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Adaptation in a heterogeneous environment.

I: Persistence versus extinction*

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Abstract

Understanding how a diversity of plants in agroecosystems affects the adaptation of pathogens is a key issue in agroecology. We analyze PDE systems describing the dynamics of adaptation of two phenotypically structured populations, under the effects of mutation, selection and migration in a two-patches environment, each patch being associated with a different phenotypic optimum. We consider two types of growth functions that depend on the n -dimensional phenotypic trait: either local and linear or nonlocal nonlinear. In both cases, we obtain existence and uniqueness results as well as a characterization of the large-time behaviour of the solution (persistence or extinction) based on the sign of a principal eigenvalue. We show that migration between the two environments decreases the chances of persistence, with in some cases a ‘lethal migration threshold’ above which persistence is not possible. Comparison with stochastic individual-based simulations shows that the PDE approach accurately captures this threshold. Our results illustrate the importance of cultivar mixtures for disease prevention and control.

Keywords: Mutation, selection, migration, heterogeneous environment, persistence, extinction.

MSC 2010: 35B30, 35B40, 35K40, 35Q92, 92D25.

1 Introduction

Phenotypic differences between populations generally appear as a consequence of differential selection regimes [19]. For instance, in the absence of migration, the adaptation of a population to local habitat conditions leads to a particular phenotypic distribution. In asexual populations, a standard way to describe the gene – environment interaction is to use Fisher’s geometrical model (FGM) [16, 24]. In this approach, each individual in the population is characterized by a multivariate phenotype at a set of n traits, *i.e.*, a vector $\mathbf{x} \in \mathbb{R}^n$. This vector \mathbf{x} determines

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the fitness $r(\mathbf{x})$ (the reproductive success of the individual) through its quadratic distance with respect to an optimum $\mathbf{O} \in \mathbb{R}^n$ associated with the considered environment:

$$r(\mathbf{x}) = r_{\max} - \frac{\|\mathbf{x} - \mathbf{O}\|^2}{2},$$

with $r_{\max} > 0$ the fitness of the optimal phenotype. Throughout the paper, $\|\cdot\|$ denotes the Euclidean norm in \mathbb{R}^n .

PDE models. Under the assumption of the FGM, recent models of asexual adaptation based on partial differential equations (PDE) [1, 2, 13] typically describe the dynamics of the phenotype distribution q of a population in a single environment, with equations of the form:

$$\forall t > 0, \forall \mathbf{x} \in \mathbb{R}^n, \quad \partial_t q(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta q(t, \mathbf{x}) + [r(\mathbf{x}) - \bar{r}(t)] q(t, \mathbf{x}),$$

where the Laplace operator describes the mutation effects on the phenotype (see [13, Appendix] for the derivation of this term in this framework), and the term $[r(\mathbf{x}) - \bar{r}(t)] q(t, \mathbf{x})$ describes the effects of selection [25], with $\bar{r}(t) = \int_{\mathbb{R}^n} r(\mathbf{x}) q(t, \mathbf{x}) d\mathbf{x}$ the mean fitness in the population at time t . Extensions to temporally changing environments (with an optimum $\mathbf{O}(t)$) have also been proposed [21]. In all those cases, it was possible to describe the full dynamics of adaptation, by deriving explicit expressions for $\bar{r}(t)$.

Here, we consider a spatially heterogeneous environment, made of two habitats, each of them corresponding to a different phenotype optimum, \mathbf{O}_1 and \mathbf{O}_2 . The main issue that we are going to deal with is to determine the respective effect of the migration between the two habitats and of the phenotypic distance between the two habitats on the faith (persistence or extinction) of the total population. This type of model has already been considered in [18], in a particular regime of parameters such that the effect of the mutation is low, while the mutation rate is large enough, and in dimension $n = 1$. The authors have used a specific method based on constrained Hamilton-Jacobi equations (*e.g.*, [4, 10, 12, 15, 20] for more details on this method), to find an accurate analytic approximation of the equilibrium phenotype distribution and the population size in each habitat. They found that, when the two environments are symmetric (same mutation parameters, same selection pressure, same competition intensity and same migration rates), there exists an explicit threshold for the migration rate, which depends on the phenotypic distance between the two habitats. When the migration rate is above this threshold, the two subpopulations are well-mixed so that the total equilibrium population is monomorphic or 'generalist'. On the contrary, when the migration is below the threshold, the two subpopulations stay different, causing dimorphism in the phenotype density for the global population: the equilibrium population is made of two 'specialists'. They also obtained some results in the general case, without the symmetry assumption.

As we focus here on persistence/extinction issues, instead of dealing with the phenotype distribution $q(t, \mathbf{x})$, we are interested in the *phenotype density* $u(t, \mathbf{x})$, *i.e.*, $u(t, \mathbf{x}) = q(t, \mathbf{x}) N(t)$, with $N(t)$ the population size at time t . We therefore deal with systems of the form:

$$\forall t \geq 0, \forall \mathbf{x} \in \mathbb{R}^n, \quad \begin{cases} \partial_t u_1(t, \mathbf{x}) &= \frac{\mu^2}{2} \Delta u_1(t, \mathbf{x}) + f_1(t, \mathbf{x}, u_1) + \delta [u_2(t, \mathbf{x}) - u_1(t, \mathbf{x})], \\ \partial_t u_2(t, \mathbf{x}) &= \frac{\mu^2}{2} \Delta u_2(t, \mathbf{x}) + f_2(t, \mathbf{x}, u_2) + \delta [u_1(t, \mathbf{x}) - u_2(t, \mathbf{x})], \end{cases} \quad (1)$$

with u_i the phenotype density in the habitat $i \in \{1, 2\}$, $\delta > 0$ the migration rate, and $\mu > 0$ a mutational parameter. Note that the migration and mutation parameters are assumed to be identical in the two habitats. This is a simplifying assumption which leads to symmetry properties of the solutions that are important for our analysis.

We may assume two different types of growth functions f_i . We first state that, in both cases, the fitness of a phenotype \mathbf{x} in the habitat i is given by:

$$r_i(\mathbf{x}) = r_{\max} - \frac{\|\mathbf{x} - \mathbf{O}_i\|^2}{2}, \quad (2)$$

Notice in particular that the fitnesses r_i are unbounded in the phenotypic space \mathbb{R}^n and, since they are involved in the definition of the growth functions f_i for both types listed below, the system (1) of unknowns (u_1, u_2) then has unbounded coefficients.

1. *The first type (Malthusian):*

$$f_i(t, \mathbf{x}, u_i) = r_i(\mathbf{x}) u_i(t, \mathbf{x}), \quad (3)$$

corresponds to the standard assumption of Malthusian population growth:

$$\forall t \geq 0, \quad \begin{cases} N_1'(t) = \bar{r}_1(t) N_1(t) + \delta [N_2(t) - N_1(t)], \\ N_2'(t) = \bar{r}_2(t) N_2(t) + \delta [N_1(t) - N_2(t)], \end{cases} \quad (4)$$

with $N_i(t)$ the population size in habitat i at time t :

$$N_i(t) = \int_{\mathbb{R}^n} u_i(t, \mathbf{x}) d\mathbf{x}, \quad (5)$$

and $\bar{r}_i(t)$ the mean fitness of the individuals located in habitat i at time t :

$$\bar{r}_i(t) = \frac{1}{N_i(t)} \int_{\mathbb{R}^n} r_i(\mathbf{x}) u_i(t, \mathbf{x}) d\mathbf{x}. \quad (6)$$

Note that, with f_i of the type (3), the system (1) is a local cooperative system since the right-hand side of the equation of each component is nondecreasing with respect to the other component, and since the right-hand side only depends on the densities for the phenotype \mathbf{x} . As a consequence, the maximum principle holds for (1) in this first type, that is, if $\mathbf{u} = (u_1, u_2)$ and $\mathbf{v} = (v_1, v_2)$ are two classical solutions of (1) which are locally bounded in time and are such that $\mathbf{u}(0, \cdot) \leq \mathbf{v}(0, \cdot)$ in \mathbb{R}^n (in the sense of componentwise inequalities), then $\mathbf{u}(t, \cdot) \leq \mathbf{v}(t, \cdot)$ in \mathbb{R}^n for all $t > 0$.

2. *The second type (density-dependent):*

$$f_i(t, \mathbf{x}, u_i) = \left(r_i(\mathbf{x}) - \int_{\mathbb{R}^n} u_i(t, \mathbf{y}) d\mathbf{y} \right) u_i(t, \mathbf{x}), \quad (7)$$

corresponds to the standard assumption of logistic population growth:

$$\forall t \geq 0, \quad \begin{cases} N_1'(t) = \bar{r}_1(t) N_1(t) - N_1(t)^2 + \delta [N_2(t) - N_1(t)], \\ N_2'(t) = \bar{r}_2(t) N_2(t) - N_2(t)^2 + \delta [N_1(t) - N_2(t)], \end{cases} \quad (8)$$

with $N_i(t)$ and $\bar{r}_i(t)$ as in (5)-(6). Note that, with f_i of the type (7), the system (1) is a nonlocal cooperative system, the nonlocality in the form of an internal competition. As a consequence, the maximum principle does not hold for (1) in this second type.

In this work, we will mainly focus our attention on the effects of the migration parameter δ and of the *habitat difference* defined by:

$$m_D := \frac{\|\mathbf{O}_1 - \mathbf{O}_2\|^2}{2} > 0. \quad (9)$$

Stochastic model. Before stating our main results, and in order to underline the interest of the PDE approach, we compare its accuracy with a standard Wright-Fisher individual-based stochastic model (IBM), with mutation, selection and migration.

In this IBM, each individual is characterized by a phenotype $\mathbf{x} \in \mathbb{R}^n$, and a corresponding fitness $r_i(\mathbf{x})$, depending on the position (*i.e.*, the habitat $i = 1$ or $i = 2$) of the individual. The populations in the two habitats are initially clonal (with all of the phenotypes set at $(\mathbf{O}_1 + \mathbf{O}_2)/2$), and of size $N_i(0) = N^0$. Then, at each time step (the model is discrete in time), the *reproduction-selection step* is simulated by drawing a Poisson number of offspring, for each individual, with rate $\exp(r_i(\mathbf{x}))$ (Darwinian fitness, the discrete-time counterpart of $r_i(\mathbf{x})$). Then, the *mutation step* is simulated by randomly drawing, for each individual, a Poisson number of mutations, with rate $U > 0$. Each single mutation has a random phenotypic effect $d\mathbf{x} \in \mathbb{R}^n$ drawn into a multivariate Gaussian distribution: $d\mathbf{x} \sim \mathcal{N}(0, \lambda I_n)$, where $\lambda > 0$ is the mutational variance at each trait, and I_n is the identity matrix of size $n \times n$. Multiple mutations in a single individual have additive effects on phenotype. Lastly, the *migration step* consists in sending individuals from the first habitat into the second (*resp.* from the second into the first): the numbers of migrants are drawn in a Poisson law with parameter $\delta N_1(t)$ (*resp.* $\delta N_2(t)$), and the migrants are randomly sampled in the populations.

Numerical comparison between the PDE and stochastic models. We simulated the IBM until a time $t = 300$, and compared the result with the numerical solution of the PDE model (1) with $\mu^2 = \lambda U$ (see [13, Appendix] for a justification of this parameter choice), and with the first type of growth function (Malthusian), as the IBM does not take density-dependence into account. The solution of the PDE was computed using the method of lines coupled with the Runge-Kutta ODE solver Matlab[®] *ode45*. The results are presented in Fig. 1. We observe a very good agreement between the results obtained with the IBM and the PDE, with in both cases a strong dependence of the persistence/extinction behaviour with respect to the parameters δ and m_D .

Aim of this paper. Our main goal is to set on a firm mathematical basis the behaviour observed in Fig. 1, based on the sign of the principal eigenvalue of a system of linear elliptic equations, and to study the dependence of this eigenvalue with respect to the model parameters. The main results are presented in the next section, and discussed in Section 3.

2 Main results

Without loss of generality, we assume that the optima \mathbf{O}_1 and \mathbf{O}_2 are located along the x_1 -axis and are symmetric with respect to the origin, *i.e.*, there exists $\beta > 0$ such that:

$$\mathbf{O}_1 = (-\beta, 0, \dots, 0), \quad \text{and} \quad \mathbf{O}_2 = (\beta, 0, \dots, 0). \quad (10)$$

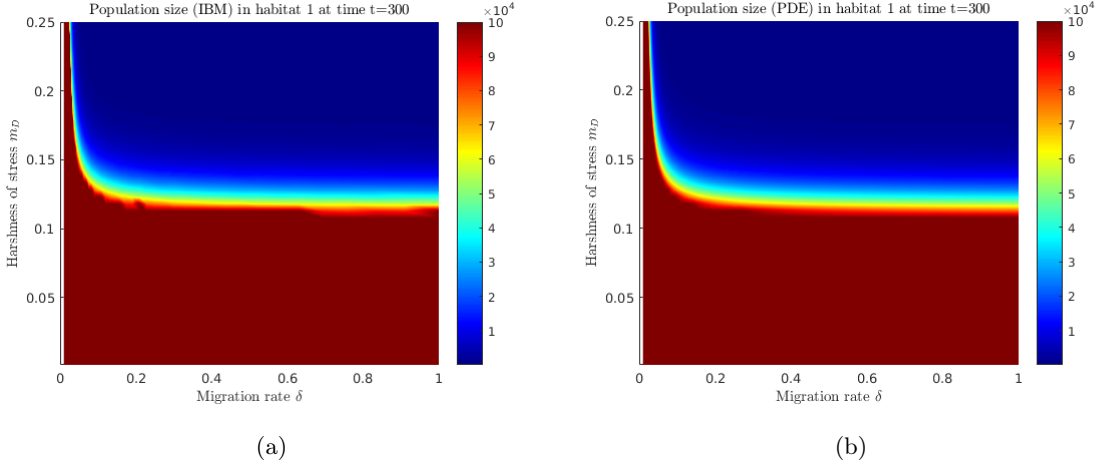


Figure 1 – **Persistence vs extinction: effect of the migration rate δ and the habitat difference m_D .** Total population size $N_1 + N_2$, given (a) by simulation of the stochastic model (average result over 50 replicate simulations) (b) by numerically solving (1) with f_1, f_2 given by (3). The parameters are $U = 1/6$, $\lambda = 1/300$, $n = 2$, $r_{\max} = 1/18$ and $\mu^2 = \lambda U$, and the results are computed at $t = 300$. Initially, each habitat $i \in \{1, 2\}$ has $N^0 = 10^4$ individuals, all of them with the phenotype $(\mathbf{O}_1 + \mathbf{O}_2)/2$.

We also assume that the two densities u_1 and u_2 are initially symmetric with respect to the hyperplane $\{\mathbf{x} = (x_1, \dots, x_n) \in \mathbb{R}^n, x_1 = 0\}$:

$$\forall \mathbf{x} \in \mathbb{R}^n, \quad u_1^0(\mathbf{x}) = u_2^0(\iota(\mathbf{x})) =: u^0(\mathbf{x}), \quad \mathbf{u}^0(\mathbf{x}) := (u_1^0(\mathbf{x}), u_2^0(\mathbf{x})) = (u^0(\mathbf{x}), u^0(\iota(\mathbf{x}))), \quad (\text{SH})$$

with:

$$\forall \mathbf{x} = (x_1, \dots, x_n) \in \mathbb{R}^n, \quad \iota(\mathbf{x}) = (-x_1, x_2, \dots, x_n). \quad (11)$$

The Cauchy problem. We first show that the Cauchy problem associated with (1) admits a unique solution, under some assumptions on the initial condition u^0 given in (SH):

(H1) $u^0 \in C^{2,\alpha}(\mathbb{R}^n)$ for some $\alpha \in (0, 1)$;

(H2) $N^0 := N(0) = \int_{\mathbb{R}^n} u^0(\mathbf{x}) \, d\mathbf{x} > 0$ and $N^0 < +\infty$;

(H3) there exists a nonincreasing function $g: \mathbb{R}_+ \rightarrow \mathbb{R}$ (with $\mathbb{R}_+ = [0, +\infty)$) such that:

(i) $0 \leq u^0(\mathbf{x}) \leq g(\|\mathbf{x} - \mathbf{O}_1\|)$ (and therefore $0 \leq u^0(\iota(\mathbf{x})) \leq g(\|\mathbf{x} - \mathbf{O}_2\|)$) for all $\mathbf{x} \in \mathbb{R}^n$;

(ii) the function $r \mapsto r^{n+1}g(r)$ belongs to $L^1(\mathbb{R}_+)$ and converges to 0 as $r \rightarrow +\infty$.

Hereafter, unless otherwise specified, we always make the assumptions (SH) and (H1)-(H3).

Our first main result provides the existence and uniqueness of the density of phenotypes, for both types (3) and (7) of growth functions f_1, f_2 .

Theorem 2.1. *Assume that f_1, f_2 are either both of the first type (3) or both of the second type (7), and that $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$ satisfies (SH) and (H1)-(H3). Then, there exists a unique solution $\mathbf{u} = (u_1, u_2) \in C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)$ of (1), such that $\mathbf{u} \in L^\infty((0, T) \times \mathbb{R}^n)$ for all $T > 0$, $u_i(t, \mathbf{x}) \rightarrow 0$ as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$, $u_i > 0$ in $(0, +\infty) \times \mathbb{R}^n$, the population sizes*

$N_i : \mathbb{R}_+ \rightarrow (0, +\infty)$ are of class C^1 , the mean fitnesses $\bar{r}_i : \mathbb{R}_+ \rightarrow \mathbb{R}$ are continuous, \mathbf{u} is symmetric in the sense that:

$$u_1(t, \mathbf{x}) = u_2(t, \iota(\mathbf{x})), \quad \text{for all } t \geq 0 \text{ and } \mathbf{x} = (x_1, \dots, x_n) \in \mathbb{R}^n, \quad (12)$$

with ι defined in (11), and:

$$N_1(t) = N_2(t) =: N(t) \quad \text{and} \quad \bar{r}_1(t) = \bar{r}_2(t) =: \bar{r}(t), \quad \text{for all } t \geq 0. \quad (13)$$

Moreover, the population sizes $N_1 = N_2$ satisfy (4) if f_1, f_2 are of the first type (3), whereas $N_1 = N_2$ satisfy (8) if f_1, f_2 are of the second type (7). In both cases, the functions u_i satisfy the nonlocal parabolic equation:

$$\partial_t u_i(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta u_i(t, \mathbf{x}) + f_i(t, \mathbf{x}, u_i) + \delta[u_i(t, \iota(\mathbf{x})) - u_i(t, \mathbf{x})], \quad (14)$$

for all $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$.

Remark 2.2. The existence and uniqueness result of Theorem 2.1 in the first type (3) can easily be extended to the non-symmetric case, *i.e.*, without assumption (SH) (but with initial conditions $\mathbf{u}^0 = (u_1^0, u_2^0)$ such that both functions u_1^0 and u_2^0 still satisfy the assumptions (H1)-(H3)). In that case, the population sizes N_1 and N_2 still satisfy (4) but the N_i and \bar{r}_i do not satisfy (13) in general and the subsequent analysis then becomes more involved. In the second type (7), the existence and uniqueness is established only for symmetric solutions satisfying (12), since the proof, which is based on a change of functions amounting to a system with the first type (3), uses as a key ingredient the equality of the corresponding population sizes.

Persistence vs extinction. Before going further on, we give a precise meaning to the notions of persistence and extinction. By extinction, we mean that the total population size $2N(t) = N_1(t) + N_2(t)$ converges to 0 as $t \rightarrow +\infty$. By persistence, we mean that the population does not get extinct at large times. To analyze the effect of the parameter values on the persistence/extinction behaviour of the system (1), we consider an eigenvalue problem (see [8] for several other examples of persistence/extinction results *via* eigenvalue problems in bounded domains).

For any $R > 0$, we denote by \mathcal{A} the self-adjoint differential operator:

$$\mathcal{A} := -\frac{\mu^2}{2} \Delta - \begin{pmatrix} r_1(\mathbf{x}) - \delta & \delta \\ \delta & r_2(\mathbf{x}) - \delta \end{pmatrix}, \quad (15)$$

acting here on functions in $[W_{loc}^{2,n}(B(0, R)) \cap C_0(\overline{B(0, R)})]^2$, with $B(0, R)$ the open Euclidean ball of \mathbb{R}^n of center 0 and radius $R > 0$, and $C_0(\overline{B(0, R)})$ the space of continuous functions in $\overline{B(0, R)}$ which vanish on $\partial B(0, R)$. It follows from [23, Theorem 1.1] that there exists a unique principal eigenvalue $\lambda^{\delta, R} \geq -r_{\max}$ and a unique (up to multiplication by a positive constant) pair of positive (in $B(0, R)$) eigenfunctions $(\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) \in [W_{loc}^{2,n}(B(0, R)) \cap C_0(\overline{B(0, R)})]^2$, satisfying:

$$\mathcal{A}(\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) = \lambda^{\delta, R}(\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) \quad \text{in } B(0, R).$$

Moreover, the functions $\varphi_i^{\delta, R}$ are of class $C_0^\infty(\overline{B(0, R)}) = C^\infty(\overline{B(0, R)}) \cap C_0(\overline{B(0, R)})$ by standard elliptic estimates, and the eigenvalue $\lambda^{\delta, R}$ is characterized by the following minmax formula:

$$\lambda^{\delta, R} = \sup_{(\psi_1, \psi_2) \in E} \inf_{\mathbf{x} \in B(0, R), i \in \{1, 2\}} \frac{(\mathcal{A}(\psi_1, \psi_2))_i(\mathbf{x})}{\psi_i(\mathbf{x})},$$

with:

$$E = \{(\psi_1, \psi_2) \in [C^2(B(0, R)) \cap C(\overline{B(0, R)})]^2, \psi_i(\mathbf{x}) > 0 \text{ for all } \mathbf{x} \in B(0, R) \text{ and } i \in \{1, 2\}\}.$$

This formula readily implies that the map $R \mapsto \lambda^{\delta, R}$ is nonincreasing. Since $\lambda^{\delta, R} \geq -r_{\max}$, the quantity $\lambda^{\delta, R}$ admits a finite limit as $R \rightarrow +\infty$:

$$\lambda^\delta := \lim_{R \rightarrow +\infty} \lambda^{\delta, R} \geq -r_{\max}. \quad (16)$$

The eigenfunctions $\varphi_1^{\delta, R}$ and $\varphi_2^{\delta, R}$ also satisfy a symmetry property.

Lemma 2.3. (Symmetry property of the eigenfunctions) *For every $R > 0$ and $\delta > 0$, the eigenfunction $(\varphi_1^{\delta, R}, \varphi_2^{\delta, R})$ satisfies $\varphi_i^{\delta, R}(\mathbf{x}) = \varphi_i^{\delta, R}(\iota(\mathbf{x}))$ for all $\mathbf{x} \in \overline{B(0, R)}$, with ι defined in (11).*

Proof. Set $\tilde{\varphi}_1(\mathbf{x}) = \varphi_2^{\delta, R}(\iota(\mathbf{x}))$ and $\tilde{\varphi}_2(\mathbf{x}) = \varphi_1^{\delta, R}(\iota(\mathbf{x}))$ for $\mathbf{x} \in \overline{B(0, R)}$. Then, from the symmetry assumption (10), one has $\mathcal{A}(\tilde{\varphi}_1, \tilde{\varphi}_2) = \lambda^{\delta, R}(\tilde{\varphi}_1, \tilde{\varphi}_2)$. By uniqueness (up to multiplication) of the pair of principal eigenfunctions, there exists $K > 0$ such that $(\tilde{\varphi}_1, \tilde{\varphi}_2) = K(\varphi_1^{\delta, R}, \varphi_2^{\delta, R})$. At $\mathbf{x} = 0$, we get that $\varphi_2^{\delta, R}(0) = \tilde{\varphi}_1(0) = K\varphi_1^{\delta, R}(0)$ and $\varphi_1^{\delta, R}(0) = \tilde{\varphi}_2(0) = K\varphi_2^{\delta, R}(0)$. Therefore $K = 1$ and the result is proved. \square

Thus, we may (and we have to) take the same normalization condition for $\varphi_1^{\delta, R}$ and $\varphi_2^{\delta, R}$. In the proofs, we either assume that $\|\varphi_i^{\delta, R}\|_{L^1(B(0, R))} = 1$ for both $i \in \{1, 2\}$, or $\varphi_i^{\delta, R}(0) = 1$ for both $i \in \{1, 2\}$.

The large time behaviour of the population size is closely related to the sign of the quantity λ^δ defined in (16). We treat separately the first and second types (3) and (7).

Theorem 2.4 (Malthusian growth: blow up vs extinction). *Assume that f_1, f_2 are of the first type (3), let $\delta > 0$ and λ^δ be given by (16). Let \mathbf{u} be the solution of (1) given by Theorem 2.1, with initial condition $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$, and let $N(t) = N_1(t) = N_2(t)$ be its population size in each habitat.*

- (i) *If $\lambda^\delta < 0$, then $N(t) \rightarrow +\infty$ as $t \rightarrow +\infty$ (blow up of the population).*
- (ii) *If $\lambda^\delta = 0$ and if u^0 is compactly supported, then:*

$$\limsup_{t \rightarrow +\infty} N(t) < +\infty \quad (\text{boundedness of the population}).$$

Furthermore, there exist bounded positive stationary solutions of (1) with finite population sizes.

- (iii) *If $\lambda^\delta > 0$ and if u^0 is compactly supported, then $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ (extinction of the population).*

Theorem 2.5 (Logistic growth: persistence vs extinction). *Assume that f_1, f_2 are of the second type (7), let $\delta > 0$ and λ^δ given by (16). Let \mathbf{u} be the solution of (1) given by Theorem 2.1, with initial condition $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$, and let $N(t) = N_1(t) = N_2(t)$ be its population size in each habitat.*

(i) If $\lambda^\delta < 0$, then:

$$0 < \liminf_{t \rightarrow +\infty} N(t) \leq \limsup_{t \rightarrow +\infty} N(t) < +\infty \quad (\text{persistence of the population}), \quad (17)$$

for some initial conditions \mathbf{u}^0 .

(ii) If $\lambda^\delta \geq 0$ and if u^0 is compactly supported, then $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ (extinction of the population).

As a consequence of Theorems 2.4-2.5, the faith of the population is determined by the sign of λ^δ , *i.e.*, by the linear stability of the steady state $\mathbf{u} = (0, 0)$, whether the growth functions f_i be of the first or second type. The main differences between the Malthusian case and the logistic case arise when this steady state $(0, 0)$ is unstable ($\lambda^\delta < 0$). Although persistence occurs with both types of growth functions, the population size remains bounded with type 2 growth functions, due to the nonlocal competition term. We conjecture that it converges to $-\lambda^\delta$, as $t \rightarrow +\infty$. Interestingly, the threshold case $\lambda^\delta = 0$ leads to very different behaviours, depending on the type of growth functions: in the absence of competition (Malthusian growth), persistence is still possible in this case, although it is not in the logistic case. Biologically, however, the particular case $\lambda^\delta = 0$ is presumably not relevant.

Remark 2.6. In part (i) of Theorem 2.5 with $\lambda^\delta < 0$, the initial conditions $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$ such that (17) holds are those which are trapped between two multiples of the principal eigenfunctions associated to the operator \mathcal{A} given by (15) but acting this time on $[W_{loc}^{2,n}(\mathbb{R}^n) \cap C_0(\mathbb{R}^n)]^2$, where $C_0(\mathbb{R}^n)$ is the space of continuous functions in \mathbb{R}^n converging to 0 at infinity. Such eigenfunctions are introduced in Lemma 4.1 below.

In the following results, we now use the above persistence/extinction criteria to study the effect of the parameters, especially the habitat difference m_D given by (9) and the migration rate δ , on the faith of the population.

Proposition 2.7. *The map $\delta \mapsto \lambda^\delta$ is continuous, increasing and concave in $(0, +\infty)$. Moreover,*

$$\lim_{\delta \rightarrow 0^+} \lambda^\delta = -r_{\max} + \frac{\mu n}{2} =: \lambda^0, \quad \text{and} \quad \lim_{\delta \rightarrow +\infty} \lambda^\delta = \frac{m_D}{4} - r_{\max} + \frac{\mu n}{2} =: \lambda^\infty.$$

Two corollaries of Theorems 2.4-2.5 and Proposition 2.7 follow immediately with straightforward proof.

Corollary 2.8. *Assume that $\lambda^0 < 0$, *i.e.*, $r_{\max} > \mu n/2$. Let $\delta > 0$, let \mathbf{u} be the solution of (1) given by Theorem 2.1, with initial condition $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$, and let $N(t) = N_1(t) = N_2(t)$ be its population size in each habitat.*

- (i) *If $\lambda^\infty \leq 0$, *i.e.*, if $m_D \leq 4(r_{\max} - \mu n/2)$, then $\lim_{t \rightarrow +\infty} N(t) = +\infty$ for the first type (3), whereas (17) is satisfied for some initial conditions \mathbf{u}^0 for the second type (7).*
- (ii) *If $\lambda^\infty > 0$, *i.e.*, if $m_D > 4(r_{\max} - \mu n/2)$, then there exists $\delta_{crit} > 0$, independent of $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$, such that:*
 - (ii-a) *if $\delta < \delta_{crit}$, then $\lim_{t \rightarrow +\infty} N(t) = +\infty$ for the first type (3), whereas (17) is satisfied for some initial conditions \mathbf{u}^0 for the second type (7);*

- (ii-b) if $\delta = \delta_{crit}$ and if u^0 is compactly supported, then $\limsup_{t \rightarrow +\infty} N(t) < +\infty$ for the first type (3) and $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ for the second type (7);
- (ii-c) if $\delta > \delta_{crit}$ and if u^0 is compactly supported, then $\lim_{t \rightarrow +\infty} N(t) = 0$ for both types (3) and (7).

Corollary 2.9. *Assume that $\lambda^0 \geq 0$, i.e., $r_{max} \leq \mu n/2$. Let $\delta > 0$, let \mathbf{u} be the solution of (1) given by Theorem 2.1, with initial condition $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$ and u^0 compactly supported, and let $N(t) = N_1(t) = N_2(t)$ be its population size in each habitat. Then $N(t) \rightarrow 0$ as $t \rightarrow +\infty$, for both types (3) and (7).*

An interpretation of Corollary 2.8 is that, when the maximal fitness r_{max} is large enough, namely $r_{max} > \mu n/2$, and the environmental stress m_D is low, namely $m_D \leq 4(r_{max} - \mu n/2)$, the population can adapt to the global environment, whichever migration rate δ . However, when the stress is high, namely $m_D > 4(r_{max} - \mu n/2)$, the population can only survive if the migration rate is low ($\delta \leq \delta_{crit}$). These results are coherent with the numerical simulations of Figure 1. Corollary 2.9 says that, on the other hand, when the maximal fitness is small enough, namely $r_{max} \leq \mu n/2$, the population, if initially compactly supported, can never adapt to the global environment, whichever migration rate δ and environmental stress m_D .

The last result is related to a unification result at each time $t > 0$ in the limit of infinite migration rates δ .

Theorem 2.10. *Let $\mathbf{u}_\delta = (u_{\delta,1}, u_{\delta,2})$ be the solution of (1) given by Theorem 2.1 and Remark 2.2, for growth functions f_1, f_2 of the first type (3), with a fixed initial condition $\mathbf{u}^0 = (u_1^0, u_2^0)$ independent of δ and such that both functions u_1^0 and u_2^0 satisfy the assumptions (H1)-(H3). Then:*

$$\lim_{\delta \rightarrow +\infty} \|u_{\delta,1}(t, \cdot) - u_{\delta,2}(t, \cdot)\|_{L^\infty(\mathbb{R}^n)} = 0, \quad \text{locally uniformly in } t \in (0, +\infty).$$

In other words, a strong migration rate δ unifies the two populations into one global population, since the exchanges between them are very large. The population then goes to be generalist at every time $t > 0$, even if it is not initially.

3 Discussion

On the biological interpretation of the main results. Proposition 2.7 together with Theorems 2.4-2.5 show that the more the two environments are connected by migration (i.e., when δ is increased), the lower are the chances of persistence. In the absence of migration, when the two habitats are not connected ($\delta = 0$), it was already known that persistence occurs if $r_{max} > \mu n/2$ [13, 17], i.e., $\lambda^0 < 0$, whereas $r_{max} < \mu n/2$ leads to extinction (for both types of growth functions). In the case $\delta = 0$, at large times, the mean fitness $\bar{r}(t)$ converges to $r_{max} - \mu n/2$. Thus, $-\mu n/2$ corresponds to the *mutation load*: the amount of maladaptation due to mutations. More precisely, if the mutation load exceeds the fitness of the optimal phenotype r_{max} , the population is doomed to extinction. This corresponds to *lethal mutagenesis* [3].

When δ becomes positive, some individuals migrate between the two environments. Generally these individuals are better adapted to their environment of origin. Thus, as shown by

Proposition 2.7, increasing the migration rate increases the global maladaptation. Ultimately, when $\delta \rightarrow +\infty$, the condition for persistence becomes $\lambda^\infty = -r_{\max} + m_D/4 + \mu n/2 < 0$: in this case, as shown by Theorem 2.10, the two phenotypic populations merge into a single one, centered at the origin, in-between the two optima. We observe that in addition to the mutation load $-\mu n/2$, a *migration load* $-m_D/4$ appears. It is proportional to the habitat difference m_D .

If $\lambda^0 < 0$ and $\lambda^\infty = -r_{\max} + m_D/4 + \mu n/2 > 0$, populations are doomed to extinction for large migration rates, but survive for small migration rates. Corollary 2.8 shows that there exists a migration threshold such that persistence is possible if the migration rate is below this threshold, but not if the migration rate is above this threshold. Thus, increasing the migration rate may imply a 'lethal migration effect', comparable to lethal mutagenesis.

Implications in agroecology. One of the fundamental principles in agroecology is to promote diversified agroecosystems rather than uniform cultures [9, 11]. Some empirical study already illustrated the higher resilience of such diversified agroecosystems [7] to plant diseases. In our case, the two environments can be interpreted as two different types of host plants (different species, or different genetic variants) and the populations of phenotypes u_1 , u_2 describe the density of a pathogen over these two types of host plants. With this interpretation, our study advocates for more diversified cultures, with strong migration of the pathogens between the host plants: it should reduce the chances of persistence of the pathogen over the agroecosystem. This is consistent, therefore, with the above-mentioned principle of plant diversification. However, we point out that this conclusion may not be valid for three environments or more: as discussed in [14], the presence of a third environment associated with a phenotype optimum between the two others may lead to higher chances of persistence of the pathogen, compared to two environments, due to a 'springboard' effect. By now, and up to our knowledge, there is no rigorous mathematical proof of this result.

On the derivation of quantitative estimates. The methods used in our paper do not allow for a computation of the dispersal load: when $\delta = 0$, as discussed above, the mean growth rate $\bar{r}(t)$ converges to $r_{\max} - \mu n/2$. With positive values of δ , it should converge to some value $r_{\max} - \mu n/2 + \text{Load}_{\text{migr}}(\delta)$, with $\text{Load}_{\text{migr}}(\delta) \in (-m_D/4, 0)$, the migration load. The determination of $\text{Load}_{\text{migr}}(\delta)$ would help disentangling the respective effect of mutation and migration on the persistence of a population. Additionally, Theorem 2.10 shows that when the migration rate is increased the two population merge into a single one, which may be qualified as 'generalist'. This is consistent with the results that have been obtained by [18] in the case $n = 1$ with methods based on constrained Hamilton-Jacobi equations. This means that the mean phenotype in each environment converges to $\mathbf{x} = 0$. With smaller migration rates, the two populations should behave as 'specialists', with mean phenotypes that converges to \mathbf{O}_1 and \mathbf{O}_2 respectively as $\delta \rightarrow 0$. In a forthcoming work, using the methods in [13] based on the analysis of moment generating functions associated with the distribution of fitness, we will aim to derive quantitative estimates for the migration load, the lethal migration threshold δ_{crit} and the respective distributions of phenotypes in the two environments.

4 Proofs

This section is devoted to the proofs of the results stated in Section 2. Section 4.1 is devoted to the proof of Theorem 2.1 on the well-posedness of the Cauchy problem (1). Section 4.2 is concerned with the proof of Theorems 2.4-2.5 on the large time behaviour of the population size, and Section 4.3 with the dependence of the fitness of the population with respect to the parameters.

4.1 The Cauchy problem (1)

Proof of Theorem 2.1. We begin by assuming that f_1, f_2 are of the first type (3). As we will see later in the proof, the results in the case where f_1, f_2 are the second type (7) are then straightforward thanks to a change of functions. Note that the proof of the existence and uniqueness of the solution of the Cauchy problem (1) for the first type (3) actually does not require the symmetry property (SH) (but the proof still uses the same sign, smoothness and decay assumptions of each component u_i^0 of the initial condition $\mathbf{u}^0 = (u_1^0, u_2^0)$, and the positivity of the initial population size in each habitat).

So, let us first assume that f_1, f_2 are of the first type (3). Thanks to the assumptions (H1)-(H3) and owing to the definition (2) of the fitnesses r_i , it follows from [6, Theorem 3] that, for any $T > 0$, the Cauchy problem:

$$\begin{cases} \partial_t v_1(t, \mathbf{x}) &= \frac{\mu^2}{2} \Delta v_1(t, \mathbf{x}) + [r_1(\mathbf{x}) - r_{\max}] v_1(t, \mathbf{x}) + \delta[v_2(t, \mathbf{x}) - v_1(t, \mathbf{x})], & t \geq 0, \mathbf{x} \in \mathbb{R}^n, \\ \partial_t v_2(t, \mathbf{x}) &= \frac{\mu^2}{2} \Delta v_2(t, \mathbf{x}) + [r_2(\mathbf{x}) - r_{\max}] v_2(t, \mathbf{x}) + \delta[v_1(t, \mathbf{x}) - v_2(t, \mathbf{x})], & t \geq 0, \mathbf{x} \in \mathbb{R}^n, \\ \mathbf{v}(0, \mathbf{x}) &= \mathbf{u}^0(\mathbf{x}) = (u_1^0(\mathbf{x}), u_2^0(\mathbf{x})), & \mathbf{x} \in \mathbb{R}^n, \end{cases}$$

admits a solution $\mathbf{v} = (v_1, v_2) \in [C^{1,2}([0, T] \times \mathbb{R}^n) \cap L^\infty((0, T) \times \mathbb{R}^n)]^2$, such that $\mathbf{v}(t, \mathbf{x}) \rightarrow (0, 0)$ as $\|\mathbf{x}\| \rightarrow +\infty$ uniformly in $t \in [0, T]$. Thus, the function $\mathbf{u} : (t, \mathbf{x}) \mapsto e^{r_{\max} t} \mathbf{v}(t, \mathbf{x})$, defined in $[0, T] \times \mathbb{R}^n$, is a bounded classical solution of (1) satisfying the same properties as \mathbf{v} . Moreover, this solution is nonnegative (componentwise) from the comparison principle [26, Lemma 1] applied to this linear cooperative system. This maximum principle also yields the uniqueness of this solution \mathbf{u} . Since the initial population density in each habitat is not identically equal to 0 by assumption (H2), the nonnegativity of each component u_i and the strong parabolic maximum principle applied to each linear operator $\partial_t - (\mu^2/2)\Delta - r_i(\mathbf{x}) + \delta$ (for $i \in \{1, 2\}$) yield the positivity of each component u_i in $(0, T] \times \mathbb{R}^n$. As $T > 0$ can be chosen arbitrarily, these existence, uniqueness and positivity results extend to $t \in (0, +\infty)$, with local boundedness in t .

Still for the first type (3), in order to show that the population sizes and mean fitnesses $N_i(t)$ and $\bar{r}_i(t)$ defined by (5)-(6) are real valued, continuous and satisfy (4), we first establish some bounds and, to do so, we construct a super-solution for $\mathbf{u} = (u_1, u_2)$. Let us set, for all $t > 0$ and $\mathbf{x} \in \mathbb{R}^n$:

$$\mathbf{h}(t, \mathbf{x}) := \begin{pmatrix} h_1(t, \mathbf{x}) \\ h_2(t, \mathbf{x}) \end{pmatrix} := e^{(r_{\max} - \delta)t} [K_t * u_1^0](\mathbf{x}) \begin{pmatrix} \cosh(\delta t) \\ \sinh(\delta t) \end{pmatrix} + e^{(r_{\max} - \delta)t} [K_t * u_2^0](\mathbf{x}) \begin{pmatrix} \sinh(\delta t) \\ \cosh(\delta t) \end{pmatrix}, \quad (18)$$

with:

$$\forall t > 0, \forall \mathbf{x} \in \mathbb{R}^n, \quad K_t(\mathbf{x}) = \frac{e^{-\|\mathbf{x}\|^2/(2\mu^2 t)}}{(2\pi\mu^2 t)^{n/2}},$$

and $\mathbf{h}(0, \mathbf{x}) = \mathbf{u}^0(\mathbf{x}) = \mathbf{u}(0, \mathbf{x})$. The function \mathbf{h} is of class $[C^\infty((0, +\infty) \times \mathbb{R}^n) \cap C([0, +\infty) \times \mathbb{R}^n)]^2$, it is locally bounded in time, it converges to $(0, 0)$ as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$, and it satisfies:

$$\partial_t \mathbf{h}(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta \mathbf{h}(t, \mathbf{x}) + \begin{pmatrix} r_{\max} - \delta & \delta \\ \delta & r_{\max} - \delta \end{pmatrix} \mathbf{h}(t, \mathbf{x}),$$

for all $t > 0$ and $\mathbf{x} \in \mathbb{R}^n$. Let $\boldsymbol{\psi}(t, \mathbf{x}) := \mathbf{u}(t, \mathbf{x}) - \mathbf{h}(t, \mathbf{x})$. We see that $\boldsymbol{\psi}(0, \mathbf{x}) = (0, 0)$ for all $\mathbf{x} \in \mathbb{R}^n$, and:

$$\partial_t \boldsymbol{\psi}(t, \mathbf{x}) - \frac{\mu^2}{2} \Delta \boldsymbol{\psi}(t, \mathbf{x}) - \begin{pmatrix} r_{\max} - \delta & \delta \\ \delta & r_{\max} - \delta \end{pmatrix} \boldsymbol{\psi}(t, \mathbf{x}) = \begin{pmatrix} m_1(\mathbf{x}) u_1(t, \mathbf{x}) \\ m_2(\mathbf{x}) u_2(t, \mathbf{x}) \end{pmatrix} \leq \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad (19)$$

for all $t > 0$ and $\mathbf{x} \in \mathbb{R}^n$, with:

$$m_i(\mathbf{x}) := r_i(\mathbf{x}) - r_{\max} = -\frac{\|\mathbf{x} - \mathbf{O}_i\|^2}{2} \leq 0. \quad (20)$$

Again, the comparison principle [26, Lemma 1] implies that $\boldsymbol{\psi} \leq 0$ (componentwise) in $\mathbb{R}_+ \times \mathbb{R}^n$, hence:

$$0 \leq \mathbf{u}(t, \mathbf{x}) \leq \mathbf{h}(t, \mathbf{x}) \quad \text{for all } (t, \mathbf{x}) \in \mathbb{R}_+ \times \mathbb{R}^n. \quad (21)$$

The strong parabolic maximum principle actually implies that the second inequality, as is the first one, is strict in $(0, +\infty) \times \mathbb{R}^n$, as follows from (19) together with the positivity of u_1 and u_2 . Moreover, for $i \in \{1, 2\}$ and $t > 0$,

$$\int_{\mathbb{R}^n} [K_t * u_i^0](\mathbf{x}) \, d\mathbf{x} = \int_{\mathbb{R}^n} u_i^0(\mathbf{x}) \, d\mathbf{x} =: N_i^0 < +\infty.$$

Thus, $\int_{\mathbb{R}^n} h_i(t, \mathbf{x}) \, d\mathbf{x} \leq (N_1^0 + N_2^0) e^{r_{\max} t}$ for all $t > 0$, and, from (21) and the positivity of u_i in $(0, +\infty) \times \mathbb{R}^n$, there holds:

$$0 < N_i(t) = \int_{\mathbb{R}^n} u_i(t, \mathbf{x}) \, d\mathbf{x} \leq (N_1^0 + N_2^0) e^{r_{\max} t}, \quad (22)$$

for all $t > 0$, as well as for $t = 0$ trivially.

Consider now any time $t \geq 0$ and let us prove that $\bar{r}_i(t)$ defined in (6) is finite, for $i \in \{1, 2\}$. First, the hypotheses (H2)-(H3) imply that $\bar{r}_i(0)$ is finite. Assume then that $t > 0$. From (20)-(21) and the positivity of u_i , we have:

$$r_{\max} N_i(t) \geq \int_{\mathbb{R}^n} r_i(\mathbf{x}) u_i(t, \mathbf{x}) \, d\mathbf{x} \geq r_{\max} N_i(t) + \int_{\mathbb{R}^n} m_i(\mathbf{x}) h_i(t, \mathbf{x}) \, d\mathbf{x}. \quad (23)$$

Thus, to show that $\bar{r}_i(t)$ is finite, we only have to show that the last term in the right-hand side of the above equation is finite. First, we note that:

$$0 \leq h_i(t, \cdot) \leq e^{r_{\max} t} K_t * (u_1^0 + u_2^0) \quad \text{in } \mathbb{R}^n. \quad (24)$$

Then, still using the assumption (H3), we have:

$$\begin{aligned}
0 &\leq \int_{\mathbb{R}^n} -m_i(\mathbf{x}) [K_t * u_i^0](\mathbf{x}) \, d\mathbf{x}, \\
&\leq \frac{1}{2(2\pi\mu^2t)^{n/2}} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{x}-\mathbf{y}\|^2/(2\mu^2t)} g(\|\mathbf{y} - \mathbf{O}_i\|) \, d\mathbf{y} \, d\mathbf{x}, \\
&= \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g(\|\mathbf{x} - \mu\sqrt{2t}\mathbf{z} - \mathbf{O}_i\|) \, d\mathbf{z} \, d\mathbf{x}, \\
&\leq \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\|\mathbf{z}\| \leq \|\mathbf{x} - \mathbf{O}_i\|/(2\mu\sqrt{2t})} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g\left(\frac{\|\mathbf{x} - \mathbf{O}_i\|}{2}\right) \, d\mathbf{z} \, d\mathbf{x} \\
&\quad + \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\|\mathbf{z}\| > \|\mathbf{x} - \mathbf{O}_i\|/(2\mu\sqrt{2t})} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g(0) \, d\mathbf{z} \, d\mathbf{x}, \\
&\leq \frac{1}{2\pi^{n/2}} \left[\pi^{n/2} \int_{\mathbb{R}^n} \|\mathbf{x} - \mathbf{O}_i\|^2 g\left(\frac{\|\mathbf{x} - \mathbf{O}_i\|}{2}\right) \, d\mathbf{x} + g(0) \int_{\mathbb{R}^n} \zeta_t(\|\mathbf{x} - \mathbf{O}_i\|) \|\mathbf{x} - \mathbf{O}_i\|^2 \, d\mathbf{x} \right],
\end{aligned}$$

where:

$$\zeta_t(r) := \int_{\|\mathbf{z}\| \geq r/(2\mu\sqrt{2t})} e^{-\|\mathbf{z}\|^2} \, d\mathbf{z} = O(e^{-r}), \quad \text{as } r \rightarrow +\infty. \quad (25)$$

The assumption (H3) thus implies that:

$$0 \leq \int_{\mathbb{R}^n} -m_i(\mathbf{x}) [K_t * u_i^0](\mathbf{x}) \, d\mathbf{x} < +\infty, \quad (26)$$

for every $t > 0$. Let us now check that $-\int_{\mathbb{R}^n} m_i(\mathbf{x}) [K_t * u_j^0](\mathbf{x}) \, d\mathbf{x} < +\infty$ for $i \neq j \in \{1, 2\}$:

$$\begin{aligned}
&\int_{\mathbb{R}^n} -m_i(\mathbf{x}) [K_t * u_j^0](\mathbf{x}) \, d\mathbf{x} \\
&\leq \frac{1}{2(2\pi\mu^2t)^{n/2}} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{x}-\mathbf{y}\|^2/(2\mu^2t)} g(\|\mathbf{y} - \mathbf{O}_j\|) \, d\mathbf{y} \, d\mathbf{x}, \\
&= \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\mathbb{R}^n} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g(\|\mathbf{x} - \mu\sqrt{2t}\mathbf{z} - \mathbf{O}_j\|) \, d\mathbf{z} \, d\mathbf{x}, \\
&\leq \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\|\mathbf{z}\| \leq \|\mathbf{x} - \mathbf{O}_j\|/(2\mu\sqrt{2t})} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g\left(\frac{\|\mathbf{x} - \mathbf{O}_j\|}{2}\right) \, d\mathbf{z} \, d\mathbf{x} \\
&\quad + \frac{1}{2\pi^{n/2}} \int_{\mathbb{R}^n} \int_{\|\mathbf{z}\| > \|\mathbf{x} - \mathbf{O}_j\|/(2\mu\sqrt{2t})} \|\mathbf{x} - \mathbf{O}_i\|^2 e^{-\|\mathbf{z}\|^2} g(0) \, d\mathbf{z} \, d\mathbf{x}, \\
&\leq \frac{1}{2\pi^{n/2}} \left[\pi^{n/2} \int_{\mathbb{R}^n} (2\|\mathbf{x} - \mathbf{O}_j\|^2 + 8\beta^2) g\left(\frac{\|\mathbf{x} - \mathbf{O}_j\|}{2}\right) \, d\mathbf{x} \right. \\
&\quad \left. + g(0) \int_{\mathbb{R}^n} \zeta_t(\|\mathbf{x} - \mathbf{O}_j\|) (2\|\mathbf{x} - \mathbf{O}_j\|^2 + 8\beta^2) \, d\mathbf{x} \right],
\end{aligned}$$

where we recall that β is defined in (10). Thus, (H3) implies that:

$$0 \leq \int_{\mathbb{R}^n} -m_i(\mathbf{x}) [K_t * u_j^0](\mathbf{x}) \, d\mathbf{x} < +\infty. \quad (27)$$

Adding (26) and (27), and using (24), we obtain that:

$$0 \leq \int_{\mathbb{R}^n} -m_i(\mathbf{x}) h_i(t, \mathbf{x}) \, d\mathbf{x} < +\infty,$$

and, together with (23), we infer that $-\infty < \bar{r}_i(t) \leq r_{\max}$ for $i \in \{1, 2\}$ and $t > 0$ (and also for $t = 0$ as already emphasized).

Finally, since the quantities $\zeta_t(r)$ given in (25) are nondecreasing with respect to $t > 0$, the same arguments as above together with Lebesgue's dominated convergence theorem yield the

continuity of the maps $t \mapsto N_i(t)$, $t \mapsto \int_{\mathbb{R}^n} m_i(\mathbf{x}) u_i(t, \mathbf{x}) d\mathbf{x}$ and $t \mapsto \bar{r}_i(t)$, in \mathbb{R}_+ (up to $t = 0$), for $i \in \{1, 2\}$. Now, for any $i \neq j \in \{1, 2\}$, $0 < \varepsilon < t$ and $R > 0$, integrating (1) over $(\varepsilon, t) \times B(0, R)$ yields:

$$\begin{aligned} \int_{B(0,R)} u_i(t, \mathbf{x}) d\mathbf{x} - \int_{B(0,R)} u_i(\varepsilon, \mathbf{x}) d\mathbf{x} &= \frac{\mu^2}{2} \int_{\varepsilon}^t \int_{\partial B(0,R)} \nu \cdot \nabla u_i(s, \mathbf{x}) d\sigma(\mathbf{x}) ds \\ &+ \int_{\varepsilon}^t \int_{B(0,R)} r_i(\mathbf{x}) u_i(s, \mathbf{x}) d\mathbf{x} ds \\ &+ \delta \int_{\varepsilon}^t \int_{B(0,R)} (u_j(s, \mathbf{x}) - u_i(s, \mathbf{x})) d\mathbf{x} ds, \end{aligned}$$

where ν and $d\sigma(\mathbf{x})$ denote the outward normal and surface measure on $\partial B(0, R)$. From (1), (21) and (24), together with (H3) and standard parabolic estimates, it follows that $\|\mathbf{x}\|^{n+1} u_i(s, \mathbf{x}) \rightarrow 0$ and $\|\mathbf{x}\|^{n-1} \|\nabla u_i(s, \mathbf{x})\| \rightarrow 0$ as $\|\mathbf{x}\| \rightarrow +\infty$, uniformly for $s \in [\varepsilon, t]$. Therefore, by passing to the limit $R \rightarrow +\infty$ in the above displayed equality, one gets that:

$$N_i(t) - N_i(\varepsilon) = \int_{\varepsilon}^t \bar{r}_i(s) N_i(s) ds + \delta \int_{\varepsilon}^t (N_j(s) - N_i(s)) ds,$$

where we also used Lebesgue's dominated convergence theorem, formula (20) and the continuity of the map $s \mapsto \int_{\mathbb{R}^n} m_i(\mathbf{x}) u_i(s, \mathbf{x}) d\mathbf{x}$ in \mathbb{R}_+ . Using the continuity of N_i , N_j and \bar{r}_i in \mathbb{R}_+ , the passage to the limit $\varepsilon \rightarrow 0^+$ yields:

$$N_i(t) - N_i(0) = \int_0^t \bar{r}_i(s) N_i(s) ds + \delta \int_0^t (N_j(s) - N_i(s)) ds.$$

Hence, each function N_i is of class $C^1(\mathbb{R}_+)$ and the pair (N_1, N_2) satisfies (4).

We now show the symmetry property of the solutions of (1), still for the first type (3). With (u_1, u_2) given as above and satisfying (SH), it follows that the pair of functions (U_1, U_2) defined by:

$$\forall t \in \mathbb{R}_+, \forall \mathbf{x} \in \mathbb{R}^n, (U_1(t, \mathbf{x}), U_2(t, \mathbf{x})) = (u_2(t, \iota(\mathbf{x})), u_1(t, \iota(\mathbf{x}))),$$

with ι as in (11), is a $C^{1,2}([0, +\infty) \times \mathbb{R}^n)^2$ solution of the Cauchy problem (1). Furthermore, each component U_i is positive in $(0, +\infty) \times \mathbb{R}^n$, bounded in $(0, T) \times \mathbb{R}^n$ for every $T > 0$, and converges to 0 as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$. By uniqueness of such solutions and by (SH), one gets that $U_1(t, \mathbf{x}) = u_1(t, \mathbf{x})$ and $U_2(t, \mathbf{x}) = u_2(t, \mathbf{x})$ for all $(t, \mathbf{x}) \in \mathbb{R}_+ \times \mathbb{R}^n$, and so $u_1(t, \mathbf{x}) = u_2(t, \iota(\mathbf{x}))$. The equation (14) then readily follows from this equality. Moreover the population sizes at time $t \geq 0$ satisfy:

$$N_1(t) = \int_{\mathbb{R}^n} u_1(t, \mathbf{x}) d\mathbf{x} = \int_{\mathbb{R}^n} u_2(t, \mathbf{x}) d\mathbf{x} = N_2(t),$$

and the mean fitnesses are also such that $\bar{r}_1(t) = \bar{r}_2(t)$ for all $t \geq 0$.

In order to complete the proof of Theorem 2.1, we now derive an equivalence between the problem (1) in the symmetric case with f_1, f_2 of the first type (3), and the problem (1) with f_1, f_2 of the second type (7), still in the symmetric case. Firstly, assume that f_1, f_2 are of the first type (3), and let u_i, N_i and \bar{r}_i be defined by the first part of the present proof, for $i \in \{1, 2\}$. From (SH) and the previous paragraph, we know that $\bar{r}_1(t) = \bar{r}_2(t) =: \bar{r}(t)$ and $N_1(t) = N_2(t) =: N(t) > 0$, with $N'(t) = \bar{r}(t) N(t)$, for all $t \geq 0$. Let $\tilde{N}(t)$ be the solution of the ODE:

$$\tilde{N}'(t) = \bar{r}(t) \tilde{N}(t) - \tilde{N}(t)^2,$$

with $\tilde{N}(0) = N(0) > 0$. Since \bar{r} is continuous in \mathbb{R}_+ , the function \tilde{N} is well defined, positive, and of class C^1 in \mathbb{R}_+ . Define, for $i \in \{1, 2\}$, the functions:

$$\forall t \in \mathbb{R}_+, \forall \mathbf{x} \in \mathbb{R}^n, \quad \tilde{u}_i(t, \mathbf{x}) = \frac{\tilde{N}(t)}{N(t)} u_i(t, \mathbf{x}),$$

where the functions u_i are recalled to satisfy (1) with f_1, f_2 of the first type (3). The pair $(\tilde{u}_1, \tilde{u}_2)$ is of class $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)^2$, it is locally bounded in time, it converges to $(0, 0)$ as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$, and it has the same initial condition as the pair (u_1, u_2) . Moreover, for all $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$, we have:

$$\frac{\tilde{N}(t)}{N(t)} \partial_t u_i(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta \tilde{u}_i(t, \mathbf{x}) + r_i(\mathbf{x}) \tilde{u}_i(t, \mathbf{x}) + \delta [\tilde{u}_j(t, \mathbf{x}) - \tilde{u}_i(t, \mathbf{x})],^1$$

and:

$$\begin{aligned} \partial_t \tilde{u}_i(t, \mathbf{x}) &= \frac{\tilde{N}(t)}{N(t)} \partial_t u_i(t, \mathbf{x}) + \left(\frac{\tilde{N}'(t) N(t) - \tilde{N}(t) N'(t)}{N^2(t)} \right) u_i(t, \mathbf{x}), \\ &= \frac{\tilde{N}(t)}{N(t)} \partial_t u_i(t, \mathbf{x}) - \frac{\tilde{N}(t)^2}{N(t)} u_i(t, \mathbf{x}) = \frac{\tilde{N}(t)}{N(t)} \partial_t u_i(t, \mathbf{x}) - \tilde{N}(t) \tilde{u}_i(t, \mathbf{x}). \end{aligned}$$

The functions \tilde{u}_i thus satisfy (with $i, j \in \{1, 2\}$ and $i \neq j$):

$$\partial_t \tilde{u}_i(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta \tilde{u}_i(t, \mathbf{x}) + [r_i(\mathbf{x}) - \tilde{N}(t)] \tilde{u}_i(t, \mathbf{x}) + \delta [\tilde{u}_j(t, \mathbf{x}) - \tilde{u}_i(t, \mathbf{x})],$$

for all $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$, and, as:

$$\int_{\mathbb{R}^n} \tilde{u}_i(t, \mathbf{x}) \, d\mathbf{x} = \tilde{N}(t),$$

for all $t \geq 0$ and $i \in \{1, 2\}$, the functions \tilde{u}_i then solve (1), with f_1, f_2 of the second type (7). These solutions \tilde{u}_i are also symmetric, in the sense that $\tilde{u}_1(t, \mathbf{x}) = \tilde{u}_2(t, \iota(\mathbf{x}))$ for all $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$, and they are positive in $(0, +\infty) \times \mathbb{R}^n$. Notice finally that:

$$\tilde{r}(t) := \frac{1}{\tilde{N}(t)} \int_{\mathbb{R}^n} r_i(\mathbf{x}) \tilde{u}_i(t, \mathbf{x}) \, d\mathbf{x} = \bar{r}(t),$$

for all $t \geq 0$ and $i \in \{1, 2\}$.

Conversely, assume that $(\tilde{u}_1, \tilde{u}_2)$ is a symmetric $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)^2$ locally bounded in time solution of (1) and converging to $(0, 0)$ as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$, with f_1, f_2 of the second type (7) and with a continuous associated population size $\tilde{N}(t)$ in each habitat, such that $\tilde{N}(0) > 0$. Since the system satisfied by $(\tilde{u}_1, \tilde{u}_2)$ can also be viewed as a linear cooperative system (with additional diagonal term $-\tilde{N}_i(t) \tilde{u}_i(t, x)$), the weak and strong comparison principle applied with respect to the trivial solution $(0, 0)$ imply that the functions \tilde{u}_i are then positive in $(0, +\infty) \times \mathbb{R}^n$. Therefore, the population size $\tilde{N}(t)$ is positive and $f_i(t, \mathbf{x}, \tilde{u}_i) \leq r_i(\mathbf{x}) \tilde{u}_i(t, \mathbf{x})$ for all $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$. As a consequence, the pair $(\tilde{u}_1, \tilde{u}_2)$ is then a subsolution of the cooperative system (1) with growth functions of the first type (3). Since the maximum principle holds for the latter system, one infers that the functions \tilde{u}_i satisfy similar bounds as (21) and (24) above for the solutions u_i in the first type (3). By arguing as above, it follows that the mean fitness

1. We use in the last term the fact that the proportionality factor between \tilde{u}_i and u_i is the same for $i \in \{1, 2\}$.

$t \mapsto \tilde{r}(t) = \tilde{N}(t)^{-1} \int_{\mathbb{R}^n} r_i(\mathbf{x}) \tilde{u}_i(t, \mathbf{x}) d\mathbf{x}$ is continuous in \mathbb{R}_+ and independent of $i \in \{1, 2\}$, and that population size \tilde{N} is of class $C^1(\mathbb{R}_+)$ and satisfies (8) (due to the additional term $-\tilde{N}(t) \tilde{u}_i(t, \mathbf{x})$ in the right-hand side of the equation satisfied by \tilde{u}_i). Finally, by inverting all the calculations of the previous paragraph and by defining $N(t)$ as the solution of $N'(t) = \tilde{r}(t) N(t)$ with $N(0) = \tilde{N}(0)$, one gets that the pair (u_1, u_2) defined by:

$$\forall t \in \mathbb{R}_+, \forall \mathbf{x} \in \mathbb{R}^n, \quad u_i(t, \mathbf{x}) = \frac{N(t)}{\tilde{N}(t)} \tilde{u}_i(t, \mathbf{x}),$$

is a symmetric solution of (1) satisfying the conditions of Theorem 2.1 with growth functions f_1, f_2 of the first type (3). The uniqueness result for the solutions in the first type (3) then leads to the uniqueness of the symmetric solutions of (1) for growth functions of the second type (7). The proof of Theorem 2.1 is thereby complete. \square

4.2 Large time behaviour

This section is devoted to the proof of Theorems 2.4-2.5. Before that, we state an auxiliary lemma on the existence of positive eigenfunctions of the operator \mathcal{A} defined in (15).

Lemma 4.1. *There exists a pair of symmetric positive eigenfunctions $(\varphi_1^\delta, \varphi_2^\delta) \in [C_0^\infty(\mathbb{R}^n) \cap L^1(\mathbb{R}^n)]^2$ such that $\mathcal{A}(\varphi_1^\delta, \varphi_2^\delta) = \lambda^\delta(\varphi_1^\delta, \varphi_2^\delta)$ in \mathbb{R}^n , with \mathcal{A} defined by (15) and λ^δ by (16). Furthermore, this pair $(\varphi_1^\delta, \varphi_2^\delta)$ is unique up to multiplication by a positive constant.*

The proof of Lemma 4.1 is postponed after that of Theorem 2.4.

Proof of Theorem 2.4. Let $\mathbf{u} = (u_1, u_2)$ be the solution of (1) given by Theorem 2.1 with an initial condition $\mathbf{u}^0 = (u^0, u^0 \circ \iota)$ satisfying (SH) and (H1)-(H3), for f_1, f_2 of the first type (3). Recall that the symmetry of the problem implies that $N_1(t) = N_2(t) =: N(t)$ for all $t \geq 0$. For $R > 0$, let $(\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) \in C_0^\infty(\overline{B(0, R)})^2$ and $\lambda^{\delta, R}$ be the principal eigenfunctions and eigenvalue of the operator \mathcal{A} defined by (15). Finally, let λ^δ be given by (16). We consider the cases $\lambda^\delta < 0$ and $\lambda^\delta \geq 0$ separately, with λ^δ given by (15).

First case: Assume that $\lambda^\delta < 0$. From assumptions (H2)-(H3), we know that $u^0 \geq 0$ and $u^0 \not\equiv 0$ in \mathbb{R}^n and, from Theorem 2.1, $u_i(1, \cdot) > 0$ in \mathbb{R}^n for each $i \in \{1, 2\}$. As $\lim_{R \rightarrow +\infty} \lambda^{\delta, R} = \lambda^\delta < 0$, we can fix $R > 0$ such that $\lambda^{\delta, R} < 0$. Let $\underline{K} > 0$ be such that $\underline{K} e^{-\lambda^{\delta, R} t} (\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) \leq \mathbf{u}(1, \cdot)$ in $\overline{B(0, R)}$. Set $\underline{H}(t, \mathbf{x}) = (\underline{H}_1, \underline{H}_2)(t, \mathbf{x}) := \underline{K} e^{-\lambda^{\delta, R} t} (\varphi_1^{\delta, R}(\mathbf{x}), \varphi_2^{\delta, R}(\mathbf{x}))$ for $t \geq 1$ and $\mathbf{x} \in \overline{B(0, R)}$. In particular, $\underline{H}(1, \cdot) \leq \mathbf{u}(1, \cdot)$ in $\overline{B(0, R)}$. We have, for all $t \geq 1$, and $i \neq j \in \{1, 2\}$,

$$\partial_t \underline{H}_i = \frac{\mu^2}{2} \Delta \underline{H}_i + r_i(\mathbf{x}) \underline{H}_i + \delta (\underline{H}_j - \underline{H}_i) \text{ in } \overline{B(0, R)} \text{ and } (\underline{H}_1, \underline{H}_2)(t, \cdot) = (0, 0) \text{ on } \partial B(0, R). \quad (28)$$

As the pair $(u_1(t, \cdot), u_2(t, \cdot))$ satisfies the same equation in $\overline{B(0, R)}$ and is positive in \mathbb{R}^n for each $t \geq 1$ and therefore on $\partial B(0, R)$, the maximum principle applied to this cooperative system implies that $u_i(t, \mathbf{x}) \geq \underline{H}_i(t, \mathbf{x})$ for all $t \geq 1$, $\mathbf{x} \in \overline{B(0, R)}$ and $i \in \{1, 2\}$. Integrating over $B(0, R)$ the above inequality and using the positivity of u_i , we get:

$$N(t) \geq \underline{K} e^{-\lambda^{\delta, R} t} \|\varphi_i^{\delta, R}\|_{L^1(B(0, R))}, \text{ for all } t \geq 1 \text{ and } i \in \{1, 2\}.$$

Since $\lambda^{\delta, R} < 0$, this implies that $N(t) \rightarrow +\infty$ as $t \rightarrow +\infty$ and this shows part (i) of Theorem 2.4.

Second case: Assume that $\lambda^\delta \geq 0$. Assume also that the initial condition u^0 is compactly supported. Then, there is $\bar{K} > 0$ large enough, one has $\bar{K}(\varphi_1^\delta, \varphi_2^\delta) \geq \mathbf{u}(0, \cdot)$ in \mathbb{R}^n . Set $\bar{H}(t, \mathbf{x}) = (\bar{H}_1, \bar{H}_2)(t, \mathbf{x}) := \bar{K} e^{-\lambda^\delta t}(\varphi_1^\delta(\mathbf{x}), \varphi_2^\delta(\mathbf{x}))$ for $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$. As for (28), the function \bar{H} satisfies the same cooperative system (1) as \mathbf{u} in $\mathbb{R}_+ \times \mathbb{R}^n$, but with a larger initial condition. The comparison principle thus implies that, for $i \in \{1, 2\}$ and $t \geq 0$:

$$0 \leq u_i(t, \mathbf{x}) \leq \bar{H}_i(t, \mathbf{x}) = \bar{K} e^{-\lambda^\delta t} \varphi_i^\delta(\mathbf{x}), \quad \text{for all } \mathbf{x} \in \mathbb{R}^n. \quad (29)$$

As the functions φ_i^δ belong to $L^1(\mathbb{R}^n)$, integrating (29) over \mathbb{R}^n yields $\lim_{t \rightarrow +\infty} N(t) = 0$ if $\lambda^\delta > 0$. If $\lambda^\delta = 0$, (29) implies that:

$$\limsup_{t \rightarrow +\infty} N(t) < +\infty.$$

Furthermore, in that case, for every $C > 0$, $C(\varphi_1^\delta, \varphi_2^\delta)$ is a pair of positive stationary solutions of (1). That shows parts (ii) and (iii) of Theorem 2.4 and the proof of Theorem 2.4 is thereby complete. \square

Proof of Lemma 4.1. For $R > 0$, the functions $(\varphi_1^{\delta, R}, \varphi_2^{\delta, R}) \in C_0^\infty(\overline{B(0, R)})^2$ satisfy:

$$\frac{\mu^2}{2} \Delta \varphi_i^{\delta, R} + (\lambda^{\delta, R} - \delta + r_i) \varphi_i^{\delta, R} + \delta \varphi_j^{\delta, R} = 0 \quad \text{in } \overline{B(0, R)},$$

with $i \neq j \in \{1, 2\}$. As the eigenvalues $\lambda^{\delta, R}$ are nonincreasing with respect to R and not smaller than $-r_{\max}$, we have $-r_{\max} \leq \lambda^{\delta, R} \leq \lambda^{\delta, 2}$ for all $R \geq 2$. For every $R' \geq 1$, it then follows from the Harnack inequality in [22, Theorem 2] (applied here with $\Omega = B(0, 2R')$) that there is a positive constant $C(R')$ such that:

$$\max_{\mathbf{x} \in \overline{B(0, R')}, i \in \{1, 2\}} \varphi_i^{\delta, R}(\mathbf{x}) \leq C(R') \min_{\mathbf{x} \in \overline{B(0, R')}, i \in \{1, 2\}} \varphi_i^{\delta, R}(\mathbf{x}),$$

for all $R \geq 2R'$. Without loss of generality, we assume the normalization condition $\varphi_i^{\delta, R}(0) = 1$ (recall that $\varphi_1^{\delta, R}(0) = \varphi_2^{\delta, R}(0)$ by the symmetry property of Lemma 2.3). Thus, we get:

$$0 < \varphi_i^{\delta, R}(\mathbf{x}) \leq C(R'), \quad \text{for all } \mathbf{x} \in \overline{B(0, R')}, \quad i \in \{1, 2\}, \quad \text{and } R \geq 2R' \geq 2.$$

Standard elliptic estimates then imply that, for every $\theta \in [0, 1)$, and for every $R' \geq 1$, the functions $\varphi_i^{\delta, R}$ are bounded in $C^{2, \theta}(\overline{B(0, R')})$, independently of $R \in [2R', +\infty)$. Thus Sobolev's injections imply that, up to the extraction of a subsequence, $\varphi_i^{\delta, R} \rightarrow \varphi_i^\delta$ in $C_{loc}^2(\mathbb{R}^n)$ as $R \rightarrow +\infty$, where the functions φ_i^δ satisfy $\mathcal{A}(\varphi_1^\delta, \varphi_2^\delta) = \lambda^\delta(\varphi_1^\delta, \varphi_2^\delta)$, are nonnegative and such that $\varphi_i^\delta(0) = 1$ for $i \in \{1, 2\}$. From the (scalar) strong elliptic maximum principle, the functions φ_i^δ are positive in \mathbb{R}^n . Furthermore, they satisfy the same symmetry property as the functions $\varphi_i^{\delta, R}$, and, again from standard elliptic estimates, they are of class $C^\infty(\mathbb{R}^n)$.

To show that the eigenfunctions φ_i^δ are in $L^1(\mathbb{R}^n)$ and converge to 0 at infinity, we use the fact that the potentials r_i are confining. In particular, we fix $R'_0 \geq 1$ large enough such that, all $R \geq 2R'_0$, there holds $\lambda^{\delta, R} + r_i(\mathbf{x}) < -\|\mathbf{x}\|^2/4$ for all $\mathbf{x} \in \overline{B(0, R)} \setminus B(0, R'_0)$ and $i \in \{1, 2\}$, hence:

$$-\frac{\mu^2}{2} \Delta(\varphi_1^{\delta, R} + \varphi_2^{\delta, R})(\mathbf{x}) + \frac{\|\mathbf{x}\|^2}{4} (\varphi_1^{\delta, R} + \varphi_2^{\delta, R})(\mathbf{x}) < 0 \quad \text{in } \overline{B(0, R)} \setminus B(0, R'_0).$$

For any such R , since $\max_{\partial B(0, R'_0)} \varphi_i^{\delta, R} \leq C(R'_0)$ and $\varphi_1^{\delta, R} + \varphi_2^{\delta, R} = 0$ on $\partial B(0, R)$, the maximum principle implies that $\varphi_1^{\delta, R} + \varphi_2^{\delta, R} \leq w$ in $\overline{B(0, R)} \setminus B(0, R'_0)$, where w denotes the solution of the equation $-(\mu^2/2)\Delta w(\mathbf{x}) + (\|\mathbf{x}\|^2/4)w(x) = 0$ in $\overline{B(0, R)} \setminus B(0, R'_0)$ with the boundary conditions $w = 0$ on $\partial B(0, R)$ and $w = 2C(R'_0)$ on $\partial B(0, R'_0)$. Consequently,

$$\varphi_1^{\delta, R}(x) + \varphi_2^{\delta, R}(x) \leq w(x) \leq 2C(R'_0) e^{(R_0'^2 - \|\mathbf{x}\|^2)/\sqrt{8\mu^2}}, \quad \text{for all } \mathbf{x} \in \overline{B(0, R)} \setminus B(0, R'_0),$$

and for all $R \geq 2R'_0$. Thus, the same inequality holds for the functions $\varphi_1^\delta + \varphi_2^\delta$ in $\mathbb{R}^n \setminus B(0, R'_0)$. This implies in particular that the eigenfunctions φ_i^δ belong to $L^1(\mathbb{R}^n)$ and converge to 0 at infinity.

Lastly, since for any $\lambda \in \mathbb{R}$ the weak maximum principle holds outside a large ball for the system $\mathcal{A}(\varphi_1, \varphi_2) = \lambda(\varphi_1, \varphi_2)$ in the class of $C_0^2(\mathbb{R}^n)$ functions (namely, there is $\rho > 0$ such that, if $\varphi_1, \varphi_2 \in C_0^2(\mathbb{R}^n)$ satisfy $\mathcal{A}(\varphi_1, \varphi_2) \leq \lambda(\varphi_1, \varphi_2)$ in $\mathbb{R}^n \setminus B(0, \rho)$ and $(\varphi_1, \varphi_2) \leq (0, 0)$ on $\partial B(0, \rho)$, then $(\varphi_1, \varphi_2) \leq (0, 0)$ in $\mathbb{R}^n \setminus B(0, \rho)$) and since the strong maximum principle holds as well in any connected open subset $\Omega \subset \mathbb{R}^n$ (namely, if $\varphi_1, \varphi_2 \in C^2(\Omega)$ are such that $\mathcal{A}(\varphi_1, \varphi_2) \leq \lambda(\varphi_1, \varphi_2)$ and $(\varphi_1, \varphi_2) \leq (0, 0)$ in Ω with $\varphi_i(x_0) = 0$ for some $i \in \{1, 2\}$ and $x_0 \in \Omega$, then $(\varphi_1, \varphi_2) \equiv (0, 0)$ in Ω), it follows with similar arguments as in [5] that the pair of eigenfunctions $(\varphi_1^\delta, \varphi_2^\delta)$ constructed above is unique, up to multiplication by a positive constant, in the class of $C_0^2(\mathbb{R}^n)$ eigenfunctions. Moreover, the eigenvalue λ^δ is the unique eigenvalue associated with a pair of positive eigenfunctions. The proof of Lemma 4.1 is thereby complete. \square

Proof of Theorem 2.5. Let $\mathbf{u} = (u_1, u_2)$ be the unique symmetric solution of (1) given by Theorem 2.1, for f_1, f_2 of the second type (7). Let $N(t) := N_1(t) = N_2(t)$ be its population size given by (5) and $\bar{r}(t) := \bar{r}_1(t) = \bar{r}_2(t)$ be its mean fitness given by (6), at each time $t \geq 0$. From Theorem 2.1, the densities u_i are positive in $(0, +\infty) \times \mathbb{R}^n$, the function \bar{r} is continuous in \mathbb{R}_+ , the function N is positive and of class C^1 in \mathbb{R}_+ , and $N'(t) = \bar{r}(t)N(t) - N(t)^2$ for all $t \in \mathbb{R}_+$.

Let also $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2)$ be the unique symmetric solution of (1) given by Theorem 2.1, for f_1, f_2 of the first type (3), with the same initial condition \mathbf{u}^0 as \mathbf{u} . Let $\tilde{N}(t) := \tilde{N}_1(t) = \tilde{N}_2(t)$ be its population size and $\tilde{r}(t) := \tilde{r}_1(t) = \tilde{r}_2(t)$ be its mean fitness, at each time $t \geq 0$. From Theorem 2.1, the densities \tilde{u}_i are positive in $(0, +\infty) \times \mathbb{R}^n$, the function \tilde{r} is continuous in \mathbb{R}_+ , the function \tilde{N} is positive and of class C^1 in \mathbb{R}_+ , and $\tilde{N}'(t) = \tilde{r}(t)\tilde{N}(t)$ for all $t \in \mathbb{R}_+$.

The correspondence between the symmetric solutions of (1) for both types (3) and (7), shown in the last part of the proof of Theorem 2.1, implies that:

$$\tilde{\mathbf{u}}(t, \mathbf{x}) = \frac{\tilde{N}(t)}{N(t)} \mathbf{u}(t, \mathbf{x}), \quad \text{for all } t \geq 0 \text{ and } \mathbf{x} \in \mathbb{R}^n,$$

hence $\tilde{r}(t) = \bar{r}(t)$ for all $t \geq 0$. Therefore, we have:

$$\frac{\tilde{N}'(t)}{\tilde{N}(t)} = \frac{N'(t)}{N(t)} + N(t),$$

for all $t \geq 0$. Integrating this equality and using $\tilde{N}(0) = N(0)$ yields:

$$N(t) = \frac{\tilde{N}(t)}{1 + \int_0^t \tilde{N}(s) ds}, \quad \text{for all } t \geq 0. \quad (30)$$

Let now $(\varphi_1^\delta, \varphi_2^\delta)$ be defined by Lemma 4.1 with the normalization $\|\varphi_i^\delta\|_{L^1(\mathbb{R}^n)} = 1$. Set:

$$H(t, \mathbf{x}) = (H_1(t, \mathbf{x}), H_2(t, \mathbf{x})) := e^{-\lambda^\delta t} (\varphi_1^\delta(\mathbf{x}), \varphi_2^\delta(\mathbf{x})),$$

for $t \geq 0$ and $\mathbf{x} \in \mathbb{R}^n$. As in the proof of Theorem 2.4, the function H satisfies (1) with growth functions f_i of the first type (3). We then treat separately the cases $\lambda^\delta \geq 0$ and $\lambda^\delta < 0$.

First case: Assume that $\lambda^\delta \geq 0$. Assume also in this case that \mathbf{u}^0 is compactly supported. Then there is $K > 0$ such that $\tilde{\mathbf{u}}(0, \cdot) = \mathbf{u}(0, \cdot) = \mathbf{u}^0 \leq K H(0, \cdot)$ in \mathbb{R}^n and the maximum principle applied to the cooperative system (1) with growth functions of the first type (3) implies that $\tilde{\mathbf{u}}(t, \cdot) \leq K H(t, \cdot)$ in \mathbb{R}^n for all $t \geq 0$, hence $\tilde{N}(t) \leq K e^{-\lambda^\delta t}$ for all $t \geq 0$. From (30) and the positivity of N and \tilde{N} , one immediately infers that $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ if $\lambda^\delta > 0$.

Consider now the sub-case $\lambda^\delta = 0$. The previous observations imply that \tilde{N} is bounded in \mathbb{R}_+ . Furthermore, on the one hand, if the integral $\int_0^{+\infty} \tilde{N}(s) ds$ diverges, then formula (30) and the boundedness of \tilde{N} imply that $N(t) \rightarrow 0$ as $t \rightarrow +\infty$. On the other hand, if the integral $\int_0^{+\infty} \tilde{N}(s) ds$ converges, then the boundedness of the function $\tilde{N}' = \tilde{r} \tilde{N}$ in \mathbb{R}_+ (which itself follows from the inequalities $0 \leq \tilde{\mathbf{u}}(t, \cdot) \leq K H(t, \cdot) = K (\varphi_1^\delta, \varphi_2^\delta)$ in \mathbb{R}^n and the exponential decay at infinity of the eigenfunctions φ_i^δ given the proof of Lemma 4.1) implies that $\tilde{N}(t) \rightarrow 0$ as $t \rightarrow +\infty$, and finally $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ by (30).

Second case: Assume that $\lambda^\delta < 0$. Assume also in this case that \mathbf{u}^0 is trapped between two positive multiples of the eigenfunctions $(\varphi_1^\delta, \varphi_2^\delta)$, namely, there exist $0 < K_1 \leq K_2$ such that:

$$K_1 (\varphi_1^\delta, \varphi_2^\delta) \leq \mathbf{u}^0 \leq K_2 (\varphi_1^\delta, \varphi_2^\delta) \quad \text{in } \mathbb{R}^n.$$

Thus, $K_1 H(0, \cdot) \leq \tilde{\mathbf{u}}(0, \cdot) = \mathbf{u}^0 \leq K_2 H(0, \cdot)$ in \mathbb{R}^n and the maximum principle applied to the cooperative system (1) with growth functions of the first type (3) implies that:

$$K_1 H(t, \cdot) \leq \tilde{\mathbf{u}}(t, \cdot) \leq K_2 H(t, \cdot) \quad \text{in } \mathbb{R}^n, \text{ for all } t \geq 0.$$

In particular, $K_1 e^{-\lambda^\delta t} \leq \tilde{N}(t) \leq K_2 e^{-\lambda^\delta t}$ for all $t \geq 0$. Together with (30) and the negativity of λ^δ , one concludes that:

$$0 < \frac{K_1}{K_2} |\lambda^\delta| \leq \liminf_{t \rightarrow +\infty} N(t) \leq \limsup_{t \rightarrow +\infty} N(t) \leq \frac{K_2}{K_1} |\lambda^\delta| < +\infty.$$

The proof of Theorem 2.5 is thereby complete. \square

4.3 Dependence with respect to the parameters

Proof of Proposition 2.7. We start with the concavity and the monotonicity in $(0, +\infty)$ of the map $\delta \mapsto \lambda^\delta$ defined in (16). Using the confining properties of the fitnesses $r_i(\mathbf{x})$, it follows from Lemma 4.1 and elementary arguments that, for any $\delta > 0$,

$$\lambda^\delta = \min_{\substack{\varphi \in H^1(\mathbb{R}^n) \setminus \{0\} \\ \mathbf{x} \mapsto \|\mathbf{x}\| \varphi(\mathbf{x}) \in L^2(\mathbb{R}^n)}} \mathcal{R}(\delta, \varphi), \quad (31)$$

with,

$$\mathcal{R}(\delta, \varphi) = \frac{\frac{\mu^2}{2} \int_{\mathbb{R}^n} \|\nabla \varphi(\mathbf{x})\|^2 d\mathbf{x} - \int_{\mathbb{R}^n} r_1(\mathbf{x}) \varphi(\mathbf{x})^2 d\mathbf{x} + \delta \int_{\mathbb{R}^n} (\varphi(\mathbf{x})^2 - \varphi(\mathbf{x}) \varphi(\iota(\mathbf{x}))) d\mathbf{x}}{\int_{\mathbb{R}^n} \varphi(\mathbf{x})^2 d\mathbf{x}},$$

and the minimum of the Rayleigh quotient $\mathcal{R}(\delta, \cdot)$ in (31) is reached only by multiples of the function φ_1^δ given in Lemma 4.1. For each $\varphi \in H^1(\mathbb{R}^n) \setminus \{0\}$ such that $\mathbf{x} \mapsto \|\mathbf{x}\| \varphi(\mathbf{x}) \in L^2(\mathbb{R}^n)$, the map $\delta \mapsto \mathcal{R}(\delta, \varphi)$ is affine in $(0, +\infty)$ and nondecreasing in $(0, +\infty)$ (from the Cauchy-Schwarz inequality). Therefore, the map $\delta \mapsto \lambda^\delta$ is concave and nondecreasing in $(0, +\infty)$.

From this characterization, it also follows that the map $\delta \mapsto \lambda^\delta$ is not only nondecreasing but also increasing in $(0, +\infty)$. Indeed, to do so, assume by way of contradiction that there are two migration rates $0 < \delta < \delta'$ such that $\lambda^\delta = \lambda^{\delta'}$. The function $\varphi_1^{\delta'}$ is a minimum of $\mathcal{R}(\delta', \varphi)$ among the functions $\varphi \in H^1(\mathbb{R}^n) \setminus \{0\}$ such that $\mathbf{x} \mapsto \|\mathbf{x}\| \varphi(\mathbf{x}) \in L^2(\mathbb{R}^n)$. Thus, the monotonicity of $\mathcal{R}(\cdot, \varphi_1^{\delta'})$ in $(0, +\infty)$ yields:

$$\lambda^\delta \leq \mathcal{R}(\delta, \varphi_1^{\delta'}) \leq \mathcal{R}(\delta', \varphi_1^{\delta'}) = \lambda^{\delta'} = \lambda^\delta,$$

hence $\lambda^\delta = \mathcal{R}(\delta, \varphi_1^{\delta'})$, that is, $\varphi_1^{\delta'}$ also minimizes $\mathcal{R}(\delta, \varphi)$ among the same set of functions φ . Therefore, there is a constant $C > 0$ such that $\varphi_1^{\delta'} \equiv C \varphi_1^\delta$ in \mathbb{R}^n , hence:

$$\delta' (\varphi_1^\delta - \varphi_1^\delta \circ \iota) \equiv \delta (\varphi_1^{\delta'} - \varphi_1^{\delta'} \circ \iota) \quad \text{in } \mathbb{R}^n,$$

from the equations satisfied by φ_1^δ and $\varphi_1^{\delta'} = C \varphi_1^\delta$. As a consequence, $\varphi_1^{\delta'} \equiv \varphi_1^\delta \circ \iota$ in \mathbb{R}^n , that is, $\varphi_1^\delta \equiv \varphi_2^\delta$ in \mathbb{R}^n by Lemma 4.1. Finally, the system $\mathcal{A}(\varphi_1^\delta, \varphi_2^\delta) = \lambda^\delta(\varphi_1^\delta, \varphi_2^\delta)$ yields $r_1 \varphi_1^\delta \equiv r_2 \varphi_1^\delta$ in \mathbb{R}^n , which is clearly impossible since $\varphi_1^\delta > 0$ in \mathbb{R}^n and $\mathbf{O}_1 \neq \mathbf{O}_2$. Therefore, the map $\delta \mapsto \lambda^\delta$ is increasing in $(0, +\infty)$.

Let us now investigate the limits of λ^δ as $\delta \rightarrow 0$ and $\delta \rightarrow +\infty$. First of all, one knows from (16) that $\lambda^\delta \geq -r_{\max}$ for all $\delta > 0$ (this property can also be viewed as a consequence of (31) since $-r_1(\mathbf{x}) = -r_{\max} + \|\mathbf{x} - \mathbf{O}_1\|^2/2 \geq -r_{\max}$ for all $\mathbf{x} \in \mathbb{R}^n$). Furthermore, by choosing a symmetric test function, such as $\varphi_0(x) = e^{-\|\mathbf{x}\|^2}$ for instance, one has $\lambda^\delta \leq \mathcal{R}(\delta, \varphi_0)$, and the quantity $\mathcal{R}(\delta, \varphi_0)$ is independent of δ , hence $\sup_{\delta > 0} \lambda^\delta < +\infty$. Therefore, there are two real numbers $\ell^0 < \ell^\infty$ in $[-r_{\max}, +\infty)$ such that $\lambda^\delta \rightarrow \ell^0$ as $\delta \rightarrow 0$ and $\lambda^\delta \rightarrow \ell^\infty$ as $\delta \rightarrow +\infty$.

By defining $\mathcal{R}(0, \varphi)$ as above by deleting the (nonnegative) third term of the numerator of the Rayleigh quotient $\mathcal{R}(\delta, \varphi)$, one has:

$$\mathcal{R}(0, \varphi) \leq \mathcal{R}(\delta, \varphi) \leq \mathcal{R}(0, \varphi) + 2\delta,$$

for every function $\varphi \in H^1(\mathbb{R}^n) \setminus \{0\}$ such that $\mathbf{x} \mapsto \|\mathbf{x}\| \varphi(\mathbf{x}) \in L^2(\mathbb{R}^n)$. Thus, as $\delta \rightarrow 0$, the minimum λ^δ of $\mathcal{R}(\delta, \varphi)$ over this set of functions φ converges to the minimum ℓ^0 of $\mathcal{R}(0, \varphi)$ over the same set, and this last minimum ℓ^0 corresponds to the principal eigenvalue of the Schrödinger operator,

$$-\frac{\mu^2}{2} \Delta - r_1(\mathbf{x}) = -\frac{\mu^2}{2} \Delta - r_{\max} + \frac{\|\mathbf{x} - \mathbf{O}_1\|^2}{2},$$

acting on the same set of functions. Since the principal eigenvalue of the operator $-\Delta + \|\mathbf{x}\|^2$ is equal to n (with ground state, namely the principal eigenfunction, $\varphi_{GS}(\mathbf{x}) = e^{-\|\mathbf{x}\|^2/2}$ up to multiplicative constants), it easily follows by translation and scaling that $\ell^0 = -r_{\max} + \mu n/2 =: \lambda^0$, with principal eigenfunction $\varphi^0(\mathbf{x}) = e^{-\|\mathbf{x} - \mathbf{O}_1\|^2/(2\mu)}$ up to multiplicative constants.

In order to identify the real number $\ell^\infty = \lim_{\delta \rightarrow +\infty} \lambda^\delta = \lim_{k \rightarrow +\infty} \lambda^k$, we consider a sequence of (positive) principal eigenfunctions $(\varphi_1^k, \varphi_2^k)_{k \in \mathbb{N}} = (\varphi_1^k, \varphi_1^k \circ \iota)_{k \in \mathbb{N}}$ given by Lemma 4.1 (with $\delta = k \in \mathbb{N}$), normalized by $\|\varphi_1^k\|_{L^2(\mathbb{R}^n)} = 1$. For each $k \in \mathbb{N}$, there holds $\lambda^k = \mathcal{R}(k, \varphi_1^k)$, hence:

$$\frac{\mu^2}{2} \int_{\mathbb{R}^n} \|\nabla \varphi_1^k(\mathbf{x})\|^2 \, d\mathbf{x} + \int_{\mathbb{R}^n} \frac{\|\mathbf{x} - \mathbf{O}_1\|^2}{2} \varphi_1^k(\mathbf{x})^2 \, d\mathbf{x} + k \int_{\mathbb{R}^n} (\varphi_1^k(\mathbf{x})^2 - \varphi_1^k(\mathbf{x}) \varphi_1^k(\iota(\mathbf{x}))) \, d\mathbf{x} = r_{\max} + \lambda^k. \quad (32)$$

Notice that the right-hand side is bounded as $k \rightarrow +\infty$, while the left-hand side is the sum of three nonnegative terms. Therefore, the sequence $(\varphi_1^k)_{k \in \mathbb{N}}$ is bounded in $H^1(\mathbb{R}^n)$ and, up to extraction of a subsequence, there exists a nonnegative function $\varphi_1 \in H^1(\mathbb{R}^n)$ such that $\varphi_1^k \rightarrow \varphi_1$ in $L^2_{loc}(\mathbb{R}^n)$ strongly, in $H^1_{loc}(\mathbb{R}^n)$ weakly, and almost everywhere in \mathbb{R}^n . Furthermore, since $\|\mathbf{x} - \mathbf{O}_1\| \rightarrow +\infty$ as $\|\mathbf{x}\| \rightarrow +\infty$, one has $\sup_{k \in \mathbb{N}} \|\varphi_1^k\|_{L^2(\mathbb{R}^n \setminus B(0,R))} \rightarrow 0$ as $R \rightarrow +\infty$, hence $\varphi_1^k \rightarrow \varphi_1$ in $L^2(\mathbb{R}^n)$ as $k \rightarrow +\infty$, and $\|\varphi_1\|_{L^2(\mathbb{R}^n)} = 1$. Fatou's lemma also implies that the function $\mathbf{x} \mapsto \|\mathbf{x} - \mathbf{O}_1\| \varphi_1(\mathbf{x})$ belongs to $L^2(\mathbb{R}^n)$, and so does the function $\mathbf{x} \mapsto \|\mathbf{x}\| \varphi_1(\mathbf{x})$. Moreover,

$$\int_{\mathbb{R}^n} (\varphi_1^k(\mathbf{x})^2 - \varphi_1^k(\mathbf{x})\varphi_1^k(\iota(\mathbf{x}))) \, d\mathbf{x} \rightarrow \int_{\mathbb{R}^n} (\varphi_1(\mathbf{x})^2 - \varphi_1(\mathbf{x})\varphi_1(\iota(\mathbf{x}))) \, d\mathbf{x}, \quad \text{as } k \rightarrow +\infty.$$

But since the left-hand side is $O(1/k)$ as $k \rightarrow +\infty$ by (32), one gets that:

$$\int_{\mathbb{R}^n} (\varphi_1(\mathbf{x})^2 - \varphi_1(\mathbf{x})\varphi_1(\iota(\mathbf{x}))) \, d\mathbf{x} = 0.$$

Since both functions φ_1 and $\varphi_1 \circ \iota$ are nonnegative and with the same $L^2(\mathbb{R}^n)$ norm (equal to 1), the case of equality in the Cauchy-Schwarz inequality implies that:

$$\varphi_1 = \varphi_1 \circ \iota,$$

almost everywhere in \mathbb{R}^n . Since each $C_0^\infty(\mathbb{R}^n)$ function $\varphi_1^k + \varphi_2^k = \varphi_1^k + \varphi_1^k \circ \iota$ obeys:

$$-\frac{\mu^2}{2} \Delta(\varphi_1^k + \varphi_2^k) - r_1 \varphi_1^k - r_2 \varphi_2^k = \lambda^k (\varphi_1^k + \varphi_2^k) \quad \text{in } \mathbb{R}^n,$$

and since $\varphi_1^k \rightarrow \varphi_1$ and $\varphi_2^k = \varphi_1^k \circ \iota \rightarrow \varphi_1 \circ \iota = \varphi_1$ in $L^2(\mathbb{R}^n)$ strongly and in $H^1_{loc}(\mathbb{R}^n)$ weakly, it then follows from a passage to the limit in the weak sense and from standard elliptic regularity theory that the function φ_1 is a $C^\infty(\mathbb{R}^n)$ solution of:

$$-\frac{\mu^2}{2} \Delta \varphi_1 - \frac{r_1 + r_2}{2} \varphi_1 = \ell^\infty \varphi_1 \quad \text{in } \mathbb{R}^n.$$

Furthermore, since $\|\varphi_1\|_{L^2(\mathbb{R}^n)} = 1$ and since φ_1 is nonnegative, the elliptic strong maximum principle implies that $\varphi_1 > 0$ in \mathbb{R}^n . The $H^1(\mathbb{R}^n)$ function φ_1 is then a ground state of the Schrödinger operator $-(\mu^2/2)\Delta - (r_1 + r_2)/2 = -(\mu^2/2)\Delta - r_{\max} + m_D/4 + \|\mathbf{x}\|^2/2$, with m_D defined in (9). As a consequence, ℓ^∞ is the principal eigenvalue of this operator and φ_1 is its principal eigenfunction. In other words, $\ell^\infty = -r_{\max} + m_D/4 + \mu n/2 =: \lambda^\infty$ and $\varphi_1(\mathbf{x}) = (\pi\mu)^{-n/4} e^{-\|\mathbf{x}\|^2/(2\mu)}$. The proof of Proposition 2.7 is thereby complete. \square

Proof of Theorem 2.10. Let $\mathbf{u}_\delta = (u_{\delta,1}, u_{\delta,2})$ be the unique $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)^2$ solution of (1) given by Theorem 2.1 and Remark 2.2, for growth functions f_1, f_2 of the first type (3), with a fixed initial condition $\mathbf{u}^0 = (u_1^0, u_2^0)$ independent of δ and such that both functions u_1^0, u_2^0 satisfy the assumptions (H1)-(H3). Let us fix two positive times $0 < T' \leq T$ and let us show that $\sup_{t \in [T', T]} \|u_{\delta,1}(t, \cdot) - u_{\delta,2}(t, \cdot)\|_{L^\infty(\mathbb{R}^n)} \rightarrow 0$ as $\delta \rightarrow +\infty$.

From the first part of the proof of Theorem 2.1, especially from (21), (24)-(25) and similar calculations as the ones between (24) and (25), it follows that there exists a constant $K \geq 0$ (independent of $\delta > 0$) such that, for all $\delta > 0$,

$$|x_1 u_{\delta,2}(t, \mathbf{x})| \leq |x_1 h_2(t, \mathbf{x})| \leq K, \quad \text{for all } t \in [0, T] \text{ and } \mathbf{x} = (x_1, \dots, x_n) \in \mathbb{R}^n, \quad (33)$$

with h_2 defined by (18) (notice that the function h_2 actually depends on δ , but the upper bound (24) is independent of $\delta > 0$). For each $\delta > 0$, one infers from (1)-(2) and (10) that the function $v_\delta := u_{\delta,1} - u_{\delta,2}$ is a classical $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)$ solution of:

$$\partial_t v_\delta(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta v_\delta(t, \mathbf{x}) + r_1(\mathbf{x}) v_\delta(t, \mathbf{x}) - 2\delta v_\delta(t, \mathbf{x}) - 2\beta x_1 u_{\delta,2}(t, \mathbf{x}),$$

such that v_δ is locally bounded in time and $v_\delta(t, x) \rightarrow 0$ as $\|\mathbf{x}\| \rightarrow +\infty$ locally uniformly in $t \in \mathbb{R}_+$. The previous relation, together with (20) and (33), implies that:

$$\begin{cases} -2\beta K \leq \partial_t v_\delta(t, \mathbf{x}) - \frac{\mu^2}{2} \Delta v_\delta(t, \mathbf{x}) - (r_{\max} + m_1(\mathbf{x})) v_\delta(t, \mathbf{x}) + 2\delta v_\delta(t, \mathbf{x}) \leq 2\beta K, & t \in [0, T], \mathbf{x} \in \mathbb{R}^n, \\ |v_\delta(0, \mathbf{x})| \leq \max(\|u_1^0\|_{L^\infty(\mathbb{R}^n)}, \|u_2^0\|_{L^\infty(\mathbb{R}^n)}) =: M, & \mathbf{x} \in \mathbb{R}^n. \end{cases}$$

Since the potential $m_1(\mathbf{x}) = -\|\mathbf{x} - \mathbf{O}_1\|^2/2$ is nonpositive, there exists a $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)$ solution $V : \mathbb{R}_+ \times \mathbb{R}^n \rightarrow [0, M]$ of:

$$\begin{cases} \partial_t V(t, \mathbf{x}) = \frac{\mu^2}{2} \Delta V(t, \mathbf{x}) + m_1(\mathbf{x}) V(t, \mathbf{x}), & t \geq 0, \mathbf{x} \in \mathbb{R}^n, \\ V(0, \mathbf{x}) = M, & \mathbf{x} \in \mathbb{R}^n. \end{cases}$$

Such a function V , which is independent of $\delta > 0$, can be obtained as the nondecreasing local limit as $R \rightarrow +\infty$ of $C^{1,2}(\mathbb{R}_+ \times \overline{B(0, R)})$ solutions $V^R : \mathbb{R}_+ \times \overline{B(0, R)} \rightarrow [0, M]$ of the same equation in $\mathbb{R}_+ \times \overline{B(0, R)}$, with Dirichlet boundary conditions $V^R = 0$ on $\mathbb{R}_+ \times \partial B(0, R)$ and initial conditions of the type $V^R(0, \mathbf{x}) = M \phi(\|\mathbf{x}\|/R)$ in $\overline{B(0, R)}$, where $\phi : [0, 1] \rightarrow [0, 1]$ is a $C^\infty([0, 1])$ nonincreasing function such that $\phi = 1$ in $[0, 1/3]$ and $\phi = 0$ in $[2/3, 1]$.

Consider now any $\delta > r_{\max}/2$ and let V_δ be the $C^{1,2}(\mathbb{R}_+ \times \mathbb{R}^n)$ function defined in $\mathbb{R}_+ \times \mathbb{R}^n$ by:

$$V_\delta(t, \mathbf{x}) = v_\delta(t, \mathbf{x}) e^{(2\delta - r_{\max})t} - \frac{2\beta K}{2\delta - r_{\max}} (e^{(2\delta - r_{\max})t} - 1).$$

A straightforward calculation shows that:

$$\partial_t V_\delta(t, \mathbf{x}) - \frac{\mu^2}{2} \Delta V_\delta(t, \mathbf{x}) - m_1(\mathbf{x}) V_\delta(t, \mathbf{x}) \leq m_1(\mathbf{x}) \frac{2\beta K}{2\delta - r_{\max}} (e^{(2\delta - r_{\max})t} - 1) \leq 0,$$

for all $(t, x) \in [0, T] \times \mathbb{R}^n$. Furthermore, $V_\delta(0, \mathbf{x}) = v_\delta(0, \mathbf{x}) \leq M = V(0, \mathbf{x})$ for all $\mathbf{x} \in \mathbb{R}^n$, and $\limsup_{\|\mathbf{x}\| \rightarrow +\infty} V_\delta(t, \mathbf{x}) \leq 0$ uniformly in $t \in [0, T]$. It follows from the maximum principle that $V_\delta(t, \mathbf{x}) \leq V(t, x)$ for all $(t, \mathbf{x}) \in [0, T] \times \mathbb{R}^n$, hence:

$$v_\delta(t, \mathbf{x}) \leq e^{(r_{\max} - 2\delta)t} V(t, \mathbf{x}) + \frac{2\beta K}{2\delta - r_{\max}} (1 - e^{(r_{\max} - 2\delta)t}), \quad \text{for all } (t, \mathbf{x}) \in [0, T] \times \mathbb{R}^n.$$

Since the function V is bounded (by M), one gets that:

$$\limsup_{\delta \rightarrow +\infty} \left(\sup_{[T', T] \times \mathbb{R}^n} v_\delta \right) \leq 0,$$

recalling that $0 < T' \leq T$. The same argument applied to the functions $-V_\delta$ and $-v_\delta$ implies that, for all $\delta > r_{\max}/2$ and $(t, \mathbf{x}) \in [0, T] \times \mathbb{R}^n$,

$$v_\delta(t, \mathbf{x}) \geq -e^{(r_{\max} - 2\delta)t} V(t, \mathbf{x}) - \frac{2\beta K}{2\delta - r_{\max}} (1 - e^{(r_{\max} - 2\delta)t}),$$

hence $\liminf_{\delta \rightarrow +\infty} \left(\inf_{[T', T] \times \mathbb{R}^n} v_\delta \right) \geq 0$. As a conclusion, $\sup_{[T', T] \times \mathbb{R}^n} |v_\delta| \rightarrow 0$ as $\delta \rightarrow +\infty$ and the proof of Theorem 2.10 is thereby complete. \square

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