular values of the parameters for which equality holds.

324 PROPOSITION 5.5. Consider the system (2.1). Let us denote $\sqrt{\ker \Theta}$ the vector
 325 space generated by the vector $(\sqrt{\delta_1}, \dots, \sqrt{\delta_n})^T$. If the vector $(\frac{1}{\alpha_1}, \dots, \frac{1}{\alpha_n})^T$ lies in
 326 $\sqrt{\ker \Theta}$, then $T_n^*(+\infty) = \sum_i K_i$.

327 *Proof.* Direct consequence of the equation (5.11). \square

328 Note that, if the matrix Θ is symmetric, then, Prop. 5.5 says that if all α_i are equal,
 329 then $T_n^*(\infty) = \sum_i K_i$, which is [14, Prop 4.4] obtained for the multi-patch logistic
 330 model with linear diffusion.

331 In the next proposition, we give two cases which ensure that $T_n^*(0)$ can be greater
 332 or smaller than $T_n^*(+\infty)$. This result can be stated as the following proposition:

333 PROPOSITION 5.6. Consider the system (2.1).

- 334 1. If $\frac{K_1}{\sqrt{\delta_1}} \leq \dots \leq \frac{K_n}{\sqrt{\delta_n}}$ and $\sqrt{\delta_1}\alpha_1 \leq \dots \leq \sqrt{\delta_n}\alpha_n$, or if $\frac{K_1}{\sqrt{\delta_1}} \geq \dots \geq \frac{K_n}{\sqrt{\delta_n}}$ and
 335 $\sqrt{\delta_1}\alpha_1 \geq \dots \geq \sqrt{\delta_n}\alpha_n$, then $T_n^*(+\infty) \geq T_n^*(0)$.
- 336 2. If $\frac{K_1}{\sqrt{\delta_1}} \geq \dots \geq \frac{K_n}{\sqrt{\delta_n}}$ and $\sqrt{\delta_1}\alpha_1 \leq \dots \leq \sqrt{\delta_n}\alpha_n$, or if $\frac{K_1}{\sqrt{\delta_1}} \leq \dots \leq \frac{K_n}{\sqrt{\delta_n}}$ and
 337 $\sqrt{\delta_1}\alpha_1 \geq \dots \geq \sqrt{\delta_n}\alpha_n$, then $T_n^*(+\infty) \leq T_n^*(0)$.

338 In both items, if at least one of the inequalities in $\frac{K_1}{\sqrt{\delta_1}} \leq \dots \leq \frac{K_n}{\sqrt{\delta_n}}$ or
 339 $\frac{K_1}{\sqrt{\delta_1}} \geq \dots \geq \frac{K_n}{\sqrt{\delta_n}}$ is strict, then the inequality is strict in the conclusion.

340 *Proof.* Apply Lemma B.2 in [15] with the following choice: $w_i = \sqrt{\delta_i}$, $u_i = \frac{K_i}{\sqrt{\delta_i}}$,
 341 and $v_i = \sqrt{\delta_i}\alpha_i$, for all $i = 1, \dots, n$. \square

342 If the matrix Θ is symmetric, one has $\delta_i = 1$, for all i , and Prop. 5.6 becomes

343 COROLLARY 5.7. Consider the system (2.1). Assume that Θ is symmetric.

- 344 1. If $K_1 \leq \dots \leq K_n$ and $\alpha_1 \leq \dots \leq \alpha_n$, or if $K_1 \geq \dots \geq K_n$ and $\alpha_1 \geq \dots \geq$
 345 α_n , then $T_n^*(+\infty) \geq T_n^*(0)$.
- 346 2. If $K_1 \geq \dots \geq K_n$ and $\alpha_1 \leq \dots \leq \alpha_n$, or if $K_1 \leq \dots \leq K_n$ and $\alpha_1 \geq \dots \geq \alpha_n$,
 347 then $T_n^*(+\infty) \leq T_n^*(0)$.

348 **6. Effect of nonlinear dispersal on total population size.** In this section,
 349 we will investigate how non linear dispersal affects the total population in all patches.
 350 In particular, when is it detrimental or beneficial to the sum of carrying capacities?
 351 Mathematically speaking, we will compare, in some particular cases of the system
 352 (2.1), the total equilibrium population $T_n^*(\beta)$, with the sum of carrying capacities
 353 $T_n^*(0) = \sum_i K_i$, when the rate of migration β varies from zero to infinity. We show
 354 that the total equilibrium population, $T_n^*(\beta)$, can either be greater than, smaller than,
 355 or equal to the sum of the carrying capacities $T_n^*(0)$ (non dispersal).

356 **6.1. Nonlinear dispersal may be unfavorable to T_n^* .** In the next proposition,
 357 we show that if the growth rates are equal in all patches, then the total equilibrium
 358 population is always smaller than the sum of the carrying capacities:

359 PROPOSITION 6.1. If $r_1 = \dots = r_n$, then the total equilibrium population, defined
 360 by (4.7) satisfies $T_n^*(\beta) \leq \sum_{i=1}^n K_i$, for all $\beta \in [0, \infty[$.

361 *Proof.* The equation of the tangent space to the ellipsoid \mathbb{E}^{n-1} , defined by (5.5),

362 at point $\mathcal{A} = (K_1, \dots, K_n)$ is given by

363 (6.1)
$$\sum_{i=1}^n (x_i - K_i) \frac{\partial \Upsilon}{\partial x_i}(\mathcal{A}) = 0,$$

364 where Υ is given by (5.5). Since $\frac{\partial \Upsilon}{\partial x_i}(\mathcal{A}) = -r_i$, (6.1) can be written as follows:

365 (6.2)
$$\sum_{i=1}^n r_i (x_i - K_i) = 0.$$

If we take $r_1 = \dots = r_n$ in (6.2), we get that the equation of the tangent plane to \mathbb{E}^{n-1} at the point \mathcal{A} is

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

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

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

366 Which completes the proof of the proposition. \square

367 The result of the previous proposition is the same as Prop. 3.1 and Prop. 6.2 in [14]
368 for the linear diffusion.

369 **6.2. Independence of T_n^* with respect to nonlinear dispersal .** In the
370 next proposition we give sufficient and necessary conditions for the total equilibrium
371 population not to depend on the migration rate.

372 **PROPOSITION 6.2.** *The equilibrium $E_n^*(\beta)$ does not depend on β if and only if*
373 *$(K_1^2, \dots, K_n^2)^T \in \ker \Theta$. In this case we have $E_n^*(\beta) = (K_1, \dots, K_n)$ for all $\beta > 0$.*

374 *Proof.* The equilibrium $E_n^*(\beta)$ is the unique positive solution of the equation

375 (6.3)
$$f(x) + \beta \Theta x^2 = 0,$$

376 where $f(x) = (f_1(x_1), \dots, f_n(x_n))^T$, and $f_i(x_i) = r_i x_i (1 - x_i / K_i)$, $i = 1, \dots, n$.
377 Suppose that the equilibrium $E_n^*(\beta)$ does not depend on β , then we replace in Equation
378 (6.3):

379 (6.4)
$$f(E_n^*(\beta)) + \beta \Theta (E_n^*(\beta))^2 = 0.$$

380 The derivative of (6.4) with respect to β gives

381 (6.5)
$$\Theta (E_n^*(\beta))^2 = 0.$$

382 Replacing the equation (6.5) in the equation (6.4), we get $f(E_n^*(\beta)) = 0$, so $E_n^*(\beta) =$
383 (K_1, \dots, K_n) . From the equation (6.5), we conclude that $(K_1^2, \dots, K_n^2)^T \in \ker \Theta$.

384 Now, suppose that $(K_1^2, \dots, K_n^2)^T \in \ker \Theta$, then (K_1, \dots, K_n) satisfies the equa-
385 tion (6.3), for all $\beta \geq 0$. So, $E_n^*(\beta) = (K_1, \dots, K_n)$, for all $\beta \geq 0$, which proves that
386 the total equilibrium population is independent of the migration rate β . \square

387 If the matrix Θ is symmetric, the previous proposition asserts that, the K_i , for
388 $i = 1, \dots, n$, are equal if and only if $E_n^* = (K, \dots, K)$, where K is the common value
389 of the K_i . This is [14, Proposition 3.2].

390 **6.3. Nonlinear dispersal may be favorable to T_n^* .** In this section, we give a
 391 situation where the non linear dispersal is favorable to the total equilibrium popula-
 392 tion. Mathematically speaking:

PROPOSITION 6.3. Assume that for all $j < i$, $\alpha_i \sqrt{\theta_{ij}} = \alpha_j \sqrt{\theta_{ji}}$. Then

$$T_n^*(\beta) \geq \sum_{i=1}^n K_i \quad \text{for all } \beta \geq 0.$$

393 Moreover, if there exist i_0 and $j_0 \neq i_0$ such that $r_{i_0} \neq r_{j_0}$, then $T_n^*(\beta) > \sum_{i=1}^n K_i$, for
 394 all $\beta > 0$.

395 *Proof.* The equilibrium point $E_n^*(\beta)$ satisfies the system

$$396 \quad (6.6) \quad 0 = \alpha_i x_i^*(\beta) (K_i - x_i^*(\beta)) + \beta \sum_{j=1, j \neq i}^n (\theta_{ij} (x_j^*(\beta))^2 - \theta_{ji} (x_i^*(\beta))^2), \quad i = 1 \cdots n.$$

Dividing (6.6) by $\alpha_i x_i^*$, one obtains

$$x_i^*(\beta) = K_i + \beta \sum_{j=1, j \neq i}^n \frac{\theta_{ij} (x_j^*(\beta))^2 - \theta_{ji} (x_i^*(\beta))^2}{\alpha_i x_i^*(\beta)}.$$

397 Taking the sum of these expressions shows that the total equilibrium population T_n^*
 398 satisfies the following relation:

$$\begin{aligned} (6.7) \\ 399 \quad T_n^*(\beta) &= \sum_{i=1}^n K_i + \beta \sum_{i=1}^n \sum_{j=1, j \neq i}^n \frac{\theta_{ij} (x_j^*(\beta))^2 - \theta_{ji} (x_i^*(\beta))^2}{\alpha_i x_i^*(\beta)} \\ 400 &= \sum_{i=1}^n K_i + \beta \sum_{j < i} \left(\frac{\theta_{ij} (x_j^*(\beta))^2 - \theta_{ji} (x_i^*(\beta))^2}{\alpha_i x_i^*(\beta)} + \frac{\theta_{ji} (x_i^*(\beta))^2 - \theta_{ij} (x_j^*(\beta))^2}{\alpha_j x_j^*(\beta)} \right) \\ 401 &= \sum_{i=1}^n K_i + \beta \sum_{j < i} \left(\sqrt{\theta_{ij}} x_j^*(\beta) + \sqrt{\theta_{ji}} x_i^*(\beta) \right) \left(\frac{\sqrt{\theta_{ij}} x_j^*(\beta) - \sqrt{\theta_{ji}} x_i^*(\beta)}{\alpha_i x_i^*(\beta)} \right. \\ 402 &\quad \left. + \frac{\sqrt{\theta_{ji}} x_i^*(\beta) - \sqrt{\theta_{ij}} x_j^*(\beta)}{\alpha_j x_j^*(\beta)} \right) = \sum_{i=1}^n K_i \\ 403 &\quad + \beta \sum_{j < i} \left(\sqrt{\theta_{ij}} x_j^*(\beta) + \sqrt{\theta_{ji}} x_i^*(\beta) \right) \frac{(\sqrt{\theta_{ij}} x_j^*(\beta) - \sqrt{\theta_{ji}} x_i^*(\beta)) (\alpha_j x_j^*(\beta) - \alpha_i x_i^*(\beta))}{\alpha_j \alpha_i x_j^*(\beta) x_i^*(\beta)}. \end{aligned}$$

The conditions $\alpha_i \sqrt{\theta_{ij}} = \alpha_j \sqrt{\theta_{ji}}$ can be written $\omega_{ij} := \alpha_i / \sqrt{\theta_{ji}} = \alpha_j / \sqrt{\theta_{ij}}$ for all $j < i$, such that $\theta_{ij} \neq 0$ and $\theta_{ji} \neq 0$. Therefore, there exists $\omega_{ij} > 0$ such that

$$\alpha_j = \omega_{ij} \sqrt{\theta_{ij}} \quad \text{and} \quad \alpha_i = \omega_{ij} \sqrt{\theta_{ji}} \quad \text{for all } i, j \text{ with } \theta_{ij} \neq 0 \text{ and } \theta_{ji} \neq 0.$$

405 Replacing α_i and α_j in (6.7), one obtains

$$406 \quad (6.8) \quad T_n^*(\beta) = \sum_{i=1}^n K_i + \beta \sum_{j < i} \frac{\omega_{ij} (\sqrt{\theta_{ij}} x_j^*(\beta) + \sqrt{\theta_{ji}} x_i^*(\beta)) (\sqrt{\theta_{ij}} x_j^*(\beta) - \sqrt{\theta_{ji}} x_i^*(\beta))^2}{\alpha_j \alpha_i x_j^*(\beta) x_i^*(\beta)}.$$

407 Therefore, $T_n^*(\beta) \geq \sum_{i=1}^n K_i$ for all $\beta \geq 0$. As the matrix Θ is assumed irreducible,
 408 then the equality holds if and only if $\beta = 0$ or $\sqrt{\theta_{ij}x_j^*(\beta)} - \sqrt{\theta_{ji}x_i^*(\beta)} = 0$, for all
 409 i and j . Let us prove that if at least two patches have different growth rates, then
 410 equality cannot hold for $\beta > 0$. Suppose that there exists $\beta^* > 0$ such that the
 411 positive equilibrium satisfies

$$412 \quad (6.9) \quad \forall i, j, \quad \sqrt{\theta_{ij}x_j^*(\beta^*)} = \sqrt{\theta_{ji}x_i^*(\beta^*)} \iff \forall i, j, \quad \theta_{ij}(x_j^*)^2(\beta^*) = \theta_{ji}(x_i^*)^2(\beta^*).$$

413 Replacing the equation (6.9) in the system (6.6), we get that $x_i^*(\beta^*) = K_i$, for all
 414 i . Therefore, from (6.9), it is seen that, for all i and j , $K_j^2\theta_{ij} = K_i^2\theta_{ji}$. From these
 415 equations and the conditions $\alpha_i\sqrt{\theta_{ij}} = \alpha_j\sqrt{\theta_{ji}}$, we get $r_i = r_j$, for all i and j . This is
 416 a contradiction with the hypothesis that there exist two patches with different growth
 417 rates. Hence the equality in (6.8) holds if and only if $\beta = 0$. \square

418 As corollary of the previous proposition, we obtain the following result:

419 **COROLLARY 6.4.** *Assume that Θ is symmetric. If $\alpha_1 = \dots = \alpha_n$, then*
 420 $T_n^*(\beta) \geq \sum_i K_i$ for all $\beta \geq 0$.

421 *Proof.* When the matrix Θ is irreducible and symmetric, the hypothesis of Prop.
 422 6.3 implies that $\alpha_i = \alpha_j$ for all i and j . Indeed if two patches i and j are connected
 423 (i.e. $\theta_{ij} = \theta_{ji} \neq 0$), then we have $\alpha_i = \alpha_j$. As the matrix Θ is irreducible, for two
 424 arbitrary patches, there exists a finite sequence (i, \dots, j) which begins in i and ends
 425 in j , such that $\theta_{ab} \neq 0$ for all successive patches a and b in (i, \dots, j) . Hence $\alpha_a = \alpha_b$
 426 for all a and b in (i, \dots, j) . Hence, $\alpha_i = \alpha_j$. \square

427 The result of the corollary 6.4 says that if all α_i are equal, non linear dispersal enhances
 428 population growth, which is [14, Prop. 3.3], which has been proven for the multi-patch
 429 logistic model with linear diffusion.

REMARK 2. *For three patches or more, if the matrix Θ does not verify the condi-*
tion ($\forall i, j, \theta_{ij} = 0 \iff \theta_{ji} = 0$), then the hypothesis of Prop. 6.3, that for all $j < i$,
 $\alpha_i\sqrt{\theta_{ij}} = \alpha_j\sqrt{\theta_{ji}}$ cannot be satisfied. Note that the hypothesis $\alpha_i\sqrt{\theta_{ij}} = \alpha_j\sqrt{\theta_{ji}}$
implies that $\alpha_i^2\theta_{ij} = \alpha_j^2\theta_{ji}$, which implies, for all $i = 1, \dots, n$, one has

$$\sum_{j=1}^n \frac{\theta_{ij}}{\alpha_j^2} = \sum_{j=1, j \neq i}^n \frac{\theta_{ij}}{\alpha_j^2} - \sum_{j=1, j \neq i}^n \frac{\theta_{ji}}{\alpha_i^2} = \sum_{j=1, j \neq i}^n \frac{\alpha_i^2\theta_{ij} - \alpha_j^2\theta_{ji}}{\alpha_i^2\alpha_j^2} = 0.$$

430 Therefore, the hypothesis of Prop. 6.3 implies that $(\frac{1}{\alpha_1^2}, \dots, \frac{1}{\alpha_n^2})^T \in \ker \Theta$.

431 **6.4. Derivative of T_n^* at $\beta = 0$.**

432 **PROPOSITION 6.5.** *The derivative of the total equilibrium population $T_n^*(\beta)$ at*
 433 $\beta = 0$ is given by:

$$434 \quad (6.10) \quad \frac{dT_n^*}{d\beta}(0) = \sum_{i=1}^n \left(\frac{1}{r_i} \sum_{j=1}^n \theta_{ij} K_j^2 \right).$$

Proof. By differentiating the equation (6.7) at $\beta = 0$, we get:

$$\frac{dT_n^*}{d\beta}(0) = \sum_{i=1}^n \sum_{j=1, j \neq i}^n \frac{\theta_{ij}(x_j^*(0))^2 - \theta_{ji}(x_i^*(0))^2}{\alpha_i x_i^*(0)},$$

435 which gives (6.10), since $x_i^*(0) = K_i$ for all $i = 1, \dots, n$. \square

The derivative (6.10) can be written in matrix form as follows:

$$\frac{dT_n^*}{d\beta}(0) = \mathcal{R}^T \Theta K^2,$$

436 with $\mathcal{R} = \left(\frac{1}{r_1}, \dots, \frac{1}{r_n}\right)^T$ and $K^2 = (K_1^2, \dots, K_n^2)^T$. Note that, if the growth rates are
 437 equal in all patches, or, (K_1^2, \dots, K_n^2) lies in the vector space $\ker \Theta$, then the derivative
 438 of the total equilibrium population T_n^* at $\beta = 0$ equal to zero.

439 **7. Two-patch case.** In this section, we concentrate on the two-patch model:

$$440 \quad (7.1) \quad \begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta (\theta_{12} x_2^2 - \theta_{21} x_1^2), \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta (\theta_{21} x_1^2 - \theta_{12} x_2^2). \end{cases}$$

441 The total equilibrium population of the model (7.1) in the perfect mixing case (i.e.
 442 $\beta \rightarrow \infty$) is given by the following formula:

$$443 \quad (7.2) \quad T_2^*(+\infty) = \left(\sqrt{\theta_{12}} + \sqrt{\theta_{21}}\right) \frac{\sqrt{\theta_{12}} r_1 + \sqrt{\theta_{21}} r_2}{\theta_{12} r_1 / K_1 + \theta_{21} r_2 / K_2},$$

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

$$445 \quad (7.3) \quad \frac{dT_2^*}{d\beta}(0) = (\theta_{12} K_2^2 - \theta_{21} K_1^2) \left(\frac{1}{r_1} - \frac{1}{r_2}\right).$$

446 The equilibrium of the system (2.1) is the solutions of the following algebraic system:

$$447 \quad (7.4) \quad \begin{cases} 0 = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta (\theta_{12} x_2^2 - \theta_{21} x_1^2), \\ 0 = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta (\theta_{21} x_1^2 - \theta_{12} x_2^2). \end{cases}$$

448 The sum of two equations of (7.4) shows that the equilibrium points are in ellipse
 449 noted \mathbb{E} , where its equation is given by:

$$450 \quad (7.5) \quad \mathbb{E} : r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) = 0.$$

451 The ellipse \mathbb{E} passes through the points $(0, 0)$, $(K_1, 0)$, $(0, K_2)$ and $\mathcal{A} := (K_1, K_2)$.
 452 Note that, it is independent of migration rate β and θ_{ij} (shown in red in Fig. 1).

Solving the first equation of system (7.4) for x_2 yields a hyperbola noted \mathcal{H}_β defined by

$$\mathcal{H}_\beta : h_\beta(x_1) := \sqrt{\frac{1}{\theta_{12}} \left(\theta_{21} x_1^2 - \frac{r_1}{\beta} x_1 \left(1 - \frac{x_1}{K_1}\right)\right)}.$$

453 As our study is limited in the positive cone, then we are interested only in the positive
 454 branch of \mathcal{H}_β . The hyperbola \mathcal{H}_β (shown in blue in Fig. 1) depend on the migration
 455 rate β . It always passes through the origin and the point $\mathcal{B} := \left(K_1, \frac{\theta_{21}}{\theta_{12}} K_1\right)$. Notice
 456 that, the hyperbola \mathcal{H}_β intersect the axis (Ox_1) at 0 and a second positive point
 457 $x_1 = \frac{r_1/\beta}{\theta_{21} + \alpha_1/\beta}$ which always smaller than K_1 . So, the equilibrium points are the

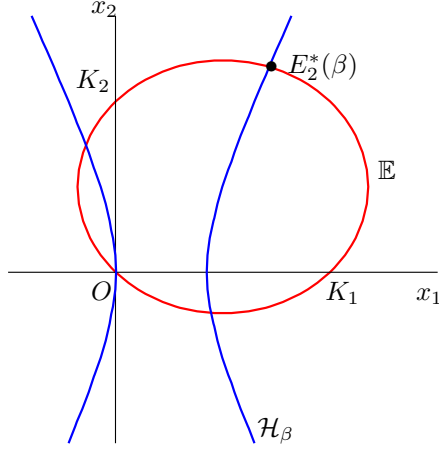


FIG. 1. The ellipse \mathbb{E} and the hyperbola \mathcal{H}_β . The equilibrium points are the intersection in the positive cone between \mathbb{E} and \mathcal{H}_β , this intersections contains the origin and a second positive point $E^*(\beta)$.

458 non negative intersection between the ellipse \mathbb{E} and \mathcal{H}_β . There are two equilibrium
 459 points. The first is the trivial point $(0, 0)$ and the second is a non trivial point
 460 $E_2^*(\beta) = (x_1^*(\beta), x_2^*(\beta))$ whose position depend on migration rate β (see Fig. 1).

When $\beta \rightarrow 0$, the left branch of hyperbola \mathcal{H}_β tend to the vertical line $x_1 = 0$
 and the right branch into the vertical line $\mathcal{H}_0 : x_1 = K_1$. Moreover, $\mathbb{E} \cap \mathcal{H}_0 =$
 $\{(K_1, 0), (K_1, K_2)\}$. In the case when $\beta \rightarrow \infty$, the hyperbola \mathcal{H}_β tend to the oblique
 line $\mathcal{H}_\infty : x_2 = \sqrt{\frac{\theta_{21}}{\theta_{12}}}x_1$. Moreover,

$$\mathbb{E} \cap \mathcal{H}_\infty = \left\{ (0, 0), \left(\sqrt{\theta_{12}} \frac{\sqrt{\theta_{12}r_1} + \sqrt{\theta_{21}r_2}}{\theta_{12}r_1/K_1 + \theta_{21}r_2/K_2}, \sqrt{\theta_{21}} \frac{\sqrt{\theta_{12}r_1} + \sqrt{\theta_{21}r_2}}{\theta_{12}r_1/K_1 + \theta_{21}r_2/K_2} \right) \right\}$$

461 It was shown by Arditi et al. [4, Proposition 2, page 54] that only three situations
 462 can occur: the case where the total equilibrium population is always greater than the
 463 sum of carrying capacities, the case where it is always smaller, and a third case, where
 464 the effect of migration is beneficial for lower values of the migration coefficient β and
 465 detrimental for the higher values. More precisely, it was shown in [4] that, if $n = 2$ in
 466 (1.7), the following trichotomy holds

- 467 • If $T_2^*(+\infty) > K_1 + K_2$ then $T_2^*(\beta) > K_1 + K_2$ for all $\beta > 0$.
- 468 • If $\frac{dT_2^*}{d\beta}(0) > 0$ and $T_2^*(+\infty) < K_1 + K_2$, then there exists $\beta_0 > 0$ such that
 469 $T_2^*(\beta) > K_1 + K_2$ for $0 < \beta < \beta_0$, $T_2^*(\beta) < K_1 + K_2$ for $\beta > \beta_0$ and
 470 $T_2^*(\beta_0) = K_1 + K_2$.
- 471 • If $\frac{dT_2^*}{d\beta}(0) < 0$, then $T_2^*(\beta) < K_1 + K_2$ for all $\beta > 0$.

472 Therefore, the condition $T_2^*(\beta) = K_1 + K_2$ holds only for $\beta = 0$ and at most for
 473 one positive value β_0 . The value β_0 exists if and only if $\frac{dT_2^*}{d\beta}(0) > 0$ and $T_2^*(+\infty) <$
 474 $K_1 + K_2$.

475 In the remainder of this section, we analyze the effect of nonlinear dispersal on
 476 the total equilibrium population for the two-patch system (7.1). Using the method of
 477 Arditi et al. [5], we describe the position affects the equilibrium $E^*(\beta)$ of (7.1) when

478 the migration rate varies from zero to infinity, we will give the condition whether T_2^*
 479 is greater or smaller than sum of carrying capacity $T_2^*(0) = K_1 + K_2$. We prove there
 480 are only three cases as in the 2-patch logistic model with linear diffusion can occur.

481 We consider the regions in the set of the parameters θ_{21} and θ_{12} , denoted \mathcal{J}_0 , \mathcal{J}_1
 482 and \mathcal{J}_2 , depicted in Fig. 2 and defined by:

$$483 \quad (7.6) \quad \left\{ \begin{array}{l} \text{If } r_2 > r_1 \text{ then} \\ \text{If } r_2 < r_1 \text{ then} \end{array} \right. \left\{ \begin{array}{l} \mathcal{J}_1 = \left\{ (\theta_{21}, \theta_{12}) : \frac{\theta_{12}}{\theta_{21}} > \frac{\alpha_2^2}{\alpha_1^2} \right\} \\ \mathcal{J}_0 = \left\{ (\theta_{21}, \theta_{12}) : \frac{\alpha_2^2}{\alpha_1^2} \geq \frac{\theta_{12}}{\theta_{21}} > \frac{K_1^2}{K_2^2} \right\} \\ \mathcal{J}_2 = \left\{ (\theta_{21}, \theta_{12}) : \frac{K_1^2}{K_2^2} > \frac{\theta_{12}}{\theta_{21}} \right\} \\ \mathcal{J}_1 = \left\{ (\theta_{21}, \theta_{12}) : \frac{\theta_{12}}{\theta_{21}} < \frac{\alpha_2^2}{\alpha_1^2} \right\} \\ \mathcal{J}_0 = \left\{ (\theta_{21}, \theta_{12}) : \frac{\alpha_2^2}{\alpha_1^2} \leq \frac{\theta_{12}}{\theta_{21}} < \frac{K_1^2}{K_2^2} \right\} \\ \mathcal{J}_2 = \left\{ (\theta_{21}, \theta_{12}) : \frac{K_1^2}{K_2^2} < \frac{\theta_{12}}{\theta_{21}} \right\} \end{array} \right.$$

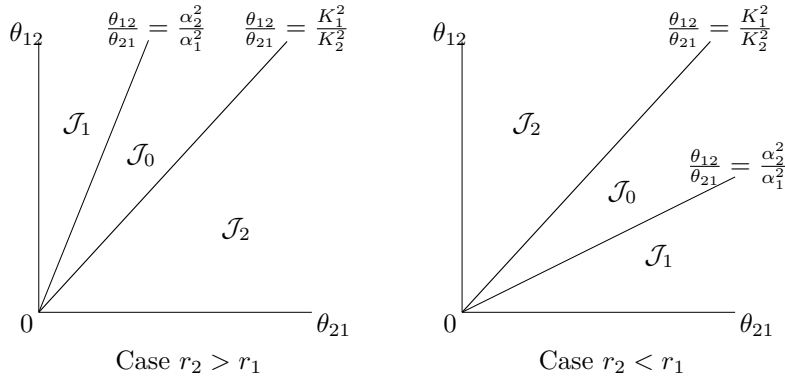


FIG. 2. The domains $\mathcal{J}_0, \mathcal{J}_1$ and \mathcal{J}_2 . In the figure $\alpha_1 = r_1/K_1$ and $\alpha_2 = r_2/K_2$.

484 We have the following result which gives the conditions for which patchiness is
 485 beneficial or detrimental in model (7.1).

486 **THEOREM 7.1.** *The total equilibrium population of (7.1) satisfies the following*
 487 *properties*

- 488 1. *If $r_1 = r_2$ then $T_2^*(\beta) \leq K_1 + K_2$ for all $\beta \geq 0$.*
 489 2. *If $r_2 \neq r_1$, let $\mathcal{J}_0, \mathcal{J}_1$ and \mathcal{J}_2 , be defined by (7.6). Then we have:*
 490 • *if $(\theta_{21}, \theta_{12}) \in \mathcal{J}_0$ then $T_2^*(\beta) > K_1 + K_2$ for any $\beta > 0$*
 • *if $(\theta_{21}, \theta_{12}) \in \mathcal{J}_1$ then $T_2^*(\beta) > K_1 + K_2$ for $0 < \beta < \beta_0$ and $T_2^*(\beta) <$
 • $K_1 + K_2$ for $\beta > \beta_0$, where*

$$\beta_0 = \frac{r_2 - r_1}{\frac{\sqrt{\theta_{12}}}{\alpha_2} - \frac{\sqrt{\theta_{21}}}{\alpha_1}} \frac{1}{\alpha_1 + \alpha_2}.$$

- 491 • *if $(\theta_{21}, \theta_{12}) \in \mathcal{J}_2$ then $T_2^*(\beta) < K_1 + K_2$ for any $\beta > 0$*
 492 • *If $\frac{\theta_{12}}{\theta_{21}} = \frac{K_1^2}{K_2^2}$, then $x_1^*(\beta) = K_1$ and $x_2^*(\beta) = K_2$ for all $\beta \geq 0$. Therefore*
 493 *$T_2^*(\beta) = K_1 + K_2$ for all $\beta \geq 0$.*

494 *Proof.* To facilitate comparison of the total equilibrium population $T_2^*(\beta)$ and
 495 $T_2^*(0) = K_1 + K_2$, we define a straight line $\Delta : x_1 + x_2 = K_1 + K_2$. If the intersection
 496 of the ellipse \mathbb{E} and the hyperbola \mathcal{H}_β , i.e., the equilibrium $(x_1^*(\beta), x_2^*(\beta))$, is on or
 497 below the line Δ , then $T_2^*(\beta) \leq T_2^*(0)$, whereas if the intersection is above the line,
 498 then $T_2^*(\beta) \geq T_2^*(0)$. The equilibrium point $E_2^*(\beta)$ is always in ellipse, then, for
 499 $\beta = 0$, the equilibrium point states at \mathcal{A} , and when β increases, $E_2^*(\beta)$ describes an
 500 arc of the ellipse and ends at point $E_2^*(\infty)$.

501 If we take $r_1 = r_2$, we get that the equation of tangent space to the ellipse \mathbb{E} at
 502 point \mathcal{A} is the equation of Δ . By Prop. 6.1, we deduce $T_2^*(\beta) \leq T_2^*(0)$ for all $\beta \geq 0$.

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

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

We denote by Σ the straight line joint the origin and C . The slope of Σ is equal to
 $\frac{\alpha_2}{\alpha_1}$. We distinguish three cases relative position of the three points \mathcal{A} , $E_2^*(\infty)$, and C ,
 or equivalently, the three lines $[O\mathcal{A}]$, \mathcal{H}_∞ and Σ whose slopes are

$$\frac{K_2}{K_1}, \quad \sqrt{\frac{\theta_{21}}{\theta_{12}}} \quad \text{and} \quad \frac{\alpha_2}{\alpha_1}.$$

503 By the method graphic of Arditi et al. [5], we conclude the complete proof. \square

504 The result of the previous theorem show that the nonlinear dispersal can lead to an
 505 increased, a decreased the total population size in two patches. This prove that, the
 506 effect of nonlinear dispersal is the same as the effect of linear dispersal in two-patch
 507 logistic model [4, 5]. Moreover, if the movement between two patches is symmetric,
 508 then we have the same results. In particular, Theorem 7.1, formula of equilibrium for
 509 large migration rate.

510 For the two-patch model (7.1), we plot in the figure 4.2, the curves of the total
 511 equilibrium population T_2^* and the line $K_1 + K_2$ in term of the migration rate β , for
 512 the sets of parameters choosing in Table 1.

TABLE 1

Parameters values of the three case used in Fig. 3-a,3-b and Fig 3-c. The perfect mixing
 abundance $T_2^*(+\infty)$ is computed with Eq. (7.2) and the derivative of the total equilibrium population
 at $\beta = 0$ is computed with Eq. (7.3).

Figure	r_1	r_2	K_1	K_2	θ_{12}	θ_{21}	$\frac{dT_2^*}{d\beta}(0)$	$T_2^*(+\infty)$
3-a	1	2	3.5	1	1	1	-5.62	2.62
3-b	6	2	5.5	1	1	1	3.75	4.30
3-c	5	1	3.5	1	1	1	9.00	4.94

513

514 **8. Two-patch model where one growth rate is much larger than the**
 515 **second one.** Recently, in [16], Elbetch is interested in some biological situations
 516 that can be found in the nature, that is, the case where several sub-populations grow
 517 with different speed. Mathematically speaking, he studied the system (1.7) under the
 518 hypothesis that some growth rates tend to infinity (i.e $r_i \rightarrow \infty$ for some i). In this
 519 section, we consider the two-patch model (2.1) and we assume that the growth rate

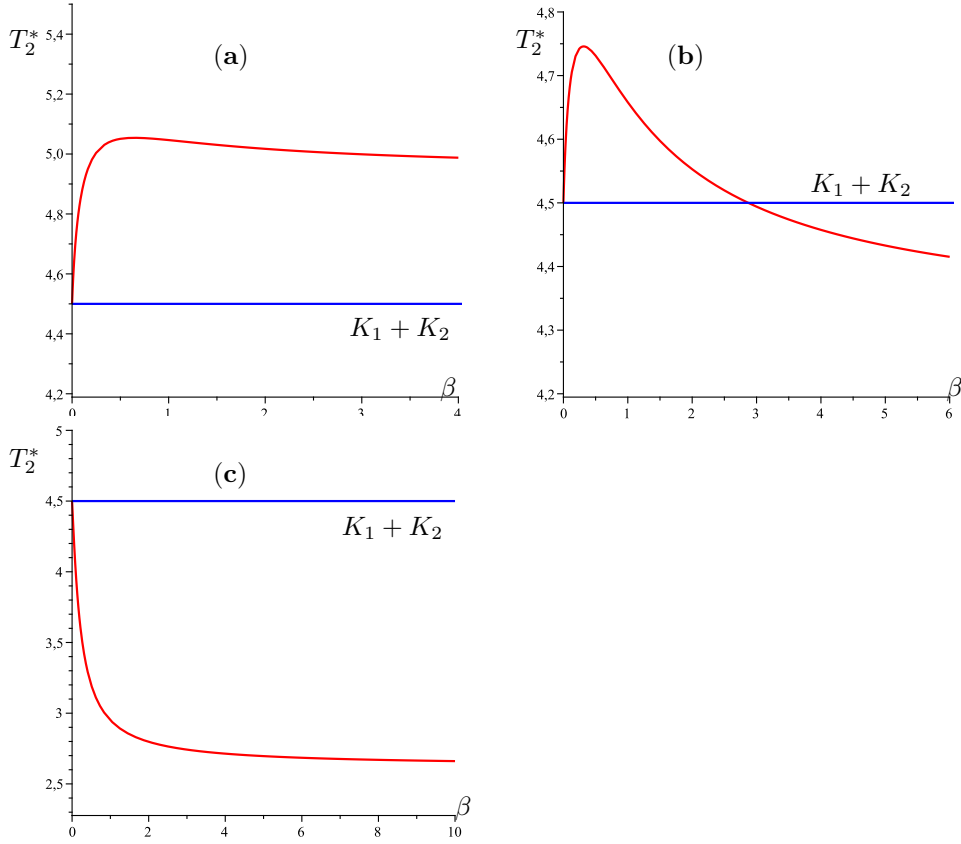


FIG. 3. Total equilibrium population T_2^* of the system (7.1) as a function of the migration rate β for the sets of the parameter values given in Table 1. The horizontal line is $K_1 + K_2$.

520 r_2 is much larger than r_1 . For simplicity we denote $\theta_2 := \theta_{12} > 0$ the migration rate
 521 from patch 2 to patch 1 and $\theta_1 := \theta_{21} > 0$ from patch 1 to patch 2. The model is
 522 written:

$$523 \quad (8.1) \quad \begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta (\theta_2 x_2^2 - \theta_1 x_1^2), \\ \frac{dx_2}{dt} = \frac{r_2}{\epsilon} x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta (\theta_1 x_1^2 - \theta_2 x_2^2), \end{cases}$$

524 where ϵ is assumed to be a small positive number. Denote $E_2^*(\beta, \epsilon) = (x_1^*(\beta, \epsilon), x_2^*(\beta, \epsilon))$
 525 the positive equilibrium of (8.1), and $T_2^*(\beta, \epsilon)$, the total equilibrium population. We
 526 recall that the derivative of $T_2^*(\beta, \epsilon)$ with respect to β at $\beta = 0$ is written as follow:

$$527 \quad (8.2) \quad \frac{dT_2^*}{d\beta}(0, \epsilon) = (\theta_2 K_2^2 - \theta_1 K_1^2) \left(\frac{1}{r_1} - \frac{\epsilon}{r_2} \right).$$

528 The total equilibrium population of the model (8.1) for perfect mixing (i.e $\beta \rightarrow \infty$)
 529 is given by the following formula:

$$530 \quad (8.3) \quad T_2^*(+\infty, \epsilon) = (\sqrt{\theta_1} + \sqrt{\theta_2}) \frac{\epsilon \sqrt{\theta_2} r_1 + \sqrt{\theta_1} r_2}{\epsilon \theta_2 \alpha_1 + \theta_1 \alpha_2},$$

531 where $\alpha_i = r_i/K_i$. First, we have the result:

532 **THEOREM 8.1.** *Let $(x_1(t, \epsilon), x_2(t, \epsilon))$ be the solution of the system (8.1) with ini-*
 533 *tial 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*
 534 *differential equation*

$$535 \quad (8.4) \quad \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta(\theta_2 K_2^2 - \theta_1 x_1^2) =: \varphi(x_1),$$

536 *with initial condition $u(0) = x_1^0$. Then, when $\epsilon \rightarrow 0$, we have*

$$537 \quad (8.5) \quad x_1(t, \epsilon) = u(t) + o_\epsilon(1), \quad \text{uniformly for } t \in [0, +\infty)$$

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

$$539 \quad (8.6) \quad x_2(t, \epsilon) = K_2 + o_\epsilon(1), \quad \text{uniformly for } t \in [t_0, +\infty).$$

540 *Proof.* When $\epsilon \rightarrow 0$, the system (8.1) is a *slow-fast* system, with one *slow variable*,
 541 x_1 , and one *fast variable*, x_2 . Tikhonov's theorem [26, 32, 33] prompts us to consider
 542 the dynamics of the fast variables in the time scale $\tau = \frac{1}{\epsilon}t$. One obtains

$$543 \quad (8.7) \quad \frac{dx_2}{d\tau} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \epsilon \beta(\theta_1 x_1^2 - \theta_2 x_2^2).$$

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

$$545 \quad (8.8) \quad \frac{dx_2}{d\tau} = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right).$$

546 The slow manifold is given by the positive equilibrium of the system (8.8), i.e $x_2 = K_2$,
 547 which is GAS in the positive axis. When ϵ goes to zero, Tikhonov's theorem ensures
 548 that after a fast transition toward the slow manifold, the solutions of (8.1) converge
 549 to the solutions of the *reduced model* (8.4), obtained by replacing $x_2 = K_2$ into the
 550 dynamics of the slow variable.

551 The differential equation (8.4) admits as a positive equilibrium

$$552 \quad (8.9) \quad x_1^*(\beta, 0^+) := 1/2 \frac{r_1 K_1 + \sqrt{r_1^2 K_1^2 + 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1}}{r_1 + \beta K_1 \theta_1}$$

554 As $\varphi(x_1) > 0$ for all $0 \leq x_1 < x_1^*(\beta, 0^+)$ and $\varphi(x_1) < 0$ for all $x_1 > x_1^*(\beta, 0^+)$ then,
 555 the equilibrium $x_1^*(\beta, 0^+)$ is GAS in the positive axis, so, the approximation given by
 556 Tikhonov's theorem holds for all $t \geq 0$ for the slow variable and for all $t \geq t_0 > 0$ for
 557 the fast variable, where t_0 is as small as we want. Therefore, let $u(t)$ be the solution
 558 of the reduced model (8.4) of initial condition $u(0) = x_1^0$, then, when $\epsilon \rightarrow 0$, we have
 559 the approximations (8.5) and (8.6). \square

560 As a corollary of the previous theorem, we have the following result which give
 561 the limit of the total equilibrium population $T_2^*(\beta, \epsilon)$ of the model (8.1) when ϵ goes
 562 to zero:

563 **COROLLARY 8.2.** *We have:*

(8.10)

$$564 \quad T_2^*(\beta, 0^+) := \lim_{\epsilon \rightarrow 0} T_2^*(\beta, \epsilon) = \lim_{\epsilon \rightarrow 0} (x_1^*(\beta, \epsilon) + x_2^*(\beta, \epsilon))$$

$$565 \quad = 1/2 \frac{r_1 K_1 + \sqrt{r_1^2 K_1^2 + 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1}}{r_1 + \beta K_1 \theta_1} + K_2.$$

567 *Proof.* According to the equations (8.5), (8.6) and (8.9), when ϵ goes to zero, the
568 equilibrium $E_2^*(\beta, \epsilon)$ of the model (8.1) is converge to $E_2^*(\beta, 0^+) := (x_1^*(\beta, 0^+), K_2)$,
569 where $x_1^*(\beta, 0^+)$ is given in (8.9). The sum of the coordinates of $E_2^*(\beta, 0^+)$ gives the
570 formula (8.10). \square

571 In the following proposition, we calculate the derivative and the formula of perfect
572 mixing (i.e when $\beta \rightarrow \infty$) of the total equilibrium population defined by (8.10).

573 **PROPOSITION 8.3.** *Consider the total equilibrium population (8.10). Then,*

$$574 \quad (8.11) \quad \frac{dT_2^*}{d\beta}(0, 0^+) := \frac{-\theta_1 K_1^2 + \theta_2 K_2^2}{r_1},$$

575 *and*

$$576 \quad (8.12) \quad T_2^*(+\infty, 0^+) := \frac{\sqrt{\theta_1} + \sqrt{\theta_2}}{\sqrt{\theta_1}} K_2.$$

577 *Proof.* The derivative of the total equilibrium population $X_T^*(\beta, 0^+)$ defined by
578 (8.10) with respect to β is:

$$(8.13) \quad \begin{aligned} 579 \quad \frac{dT_2^*}{d\beta}(\beta, 0^+) = & -1/2 \frac{\left(r_1 K_1 + \sqrt{r_1^2 K_1^2 + 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1} \right) K_1 \theta_1}{(r_1 + \beta K_1 \theta_1)^2} \\ 580 \quad & + 1/4 \frac{4 K_1 \theta_2 K_2^2 r_1 + 8\beta K_1^2 \theta_2 K_2^2 \theta_1}{(r_1 + \beta K_1 \theta_1) \sqrt{r_1^2 K_1^2 + 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1}}. \end{aligned}$$

582 In particular, the derivative of the total equilibrium population at $\beta = 0$ is given by
583 the formula (8.11).

584 By taking the limit of (8.10) when $\beta \rightarrow \infty$, we get that the total equilibrium
585 population $X_T^*(\beta, 0^+)$ tend to (8.12). \square

586 **REMARK 3.** *We can deduce $\frac{dT_2^*}{d\beta}(0, 0^+)$ by using the equation (8.2). Indeed, the*
587 *limit of (8.2) when ϵ goes to zero gives:*

$$588 \quad \lim_{\epsilon \rightarrow 0} \frac{dT_2^*}{d\beta}(0, \epsilon) = \lim_{\epsilon \rightarrow 0} \left[(\theta_2 K_2^2 - \theta_1 K_1^2) \left(\frac{1}{r_1} - \frac{\epsilon}{r_2} \right) \right] = \frac{-\theta_1 K_1^2 + \theta_2 K_2^2}{r_1} = \frac{dT_2^*}{d\beta}(0, 0^+).$$

589 *We can also deduce $T_2^*(+\infty, 0^+)$ by compute the limit of (8.3) when ϵ goes to zero:*

$$590 \quad \lim_{\epsilon \rightarrow 0} T_2^*(\infty, \epsilon) = \lim_{\epsilon \rightarrow 0} \left[(\sqrt{\theta_1} + \sqrt{\theta_2}) \frac{\epsilon \sqrt{\theta_2} r_1 + \sqrt{\theta_1} r_2}{\epsilon \theta_2 \alpha_1 + \theta_1 \alpha_2} \right] = \frac{\sqrt{\theta_1} + \sqrt{\theta_2}}{\sqrt{\theta_1}} K_2 = T_2^*(\infty, 0^+).$$

591 We consider the regions in the set of the parameters θ_1 and θ_2 , denoted \mathcal{J}_0 and
592 \mathcal{J}_1 defined by:

$$593 \quad (8.14) \quad \mathcal{J}_0 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} > \frac{K_1^2}{K_2^2} \right\}, \quad \mathcal{J}_1 = \left\{ (\theta_1, \theta_2) : \frac{\theta_2}{\theta_1} < \frac{K_1^2}{K_2^2} \right\}.$$

594 We have the following result which gives the conditions for which patchiness is bene-
595 ficial or detrimental in model (8.1) when ϵ goes to zero.

596 **THEOREM 8.4.** *Let \mathcal{J}_0 and \mathcal{J}_1 be the domains defined in (8.14). Consider the*
597 *total equilibrium population $T_2^*(\beta, 0^+)$ given by (8.10). Then, we have:*

- 598 • If $(\theta_1, \theta_2) \in \mathcal{J}_0$ then $T_2^*(\beta, 0^+) > K_1 + K_2$, for all $\beta > 0$.
- 599 • If $(\theta_1, \theta_2) \in \mathcal{J}_1$ then $T_2^*(\beta, 0^+) < K_1 + K_2$, for all $\beta > 0$.
- 600 • If $\frac{\theta_2}{\theta_1} = \frac{K_1^2}{K_2^2}$, then $x_1^*(\beta, 0^+) = K_1$ and $x_2^*(\beta, 0^+) = K_2$ for all $\beta \geq 0$. Therefore
- 601 $T_2^*(\beta, 0^+) = K_1 + K_2$ for all $\beta \geq 0$.

602 *Proof.* First, we try to solve the equation $T_2^*(\beta, 0^+) = K_1 + K_2$ with respect to β ,
603 the solutions of this last equation give the points of intersection between the curve of
604 the total equilibrium population $\beta \mapsto T_2^*(\beta, 0^+)$ and the straight line $\beta \mapsto K_1 + K_2$.
605 For any $\beta > 0$, we have

$$\begin{aligned}
606 \quad T_2^*(\beta, 0^+) &= K_1 + K_2 \\
607 \quad &\iff \frac{1}{2} \frac{r_1 K_1 + \sqrt{r_1^2 K_1^2 + 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1}}{r_1 + \beta K_1 \theta_1} = K_1 \\
608 \quad &\iff 4\beta K_1 \theta_2 K_2^2 r_1 + 4\beta^2 K_1^2 \theta_2 K_2^2 \theta_1 - 4r_1 K_1^3 \beta \theta_1 - 4\beta^2 K_1^4 \theta_1^2 \\
609 \quad &\iff = (\theta_2 K_2^2 - \theta_1 K_1^2)(4\theta_1 K_1^2 \beta^2 + 4r_1 K_1 \beta) = 0 \\
610 \quad &\iff \theta_2 K_2^2 = \theta_1 K_1^2 \\
611 \quad &\iff \frac{dT_2^*}{d\beta}(0, 0^+) = 0. \\
612
\end{aligned}$$

613 So, if $\frac{dT_2^*}{d\beta}(0, 0^+) \neq 0$ then $\beta = 0$ and the curve of the total equilibrium population
614 intersects the straight line $\beta \mapsto K_1 + K_2$ in a unique point which is $(0, K_1 + K_2)$.
615 Therefore, we conclude that the first and second items of the theorem are hold. \square

616 **9. Concluding remarks.** In summary, this work was aimed to find out whether
617 the total equilibrium population of the n patches connected by nonlinear migration
618 asymmetrical migrations can be greater than the sum of the carrying capacities of the
619 n isolated patches, i.e. at equilibrium. Is there a way to make connections between
620 patches that increases the total population? we have assumed that the population
621 obey a logistic type growth at each patches.

622 We have shown that if the growth rates are equal in all patches, then the total
623 equilibrium population on the n connected patches is always less than or equal to the
624 sum of carrying capacity of the isolated patches. This result can be seen as negative
625 but constitutes in our eyes an interesting result. We then addressed this issue in the
626 general case when the growth rates are different, we have determined criteria for which
627 the total population size of the n connected patches at equilibrium may be greater
628 than the sum of carrying capacities of n isolated patches. we have shown that for high
629 movement rates between the patches, the total equilibrium population cloud exceed
630 total carrying capacity of the n patches for certain combinations of the parameters
631 r_i, K_i and δ_i . For two-patch model, the parameter space is fully classified as to
632 whether nonlinear dispersal is beneficial or detrimental to the sum of two carrying
633 capacities.

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