

## INFLUENCE OF A SPATIAL STRUCTURE ON THE LONG TIME BEHAVIOR OF A COMPETITIVE LOTKA-VOLTERRA TYPE SYSTEM

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**ABSTRACT.** To describe population dynamics, it is crucial to take into account jointly evolution mechanisms and spatial motion. However, the models which include these both aspects, are not still well-understood. Can we extend the existing results on type structured populations, to models of populations structured by type and space, considering diffusion and nonlocal competition between individuals?

We study a nonlocal competitive Lotka-Volterra type system, describing a spatially structured population which can be either monomorphic or dimorphic. Considering spatial diffusion, intrinsic death and birth rates, together with death rates due to intraspecific and interspecific competition between the individuals, leading to some integral terms, we analyze the long time behavior of the solutions. We first prove existence of steady states and next determine the long time limits, depending on the competition rates and the principal eigenvalues of some operators, corresponding somehow to the strength of traits. Numerical computations illustrate that the introduction of a new mutant population can lead to the long time evolution of the spatial niche.

**Introduction.** The spatial aspect of populations is an important ecological issue which has been extensively studied (see [17], [18], [23], [25], [28]). The interplay between space and evolution is particularly crucial in the emergence of polymorphism and spatial patterns and the heterogeneity of the environment is considered as essential ([21], [22]). The combination of spatial motion and mutation-selection processes is also known for a long time to have important effects on population dynamics ([19], [24]). Recently biological studies observed that classical models could underestimate the invasion speed and suggested that invasion and evolution are closely related. The ecological parameters can have a strong effect on the expansion

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of invading species and conversely, the evolution can be conditioned by the spatial behavior of individuals related to the resources available. The paper by Philipps and Co [26] shows the strong impact of the morphologic parameters of the cane toads on the expansion of their invasion.

In this context, the study of space-related traits, such as dispersal speed or sensibility to heterogeneously distributed resources, is fundamental and has been the object of mathematical developments. In Champagnat-Méléard [12], a stochastic individual-based model is introduced where individuals are characterized both by their location and one or several phenotypic and heritable traits. The individuals move, reproduce with possible mutation and die of natural death or because of competition for resources. The spatial motion is modeled as a diffusion and the spatial interaction between individuals is modeled by a convolution kernel in some spatial range. In a large population scale, it is shown that this microscopic stochastic model can be approximated by a nonlinear nonlocal reaction-diffusion equation defined on the space of traits and space. The latter has been studied in Ferrière-Desvillettes-Prévost [16] and Arnold-Desvillettes-Prévost [2] and existence and uniqueness of the solution, numerical simulations and steady states are studied. Propagation phenomena and existence of traveling waves are explored numerically and theoretically for different variants of such models in [1], [3], [4], [6]. This problem has also been studied from an asymptotic point of view using Hamilton-Jacobi equations [7], [8].

Despite several recent attempts to study such models, dynamics of populations structured by trait and space are not completely understood and several interesting and challenging questions remain to be resolved in this field (see for instance [7]). In particular, the works quoted above concentrate on the case where the mutations are frequent such that the diffusion in space and the mutations are modeled in the same time scale. Our objective is to understand the framework of adaptive dynamics where the mutations are rare enough such that between two mutations the dynamics is driven by a system of nonlocal reaction-diffusion equations, each of them describing the dynamics and the spatial distribution of one trait. We study the steady states and the long time behavior of such systems. Note that although the existence of steady states for a model with continuous trait and space is provided in [2], the long time behavior of solutions is not known, to our knowledge, for discrete or continuous traits. However, in the case of a single trait and considering only homogeneous environments, [5] provides a study of steady states and traveling waves.

**1. Models and main results.** In this paper we focus on this problem for the simplest case where the population is dimorphic (the population is composed of two-type subpopulations). We will also study the monomorphic case (a single type is involved).

Let us first introduce some notation: The space set  $\mathcal{X}$  is an open bounded subset of  $\mathbb{R}^d$  with a boundary of class  $C^3$ . We will denote by  $\mathbb{L}^k$  the Lebesgue space on  $\mathcal{X}$  of order  $k \in \mathbb{N}^*$  and by  $\mathbb{H}^k$  the Sobolev space on  $\mathcal{X}$  of order  $k \in \mathbb{N}^*$ . We denote by  $C^{0,1}$  the space of Lipschitz continuous functions on  $\mathcal{X}$ .

For all  $x \in \partial\mathcal{X}$ , we denote by  $n(x)$  the outward normal to the boundary  $\partial\mathcal{X}$  at point  $x$ . For a sufficiently smooth function  $u$  and  $x \in \partial\mathcal{X}$ , we denote by  $\partial_n u(x)$  the scalar product  $\nabla u(x) \cdot n(x)$ .

In the dimorphic case, the spatial density of the population is modeled by the system of nonlinear partial differential equations of parabolic type

$$\left\{ \begin{array}{l} \partial_t g_1(t, x) = m_1 \Delta_x g_1(t, x) + \left( a_1(x) - \int_{\mathcal{X}} I_{11}(y) g_1(t, y) dy \right. \\ \qquad \qquad \qquad \qquad \qquad \qquad \qquad \left. - \int_{\mathcal{X}} I_{12}(y) g_2(t, y) dy \right) g_1(t, x), \\ \partial_n g_1(t, x) = 0, \quad \forall (t, x) \in \mathbb{R}^+ \times \partial\mathcal{X}, \\ g_1(0, x) = g_1^0(x), \quad \forall x \in \mathcal{X}, \\ \partial_t g_2(t, x) = m_2 \Delta_x g_2(t, x) + \left( a_2(x) - \int_{\mathcal{X}} I_{21}(y) g_1(t, y) dy \right. \\ \qquad \qquad \qquad \qquad \qquad \qquad \qquad \left. - \int_{\mathcal{X}} I_{22}(y) g_2(t, y) dy \right) g_2(t, x), \\ \partial_n g_2(t, x) = 0, \quad \forall (t, x) \in \mathbb{R}^+ \times \partial\mathcal{X}, \\ g_2(0, x) = g_2^0(x), \quad \forall x \in \mathcal{X}. \end{array} \right. \quad (1)$$

where  $g_1(t, x)$  (respectively  $g_2(t, x)$ ) denotes the density of individuals of type 1 (resp. of type 2), in position  $x$  at time  $t$ . The density dynamics is driven by growth rates  $a_1$  and  $a_2$  which depend on the spatial position of individuals and on their type. Laplacian terms describe the diffusion of individuals in space with infinitesimal variances  $m_1$  and  $m_2$ . The competition is modeled by nonlocal death rates depending on the environment heterogeneity through the kernels  $I_{ij}$ ,  $i, j = 1, 2$ . We make the following assumptions on the coefficients: for  $i, j \in \{1, 2\}$ ,

$$a_i \in C^{0,1}(\mathcal{X}), \quad \text{and} \quad |a_i(x)| \leq a_\infty, \quad \text{for all } x \in \mathcal{X}, \quad (2)$$

$$\left\{ \begin{array}{l} \|I_{ij}\|_{\mathbb{L}^2} < +\infty, \quad \text{for } i, j \in \{1, 2\}, \\ \exists I_- > 0 / \forall x \in \mathcal{X}, \quad I_{ii}(x) \geq I_-, \quad \text{for } i = 1, 2. \end{array} \right. \quad (3)$$

We also assume that the initial condition satisfies

$$g_i^0 \in \mathbb{L}^2, \quad \text{for } i = 1, 2. \quad (4)$$

We will show that this system admits 4 non-negative steady states depending on the ecological parameters. The stability of these states is based on the sign of the principal eigenvalues

$$\begin{aligned} H_1 &= - \min_{\substack{u \in \mathbb{H}^1 \\ u \neq 0}} \frac{1}{\|u\|_{\mathbb{L}^2}^2} \left[ \int_{\mathcal{X}} m_1 |\nabla u|^2 dx - \int_{\mathcal{X}} a_1(x) u^2(x) dx \right], \\ H_2 &= - \min_{\substack{u \in \mathbb{H}^1 \\ u \neq 0}} \frac{1}{\|u\|_{\mathbb{L}^2}^2} \left[ \int_{\mathcal{X}} m_2 |\nabla u|^2 dx - \int_{\mathcal{X}} a_2(x) u^2(x) dx \right]. \end{aligned} \quad (5)$$

We also denote by  $A_1^1$  (resp.  $A_1^2$ ) the positive eigenfunction associated with the eigenvalue  $H_1$  (resp.  $H_2$ ) such that  $\int_{\mathcal{X}} A_1^i(x) dx = 1$  and for  $i, j \in \{1, 2\}$ ,

$$\mu_{ij} = \int_{\mathcal{X}} I_{ij}(x) A_1^j(x) dx. \quad (6)$$

From (3), we notice that  $\mu_{11} \neq 0$  and  $\mu_{22} \neq 0$ . Finally, we make the following assumption on the variables  $\mu_{ij}$  to exclude the degenerate case

$$\mu_{11}\mu_{22} - \mu_{12}\mu_{21} \neq 0. \quad (7)$$

We identify now the steady states of Equation (1).

**Lemma 1.1.** *Assume (2), (3) and (7). Then, the only non-negative steady states of Equation (1) are*

- the trivial steady state  $(0, 0)$ ,
- the state  $(\bar{g}_1, 0)$  with  $\bar{g}_1 = \frac{H_1}{\mu_{11}}A_1^1$ , which is non-negative and non-trivial if and only if  $H_1 > 0$ ,
- the state  $(0, \bar{g}_2)$  with  $\bar{g}_2 = \frac{H_2}{\mu_{22}}A_1^2$ , which is non-negative and non-trivial if and only if  $H_2 > 0$ ,
- the state  $(\hat{g}_1, \hat{g}_2)$  where  $\hat{g}_1 = r_1A_1^1$  and  $\hat{g}_2 = r_2A_1^2$ , with  $r_1$  and  $r_2$  positive constants satisfying

$$\begin{pmatrix} H_1 \\ H_2 \end{pmatrix} = \begin{pmatrix} \mu_{11} & \mu_{12} \\ \mu_{21} & \mu_{22} \end{pmatrix} \begin{pmatrix} r_1 \\ r_2 \end{pmatrix}. \quad (8)$$

This steady state exists if and only if  $(H_2\mu_{11} - H_1\mu_{21})(H_1\mu_{22} - H_2\mu_{12}) > 0$ ,  $H_1 > 0$  and  $H_2 > 0$ .

The first steady state is the trivial one  $(0, 0)$  describing the population extinction. The second and third ones describe the long term specialization of the population on a single type : one subpopulation has a non trivial long time behavior and the subpopulation with the other type goes to extinction. The last case describes the co-existence case where individuals with two types exist in a long time scale.

Our main results concern the long time behavior of solutions of (1). We give explicit conditions determining whether or not the population goes extinct or whether or not there is co-existence of the two types at equilibrium. The first theorem shows the convergence of the solution when time goes to infinity and gives sufficient conditions for convergence to the globally asymptotically stable states. The second theorem explores the more delicate cases, where there are several stable equilibria and different basins of attraction.

**Theorem 1.2.** *Assume (2), (3), (4) and (7).*

1. For any initial condition, as  $t \rightarrow \infty$ , the unique solution of the parabolic system (1) tends to one of the steady states described in Lemma 1.1.
2. If  $H_1 \leq 0$  and  $H_2 \leq 0$  then for any initial condition and as  $t \rightarrow \infty$ , the solution of (1) tends to  $(0, 0)$ , i.e. the population goes extinct.
3. If

$$H_1 > 0, H_2\mu_{11} - H_1\mu_{21} \leq 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} > 0,$$

then for any initial condition such that  $g_1^0$  is not identically zero and as  $t \rightarrow \infty$ , the solution converges to  $(\bar{g}_1, 0)$ . We thus have fixation of type 1 in the population.

4. If

$$H_2 > 0, H_2\mu_{11} - H_1\mu_{21} > 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} \leq 0,$$

then for any initial condition such that  $g_2^0$  is not identically zero and as  $t \rightarrow \infty$ , the solution converges to  $(0, \bar{g}_2)$ . We thus have fixation of type 2 in the population.

5. If

$$H_1 > 0, H_2 > 0, H_2\mu_{11} - H_1\mu_{21} > 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} > 0,$$

then for any initial condition such that  $g_1^0$  and  $g_2^0$  are not identically zero and as  $t \rightarrow \infty$ , the solution converges to  $(\hat{g}_1, \hat{g}_2)$ , i.e. we have co-existence of types 1 and 2.

Next, to give a complete picture of the long time behavior of the solution, let us study the last cases where several equilibria can be reached.

**Theorem 1.3.** Assume (2), (3), (4) and (7).

1. If

$$H_1 > 0, H_2 > 0, H_2\mu_{11} - H_1\mu_{21} < 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} < 0,$$

then the steady states  $(\bar{g}_1, 0)$  and  $(0, \bar{g}_2)$  are both asymptotically stable and  $(\hat{g}_1, \hat{g}_2)$  is unstable. Nevertheless some solutions will converge to the latter.

2. If

$$H_1 > 0, H_2 > 0, H_2\mu_{11} - H_1\mu_{21} < 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} = 0,$$

then the steady state  $(\bar{g}_1, 0)$  is asymptotically stable and  $(0, \bar{g}_2)$  is unstable. Nevertheless some solutions will converge to the latter.

3. If

$$H_1 > 0, H_2 > 0, H_2\mu_{11} - H_1\mu_{21} = 0 \text{ and } H_1\mu_{22} - H_2\mu_{12} < 0,$$

then the steady state  $(\bar{g}_2, 0)$  is asymptotically stable and  $(0, \bar{g}_1)$  is unstable. Nevertheless some solutions will converge to the latter.

**Remark 1.** One can check that, excluding the degenerate case (7), all the possible values of  $(H_1, H_2) \in \mathbb{R}^2$  are covered by the statements of Theorems 1.2 and 1.3.

These results are new and interesting by themselves but they will also be the first step in an adaptive dynamics framework, if we want to understand how mutant individuals invade the population at an evolutive scale (see [11], [13]).

The above theorems provide assumptions based on spectral parameters and competitive kernels under which the solutions of the system (1) converge to one of the steady states, as time goes to infinity. Equilibria of System (1) and their stability are characterized by the parameters  $(H_i)_{i=1,2}$  and  $(\mu_{ij})_{i,j=1,2}$  even if these parameters are not sufficient to understand the complete dynamics. As  $A_1^i$ , which defines the density landscape of steady states on space  $\mathcal{X}$ ,  $H_i$  is a spectral parameter depending only on the diffusion part and the intrinsic growth rate of population  $i$ . The competitive parameter  $\mu_{ij}$  can be seen as the mean of the competitive kernel  $I_{ij}$  under the specific spectral measure  $A_1^j(x)dx$ . Thus,  $\mu_{ij}$  times the mass of population  $j$  is the competitive pressure that population  $j$ , in the case of a stationary density, puts on an individual  $i$ . Note that here  $H_i$  corresponds somehow to the strength of trait  $i$ . To determine which trait would persist in long time, one should compare the trait strength values  $H_i$  weighted by the competition parameters  $\mu_{i,j}$ , as stated in Theorems 1.2 and 1.3.

Furthermore, the conditions presented in Theorems 1.2, 1.3 can be compared with survival and extinction conditions of the following Lotka-Volterra system (see for example p.186 of [10] or part 3.5 of [25]):

$$\begin{cases} r_1'(t) = r_1(t) (H_1 - \mu_{11}r_1(t) - \mu_{12}r_2(t)), \\ r_2'(t) = r_2(t) (H_2 - \mu_{21}r_1(t) - \mu_{22}r_2(t)). \end{cases} \quad (9)$$

Indeed, by integrating the equations of System (1) over  $\mathcal{X}$ , we will prove that the masses of the two populations satisfy a slightly perturbed system close to (9) and with similar conditions for survival and extinction. The system satisfied by the masses is not a closed system in the general case. But it is closed in the case where functions  $(a_i)_{i=1,2}$  and  $(I_{ij})_{i,j=1,2}$  are constant (homogeneous environment),  $a_i \equiv \bar{a}_i$ ,  $I_{ij} \equiv \bar{I}_{ij}$ , for  $i, j = 1, 2$ . Thanks to Definition (5), notice that in this case,  $H_i$  is equal to  $\bar{a}_i$ . Moreover,  $\mu_{ij} = \bar{I}_{ij}$ . Thus, the masses satisfy exactly System (9).

Before proving those theorems, we need to consider the case of a monomorphic population where all individuals have the same type.

As above, the density dynamics is driven by a nonlinear partial differential equation of parabolic type with a non-local competition term.

$$\begin{cases} \partial_t g(t, x) = m\Delta_x g(t, x) + a(x)g(t, x) - \left( \int_{\mathcal{X}} I(y)g(t, y)dy \right) g(t, x), \quad \forall x \in \mathcal{X} \\ \partial_n g(t, x) = 0, \quad \forall x \in \partial\mathcal{X}, \quad \forall t \in \mathbb{R}, \\ g(0, x) = g^0(x), \quad \forall x \in \mathcal{X}. \end{cases} \quad (10)$$

Here  $g(t, x)$  denotes the density of individuals in position  $x$  and at time  $t$ . As before, the Laplacian term models the spatial behaviour of individuals and  $m$  is the diffusion coefficient. The intrinsic growth rate is given by a function  $a(x)$ , which depends on the position  $x$  of the individuals. Finally, the last term corresponds to the mortality induced by competition where the function  $I(y)$  is the competition kernel.

We prove that there exists at most one steady state for (10) to which the solution converges in long time. To this end, we make the following assumptions on the coefficients:

$$a \in C^{0,1}(\mathcal{X}), \quad \text{and} \quad |a(x)| \leq a_\infty, \quad \text{for all } x \in \mathcal{X}, \quad (11)$$

$$I \in \mathbb{L}^2 \quad \text{and there exists } I_- > 0, \quad \text{for all } y \in \mathcal{X}, \quad I(y) \geq I_-. \quad (12)$$

We also assume that the initial condition satisfies

$$g^0 \in \mathbb{L}^2. \quad (13)$$

To state our result we also need to define the principal eigenvalue of the problem

$$H = - \min_{\substack{u \in \mathbb{H}^1 \\ u \neq 0}} \frac{1}{\|u\|_{\mathbb{L}^2}^2} \left[ \int_{\mathcal{X}} m|\nabla u|^2 dx - \int_{\mathcal{X}} a(x)u^2(x) dx \right]. \quad (14)$$

We are now ready to state the result:

**Theorem 1.4.** *Assume (11), (12) and (13). If  $H > 0$ , any positive  $C^2$ -solution to (10) tends in  $\mathbb{L}^\infty$  to the unique positive solution to*

$$\begin{cases} -m\Delta \bar{g}(x) = a(x)\bar{g}(x) - \left( \int_{\mathcal{X}} I(y)\bar{g}(y)dy \right) \bar{g}(x), \quad \forall x \in \mathcal{X} \\ \partial_n \bar{g}(x) = 0, \quad \forall x \in \partial\mathcal{X}, \quad \forall t \in \mathbb{R}. \end{cases} \quad (15)$$

Moreover, if  $H \leq 0$ ,  $g(t, \cdot) \xrightarrow[t \rightarrow +\infty]{\mathbb{L}^\infty} 0$ .

Notice that  $H > 0$  is a necessary and sufficient condition to obtain a positive limit as  $t \rightarrow \infty$ . Hence, only the diffusion parameter and the growth rate  $a(x)$  have an influence on the non-extinction of the population in long time. The competition

rate affects the total population size at the limit, but not its persistence.

We can explicit a simple example where the assumption  $H > 0$  is satisfied : if the growth rate  $a(x)$  is a positive function, that is, if the birth rate is greater than the death rate everywhere, then  $H$  is positive. Theorem 1.4 allows us to conclude that the population will survive, which corresponds to the intuition. Conversely, if  $a(x)$  is a negative function, it is easy to deduce that  $H$  is negative and that the population goes to extinction.

**Remark 2.** In [14], the steady states and the long time behavior of the solution of a similar model are studied using different techniques, specific for the monomorphic case. However, we provide a shorter result for the long time convergence of solutions to (10), which is easily generalizable to dimension 2.

The first step of our proof is to study the steady states of Equation (10). In fact, we can prove the existence of a steady state in the case of a more heterogeneous competition term  $I$ .

In the end of this section, the function  $I$  is a function on  $\mathcal{X} \times \mathcal{X}$  and for all  $x, y \in \mathcal{X} \times \mathcal{X}$ ,  $I(x, y)$  denotes the competition rate between individuals with respective positions  $x$  and  $y$ . The dynamics is so the following, on  $\mathbb{R}^+ \times \mathcal{X}$ ,

$$\begin{cases} \partial_t g(t, x) = m\Delta g(t, x) + a(x)g(t, x) - \left( \int_{\mathcal{X}} I(x, y)g(t, y)dy \right) g(t, x), \\ \partial_n g(t, x) = 0, \forall (t, x) \in \mathbb{R}^+ \times \partial\mathcal{X}. \end{cases} \quad (16)$$

Unfortunately, the long-time behavior of the solution of (16) with this general competition kernel  $I(x, y)$  is not yet understood to our knowledge. Here we prove the existence of a positive steady state. Let us assume that  $I$  satisfies

$$\begin{aligned} & I(\cdot, \cdot) \in C(\bar{\mathcal{X}} \times \bar{\mathcal{X}}) \text{ is nonnegative} \\ & \text{and Lipschitz continuous with respect to the first variable,} \\ & \begin{cases} \text{if } d = 1 : \exists I_- > 0 / \forall x \in \mathcal{X}, I(x, x) \geq I_-, \\ \text{if } d > 1 : \exists I_- > 0 / \forall (x, y) \in \mathcal{X} \times \mathcal{X}, I(x, y) \geq I_-. \end{cases} \end{aligned} \quad (17)$$

**Theorem 1.5 (Existence of a steady state).** *Assume (11), (17).*

(i) *If  $H \leq 0$ , then there is no non-trivial nonnegative steady solution for (16).*

(ii) *If  $H > 0$ , then (16) has a strictly positive steady solution  $\bar{g} \in C^2(\mathcal{X})$ , i.e.  $\bar{g}$  solves*

$$\begin{cases} -m\Delta \bar{g}(x) = \left( a(x) - \int_{\mathcal{X}} I(x, y)\bar{g}(y)dy \right) \bar{g}(x), \forall x \in \mathcal{X} \\ \partial_n \bar{g}(x) = 0, \forall x \in \partial\mathcal{X}. \end{cases} \quad (18)$$

The proofs of the theorems rely on the spectral decomposition of compact operators, fixed point arguments and the study of perturbed Lotka-Volterra type systems.

The rest of the paper is organized as follows. In Section 2 we provide the proofs of our results in the case of a monomorphic population. Section 3 is devoted to the two-type case of dimorphic population. We provide the proofs of our main Theorems 1.2 and 1.3. Finally in Section 4, we present some numerical results

which are linked with evolution. The appearance of a mutant population within a well-established population can dramatically affect the landscape of that resident population, leading to coexistence or extinction. We will study an example with evolution of spatial niches.

## 2. Monomorphic population.

**2.1. Existence of a steady state.** In this section, we prove Theorem 1.5 and give a necessary and sufficient condition for (16) to have a steady solution.

We need the following lemma which can be derived easily from Krein-Rutman's Theorem (see for instance the chapter 6 of [20]) and its proof is left to the reader.

**Lemma 2.1 (Eigenvalue problem).** *There exists a principal eigenvalue  $H$  to the following eigenvalue problem:*

$$\begin{cases} m\Delta\bar{u}(x) + a(x)\bar{u} = H\bar{u}, & \forall x \in \mathcal{X}, \\ \partial_n\bar{u}(x) = 0, & \forall x \in \partial\mathcal{X}. \end{cases} \quad (19)$$

*This eigenvalue is simple and the corresponding eigenfunction  $\bar{u}$  is the only eigenfunction which is strictly positive in  $\mathcal{X}$ . Moreover,  $H$  can be computed from the following variational problem given by (14):*

$$H = - \min_{\substack{u \in \mathbb{H}^1 \\ u \neq 0}} \frac{1}{\|u\|_{\mathbb{L}^2}^2} \left[ \int_{\mathcal{X}} m|\nabla u|^2 dx - \int_{\mathcal{X}} a(x)u^2(x) dx \right].$$

(i) Let  $H \leq 0$ . We prove by contradiction that there is no nonnegative solution to (18). To this end, we suppose that  $0 \leq \bar{g} \in C^2(\mathcal{X})$  solves (18). Supposing that  $\bar{g}$  is non-trivial, from the maximum principle we obtain that  $\bar{g}$  is strictly positive and in particular

$$\int_{\mathcal{X} \times \mathcal{X}} I(x, y)\bar{g}(y)\bar{g}(x)\bar{u}(x) dx dy > 0.$$

We now multiply (18) by  $\bar{u}$  and integrate with respect to  $x$  to obtain from (19),

$$H \int_{\mathcal{X}} \bar{u}\bar{g} dx = \int_{\mathcal{X} \times \mathcal{X}} I(x, y)\bar{g}(y)\bar{g}(x)\bar{u}(x) dx dy > 0.$$

This is in contradiction with the assumption  $H \leq 0$ .

(ii) We now suppose that  $H > 0$ . To prove that (18) has a steady solution, we construct a mapping

$$\Upsilon : \begin{pmatrix} \mathbb{L}^2 & \rightarrow & \mathbb{L}^2 \\ h & \mapsto & g \end{pmatrix},$$

such that any fixed point of this mapping will be a steady state of our problem, as follows.

Thanks to (11), we can choose  $\delta > 0$  small enough such that  $1 - \delta a(x) > 0$  for all  $x \in \mathcal{X}$ . Let  $h \in \mathbb{L}^2$ . We define  $\psi(h) = h(1 - \delta \int I(\cdot, y)h(y)dy)$ , and  $\Upsilon(h) = g$ , where  $g \in \mathbb{H}^1$  is the unique solution of the following equation

$$\begin{cases} -m\delta\Delta g(x) - \delta a(x)g(x) + g(x) = \psi(h)(x), & \text{in } \mathcal{X}, \\ \partial_n g(x) = 0, & \text{on } \partial\mathcal{X}. \end{cases} \quad (20)$$

Notice that fixed points of the mapping  $\Upsilon$  are steady solutions of our problem and conversely. So the last step is to show that  $\Upsilon$  has a fixed point. We establish this



result thanks to Schauder's fixed point Theorem (see for instance Theorem (4.1) in [15]).

We first notice from the choice of  $\delta$  that  $(-m\delta\Delta + (1 - \delta a)Id)^{-1}$  is a continuous and compact mapping. As  $\psi : \mathbb{L}^2 \rightarrow \mathbb{L}^2$  is a well-defined continuous mapping, we deduce the continuity and compactness of  $\Upsilon$ .

We will split the rest of the proof into two cases depending on the dimension  $d$  of the domain  $\mathcal{X}$ .

But, first, let us remark that, consequently to Assumptions (17), there exists a positive constant  $I^+$  such that

$$I(x, y) \leq I^+, \quad \text{for all } x, y \in \mathcal{X}. \quad (21)$$

• If  $d > 1$ , using Lemma 2.1, there exists a positive eigenfunction  $\bar{u}$  associated with the positive eigenvalue  $H$ . We denote by  $\bar{u}^+$  and  $\bar{u}_-$  its maximum and minimum values on  $\mathcal{X}$ . Then we define

$$\lambda^+ = \frac{H\bar{u}^+}{I_-} \quad \text{and} \quad \lambda_- = \frac{H\bar{u}_-}{I^+} \quad (22)$$

and choose  $\delta > 0$  small enough such that

$$\lambda^+ \leq \frac{\bar{u}_-}{2\delta I^+} \quad \text{and} \quad 1 - \delta H > 0. \quad (23)$$

Let us now introduce the convex closed subset of  $\mathbb{L}^2$

$$\mathcal{Y} = \left\{ g \in \mathbb{L}^2 \mid g \geq 0, \lambda_- \leq \int_{\mathcal{X}} g\bar{u} \leq \lambda^+ \right\}.$$

We now prove that  $\Upsilon$  maps  $\mathcal{Y}$  into itself.

Let  $h$  be in  $\mathcal{Y}$ , and  $g = \Upsilon(h)$ , they satisfy

$$-m\delta\Delta g(x) - \delta a(x)g(x) + g(x) = h(x) \left( 1 - \delta \int_{\mathcal{X}} I(x, y)h(y)dy \right), \quad \text{on } \mathcal{X}. \quad (24)$$

As  $h$  is a positive function in  $\mathcal{Y}$ , and using (23),

$$\psi(h) \geq h \left( 1 - \delta \int_{\mathcal{X}} \frac{I(\cdot, y)}{\bar{u}(y)} h(y)\bar{u}(y)dy \right) \geq h \left( 1 - \delta \frac{I^+}{\bar{u}_-} \lambda^+ \right) \geq \frac{h}{2} \geq 0.$$

We deduce that  $g$  is positive on  $\mathcal{X}$  thanks to the maximum principle.

Then we multiply (24) by  $\bar{u}$  and integrate it over  $\mathcal{X}$ ,

$$\int_{\mathcal{X}} (-m\delta\Delta g - \delta a g)\bar{u} + \int_{\mathcal{X}} g\bar{u} = \int_{\mathcal{X}} h\bar{u} - \delta \int_{\mathcal{X} \times \mathcal{X}} \frac{I(x, y)}{\bar{u}(y)} h(y)\bar{u}(y)h(x)\bar{u}(x)dydx.$$

From an integration by parts, (19), (21) and (17), we find the following inequalities:

$$\int_{\mathcal{X}} h\bar{u} \left( 1 - \delta \frac{I_-}{\bar{u}^+} \int_{\mathcal{X}} h\bar{u} \right) \geq (1 - \delta H) \int_{\mathcal{X}} g\bar{u} \geq \int_{\mathcal{X}} h\bar{u} \left( 1 - \delta \frac{I^+}{\bar{u}_-} \int_{\mathcal{X}} h\bar{u} \right).$$

Thanks to (23), the two polynomial functions  $r \mapsto r(1 - \delta \frac{I_-}{\bar{u}^+} r)$  and  $r \mapsto r(1 - \delta \frac{I^+}{\bar{u}_-} r)$  are increasing on interval  $[\lambda_-, \lambda^+]$ , and, as  $\int_{\mathcal{X}} h\bar{u} \in [\lambda_-, \lambda^+]$ ,

$$\lambda^+ \left( 1 - \delta \frac{I_-}{\bar{u}^+} \lambda^+ \right) \geq (1 - \delta H) \int_{\mathcal{X}} g\bar{u} \geq \lambda_- \left( 1 - \delta \frac{I^+}{\bar{u}_-} \lambda_- \right).$$

Finally we obtain from (22) and (23) that  $\lambda^+ \geq \int_{\mathcal{X}} g \bar{u} \geq \lambda_-$ , thus  $g \in \mathcal{Y}$ .

We conclude from the Schauder's fixed point theorem that  $\Upsilon$  has a positive fixed point.

• For  $d = 1$ , the previous proof is valid if  $I$  is strictly positive in  $\mathcal{X}$  but we can relax this assumption to the one in (17) thanks to the following method. We first prove the following lemma

**Lemma 2.2.** *Assume (11) and (17). There exists  $R > 0$  such that for all positive function  $g \in \mathbb{L}^2$  and  $t \in [0, 1[$  satisfying  $g = t\Upsilon(g)$ , we have  $\|g\|_{\mathbb{L}^2} < R$ .*

*Proof.* We use an argument which is similar to the one presented in [5]. Let  $g \in \mathbb{L}^2$ , positive and  $t \in ]0, 1[$  such that  $g = t\Upsilon(g)$ .  $g$  attain its maximum value at a point  $x_0 \in \bar{\mathcal{X}}$ . As  $g$  satisfies Neumann boundary conditions, we have  $g'(x_0) = 0$  and  $g''(x_0) \leq 0$ . Using  $g = t\Upsilon(g)$  at the point  $x_0$  and since  $t < 1$  and  $(1 - \delta a(x_0))g(x_0) > 0$ , we get

$$\int_{\mathcal{X}} I(x_0, y)g(y)dy \leq a_\infty. \quad (25)$$

We then use Taylor-Lagrange's formula for the function  $g$  at point  $x_0$ . For all  $y \in \bar{\mathcal{X}}$ , there exists  $\xi \in ]x_0, y[$  or  $]y, x_0[$  such that

$$g(y) = \|g\|_\infty + (y - x_0)^2 g''(\xi)/2.$$

Additionally, using again  $g = t\Upsilon(g)$  and that  $1 - 1/t < 0$ , we obtain, for all  $\xi \in \bar{\mathcal{X}}$ ,  $g''(\xi) \geq -(\|g\|_\infty a_\infty)/m$ . We deduce that  $g(y) \geq \|g\|_\infty \left(1 - a_\infty \frac{(y - x_0)^2}{2m}\right)_+$ .

Therefore (25) implies

$$\|g\|_\infty \leq a_\infty \left( \int_{\mathcal{X}} I(x_0, y) \left(1 - a_\infty \frac{(y - x_0)^2}{2m}\right)_+ dy \right)^{-1} < +\infty,$$

which is bounded since  $I(x_0, \cdot)$  is positive in a neighborhood of  $x_0$  from (17) and we conclude easily.  $\square$

Thanks to this lemma, we choose  $\delta$  satisfying

$$\delta < \min \left( \frac{\bar{u}_-}{2RI^+ \|\bar{u}\|_{\mathbb{L}^2}}, \frac{1}{I^+ R \sqrt{|\mathcal{X}|}} \right). \quad (26)$$

Then we define the convex closed subset

$$\mathcal{Y} = \{h \in \mathbb{L}^2 | h \geq 0, \|h\|_{\mathbb{L}^2} \leq R, \int_{\mathcal{X}} h \bar{u} \geq \lambda_-\},$$

where  $\lambda_-$  is defined as before by (22). For  $h \in \mathcal{Y}$ , we have  $\int_{\mathcal{X}} I(x, y)h(y)dy \leq I^+ R \sqrt{|\mathcal{X}|} < \frac{1}{\delta}$  which implies that  $\psi(h)$  and  $g = \Upsilon(h)$  are positive functions. Moreover, following similar arguments as in the case  $d > 1$ , and noticing that Assumption (26) guarantees that  $\int_{\mathcal{X}} h \bar{u} dx \in [\lambda_-, \frac{\bar{u}_-}{2\delta I^+}]$ , we obtain that  $\int_{\mathcal{X}} g \bar{u} \geq \lambda_-$ .

As we are not sure that  $\|\Upsilon(h)\|_{\mathbb{L}^2} \leq R$ , we use the following method inspired by the proof of Schaefer's fixed point theorem: we introduce a new function  $\tilde{\Upsilon} : \mathbb{L}^2 \rightarrow \mathbb{L}^2$ ,

$$\tilde{\Upsilon}(h) = \begin{cases} \Upsilon(h), & \text{if } \|\Upsilon(h)\|_{\mathbb{L}^2} \leq R \\ \frac{R}{\|\Upsilon(h)\|_{\mathbb{L}^2}} \cdot \Upsilon(h), & \text{if } \|\Upsilon(h)\|_{\mathbb{L}^2} > R. \end{cases}$$

Thus  $\tilde{\Upsilon}$  is a continuous and compact function mapping  $\mathcal{Y}$  into itself. From the Schauder's fixed point theorem, we deduce that it has a fixed point  $\bar{g}$ . Suppose that  $\|\Upsilon(\bar{g})\|_{\mathbb{L}^2} > R$ , then  $\tilde{\Upsilon}(\bar{g}) = \frac{R}{\|\Upsilon(\bar{g})\|_{\mathbb{L}^2}} \Upsilon(\bar{g}) = \bar{g}$  and  $\|\tilde{\Upsilon}(\bar{g})\|_{\mathbb{L}^2} = \|\bar{g}\|_{\mathbb{L}^2} = R$ . However, since  $\bar{g} = t\Upsilon(\bar{g})$  with  $t = \frac{R}{\|\Upsilon(\bar{g})\|_{\mathbb{L}^2}} < 1$ , this is in contradiction with Lemma 2.2. Hence  $\|\Upsilon(\bar{g})\|_{\mathbb{L}^2} \leq R$  and  $\bar{g}$  is a fixed point of  $\Upsilon$ . That ends the proof of Theorem 1.5.

**2.2. Convergence to steady state solution.** We now prove Theorem 1.4, i.e. we study the long time behavior of the solution to (16) for the particular case, where  $I(x, y) \equiv I(x)$ .

We first check that there exists only one positive steady state in the case  $H > 0$ . Let  $\bar{g}, \bar{h} \in \mathbb{H}^1$  be two positive solutions to (15). Hence  $\bar{g}, \bar{h}$  are positive eigenvectors of the operator  $\mathcal{L} = m\Delta(\cdot) + a$ . which is compact and continuous. As Lemma 2.1 implies the uniqueness of a positive eigenvector up to a multiplicative constant,  $\bar{g} = s \cdot \bar{h}$  with  $s \in \mathbb{R}^+$ . Moreover, from (15), we deduce that the principal eigenvalue  $H$  is equal to  $(\int_{\mathcal{X}} I(y)\bar{g}(y)dy)$  and the same result holds for  $\bar{h}$ . It follows that  $\bar{g} = \bar{h}$ . We now denote by  $\bar{g}$  the unique solution of (15).

The next step is to show the convergence in  $\mathbb{L}^\infty$  towards the positive steady state if  $H > 0$  and towards 0 if  $H \leq 0$ . Let us make the following change of variable function

$$\forall (t, x) \in \mathbb{R} \times \mathcal{X}, \quad v(t, x) = g(t, x) \exp\left(\int_0^t \left(\int_{\mathcal{X}} I(y)g(s, y)dy\right)ds\right).$$

Thus  $v$  is a solution of the equation

$$\begin{cases} \partial_t v(t, x) - m\Delta v(t, x) = a(x)v(t, x), & \forall (t, x) \in \mathbb{R} \times \mathcal{X}, \\ \partial_n v(t, x) = 0, & \forall (t, x) \in \mathbb{R} \times \partial\mathcal{X}, \\ v(0, x) = g^0(x), & \forall x \in \partial\mathcal{X}. \end{cases} \quad (27)$$

It is well-known from the spectral decomposition of the operator  $\mathcal{L}$  and the regularizing property of the Laplace operator that  $v(t, \cdot)e^{-Ht}$  tends uniformly to  $\beta\bar{g}$ , a principal eigenvector of the operator  $\mathcal{L}$ , that is, for some positive constant  $\beta$ ,

$$g(t, x) \exp\left(\int_0^t \left(\int_{\mathcal{X}} I(y)g(s, y)dy\right)ds - Ht\right) \xrightarrow[t \rightarrow +\infty]{\mathbb{L}^\infty} \beta\bar{g}. \quad (28)$$

We divide this limit by an integrated version of it to obtain

$$\frac{g(t, \cdot)}{\rho(t)} \xrightarrow[t \rightarrow +\infty]{\mathbb{L}^\infty} \frac{\bar{g}(\cdot)}{\int_{\mathcal{X}} \bar{g}dx} > 0, \quad (29)$$

where  $\rho(t) = \int_{\mathcal{X}} g(t, y)dy$ , and the r.h.s. is positive since  $\bar{g}$  is a principal eigenvector of  $\mathcal{L}$ .

It remains to show that  $\rho(t)$  has a finite limit when  $t$  tends to infinity. Integrating (10), we find that  $\rho$  is a solution to

$$\frac{d}{dt}\rho(t) = \left(\int_{\mathcal{X}} a(y)\frac{g(t, y)}{\rho(t)}dy - \int_{\mathcal{X}} I(y)\frac{g(t, y)}{\rho(t)}dy \cdot \rho(t)\right)\rho(t), \quad \forall t \in \mathbb{R}.$$

Moreover, using definitions of  $H$  and  $\bar{g}$ ,  $-m\Delta\bar{g} = a\bar{g} - H\bar{g}$  holds, that leads to  $\int_{\mathcal{X}} a(x)\bar{g}(x)dx = H \int_{\mathcal{X}} \bar{g}(x)dx$ . Therefore (29) implies

$$\int_{\mathcal{X}} a(y) \frac{g(t, y)}{\rho(t)} dy \xrightarrow{t \rightarrow +\infty} \int_{\mathcal{X}} a(y) \frac{\bar{g}(y)}{\int_{\mathcal{X}} \bar{g}} dy = H$$

and

$$\int_{\mathcal{X}} I(y) \frac{g(t, y)}{\rho(t)} dx \xrightarrow{t \rightarrow +\infty} \mu := \int_{\mathcal{X}} \frac{I(y)\bar{g}(y)}{\int_{\mathcal{X}} \bar{g}} dy.$$

Thus,  $\rho$  is solution to the equation  $\frac{d}{dt}\rho(t) = \rho(t)(H + \mathcal{D}(t) - \mu\rho(t))$ , where

$$\mathcal{D}(t) = \int_{\mathcal{X}} a(y) \frac{g(t, y)}{\rho(t)} dy - H + \left( \int_{\mathcal{X}} I(y) \frac{g(t, y)}{\rho(t)} dy - \mu \right) \rho(t) \xrightarrow{t \rightarrow +\infty} 0$$

Indeed, since  $I$  is positive, we have  $\frac{d}{dt}\rho(t) \leq (a_{\infty} - I_{-}\rho(t))\rho(t)$ , that is sufficient to conclude that  $\sup_{t \in \mathbb{R}^+} \rho(t) < +\infty$ , and  $\mathcal{D}(t) \rightarrow 0$ , as  $t \rightarrow +\infty$ .

Next, we show that  $\rho(t)$  tends to  $H/\mu$  if  $H > 0$  and to 0 if  $H \leq 0$  thanks to the following lemma.

**Lemma 2.3.** *Let  $\mu \in \mathbb{R}_*^+$ , and  $\rho$  be a positive solution on  $\mathbb{R}$  to  $\frac{d}{dt}\rho(t) = \rho(t)(r + \mathcal{E}(t) - \mu\rho(t))$ , where  $\mathcal{E}(t) \xrightarrow{t \rightarrow +\infty} 0$ , then  $\rho(t)$  tends to  $\frac{r}{\mu}$  if  $r \geq 0$  or to 0 if  $r < 0$  as  $t$  tends to  $+\infty$ .*

Finally, we conclude from (29) and the above lemma that, for  $H > 0$ ,

$$g(t, \cdot) \xrightarrow{t \rightarrow +\infty} \frac{H}{\mu} \frac{\bar{g}}{\int_{\mathcal{X}} \bar{g} dx} = \bar{g}, \quad \text{since} \quad \int_{\mathcal{X}} \bar{g} dx = \frac{H}{\mu},$$

and for  $H \leq 0$ ,

$$g(t, \cdot) \xrightarrow{t \rightarrow +\infty} 0.$$

*Proof of Lemma 2.3.* We split this proof into two parts, depending on the value of  $r$ .

- If  $r < 0$ , there exists  $t_0 \in \mathbb{R}^+$  such that for all  $t \leq t_0$ ,  $r + \mathcal{E}(t) - \mu\rho(t) < \frac{r}{2}$ , i.e.  $\partial_t \rho(t) \leq \frac{r}{2}\rho(t)$  and we conclude with Gronwall's lemma.
- If  $r \geq 0$ , fix  $\varepsilon_0 > 0$ . there exists  $t_0$  such that for all  $t \geq t_0$ ,  $|\mathcal{E}(t)| \leq \varepsilon_0$ , that is

$$\rho(t)(r - \varepsilon_0 - \mu\rho(t)) \leq \partial_t \rho(t) \leq \rho(t)(r + \varepsilon_0 - \mu\rho(t)).$$

That means

$$\frac{r - \varepsilon_0}{\mu} \leq \liminf_{t \rightarrow +\infty} \rho(t) \leq \limsup_{t \rightarrow +\infty} \rho(t) \leq \frac{r + \varepsilon_0}{\mu}.$$

As this is true for all  $\varepsilon_0 > 0$ , we can conclude.  $\square$

**3. Dimorphic population.** In this section we present the proof of the main Theorems 1.2 and 1.3.

Similarly to the case of a monomorphic population, the long time behavior depends on the values of spectral parameters. To this end we use the spectral decomposition of compact operators:

**Lemma 3.1** (Spectral decomposition of compact operators (see chapter VI.4 of [9])). *For  $i \in \{1, 2\}$ , there exists a spectral basis  $(\lambda_k^i, A_k^i)_{k \geq 1}$ , for the operator  $\mathcal{L}^i(u) = m_i \Delta u + a_i u$  with Neumann boundary condition, that is,*

(i)  $\lambda_k^i$  is a nondecreasing sequence with  $H_i := \lambda_1^i > \lambda_2^i \geq \lambda_3^i \geq \dots \geq \lambda_k^i \geq \dots$  and  $\lambda_k^i \rightarrow -\infty$  as  $t \rightarrow \infty$ .

(ii)  $(\lambda_k^i, A_k^i)$  are eigenpairs, that is for all  $k \geq 1$  and  $i = 1, 2$ ,

$$\begin{cases} m_i \Delta A_k^i(x) + a_i(x) A_k^i = \lambda_k^i A_k^i, & \forall x \in \mathcal{X}, \\ \partial_n A_k^i(x) = 0, & \forall x \in \partial \mathcal{X}. \end{cases} \quad (30)$$

(iii)  $(A_k^i)_{k \geq 1}$  is an orthogonal basis of  $\mathbb{L}^2$ . We normalize them by

$$\int_{\mathcal{X}} |A_k^i(x)| dx = 1.$$

(iv) The first eigenvalue  $H_i$  is simple and is given by

$$H_i = - \min_{\substack{u \in \mathbb{H}^1 \\ u \neq 0}} \frac{1}{\|u\|_{\mathbb{L}^2}^2} \left[ \int_{\mathcal{X}} m_i |\nabla u|^2 dx - \int_{\mathcal{X}} a_i(x) u(x)^2 dx \right].$$

The first eigenfunction  $A_1^i$  is positive, unlike the eigenfunctions corresponding to the other eigenvalues. Those eigenfunctions are smooth.

Let us recall the following notation for  $i, j \in \{1, 2\}$

$$\mu_{ij} = \int_{\mathcal{X}} I_{ij}(x) A_1^j(x) dx. \quad (31)$$

**3.1. Studies of the steady states.** This part is devoted to the proof of Lemma 1.1 that identifies the steady states of the equation (1).

The conditions on the existence of the three first steady states are immediate from Theorem 1.5. Moreover, it follows from Lemma 3.1 that there is no nonnegative steady state other than the ones stated above. We only prove the last point corresponding to the steady state with two positive exponents.

We first suppose that  $r_1$  and  $r_2$  given by (8) are positive. It is then easy to verify, from (30) and (6), that  $(r_1 A_1^1, r_2 A_1^2)$  is a steady solution of (1).

We next notice using (7) that the matrix in (8) is invertible, and  $r_1$  and  $r_2$  are positive if and only if

$$r_i = \frac{H_i \mu_{jj} - H_j \mu_{ij}}{\mu_{jj} \mu_{ii} - \mu_{ji} \mu_{ij}} > 0, \text{ for } (i, j) \in \{(1, 2), (2, 1)\}.$$

This is equivalent to  $(H_2 \mu_{11} - H_1 \mu_{21})(H_1 \mu_{22} - H_2 \mu_{12}) > 0$  and  $H_1, H_2 > 0$ . Indeed, if  $H_2 \mu_{11} - H_1 \mu_{21}$  and  $H_1 \mu_{22} - H_2 \mu_{12}$  have the same sign, then

$$\mu_{11} \mu_{22} - \mu_{12} \mu_{21} = \frac{\mu_{11}}{H_1} (H_1 \mu_{22} - H_2 \mu_{12}) + \frac{\mu_{12}}{H_1} (H_2 \mu_{11} - H_1 \mu_{21}),$$

has also the same sign if and only if  $H_1 > 0$ . We conclude easily.

**3.2. Long time behavior of the system (proof of Theorem 1.2).** In this section, we prove Theorem 1.2. To this end, noticing that the total density of the population is not constant, we will first study the limit of population densities normalized by the masses. Then we will study the long time behavior of a system of differential equations which describes the dynamics of the two masses (see Lemma 3.2).

Similarly to the proof of Theorem 1.4, we make the following change of variables, for  $i \in \{1, 2\}$ ,

$$v_i(t, x) = g_i(t, x) \exp \left( \int_0^t \left( \int_{\mathcal{X}} I_{i1}(y) g_1(s, y) dy + \int_{\mathcal{X}} I_{i2}(y) g_2(s, y) dy \right) ds \right).$$

Following similar arguments as in subsection 2.2, we find a similar limit as (28) for  $g_i$ , which leads to

$$\frac{g_1(t, \cdot)}{\int_{\mathcal{X}} g_1(t, y) dy} \xrightarrow[t \rightarrow +\infty]{\mathbb{L}^\infty} A_1^1 \quad \text{and} \quad \frac{g_2(t, \cdot)}{\int_{\mathcal{X}} g_2(t, y) dy} \xrightarrow[t \rightarrow +\infty]{\mathbb{L}^\infty} A_1^2. \quad (32)$$

Let  $\rho_i(t) = \int_{\mathcal{X}} g_i(t, y) dy$  for  $i \in \{1, 2\}$ . We deduce the following limits from (32), for  $i, j \in \{1, 2\}$ ,

$$\int_{\mathcal{X}} \frac{a_i(y) g_i(t, y)}{\rho_i(t)} dy \xrightarrow[t \rightarrow +\infty]{} H_i \quad \text{and} \quad \int_{\mathcal{X}} \frac{I_{ji}(y) g_i(t, y)}{\rho_i(t)} dy \xrightarrow[t \rightarrow +\infty]{} \mu_{ji}.$$

It remains now to understand the behavior of  $(\rho_1(t), \rho_2(t))$ . Integrating (1) on  $\mathcal{X}$  and using the previous limits, we find that  $(\rho_1, \rho_2)$  is a solution to

$$\begin{cases} \frac{d}{dt} \rho_1(t) = \rho_1(t) (H_1 + \mathcal{D}_1(t) - \mu_{11} \rho_1(t) - \mu_{12} \rho_2(t)), \\ \frac{d}{dt} \rho_2(t) = \rho_2(t) (H_2 + \mathcal{D}_2(t) - \mu_{21} \rho_1(t) - \mu_{22} \rho_2(t)), \end{cases} \quad (33)$$

with, for  $i \in \{1, 2\}$ ,

$$\mathcal{D}_i(t) = \int_{\mathcal{X}} a_i(y) \frac{g_i(t, y)}{\rho_i(t)} dy - H_i + \sum_{j=1,2} \left( \int_{\mathcal{X}} I_{ij}(y) \frac{g_j(t, y)}{\rho_j(t)} dy - \mu_{ij} \right) \rho_j(t) \xrightarrow[t \rightarrow +\infty]{} 0.$$

Here we have used the fact that, in view of (2) and (3),  $\rho_j$  is a positive solution to

$$\partial_t \rho_j(t) \leq (a_\infty - I_- \rho_j(t)) \rho_j(t)$$

and hence  $\rho_j$  is bounded, for  $j \in \{1, 2\}$ .

To go further we need the following lemma.

**Lemma 3.2.** *Let  $(\rho_1(t), \rho_2(t))$  be a positive solution to*

$$\begin{cases} \frac{d}{dt} \rho_1(t) = \rho_1(t) (H_1 + \mathcal{E}_1(t) - \mu_{11} \rho_1(t) - \mu_{12} \rho_2(t)), \\ \frac{d}{dt} \rho_2(t) = \rho_2(t) (H_2 + \mathcal{E}_2(t) - \mu_{21} \rho_1(t) - \mu_{22} \rho_2(t)), \end{cases}$$

where  $\mathcal{E}_i(t) \xrightarrow[t \rightarrow +\infty]{} 0$  for  $i \in \{1, 2\}$ .

- If  $H_1 \leq 0$  and  $H_2 \leq 0$ , then  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} (0, 0)$ .

Also if at least one of the two eigenvalues is positive and

- if  $H_2 \mu_{11} - H_1 \mu_{21} \leq 0$  and  $H_1 \mu_{22} - H_2 \mu_{12} > 0$ , then  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} \left( \frac{H_1}{\mu_{11}}, 0 \right)$ ,
- if  $H_2 \mu_{11} - H_1 \mu_{21} > 0$  and  $H_1 \mu_{22} - H_2 \mu_{12} \leq 0$ , then  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} \left( 0, \frac{H_2}{\mu_{22}} \right)$ ,
- if  $H_2 \mu_{11} - H_1 \mu_{21} > 0$  and  $H_1 \mu_{22} - H_2 \mu_{12} > 0$  then  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} (r_1, r_2)$ , where  $r_1$  and  $r_2$  are given by (8),

- if  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} = 0$ , or if  $H_2\mu_{11} - H_1\mu_{21} = 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$ , then  $(\rho_1(t), \rho_2(t))$  has a limit which can be  $\left(\frac{H_1}{\mu_{11}}, 0\right)$  or  $\left(0, \frac{H_2}{\mu_{22}}\right)$ , depending on the initial condition, on the parameters and on the functions  $(\mathcal{E}_i)_{i=1,2}$ ,
- finally, if  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$ , then  $(\rho_1(t), \rho_2(t))$  has a limit which can be one of the three non-zero limits, depending on the initial condition, on the parameters and on the functions  $(\mathcal{E}_i)_{i=1,2}$ .

This lemma and expressions (32) are sufficient to prove all the statements of the theorem:

(1) One can verify using (7) that all possible values of  $(H_1, H_2) \in \mathbb{R}^2$  are covered by Lemma 3.2 and hence, in all cases, the solution to (33) has a limit when  $t$  tends to  $+\infty$  for any initial condition.

(2) If  $H_1 \leq 0$  and  $H_2 \leq 0$ ,  $(\rho_1(t), \rho_2(t))$  tends to  $(0, 0)$ , so for any initial condition,  $(g_1(t, \cdot), g_2(t, \cdot))$  tends to  $(0, 0)$ .

(3) If  $H_1 > 0$ ,  $H_2\mu_{11} - H_1\mu_{21} \leq 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$ ,  $(\rho_1(t), \rho_2(t))$  tends to  $\left(\frac{H_1}{\mu_{11}}, 0\right)$  and  $\int_{\mathcal{X}} \bar{g}_1(x) dx = \frac{H_1}{\mu_{11}}$ . Therefore, for any initial condition,  $(g_1(t, \cdot), g_2(t, \cdot))$  tends to  $(\bar{g}_1, 0)$ .

(4) If  $H_2 > 0$ ,  $H_2\mu_{11} - H_1\mu_{21} > 0$  and  $H_1\mu_{22} - H_2\mu_{12} \leq 0$ ,  $(\rho_1(t), \rho_2(t))$  tends to  $\left(0, \frac{H_2}{\mu_{22}}\right)$  and  $\int_{\mathcal{X}} \bar{g}_2(x) dx = \frac{H_2}{\mu_{22}}$ . Therefore, for any initial condition,  $(g_1(t, \cdot), g_2(t, \cdot))$  tends to  $(0, \bar{g}_2)$ .

(5) If  $H_1 > 0$ ,  $H_2 > 0$ ,  $H_2\mu_{11} - H_1\mu_{21} > 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$ ,  $(\rho_1(t), \rho_2(t))$  tends to  $(r_1, r_2)$  and we have, from Lemma 1.1, that  $r_1 = \int_{\mathcal{X}} \hat{g}_1(x) dx$  and  $r_2 = \int_{\mathcal{X}} \hat{g}_2(x) dx$ . It follows that  $(g_1(t, \cdot), g_2(t, \cdot))$  tends to  $(\hat{g}_1, \hat{g}_2)$  for any initial condition.

*Proof of Lemma 3.2.* We split the proof into several cases depending on the values of  $H_1$  and  $H_2$ .

**Case 1:** First of all, we will consider that at least one of the two variables is non-positive. For example, let assume that  $H_1 \leq 0$ .

Let  $\varepsilon > 0$  and  $t_\varepsilon > 0$  such that for all  $t \geq t_\varepsilon$ ,  $|\mathcal{E}_1(t)| \leq \mu_{11}\varepsilon$ . So for all  $t \geq t_\varepsilon$ ,  $\partial_t \rho_1(t) \leq \rho_1(t)(\mu_{11}\varepsilon - \mu_{11}\rho_1(t))$ . Thanks to the results on the logistic equation, we conclude easily that  $\limsup_{t \rightarrow +\infty} \rho_1(t) \in [0, \varepsilon]$ . As this is true for all  $\varepsilon > 0$ ,  $\rho_1(t)$  tends toward 0 when  $t$  approaches infinity. Therefore,  $\rho_2$  solves

$$\partial_t \rho_2(t) = \rho_2(t)(H_2 + \mathcal{E}'(t) - \mu_{22}\rho_2(t)) \text{ where } \mathcal{E}'(t) = \mathcal{E}_2(t) - \mu_{21}\rho_1(t) \xrightarrow{t \rightarrow +\infty} 0.$$

We conclude that  $\rho_2$  converges and we evaluate its limit thanks to Lemma 2.3.

We consider now that  $H_1$  and  $H_2$  are positive. We will detail only three cases here, the other ones can be adapted from those three cases.

**Case 2:** Let  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$ ; the case where  $H_2\mu_{11} - H_1\mu_{21} > 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$ , can be studied following similar arguments.

Let  $\varepsilon > 0$  be small enough to satisfy

$$\min \left\{ \frac{H_1 - \varepsilon}{\mu_{12}} - \frac{H_2 + \varepsilon}{\mu_{22}}, \frac{H_1 - \varepsilon}{\mu_{11}} - \frac{H_2 + \varepsilon}{\mu_{21}}, \frac{H_2 - \varepsilon}{\mu_{22}}, \frac{H_2 - \varepsilon}{\mu_{21}} \right\} > 0. \quad (34)$$

We split  $(\mathbb{R}_+)^2$  into the next five disjoint sets drawn on Figure 1:

$$D_1 = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \leq -\varepsilon\}$$

$$D_2 = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \geq \varepsilon\}$$

$$D_3 = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \geq \varepsilon, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \leq -\varepsilon\}$$

$$D_4 = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \geq -\varepsilon, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \leq \varepsilon\}$$

$$D_5 = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \geq -\varepsilon, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \leq \varepsilon\}.$$

There exists  $t_\varepsilon > 0$  such that for all  $t \geq t_\varepsilon$ ,  $\max\{|\mathcal{E}_1(t)|, |\mathcal{E}_2(t)|\} \leq \frac{\varepsilon}{2}$ . It is then

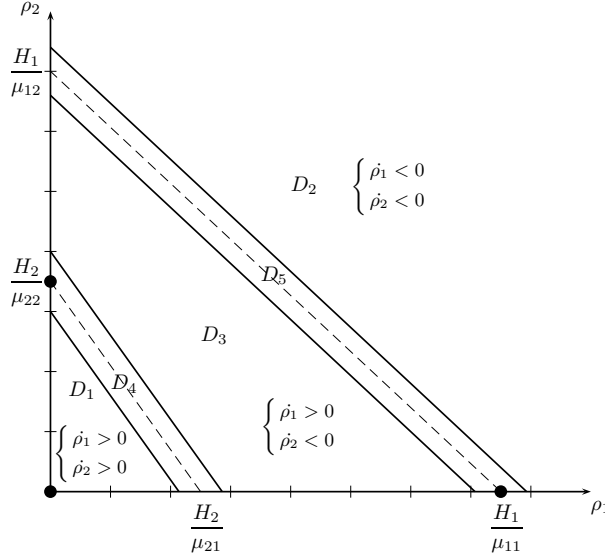


FIGURE 1. Plan arrangement for case 2, i.e.  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$

easy to verify that, for  $i = 1, 2$ ,  $\frac{d}{dt}\rho_i \geq \frac{\varepsilon}{2}\rho_i$  in  $D_1$  and  $\frac{d}{dt}\rho_i \leq -\frac{\varepsilon}{2}\rho_i$  in  $D_2$ . Moreover,  $\frac{d}{dt}\rho_1 \geq \frac{\varepsilon}{2}\rho_1$  and  $\frac{d}{dt}\rho_2 \leq -\frac{\varepsilon}{2}\rho_2$  in  $D_3$ .

As  $\rho_1$  satisfies  $\frac{d}{dt}\rho_1(t) \geq \frac{\varepsilon}{2}\rho_1(t)$  in  $D_1$ , for all  $t \geq t_\varepsilon$ , if  $(\rho_1(\bar{t}), \rho_2(\bar{t}))$  belongs to  $D_1$  for some  $\bar{t} \geq t_\varepsilon$ , it will quit this domain after a finite time  $t_0$  and reach the set  $D' = D_3 \cup D_4 \cup D_5$ . Same kind of results holds in  $D_2$ . Thus after a finite time  $t_0 \geq t_\varepsilon$ , the trajectory of the solution reaches  $D'$ . Moreover it cannot quit this domain according to the signs of derivatives of  $\rho_1$  and  $\rho_2$  at the boundaries of  $D'$ . The next step is to study the dynamics in  $D'$ . Suppose that the trajectory belongs



to  $D_3 \cup D_4$ , it cannot stay in that area for all  $t \geq t_0$ , so there exists  $t_1$  such that  $(\rho_1(t_1), \rho_2(t_1)) \in D_5$ . We denote the entry point in  $D_5$  by  $x_1$ , drawn in Figure 2. According to the derivatives of  $\rho_1$  and  $\rho_2$ , the trajectory of the solution does not quit the set:

$$D_{x_1} = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, \rho_1 \geq \rho_1^{x_1}, \rho_2 \leq \rho_2^{x_1}\} \cap D',$$

where  $(\rho_1^{x_1}, \rho_2^{x_1})$  are the coordinates of  $x_1$ . This set is represented by the hatched area on the left scheme of Figure 2. Moreover, as long as the trajectory stays in  $D_3 \cup D_5$ ,  $\rho_2$  satisfies  $\partial_t \rho_2(t) \leq -\frac{\varepsilon}{2} \rho_2(t)$ . So two cases can happen:

- (a) either  $\rho_2(t) \xrightarrow[t \rightarrow +\infty]{} 0$ , and thus  $\rho_1$  tends to  $\frac{H_1}{\mu_{11}}$  from Lemma 2.3,
- (b) or there exists  $t_2 > t_1$  where the trajectory reaches  $D_4$ . Let us denote  $x_2 = (\rho_1^{x_2}, \frac{H_2 + \varepsilon - \mu_{21} \rho_1^{x_2}}{\mu_{22}})$ . As the trajectory stays in  $D_{x_1}$ , it reaches  $D_4 \cap D_{x_2}$ , where  $D_{x_2} = \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, \rho_1 \geq \rho_1^{x_2}, \rho_2 \leq \rho_2^{x_2}\} \cap D'$ . Moreover, for all  $t \geq t_2$ , the trajectory stays in  $D_{x_2}$  (see the hatched area on the right scheme of Figure 2).

Iterating the previous step, we construct a decreasing sequence of areas denoted by  $(D_{x_n})_{n \geq 0}$  which will be necessarily finite. Indeed, the choice of  $\varepsilon$  (34) implies that there exists  $m \in \mathbb{N}$  such that  $D_{x_{2m}} \cap D_4 = \emptyset$ . Then we conclude as in the case (a) above.

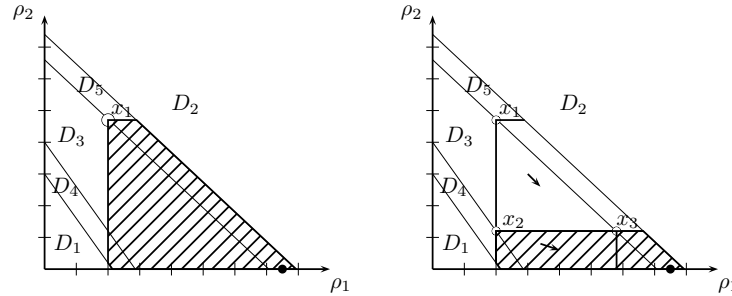


FIGURE 2. Dynamics for the case 2:  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$

The next case is quite similar except for the end of the proof.

**Case 3:** Let  $H_2\mu_{11} - H_1\mu_{21} = 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$ ; the case where  $H_2\mu_{11} - H_1\mu_{21} > 0$  and  $H_1\mu_{22} - H_2\mu_{12} = 0$  and the one where  $H_2\mu_{11} - H_1\mu_{21} > 0$  and  $H_1\mu_{22} - H_2\mu_{12} > 0$  can be proven using same kind of arguments.

Let  $k \geq 1$  and  $\varepsilon > 0$  be such that

$$\max \left\{ \frac{\mu_{11}}{\mu_{21}}, \frac{\mu_{21}}{\mu_{11}} \right\} < k \quad \text{and} \quad \min \left\{ \frac{H_1 - \varepsilon}{\mu_{21}} - \frac{H_2 + \varepsilon}{\mu_{22}}, \frac{H_2 - k\varepsilon}{\mu_{22}}, \frac{H_2 - k\varepsilon}{\mu_{21}} \right\} > 0.$$

We divide the plan  $(\mathbb{R}_+)^2$  as presented in Figure 3, where  $D_1, D_2, D_3, D_4, D_5$  and  $D'$  are defined as follows

$$\begin{aligned} D_1 &= \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \leq -k\varepsilon\} \\ D_2 &= \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \geq k\varepsilon\} \\ D_3 &= \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \geq \varepsilon, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \leq -\varepsilon\} \\ D_4 &= \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \geq -k\varepsilon, -H_2 + \mu_{21}\rho_1 + \mu_{22}\rho_2 \leq \varepsilon\} \\ D_5 &= \{(\rho_1, \rho_2) \in (\mathbb{R}_+^*)^2, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \geq -\varepsilon, -H_1 + \mu_{11}\rho_1 + \mu_{12}\rho_2 \leq k\varepsilon\} \\ D' &= D_3 \cup D_4 \cup D_5. \end{aligned}$$

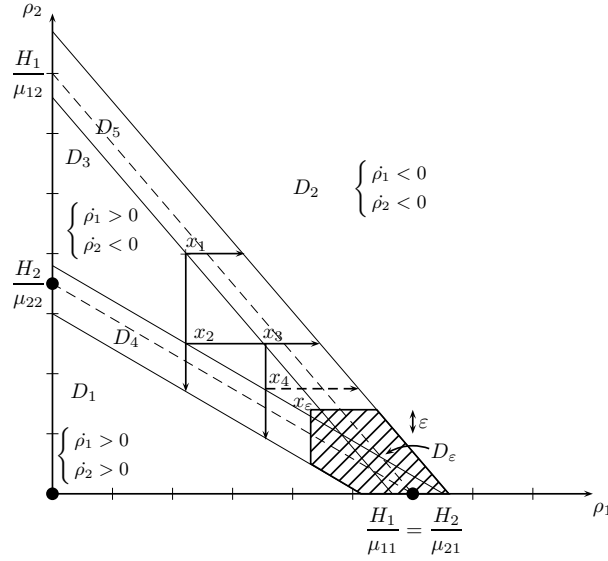


FIGURE 3. Arrangement for the case 3, i.e.  $H_2\mu_{11} - H_1\mu_{21} = 0$  et  $H_1\mu_{22} - H_2\mu_{12} > 0$

The constant  $k$  is chosen such that  $D_1 \cap D_5 = \emptyset$  and  $D_2 \cap D_4 = \emptyset$  and  $t_\varepsilon$  is defined as before. There exists  $t_0 \geq t_\varepsilon$  such that for all  $t \geq t_0$ , the trajectory is belonging to  $D'$ . Then we construct a sequence of sets  $(D_{x_n})_{n \geq 1}$  as before, but now, this sequence can be infinite. So let  $D_\varepsilon$  be the set

$$\begin{aligned} D_\varepsilon &= D' \cap \left\{ (\rho_1, \rho_2) \in (\mathbb{R}^+)^2, \rho_2 \leq \varepsilon \left( \frac{\mu_{11} + \mu_{21}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}} + 1 \right) \right. \\ &\quad \left. \text{and } \rho_1 \geq \frac{H_1}{\mu_{11}} - \varepsilon \left( \frac{\mu_{22} + \mu_{12}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}} + 1 \right) \right\}. \end{aligned}$$

There exists  $n$  such that  $D_{x_n}$  is included in  $D_\varepsilon$ , i.e. the trajectory is belonging to  $D_\varepsilon$  after a finite time. As this is true for all  $\varepsilon > 0$ ,  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} \left( \frac{H_1}{\mu_{11}}, 0 \right)$ .

The last case that we detail is a case where several limits are possible.

**Case 4:** Let  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} = 0$ ; we can deal with the case  $H_2\mu_{11} - H_1\mu_{21} = 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$  and the one with  $H_2\mu_{11} - H_1\mu_{21} < 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$  thanks to similar arguments.

Let  $k \geq 1$  and  $\varepsilon > 0$  such that

$$\max \left\{ \frac{\mu_{22}}{\mu_{12}}, \frac{\mu_{12}}{\mu_{22}} \right\} < k \quad \text{and} \quad \min \left\{ \frac{H_1 - \varepsilon}{\mu_{11}} - \frac{H_2 + \varepsilon}{\mu_{21}}, \frac{H_2 - k\varepsilon}{\mu_{22}}, \frac{H_2 - k\varepsilon}{\mu_{21}} \right\} > 0.$$

We divide the plan  $(\mathbb{R}_+)^2$  as presented in Figure 4, where  $D_3, D_4, D_5, D'$  are defined as in the case 3 and  $D_\varepsilon$  is defined as follows

$$D_\varepsilon = D' \setminus \left\{ (\rho_1, \rho_2) \in (\mathbb{R}^+)^2, \rho_1 > \varepsilon \frac{\mu_{21} + \mu_{22}}{\mu_{12}\mu_{21} - \mu_{11}\mu_{22}} \right. \\ \left. \text{and } \rho_2 < \frac{H_2}{\mu_{22}} - \varepsilon \frac{\mu_{12} + \mu_{11}}{\mu_{12}\mu_{21} - \mu_{11}\mu_{22}} \right\}$$

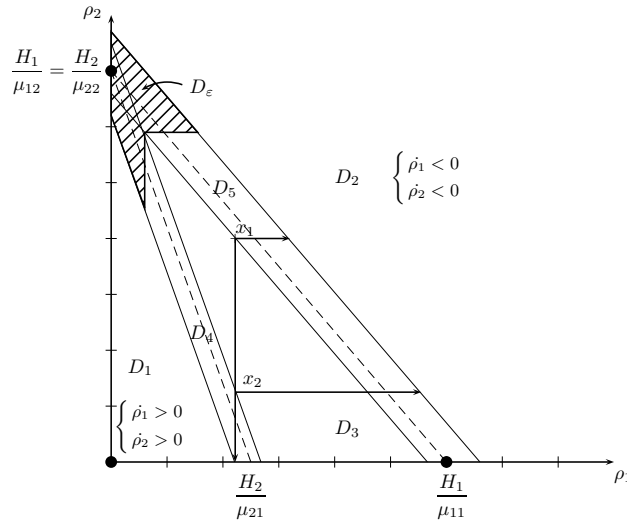


FIGURE 4. Arrangement for the case 4, i.e.  $H_2\mu_{11} - H_1\mu_{21} < 0$  et  $H_1\mu_{22} - H_2\mu_{12} = 0$

As before, we find  $t_0 \geq t_\varepsilon$  such that for all  $t \geq t_0$ , the trajectory of the solution belongs to  $D'$ . Then there exist two possibilities.

- Either for all  $\varepsilon > 0$ , there exists  $\tau_\varepsilon > t_\varepsilon$  such that for all  $t \geq \tau_\varepsilon$  the trajectory belongs to  $D_\varepsilon$ , that is,  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} \left(0, \frac{H_2}{\mu_{22}}\right)$ .
- Or there exists  $\varepsilon > 0$  and  $\tau_\varepsilon > t_\varepsilon$  when the trajectory is belonging to  $D' \setminus D_\varepsilon$ . Using same kind of arguments as before, we obtain that the trajectory won't quit this set for all  $t \geq \tau_\varepsilon$ , and we construct a sequence of decreasing sets to conclude that  $(\rho_1(t), \rho_2(t)) \xrightarrow[t \rightarrow +\infty]{} \left(\frac{H_1}{\mu_{11}}, 0\right)$ .

□

**3.3. Cases with several equilibria (proof of Theorem 1.3).** In this section we prove Theorem 1.3.

(1) Let us deal with the first case where  $H_1 > 0$ ,  $H_2 > 0$ ,  $H_2\mu_{11} - H_1\mu_{21} < 0$ , and  $H_1\mu_{22} - H_2\mu_{12} < 0$ . Thanks to the last statement of Lemma 3.2, we already know that any solution tends towards one of the non-trivial steady states. We precise the stability of each state.

(1a) This point is devoted to show the asymptotic stability of  $(\bar{g}_1, 0)$  if  $H_1 > 0$  and  $H_2\mu_{11} - H_1\mu_{21} < 0$ . Using symmetric arguments, it then can be shown that if  $H_2 > 0$  and  $H_1\mu_{22} - H_2\mu_{12} < 0$ ,  $(0, \bar{g}_2)$  is stable.

Precisely, we show that if the positive initial condition  $(g_1(0, \cdot), g_2(0, \cdot))$  satisfies the following condition: there exist  $C_1 > 0$  and  $C_2 > 0$  such that

$$\max_{i=1,2} \{ \|g_i(0, \cdot) - \bar{g}_i\|_{\mathbb{L}^2} \|I_{i1}\|_{\mathbb{L}^2} \} \leq C_1, \quad (35)$$

$$\|g_2(0, \cdot)\|_{\mathbb{L}^2} \|I_{12}\|_{\mathbb{L}^2} \leq C_2, \quad (36)$$

where the above constants satisfy the following compatibility conditions

$$C = 2 \left( (C_1 + C_2) \cdot \max \left\{ 1, \frac{\mu_{21}}{\mu_{11}} \right\} + C_1 \right) < \min \left\{ H_1 - \lambda_2^1, \frac{\mu_{21}}{\mu_{11}} H_1 - H_2 \right\}, \quad (37)$$

then the solution to the equation (1) tends to the steady state  $(\bar{g}_1, 0)$ .

Let us express  $g_1$  in the basis  $(A_k^1, k \in \mathbb{N}^*)$ ,  $\forall x \in \mathcal{X}$

$$g_1(t, x) = \int_{\mathcal{X}} \bar{g}_1(x) dx A_1^1(x) + \sum_{k=1}^{\infty} \alpha_k(t) A_k^1(x),$$

and denote for all  $t \in \mathbb{R}^+$

$$\kappa(t) = \int_{\mathcal{X}} \bar{g}_1(x) dx + \alpha_1(t).$$

From (1) and the representation of  $g_1$  and  $\partial_t g_1$  with respect to the basis  $(A_k^1, k \in \mathbb{N}^*)$ , we find the following dynamical system

$$\begin{cases} \frac{d}{dt} \alpha_k(t) = \alpha_k(t) \left( \lambda_k^1 - H_1 - \sum_{\ell=1}^{\infty} \alpha_{\ell}(t) \int_{\mathcal{X}} (I_{11} A_{\ell}^1) - \int_{\mathcal{X}} (I_{12} g_2(t, \cdot)) \right), \quad \forall k \geq 2, \\ \frac{d}{dt} \kappa(t) = \kappa(t) \left( H_1 - \sum_{\ell=2}^{\infty} \alpha_{\ell}(t) \int_{\mathcal{X}} (I_{11} A_{\ell}^1) - \int_{\mathcal{X}} (I_{12} g_2(t, \cdot)) - \mu_{11} \kappa(t) \right). \end{cases} \quad (38)$$

Here, we have used the fact that since, from Lemma 3.1,  $L_N = \int_{\mathcal{X}} \bar{g}_1 dx A_1^1 + \sum_{k=1}^N \alpha_k A_k^1$  tends to  $g_1$  in  $\mathbb{L}^2$  as  $N \rightarrow \infty$ , and since the domain  $\mathcal{X}$  is bounded,  $L_N$  tends to  $g_1$  in  $\mathbb{L}^1$ .

We will show that for all  $t \geq 0$ ,

$$\min_{i=1,2} \left\{ \sum_{k=1}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1}(y) A_k^1(y)) dy \right\} \geq -C. \quad (39)$$

We notice that this is true for  $t = 0$  thanks to (35): for  $i \in \{1, 2\}$ ,

$$\begin{aligned} \left| \sum_{k=1}^{\infty} \alpha_k(0) \int_{\mathcal{X}} (I_{i1} A_k^1) \right| &\leq \left( \sum_{k=1}^{\infty} \alpha_k(0)^2 \int_{\mathcal{X}} |A_k^1|^2 \right)^{1/2} \left( \sum_{k=1}^{\infty} \frac{(\int_{\mathcal{X}} I_{i1} A_k^1)^2}{\int_{\mathcal{X}} |A_k^1|^2} \right)^{1/2} \\ &\leq \|g_1(0, \cdot) - \bar{g}_1\|_{\mathbb{L}^2} \|I_{i1}\|_{\mathbb{L}^2} \\ &\leq C_1 < C. \end{aligned}$$

The second line is justified using the representation of  $I_{i1}$  with respect to the orthonormal basis  $\{A_k^1/\|A_k^1\|_{\mathbb{L}^2}\}_{k \geq 1}$  which is  $\{(\int_{\mathcal{X}} I_{i1} A_k^1)/\|A_k^1\|_{\mathbb{L}^2}\}_{k \geq 1}$ .

We prove the result (39) by contradiction. Denote

$$t_0 = \inf \left\{ t > 0 \mid \min_{i=1,2} \left\{ \sum_{k=1}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1}(y) A_k^1(y)) dy \right\} \leq -C \right\}$$

and suppose that  $t_0$  is finite. Thus, for  $i \in \{1, 2\}$ ,

$$\forall t \leq t_0, \quad \sum_{k=1}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1}(y) A_k^1(y)) dy \geq -C. \quad (40)$$

In fact, from (40), we will find a lower bound greater than  $-C$  for any  $t \leq t_0$  which is a contradiction with the fact that  $t_0$  is finite.

First, let us deal with the expression  $\sum_{k=2}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1} A_k^1) dx$ . We multiply the first equation of (38) by  $\alpha_k$ . Then, using the positivity of  $g_2$ , the assumption (37) and Gronwall's lemma, we get for all  $t \leq t_0$ ,  $\alpha_k(t)^2 \leq \alpha_k(0)^2 e^{2(\lambda_k^1 - H_1 + C)t} \leq \alpha_k(0)^2$ . Thus, for all  $t \leq t_0$ , for  $i \in \{1, 2\}$ ,

$$\begin{aligned} \left| \sum_{k=2}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1} A_k^1) \right| &\leq \left( \sum_{k=2}^{\infty} \alpha_k(t)^2 \int_{\mathcal{X}} |A_k^1|^2 \right)^{1/2} \left( \sum_{k=2}^{\infty} \frac{(\int_{\mathcal{X}} I_{i1} A_k^1)^2}{\int_{\mathcal{X}} |A_k^1|^2} \right)^{1/2} \\ &\leq \left( \sum_{k=2}^{\infty} \alpha_k(0)^2 \int_{\mathcal{X}} |A_k^1|^2 \right)^{1/2} \left( \sum_{k=2}^{\infty} \frac{(\int_{\mathcal{X}} I_{i1} A_k^1)^2}{\int_{\mathcal{X}} |A_k^1|^2} \right)^{1/2} \\ &\leq \|g_1(0, \cdot) - \bar{g}_1\|_{\mathbb{L}^2} \|I_{i1}\|_{\mathbb{L}^2} < C_1. \end{aligned} \quad (41)$$

Then, in view of finding a lower bound to  $\kappa$ , we are concerned with  $\int_{\mathcal{X}} I_{12} g_2(t, \cdot) dx$ . We multiply the second equation in (1) by  $g_2$  and integrate it over  $\mathcal{X}$ :

$$\begin{aligned} \frac{1}{2} \frac{d}{dt} \|g_2(t, \cdot)\|_{\mathbb{L}^2}^2 &\leq \left( H_2 - \mu_{21} \frac{H_1}{\mu_{11}} - \sum_{k=1}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{21} A_k^1) \right. \\ &\quad \left. - \int_{\mathcal{X}} I_{22}(y) g_2(t, y) dy \right) \cdot \|g_2(t, \cdot)\|_{\mathbb{L}^2}^2 \end{aligned}$$

From Assumption (40) for  $i = 2$ , the positivity of  $g_2$  and the Gronwall's lemma, we get that for all  $t \leq t_0$ ,

$$\|g_2(t, \cdot)\|_{\mathbb{L}^2}^2 \leq \exp \left\{ 2 \left( H_2 - \mu_{21} \frac{H_1}{\mu_{11}} + C \right) t \right\} \cdot \|g_2(0, \cdot)\|_{\mathbb{L}^2}^2 \leq \|g_2(0, \cdot)\|_{\mathbb{L}^2}^2, \quad (42)$$

as  $H_2 - (\mu_{21} H_1)/\mu_{11} + C$  is negative by Assumptions (37). That is, with the assumption (36), for all  $t \leq t_0$ ,  $0 \leq \int_{\mathcal{X}} (I_{12} g_2(t, \cdot)) \leq \|I_{12}\|_{\mathbb{L}^2} \|g_2(t, \cdot)\|_{\mathbb{L}^2} \leq C_2$ .

We use this inequality and (41) to show that  $\kappa$  satisfies, for all  $t \leq t_0$ ,

$$\kappa(t) (H_1 - C_1 - C_2 - \mu_{11} \kappa(t)) \leq \partial_t \kappa(t).$$

Moreover, from (35),  $|\kappa(0) - \frac{H_1}{\mu_{11}}| \cdot \mu_{11} \leq C_1$ . Using classical results on logistic equation, we deduce the following lower bound

$$\frac{-C_1 - C_2}{\mu_{11}} \leq \kappa(t) - \frac{H_1}{\mu_{11}} = \alpha_1(t), \quad \forall t \leq t_0. \quad (43)$$

Finally, we conclude with inequalities (41), (43), assumption (37) and definitions of  $\mu_{i1}$ : for all  $t \leq t_0$ , for  $i \in \{1, 2\}$

$$\sum_{k=1}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1} A_k^1) \geq \alpha_1(t) \mu_{i1} + \sum_{k=2}^{\infty} \alpha_k(t) \int_{\mathcal{X}} (I_{i1} A_k^1) \geq -(C_1 + C_2) \frac{\mu_{i1}}{\mu_{11}} - C_1 \geq -\frac{C}{2}.$$

This is the contradiction that we wanted to reach, thus,  $t_0 = +\infty$ .

Moreover, Theorem 1.2 guarantees the existence of a limit for  $(g_1(t, \cdot), g_2(t, \cdot))$ . Let us identify that limit. On the one hand, we note that (42) holds for all  $t \geq 0$ , since  $t_0 = +\infty$ , and hence  $\int_{\mathcal{X}} |g_2(t, x)|^2 dx$  tends to 0, as  $t$  approaches infinity.

On the other hand, thanks to the equation (43), which holds for all  $t \geq 0$ , and (37),

$$\begin{aligned} \int_{\mathcal{X}} |g_1(t, x)|^2 dx &\geq \sum_{k=2}^{\infty} \alpha_k(t)^2 \int_{\mathcal{X}} |A_k^1|^2 + \kappa(t)^2 \int_{\mathcal{X}} |A_1^1|^2 \\ &\geq 0 + \left( \frac{H_1 - C_1 - C_2}{\mu_{11}} \right)^2 \int_{\mathcal{X}} |A_1^1|^2 > 0. \end{aligned}$$

Thus, the limit of  $\|g_1(t, \cdot)\|_{\mathbb{L}^2}$  is positive. The limit of the solution is hence the steady state  $(\bar{g}_1, 0)$ .

(1b) Here, we show that if  $H_2 \mu_{11} - H_1 \mu_{21} < 0$  and  $H_1 \mu_{22} - H_2 \mu_{12} < 0$ , the steady state  $(\hat{g}_1, \hat{g}_2)$  is unstable, precisely in any neighborhood of  $(\hat{g}_1, \hat{g}_2)$ , there exists a solution to (1) that does not tend towards  $(\hat{g}_1, \hat{g}_2)$ , but there also exist some solutions that tend towards it.

We use a solution to (1) with an initial condition which belongs to the subspace  $\text{vect}(\hat{g}_1) \times \text{vect}(\hat{g}_2)$ . Let us notice, using the form of the equation (1) satisfied by  $(g_1, g_2)$ , that, if the initial condition belongs to a subspace  $\text{vect}(A_k^1)_{k \in K} \times \text{vect}(A_\ell^2)_{\ell \in L}$  with  $K$  and  $L$  subsets of  $\mathbb{N}$ , then for all  $t \geq 0$ , the solution  $(g_1(t, \cdot), g_2(t, \cdot))$  belongs to that subspace. Thus, for all  $t \geq 0$ ,  $g_1(t, x) = \alpha(t) \hat{g}_1(x)$  and  $g_2(t, x) = \beta(t) \hat{g}_2(x)$ . We get the following system

$$\begin{cases} \frac{d}{dt} \alpha(t) = \alpha(t) \left( H_1 - \mu_{11} \left( \int_{\mathcal{X}} \hat{g}_1 \right) \alpha(t) - \mu_{12} \left( \int_{\mathcal{X}} \hat{g}_2 \right) \beta(t) \right) \\ \frac{d}{dt} \beta(t) = \beta(t) \left( H_2 - \mu_{21} \left( \int_{\mathcal{X}} \hat{g}_1 \right) \alpha(t) - \mu_{22} \left( \int_{\mathcal{X}} \hat{g}_2 \right) \beta(t) \right). \end{cases}$$

We first notice that  $(1, 1)$  is obviously a steady state here. Moreover, the determinant of the Jacobian matrix of the linearized dynamical system at point  $(1, 1)$  is  $(\mu_{11} \mu_{22} - \mu_{12} \mu_{21}) \int_{\mathcal{X}} \hat{g}_1 \int_{\mathcal{X}} \hat{g}_2 < 0$ . So the linearized system around  $(1, 1)$  is hyperbolic. From Hartman-Grobman Theorem (see part 9.3 in [27]) concerning the linearized system, we can conclude that  $(\hat{g}_1, \hat{g}_2)$  is unstable, but that there exists some solutions tending towards it.

(2) It remains to deal with the last uncertain case :  $H_1 > 0$ ,  $H_2 > 0$ ,  $H_2 \mu_{11} - H_1 \mu_{21} < 0$  and  $H_1 \mu_{22} - H_2 \mu_{12} = 0$ . The point (3) where  $H_2 \mu_{11} - H_1 \mu_{21} = 0$  and

$H_1\mu_{22} - H_2\mu_{12} < 0$  can be studied following similar arguments.

Thanks to point (1a), we already know that the steady state  $(\bar{g}_1, 0)$  is stable. We prove that the steady state  $(0, \bar{g}_2)$  is unstable; more precisely, we show that in any neighborhood of  $(0, \bar{g}_2)$ , there exists a solution to (1) that does not tend to  $(0, \bar{g}_2)$  as  $t \rightarrow \infty$ , but there also exist some solutions tending towards it.

To prove that this steady state is unstable, we consider solutions of the form  $(g_1, g_2) = (\alpha(t)A_1^1, \beta(t)A_1^2)$ . The dynamics is then given by the following Lotka-Volterra system

$$\begin{cases} \frac{d}{dt}\alpha(t) = \alpha(t) (H_1 - \mu_{11}\alpha(t) - \mu_{12}\beta(t)), \\ \frac{d}{dt}\beta(t) = \beta(t) (H_2 - \mu_{21}\alpha(t) - \mu_{22}\beta(t)). \end{cases}$$

In view of the conditions on the parameters in this case, any solution with  $\alpha(0) > 0$ , converges to  $(\frac{H_1}{\mu_{11}}, 0)$  (see [10], p.186 Theorem 1(c)) and thus  $(\alpha(t)A_1^1, \beta(t)A_1^2)$  converges to  $(\bar{g}_1, 0)$ . Since one can choose  $\alpha(0)$  and  $\beta(0)$  to make  $(\alpha(0)A_1^1, \beta(0)A_1^2)$  be arbitrarily close to  $(0, \bar{g}_2)$ , we obtain that this point is unstable.

Finally, in order to find a solution that tends towards the steady state, we consider the initial condition  $(g_1^0, g_2^0) = (0, g_2^0)$ , with a nonnegative and non-trivial function  $g_2^0 \in \mathbb{L}^2(\mathcal{X})$ . Then, since for all  $t \geq 0$ ,  $g_1(t, x) = 0$ , it follows from Theorem 1.4 that  $g_2(t, x) \rightarrow \bar{g}_2(x)$  in  $\mathbb{L}^\infty$  as  $t \rightarrow \infty$ .

**4. Numerics.** In this last section, we illustrate the main theorem 1.2 with some numerical examples. The numerics are computed with an algorithm based on finite difference method. Our aim is to illustrate the behavior of mutant individuals that appear in a well established population.

First of all, thanks to Theorem 1.4, we have a mean to compute the principal eigenvalues  $H_i$  when they are positive. In fact, in this case, Theorem 1.4 guarantees that any positive solution to  $\partial_t u = m_i \Delta_x(u) + (a_i - \int_{\mathcal{X}} I_{ii} u)u$  with Neumann boundary conditions tends to the steady state  $\bar{g}_i$ , and

$$H_i = \int_{\mathcal{X}} I_{ii}(x)\bar{g}_i(x)dx. \tag{44}$$

Thus, with the finite difference method, we resolve numerically the previous parabolic equation. After a long time, the solution is stable, so we consider that it has reached the steady state. We calculate then  $H_i$  thanks to the simple formula (44). With same ideas, we can also calculate  $\mu_{i,j}$  for  $i, j \in \{1, 2\}$ . Thus we can check the conditions of Theorem 1.2 for the following numerical examples whose parameters values are given in Figure 5.

Let us now describe our numerical simulations. We consider that the growth rates of the two populations are maximal at two different spatial positions. For instance, the space state can represent a variation of resources, as seed size for some birds, and so the two populations are not best-adapted to same resources. Different values of  $\bar{a}_2$ , the maximum of the growth rate of the mutant population, will be explored,

while the other parameters are fixed,

$$\begin{aligned} \mathcal{X} &= [0, 1], \quad u_1 = 0.3, \quad \bar{a}_1 = 1, \quad u_2 = 0.5, \\ a_i(x) &= \max\{\bar{a}_i(1 - 20(x - u_i)^2), -1\}. \end{aligned} \quad (45)$$

Notice that around the trait  $u_i$ , the growth rate of the population  $i$  is positive but far from this position, it becomes negative. Thus positions around  $u_i$  are favorable for population  $i$ , and we suppose that the intraspecific competition is greater around that position:

$$I_{ii}(x) = \begin{cases} 1, & \text{if } |x - u_i| < 0.25, \\ 0.1, & \text{else.} \end{cases} \quad (46)$$

Then, we define the interspecific competition from the previous kernels by  $I_{12} = I_{21} = \min\{I_{11}, I_{22}\}$ . Finally, we suppose that all individuals move with the same diffusion constant  $m_1 = m_2 = 0.01$ .

As we want to illustrate the invasion of a mutant, we suppose that the initial condition is near  $(\bar{g}_1, 0)$ , as presented in figure 5(a). We resolve numerically the system of parabolic equations (1) and present the solution after a long time, that is, when the densities are almost stable, see figure 5. When  $\bar{a}_2$  is small, the mutant population is

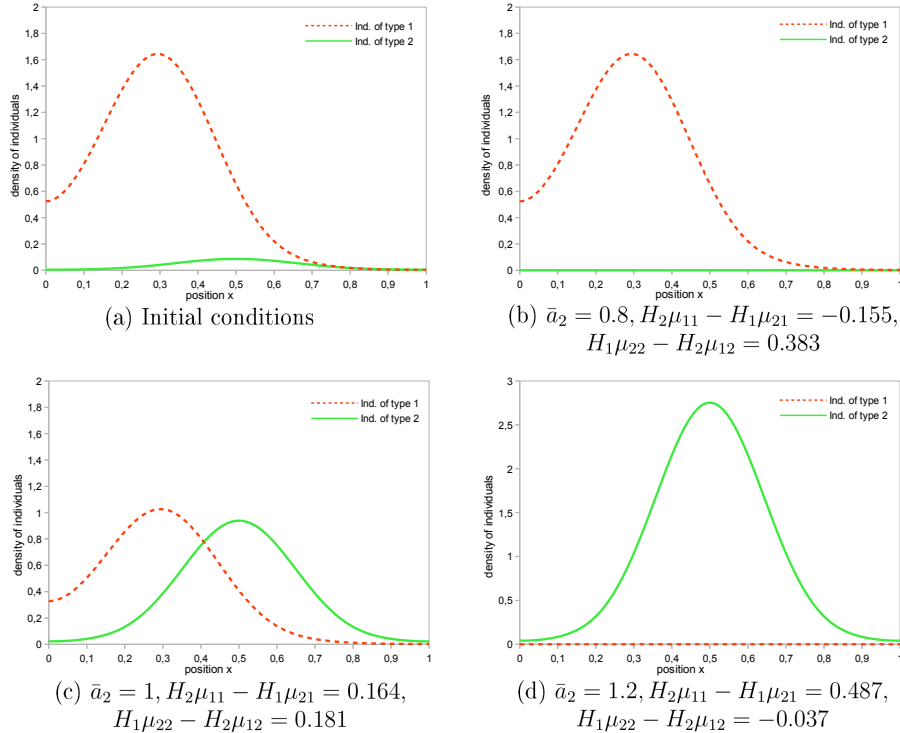


FIGURE 5. The numerical resolution of (1) with parameters given by (45)–(46). (a) presents the densities of each population initially. (b), (c) and (d) present the densities at time  $t = 1000$  for different values of  $\bar{a}_2$ , the red dashed curves represent the density of the resident population and the green continuous curves represent the density of the mutants.

not able to survive (case (b)). But when  $\bar{a}_2$  is large enough, coexistence (case (c))



and even invasion (case (d)) can appear. On the two last cases, the new population that has invaded the space does not live on the same spatial position as the previous one. From an ecological viewpoint, such examples are very interesting because we observe a change of spatial niche due to a selection event.

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