Qualitative properties of the spreading speed of a population structured in space and in phenotype

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Abstract

We consider a nonlocal Fisher-KPP equation that models a population structured in space and in phenotype. The population lives in a heterogeneous periodic environment: the diffusion coefficient, the mutation coefficient and the fitness of an individual may depend on its spatial position and on its phenotype.

We first prove a Freidlin-Gärtner formula for the spreading speed of the population. We then study the behaviour of the spreading speed in different scaling limits (small and large period, small and large mutation coefficient). Finally, we exhibit new phenomena arising thanks to the phenotypic dimension. Our results are also valid when the phenotype is seen as another spatial variable along which the population does not spread.

Keywords. Reaction-diffusion equations; long-time behaviour; population dynamics; elliptic equations; principal eigenvalue.
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Contents

1 Introduction

Our goal is to study the spreading properties of a population structured in space and in phenotype, and which evolves according to a reaction-diffusion equation. A particular case of our model reads:

$$\begin{cases} \partial_t u = a\Delta_x u + m\Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), & t>0,\,(x,\theta)\in\mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta u = 0, & t>0,\,(x,\theta)\in\mathbb{R}\times\partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta)\in\mathbb{R}\times\Theta, \end{cases} \tag{1}$$

with

$$\rho(t,x) := \int_\Theta u(t,x,\sigma)\,\mathrm{d}\sigma.$$

Here $\Theta\subset\mathbb{R}^P$ is a smooth open bounded domain with outward normal ν. The initial condition u_0 is assumed to be nonnegative, continuous and bounded.

We call $x\in\mathbb{R}$ the space variable and $\theta\in\Theta$ the phenotype variable, and we see $u(t,x,\theta)$ as the density of individuals of phenotype $\theta\in\Theta$ living at position $x\in\mathbb{R}$ and at time $t\geqslant 0$. With this viewpoint, $r(x,\theta)$ is the fitness of an individual of phenotype θ at position x, while $a>0$ is the motility and $m>0$ is the mutation coefficient (m corresponds to the product between the mutation rate and the mutational variance, see e.g. [26, Appendix A]). Later, we shall rather see m as a scaling parameter. We assume that the environment is periodic in space, which we translate into our framework by assuming that r is periodic in the variable x.

We will show that a population modelled by Equation (1) invades its environment at some finite speed, which we will call the *spreading speed*. We will compute the spreading speed for different scaling limits: when the period of the environment is large or small, and when the mutation coefficient is large or small. Finally, we will show that there exists a mutation coefficient m which maximises the spreading speed.

Simpler models. Before describing our precise assumptions and our results, let us explain where Equation (1) comes from. The Fisher-KPP equation was introduced in 1937 by Fisher [19] and Kolmogorov, Petrovsky and Piskounov [31]. It reads:

$$\partial_t u(t,x) = a\Delta_x u + ru - u^2, \tag{2}$$

where $a > 0$ and $r > 0$ are constant. A motivation for Equation (2) comes from biology: $u(t,x)$ can be seen as the density of individuals living at position $x \in \mathbb{R}$ and at time $t \geqslant 0$. The term $a\Delta_x u$ means that the individuals move according to a (time-changed) Brownian motion. The linear term ru stands for the demography in the absence of interactions. The population is regulated logistically through the nonlinear term $-u^2$, which accounts for the additional deaths due to the competition between individuals.

One very important feature of the Fisher-KPP equation is the emergence of invasions of the environment by the population. Namely, there exists a *spreading speed* $c_{KPP} := 2\sqrt{ar}$ satisfying the following property. If the initial condition is nonnegative, is nonzero and has a support bounded from above, then, for all $c' > c_{KPP}$,

$$\lim_{t\to+\infty} u(t,c't) = 0,$$

and for all $c'' \in (0, c_{KPP})$,

$$\lim_{t\to+\infty} u(t,c''t) = r.$$

Moreover, for all $c \geqslant c_{KPP}$, there exists a profile U_c such that $u(t,x) := U_c(x-ct)$ solves (2). Such a self-similar solution is called a *travelling wave*.

The simplicity of the Fisher-KPP equation, together with these invasion properties, have made it a central tool in ecology and in biology (e.g. [39–41]). However, because of its simplicity, the Fisher-KPP equation misses phenomena which may play an important role in invasions. Equation (1) is a variant that tries to take two such phenomena into account: the heterogeneity of the environment and the heterogeneity of the population.

Heterogeneous environment. A first phenomenon which is missed by the classical Fisher-KPP equation is the heterogeneity of the environment. This can be (partially) overcome by considering the following periodic heterogeneous version of the Fisher-KPP equation:

$$\partial_t u(t,x) = a\Delta_x u + r(x)u - u^2, \tag{3}$$

where the function r is smooth and 1-periodic. In this setting, if the population persists, there still exists a minimal spreading speed c_{het} (which plays a role analogous to c_{KPP} but in the heterogeneous setting). Gärtner and Freidlin [21] found a variational formula for c_{het}. For $\lambda > 0$, they consider the operator

$$\mathcal{L}^\lambda := a\Delta_x - 2\lambda a\partial_x + (r(x) + \lambda^2 a)$$

acting on 1-periodic functions. The principal eigenvalue k^λ of this operator is the unique real number such that there exists a 1-periodic function $\phi > 0$ satisfying $\mathcal{L}^\lambda\phi = k^\lambda\phi$. Gärtner

and Freidlin show that if $k^0 > 0$, then the population persists and an invasion occurs at speed

$$c_{het} := \inf_{\lambda>0} \frac{k^\lambda}{\lambda}. \tag{4}$$

Since Gärtner and Freidlin, numerous work have proved different versions of Equation (4) for various settings, e.g. [6, 7, 23, 25, 42]. In the heterogeneous setting, the existence of travelling waves cannot be expected, due to the heterogeneity. Still, there exist *pulsating travelling waves* for all speeds no less than the minimal spreading speed c_{het}. A pulsating travelling wave with speed $c \geqslant c_{het}$ is a solution v of (3) such that $(t,x) \mapsto v(t,x+ct)$ is periodic in time and which has the following limits: for all $c' > c_{het}$, $v(t,c't)$ converges to 0, and for all $c'' < c_{het}$, the profile $x \mapsto v(t,c''t+x)$ converges locally, up to a time-dependent shift, to the unique $\phi > 0$ satisfying $a\Delta_x\phi + r(x)\phi - \phi^2 = 0$. The limiting profile ϕ is called the stationary state of the equation and, by uniqueness, is 1-periodic. See also [5, 8]. In [43], Xin gives a survey of results and methods for reaction-diffusion equation in heterogeneous environments.

Heterogeneous population. A second phenomenon which is missed by the basic Fisher-KPP equation (2) is the heterogeneity of the population, i.e. some individuals may react differently to the same environmental conditions. Thus we add a new variable $\theta \in \Theta$ representing the phenotype of the individuals. If we do this directly on (3), we get

$$\partial_t u(t,x,\theta) = a\Delta_x u + m\Delta_\theta u + r(x,\theta)u - u^2, \qquad x \in \mathbb{R}, \theta \in \Theta, \tag{5}$$

together with the boundary condition $\nu \cdot \nabla_\theta u = 0$ on $\partial\Theta$. Here $m\Delta_\theta$ accounts for the mutations, with a mutation coefficient m. Then the Freidlin-Gärtner formula also holds [42], and pulsating travelling waves also exist [6, 7].

The only difference between Equation (1) and Equation (5) is the nonlocal term ρ. The nonlocal term ρ comes from the fact that in our model, the competition to which an individual is subject should depend on *all* the individuals that are located at the same position, regardless of their phenotypes. Thus the competition term $-u^2$ must be replaced by $-\rho u$. An equation similar to (1) (with rarer but larger mutations) appeared for the first time in the work of Prévost [37] and was then derived by Champagnat and Méléard [15] as a large population limit of an individual-based model.

The discussion above implies that (5) is more adapted to populations that depend on variables x and θ which are of the same nature (for example, x and θ could be the coordinates of a spatial position), while we should better use (1) if we want the variable θ to represent a phenotype. Although we shall concentrate on Equation (1), our results only depend on the linear problem, so they are valid for the local equation (5) as well (in the latter setting, however, our results may be harder to interpret from a biological viewpoint).

For the sake of example, let us assume temporarily that the fitness r only depends on the phenotype θ in (1), so that the environment becomes homogeneous (i.e. independent of the spatial position). Then, there may be individuals, say with phenotype θ_1, which are more favoured than others, say with phenotype θ_2. It can then be expected that individuals of

phenotype θ_1 will drive the invasions, while individuals of phenotype θ_2 will slow it down. Let us now try to understand the influence of this heterogeneity on the spreading speed. Let H be the principal eigenvalue of the operator

$$m\Delta_\theta + r(\theta)$$

acting on the functions $\psi \in \mathcal{C}^2(\overline{\Theta})$ such that $\nu \cdot \nabla_\theta \psi = 0$ on $\partial\Theta$. Namely, H is the only real number such that there exists a function $\psi > 0$ satisfying

$$m\Delta_\theta \psi + r(\theta)\psi = H\psi, \qquad \nu \cdot \nabla_\theta \psi = 0.$$

Assume $H > 0$. Then, if u_0 is nonnegative, not uniformly equal to 0 and has a support bounded from above, then the solution of (1) spreads at a speed $c_{phenotype} = 2\sqrt{aH}$, in the sense that for all $c' > c_{phenotype}$

$$\lim_{t\to+\infty} \rho(t, c't) = 0,$$

and for all $c'' \in \left(0, c_{phenotype}\right)$,

$$\liminf_{t\to+\infty} \rho(t, c''t) > 0.$$

Moreover, for all $c \geqslant c_{phenotype}$, there exists a profile U_c such that $u(t,x,\theta) := U(x - ct, \theta)$ solves (1). See [9]. Note that H plays a role similar to r for the usual Fisher-KPP speed c_{KPP}.

We now go back to the general case of a heterogeneous environment and a heterogeneous population with a continuous phenotype.

Heterogeneous environment and population. In [2, 36], the authors studied the case where the population evolves along an environmental gradient, that is:

$$r(x,\theta) = R(x - B\theta), \qquad B > 0,$$

with

$$\begin{aligned} R &> 0 \quad \text{on } (-1,1), \\ R &< 0 \quad \text{on } \mathbb{R} \setminus [-1,1]. \end{aligned}$$

In this model, the phenotype of the individuals must be higher and higher as the population moves to the right: evolution is necessary for the propagation of the population. This is relevant when we want to study a propagation along the north-south axis, or uphill or downhill if the population lives on a mountain. In [36], Peltier showed that if the tail of the initial condition is heavy enough, then an accelerating invasion arises, as in the 1-dimensional case [29]. In [2], Alfaro, Coville and Raoul gave a criterion, based on the principal eigenvalue of an elliptic operator, to determine whether the population persists or gets extinct. They also showed the existence of a travelling wave.

The authors of [1] added a heterogeneity in time corresponding to climate change. In this new setting, the growth rate $r(x,\theta)$ is replaced by $r(t,x,\theta) = R(x - ct, \theta)$. They study different

shapes of the favourable space-phenotype zone (confined zone, environmental gradient, or a mixing between a confined zone and an environmental gradient). In each case, they found a criterion for the persistence of the species, and found a formula for the spreading speed.

An interesting case of equations with phenotype is the *cane-toad equation*, where $\Theta \subset (0, +\infty)$ may be unbounded, and the diffusivity a is nonconstant and proportional to the phenotype: $a(\theta) = \theta$. In this case, accelerating invasions may arise [11]. Then the interplay with the phenotype has a striking behaviour with respect to the spreading properties and real world biological consequences. In this work, however, most results do not apply to the cane-toad equation.

There are also works about periodic environments, as modelled by our equation (1). In [3], Alfaro and Peltier study the effect of small perturbations of the homogeneous case on the spreading speed and the travelling waves. They also deal with a non-gradient and non-periodic heterogeneity. In [12], Bouin and Mirrahimi study the effect of large periods and get the precise position of the invasion, using Hamilton-Jacobi equation techniques. In [14], Boutillon and Rossi focused on the same equation (1) but possibly set in an unbounded phenotype space. They gave a criterion (based on a generalised principal eigenvalue) for persistence and optimisation results for the ability of persistence.

As a concluding remark, we mention that another way to study heterogeneous populations is to use a system of Fisher-KPP equations: each equation of the system represents a variant which competes with the other ones. We mention [23, 24] for homogeneous environments, and [25, 38] for heterogeneous environments.

Problematic and layout. Our main goal is to study the spreading speed of a population modelled by equations of the form (1). In the next section, we present our results. We first give our general assumptions and the general form of the equation on which we shall work. In Subsection 2.1, we shall give a variational formula analogous to the Freidlin-Gärtner formula.

From a biological point of view, it is important to note that movements of individuals and mutations are phenomena of different nature; therefore, there is no reason why they should occur on the same timescales. It is thus important to understand the interplay between the mutation coefficient and the period at different scales. What is the spreading speed for large and small periods? What is the spreading speed for large and small mutation coefficients? Subsection 2.2 is devoted to these questions. We shall see that in these limits, one can often get back to the study of equations without the phenotypic dimension.

A specificity of Equation (1) is that the population modelled by the equation is heterogeneous. What are the new phenomena which can occur? What is their biological interpretation? In Subsection 2.3, we shall give several results which are invisible when we forget the phenotypic dimension.

2 Main results

Now, we describe our general model and our general assumptions.

We consider a mutation coefficient $m > 0$ and a period $L > 0$. We let Θ be an open bounded domain with $\mathcal{C}^2$ boundary.

We fix $\alpha \in (0,1)$. We take $a \in \mathcal{C}^{1,\alpha}(\mathbb{R} \times \overline{\Theta})$, $\mu \in \mathcal{C}^{1,\alpha}(\mathbb{R} \times \overline{\Theta})$ and $r \in \mathcal{C}^{0,\alpha}(\mathbb{R} \times \overline{\Theta})$ such that for all $\theta \in \overline{\Theta}$, the functions $x \mapsto a(x,\theta)$, $x \mapsto \mu(x,\theta)$ and $x \mapsto r(x,\theta)$ are 1-periodic (we say that a, μ and r are 1-*periodic in* x).

The functions a and μ represent the heterogeneity of the diffusion in the directions x and θ respectively. We make an assumption of uniform ellipticity of the operator, that is, we assume that there exists a constant $\eta > 0$ such that $a \geqslant \eta$ and $\mu \geqslant \eta$.

As we shall be interested in the behaviour of the spreading speed for various scales of the period and of the mutation coefficient, we first write out our model in a way that makes explicit the dependence in these parameters. We note

$$a_L(x,\theta) := a\left(\frac{x}{L},\theta\right), \qquad \mu_L(x,\theta) := \mu\left(\frac{x}{L},\theta\right), \qquad r_L(x,\theta) := r\left(\frac{x}{L},\theta\right)$$

the L-periodic versions of a, μ and r respectively. We define an operator $\mathcal{T}_{m,L}$ by

$$\mathcal{T}_{m,L}\phi := \partial_x\left(a_L(x,\theta)\partial_x\phi\right) + m\nabla_\theta \cdot \left(\mu_L(x,\theta)\nabla_\theta\phi\right) + r_L(x,\theta)\phi, \tag{6}$$

and we write a general version of main model (1) as:

$$\begin{cases} \partial_t u_{m,L} = \mathcal{T}_{m,L}u_{m,L} - u_{m,L} \times \rho_{m,L}(t,x), & t > 0,\ (x,\theta) \in \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta u_{m,L} = 0, & t > 0,\ (x,\theta) \in \mathbb{R} \times \partial\Theta, \\ u_{m,L}(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R} \times \Theta, \end{cases} \tag{7}$$

with

$$\rho_{m,L}(t,x) := \int_\Theta u_{m,L}(t,x,\sigma)\,\mathrm{d}\sigma.$$

We also require that $u_0 \in \mathcal{C}^0(\mathbb{R} \times \overline{\Theta})$ is nonnegative, bounded and has a support bounded from above. Contrarily to (1), the diffusion coefficient a and the mutation coefficient $m\mu$ are now allowed to depend on x and θ. These dependencies will be restricted in several of our results below. We keep the variable m as a real number which will serve as a scaling parameter in the sequel. Since the heterogeneity μ is fixed, we will for convenience call m the mutation coefficient (instead of $m\mu$).

Theorem 1.1 of [14] ensures that the problem (7) has a unique weak solution in $W^{1,2}_{p,loc}([0,+\infty) \times (\mathbb{R} \times \overline{\Theta}))$ for all $p > 1$ (i.e. the solution, its first derivatives with respect to t, and all its derivatives with respect to (x,θ) up to the second order, belong to L^p_{loc}). Moreover, the unique solution u and the corresponding ρ are globally bounded and nonnegative. If u_0 is nonzero, then u and ρ are strictly positive at all positive times.

2.1 The Freidlin-Gärtner formula

We first introduce a family of principal eigenvalues which will be central in the statement of the Freidlin-Gärtner formula. For $\lambda > 0$, we let $\mathcal{L}^\lambda_{m,L}$ be the linear operator defined by:

$$\mathcal{L}^\lambda_{m,L} := \mathcal{T}_{m,L} - 2\lambda a_L\partial_x + \left(\lambda^2 a_L - \lambda\partial_x a_L\right),$$

or, equivalently,

$$\mathcal{L}^{\lambda}_{m,L}\phi(x,\theta) := e^{\lambda x}\mathcal{T}_{m,L}(e^{-\lambda\cdot}\phi(\cdot,\theta)).$$

We let $(\varphi^{\lambda}_{m,L}, k^{\lambda}_{m,L}) \in \mathcal{C}^2(\mathbb{R}\times\overline{\Theta})\times\mathbb{R}$ be the unique solution of the principal eigenvalue problem:

$$\begin{cases} (\mathcal{L}^{\lambda}_{m,L})(\varphi^{\lambda}_{m,L}) = (k^{\lambda}_{m,L})(\varphi^{\lambda}_{m,L}) & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta(\varphi^{\lambda}_{m,L}) = 0 & \text{over } \mathbb{R}\times\partial\Theta, \\ \varphi^{\lambda}_{m,L} > 0 & \text{in } \mathbb{R}\times\Theta, \\ \varphi^{\lambda}_{m,L} & \text{is } L\text{-periodic in } x, \end{cases} \tag{8}$$

such that

$$\int_{[0,L]\times\Theta}\varphi^{\lambda}_{m,L} = 1.$$

Due to the periodicity of x of the model and to the smoothness of $\partial\Theta$, we are in a compact setting. Therefore, the existence and uniqueness of such a couple $(\varphi^{\lambda}_{m,L}, k^{\lambda}_{m,L}) \in \mathcal{C}^2(\mathbb{R}\times\overline{\Theta})\times\mathbb{R}$ follows from the standard Krein-Rutman theory [32].

Our first result means that the solutions of the equations of the type (7) have a spreading speed, and that the spreading speed is given by a formula analogous to the Freidlin-Gärtner formula (see Equation (4)). First, we extend the definition of the spreading speed to our framework.

Definition 2.1. *Let $c>0$. We say that a solution u of (7) spreads at speed c if for all $c'>c$,*

$$\lim_{t\to+\infty}\rho(t,c't) = 0,$$

and for all $c''<c$,

$$\liminf_{t\to+\infty}\rho(t,c''t) > 0.$$

We call c the spreading speed of u.

Remark 2.2. Using a parabolic Harnack equality (see below), we may infer that u spreads at speed c if and only if: for all $c'>c$,

$$\lim_{t\to+\infty}\left(\sup_{\theta\in\overline{\Theta}}u(t,c't,\theta)\right) = 0,$$

and for all $c''<c$,

$$\liminf_{t\to+\infty}\left(\inf_{\theta\in\overline{\Theta}}u(t,c''t,\theta)\right) > 0.$$

As we are interested in the spreading of a population, the least that we should require is that the population does not get extinct. Theorem 1.3 in [14] implies that the population persists as long as the mutation coefficient $m>0$ and the period $L>0$ satisfy

$$k^{0}_{m,L} > 0.$$

We shall only work with such mutation coefficients and periods. We now have all the tools at hand to state the Freidlin-Gärtner formula in our context.

Theorem 2.3 (Freidlin-Gärtner formula)**.** *Take $m > 0$ and $L > 0$ and assume that $u_0 \in \mathcal{C}^0(\mathbb{R} \times \overline{\Theta})$ is nonnegative, not identically equal to 0, bounded and has a support bounded from above.*

(i) If $k^0_{m,L} < 0$, then the solution of (7) gets extinct: $\|\rho(t,\cdot)\|_\infty \to 0$ as $t \to +\infty$;

(ii) If $k^0_{m,L} > 0$, then the solution of (7) has a positive spreading speed $c_{m,L}$ (in the sense of Definition 2.1). The spreading speed $c_{m,L}$ is given by

$$c_{m,L} := \inf_{\lambda > 0} \frac{k^\lambda_{m,L}}{\lambda}. \tag{9}$$

Remark 2.4. As mentioned in [14], the behaviour of the solution (extinction or persistence) in the borderline case $k^0_{m,L} = 0$ is not known.

2.2 The spreading speed for different scales

In this section, we shall compute the spreading speed for different scaling limits. We will often go back to the study of equations without the phenotypic dimension. It will thus be convenient to use the notation $c^1(A,R)$ for the spreading speed of a population not structured in phenotype, living in an environment with periodic diffusion coefficient $A \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ and with periodic intrinsic growth rate $R \in \mathcal{C}^{0,\alpha}(\mathbb{R})$, with the same period as A.

Let us precisely define $c^1(A,R)$ for two functions A, R which are periodic with a common period $L > 0$. We let $\kappa^1(\lambda; A, R)$ be the principal eigenvalue corresponding to the operator $\mathcal{L}^{1,\lambda}$ defined by

$$\mathcal{L}^{1,\lambda}\phi := (A\phi')' - 2\lambda A\phi' + (R + \lambda^2 A - \lambda A')\phi, \qquad \phi \in \mathcal{C}^{2,\alpha}(\mathbb{R}),$$

acting on L-periodic functions. This means that $\kappa^1(\lambda; A, R)$ is the only real number such that there exists a L-periodic function $\varphi^{1,\lambda} \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ satisfying

$$\mathcal{L}^{1,\lambda}\varphi^{1,\lambda} = \kappa^1(\lambda; A, R)\varphi^{1,\lambda}, \qquad \varphi^{1,\lambda} > 0.$$

We point out that $\kappa^1(\lambda; A, R)$ does not depend on the common period of A and R that we choose. Then, we set

$$c^1(A,R) := \inf_{\lambda > 0} \frac{\kappa^1(\lambda; A, R)}{\lambda},$$

which, by the classical Freidlin-Gärtner formula (4), does indeed correspond to the spreading speed of a population not structured in phenotype, with diffusion coefficient A and with intrinsic growth rate R.

Unless otherwise specified, we allow a and μ to depend on both variables x and θ.

As $L \to +\infty$: Possible to forget the phenotype. First, we compute the limit of the spreading speed as the period goes to infinity. We assume that $a = a(x)$ is independent of θ and that $\mu = \mu(\theta)$ is independent of x. For all $x \in \mathbb{R}$, we say that $(\psi_x, H_m(x)) \in \mathcal{C}^2(\overline{\Theta}) \times \mathbb{R}$ solves the *local principal eigenvalue problem* if:

$$\begin{cases} m\nabla_\theta \cdot (\mu \nabla_\theta \psi_x) + r(x,\cdot)\psi_x = H_m(x)\psi_x & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \psi_x = 0 & \text{over } \partial\Theta, \\ \psi_x > 0 & \text{in } \Theta. \end{cases} \tag{10}$$

We call $H_m(x)$ the *local principal eigenvalue*. As mentioned in the introduction, if a and μ are constant and r only depends on θ, then H_m is independent of x and the spreading speed of the solution is $2\sqrt{aH_m}$. This is reminiscent of the spreading speed for the Fisher-KPP equation: hence H_m plays the role of a local growth rate.

Theorem 2.5. *Fix $m > 0$ and assume that $k^0_{m,L_0} > 0$ for some $L_0 > 0$. Assume that $a = a(x)$ is independent of θ and that $\mu = \mu(\theta)$ is independent of x. Then $c_{m,L}$ converges as $L \to +\infty$ and*

$$\lim_{L\to+\infty} c_{m,L} = \lim_{L\to+\infty} c^1\left(a_L, (H_m)_L\right),$$

where, with the usual notation, $(H_m)_L(x) = H_m(x/L)$ is the L-periodic version of H_m.

Theorem 2.5 allows one to find a more or less explicit formula for the limit, given in Proposition 4.3 below (see also [28]). This formula, in fact, is counter-intuitive. Let us try – and fail – to guess what it should be. For $x \in \mathbb{R}$, let $c(x) = 2\sqrt{a(x)H_m(x)}$ be the spreading speed corresponding to the equation with coefficients "frozen" at x. Since the period is very large, the environment is locally almost homogeneous. Hence, we expect that at position x, the instantaneous speed of the invasion is $c(x)$. Averaging over the period, the resulting spreading speed should be the harmonic mean of $x \mapsto c(x)$:

$$c_H := \left(\int_0^1 \frac{1}{c(y)}\,\mathrm{d}y\right)^{-1}.$$

Unfortunately, this is not the case in general. We have indeed, if a is constant and H is not constant:

$$c_H < \lim_{L\to+\infty} c_{m,L}. \tag{11}$$

This is proved after the proof of Theorem 2.5. The same phenomenon also occurs for the equation without the phenotypic dimension (see [28]). For bistable equations, the above heuristic does work, see [16].

This counter-intuitive phenomenon has been dubbed the "tail problem" and is due to the fact that the front is pulled by an extremely small sub-population [20, 30]. This is a true caveat in the modelling properties of equations of the Fisher-KPP type. A first possibility to overcome it is to consider the bistable case by adding an Allee effect [27]. Biologically, this means that cooperation is needed for propagation, so that a small population cannot survive by itself. A second possibility is to first work in finite populations, consider first the limit $L \to +\infty$, and only then consider the infinite population limit; with this respect, see [33].

As $L \to 0$: Impossible to forget the phenotype. Second, we compute the limit of $c_{m,L}$ as $L \to 0$. Here, we shall not be able to express the limit in terms of 1-dimensional speeds $c^1(A, R)$.

We introduce a "homogenised" principal eigenvalue problem. For a function $f : \mathbb{R} \times \Theta \to \mathbb{R}$ which is 1-periodic in x, we let

$$\widetilde{f}^A(\theta) := \int_0^1 f(x, \theta)\, \mathrm{d}x$$

be the arithmetic mean on a period in the direction $\mathbb{R}$. If $f > 0$, we let

$$\widetilde{f}^H(\theta) := \left(\int_0^1 \frac{\mathrm{d}x}{f(x, \theta)} \right)^{-1}$$

be the harmonic mean on a period in the direction $\mathbb{R}$. We say that $(\widetilde{\psi}_m^\lambda, \widetilde{k}_m^\lambda) \in \mathcal{C}^2(\overline{\Theta}) \times \mathbb{R}$ solves the *homogenised principal eigenvalue problem* if:

$$\begin{cases} m \nabla_\theta \cdot \left(\widetilde{\mu}^A \nabla_\theta \widetilde{\psi}_m^\lambda \right) + \left(\widetilde{r}^A + \lambda^2 \widetilde{a}^H \right) \widetilde{\psi}_m^\lambda = \widetilde{k}_m^\lambda \widetilde{\psi}_m^\lambda & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \widetilde{\psi}_m^\lambda = 0 & \text{over } \partial\Theta, \\ \widetilde{\psi}_m^\lambda > 0 & \text{in } \Theta. \end{cases} \tag{12}$$

We call $\widetilde{k}_m^\lambda$ the *homogenised principal eigenvalue*.

Theorem 2.6. *Fix $m > 0$ and assume that $\widetilde{k}_m^0 > 0$. Then the limit of $c_{m,L}$ as $L \to 0$ exists and*

$$\lim_{L \to 0} c_{m,L} = \inf_{\lambda > 0} \frac{\widetilde{k}_m^\lambda}{\lambda}.$$

Moreover, we have the following variational formula:

$$\lim_{L \to 0} c_{m,L} = 2 \max_{\psi \in H^1(\Theta),\, \|\psi\|_{L^2(\Theta)} = 1,\, R_\psi > 0} \left(\sqrt{A_\psi R_\psi} \right),$$

where $A_\psi := \displaystyle\int_\Theta \widetilde{a}^H \psi^2$ *and* $R_\psi := \displaystyle\int_\Theta \left(\widetilde{r}^A \psi^2 - m \widetilde{\mu}^A |\nabla \psi|^2 \right)$.

If the coefficients a, μ and r are independent of the phenotype θ, then so is $\widetilde{\psi}_m^\lambda$; thus

$$\widetilde{k}_m^\lambda = \widetilde{r}^A + \lambda^2 \widetilde{a}^H$$

and we obtain, by the first equality in Theorem 2.6,

$$\lim_{L \to 0} c_{m,L} = 2 \sqrt{\widetilde{a}^H \widetilde{r}^A}.$$

This is the result proved in [17] for the equation without the phenotypic variable.

As $m \to 0$ or $m \to +\infty$: Possible to forget the phenotype. Last, we compute the limits of the spreading speed as the mutation scaling parameter m goes to zero or infinity. For a function f defined on $\mathbb{R} \times \Theta$, we let

$$\overline{f}(x) := \frac{1}{|\Theta|} \int_\Theta f(x,\theta)\, \mathrm{d}\theta$$

be the arithmetic mean of f in the direction Θ. Note that $\overline{f}$ differs from the notation $\widetilde{f}^A$, which is the arithmetic mean of f on a period in the direction $\mathbb{R}$.

Theorem 2.7. *Fix $L > 0$.*

(i) Assume that $a = a(x)$ and $\mu = \mu(x)$ are independent of θ. Assume moreover that $\kappa^1(0; a, \overline{r}) > 0$. Then the limit of $c_{m,L}$ as $m \to +\infty$ exists and

$$\lim_{m\to+\infty} c_{m,L} = c^1(a, \overline{r}).$$

(ii) Assume that $a = a(x)$ is independent of θ and that $\mu = \mu(\theta)$ is independent of x. Assume moreover that there exists $\theta \in \overline{\Theta}$ such that $\kappa^1(0; a(\cdot), r(\cdot, \theta)) > 0$. Then the limit of $c_{m,L}$ as $m \to 0$ exists and

$$\lim_{m\to 0} c_{m,L} = \max_{\theta\in\overline{\Theta} \ / \ \kappa^1(0;a(\cdot),r(\cdot,\theta))>0} c^1(a(\cdot), r(\cdot, \theta)).$$

(iii) If the conditions for the first point and second points are satisfied, then

$$\lim_{m\to+\infty} c_{m,L} \leqslant \lim_{m\to 0} c_{m,L}.$$

In this theorem, the assumptions that $\kappa^1(0; a, \overline{r}) > 0$ and that $\kappa^1(0; a(\cdot), r(\cdot, \theta)) > 0$ for some $\theta \in \overline{\Theta}$ ensure that in the limiting regime, there is indeed a spreading speed.

2.3 The effect of the mutations

Using the previous technical mathematical results, we are ready to give several consequences which have an easy biological interpretation and which highlight the role of the phenotypic dimension in the qualitative behaviour of the population. We assume throughout Subsection 2.3 that $a = a(x)$ is independent of θ and that $\mu = \mu(\theta)$ is independent of x. We define

$$\gamma := \lim_{m\to 0} \lim_{L\to+\infty} c_{m,L} - \lim_{L\to+\infty} \lim_{m\to 0} c_{m,L}.$$

We assume that there is no phenotype which is the best everywhere:

$$\forall \theta \in \overline{\Theta}, \quad \exists (x, \sigma) \in \mathbb{R} \times \overline{\Theta}, \qquad r(x, \sigma) > r(x, \theta). \tag{13}$$

The following theorem shows that γ is well-defined, and that under assumption (13), γ is positive and can be interpreted as the maximal potential effect of mutations on the spreading speed.

Theorem 2.8. *We assume that a is independent of θ and that μ is independent of x. We also assume that there exist $\underline{L} > 0$ and $\theta \in \overline{\Theta}$ such that $\kappa^1(0; a, r_{\underline{L}}(\cdot, \theta)) > 0$. Finally, we assume that (13) holds. Then, there exists $L_0 > 0$ such that for all $L > L_0$, there exists an optimal mutation coefficient $m^*(L) > 0$, in the sense that*

$$c_{m^*(L),L} = \sup_{m>0} c_{m,L}.$$

Moreover, γ is well-defined, is positive, and for all $\varepsilon > 0$, there exists $L^\varepsilon \geqslant L_0$ such that for all $L > L^\varepsilon$,

$$c_{m^*(L),L} > \lim_{m\to 0} c_{m,L} + \gamma - \varepsilon$$

Let us comment on this theorem.

First, the fact that there is an optimal mutation coefficient $m^*(L) > 0$, together with the inequalities, suggest that there is a trade-off between two phenomena: too small a mutation coefficient implies that the population cannot benefit from the diversity of phenotypes; too high a mutation coefficient implies that the population suffers from a mutation load, i.e. suffers from the influence of the least adapted phenotypes. As the following proposition shows, this trade-off disappears in the limits $L \to +\infty$ and $L \to 0$: in both cases, the environment is "almost homogeneous", so that having a higher capacity of adaptation is useless, but increases the mutation load.

Proposition 2.9. *We assume that a is independent of θ and that μ is independent of x. We let $I \subset (0, +\infty)$ be an interval.*

(*i*) *Assume that $\widetilde{k}^0_m > 0$ for all $m \in I$. Then the function*

$$m \in I \mapsto \lim_{L\to 0} c_{m,L}$$

is well-defined and nonincreasing.

(*ii*) *Assume that there exists $L_0 > 0$ such that for all $m \in I$, we have $k^0_{m,L_0} > 0$. Then the function*

$$m \in I \mapsto \lim_{L\to+\infty} c_{m,L}$$

is well-defined and nonincreasing.

Moreover, if there exists $x \in \mathbb{R}$ such that $\theta \mapsto r(x, \theta)$ is not constant, then we can replace "nonincreasing" by "strictly decreasing" in both statements.

Second, the fact that $\gamma > 0$ means that for an "infinite period", very small mutations have a non-vanishing effect on the spreading speed. The value γ describes the maximal effect on the speed which mutations can have. With this respect, see also [18, 34, 38].

Third, we state a slightly counter-intuitive result.

Proposition 2.10. *Fix $L > 0$. The function $m \mapsto k^0_{m,L}$ is nonincreasing.*

Theorem 2.8 implies that for L large enough, $m \mapsto c_{m,L}$ is not nonincreasing. But, as mentioned above, the ability of persistence can be measured by the value of $k^0_{m,L}$. Thus, Proposition 2.10 means that *making the persistence easier is not equivalent to increasing the spreading speed.*

Last, we state a proposition which brings out the different qualitative properties of the two phenomena, spreading and mutation. For the period, there is no trade-off: the higher the period, the higher the speed. This property also holds when the phenotype is not taken into account [35].

Proposition 2.11. *Fix $m > 0$. Let $L_0 > 0$ such that $k^0_{m,L_0} > 0$. The function $L \mapsto c_{m,L}$ is positive, continuous and nondecreasing on $[L_0, +\infty)$.*

In Section 3, we will show that solutions of equations of the type (7) have a spreading speed which is given by a formula analogous to the Freidlin-Gärtner formula (Theorem 2.3). Using this formula, we will then look at the behaviour of the spreading speed of the solution of (7) as $L \to 0$, $L \to +\infty$ (Section 4), $m \to 0$ and $m \to +\infty$ (Section 5). The qualitative properties about the effect of the mutations are proved in Subsections 4.1, 5.3 and 5.4.

3 The Freidlin-Gärtner formula (Theorem 2.3)

In this part, we prove Theorem 2.3. For notational convenience, we shall assume throughout that $L = 1$ and $m = 1$. The notations thus simplify:

$$c = c_{m,L}, \qquad k^\lambda = k^\lambda_{m,L}, \qquad \varphi^\lambda = \varphi^\lambda_{m,L}.$$

3.1 Harnack inequalities

We state a nonstandard version of the parabolic Harnack inequality, which was found by Alfaro, Berestycki and Raoul in [1] and which is well adapted to our context. Contrarily to the standard parabolic Harnack inequality, in this new inequality, there is no delay in time. Recall that there exists $\eta > 0$ such that $a \geqslant \eta$, $\mu \geqslant \eta$, and that $\Theta \subset \mathbb{R}^P$.

Theorem 3.1 ([1])**.** *Let $K > 0$ and $f \in L^\infty([0,+\infty) \times \mathbb{R} \times \Theta)$ such that $\|f\|_\infty < K$, $\|a\|_\infty < K$, $\|\partial_x a\|_\infty < K$ and $\|\mu\|_\infty < K$. Let $U > 0$ and $\delta > 0$. Then there exists a constant $C > 0$ depending only on K, U, δ, η, P and $\mathrm{diam}(\Theta)$ such that a nonnegative function $u(t,x,\theta)$ which satisfies $\|u\|_\infty \leqslant U$ and*

$$\begin{cases} \partial_t u(t,x,\theta) = \partial_x(a\partial_x u) + \nabla_\theta \cdot (\mu \nabla_\theta u) + f(t,x,\theta)u, & t > 0, (x,\theta) \in \mathbb{R} \times \Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta u(t,x,\theta) = 0, & (x,\theta) \in \mathbb{R} \times \partial\Theta, \end{cases} \tag{14}$$

satisfies also, for all $t_0 \geqslant 1$, for all $x_0 \in \mathbb{R}$,

$$\sup_{\theta \in \Theta} u(t_0, x_0, \theta) \leqslant C \inf_{\theta \in \Theta} u(t_0, x_0, \theta) + \delta.$$

Proof. The proof is almost the same as that of [1, Theorem 2.6], which holds only in the full space. We only need to deal with the boundary $\partial\Theta$. We prove the result for $t_0 = 2$ and $x_0 = 0$. We take $R > diam(\Theta)$. As in [1], we introduce the following function, defined on $[0, +\infty) \times \mathbb{R} \times \Theta$ and independent of the variable θ:

$$\phi(t,x,\theta) := e^{K(t-1)} \left[\max_{|x'| \leqslant \beta R, \theta' \in \Theta} u(1,x',\theta') + \frac{2U}{(\beta R)^2} K(1+\beta R)(t-1) + \frac{Ux^2}{(\beta R)^2} \right],$$

for some $\beta > 1$ to be determined later. We have:

$$\begin{aligned} &\partial_t \phi(t,x,\theta) - \partial_x(a\partial_x\phi) - \nabla_\theta \cdot (\mu \nabla_\theta \phi) - f(t,x,\theta)\phi \\ &\qquad \geqslant \left(K\phi + e^{K(t-1)} \times \frac{2U}{(\beta R)^2} K(1+\beta R) \right) - e^{K(t-1)} \times \frac{2U}{(\beta R)^2} (a + x\partial_x a) - 0 - K\phi. \end{aligned}$$

Therefore, since $\|a\|_\infty \leqslant K$ and $\|\partial_x a\|_\infty \leqslant K$, we have

$$\partial_t \phi(t,x,\theta) - \partial_x(a\partial_x\phi) - \nabla_\theta \cdot (\mu \nabla_\theta \phi) - f(t,x,\theta)\phi \geqslant 0$$

on $(1,2) \times B(0,\beta R) \times \Theta$. We also have the boundary conditions: $\phi(1,x,\theta) \geqslant u(1,x,\theta)$ on $B(0,\beta R) \times \Theta$ and $\phi(t,x,\theta) \geqslant u(t,x,\theta)$ on $(\partial B(0,\beta R)) \times \Theta$. Finally, we have $\nu \cdot \nabla_\theta \phi = 0$ and $\nu \cdot \nabla_\theta u = 0$ on $B(0,\beta R) \times \partial\Theta$. Therefore we can apply the comparison principle:

$$\phi \geqslant u \quad \text{ on } [1,2] \times B(0,\beta R) \times \Theta.$$

In particular,

$$\begin{aligned} \sup_{|x|<R, \theta \in \Theta} u(2,x,\theta) &\leqslant \sup_{|x|<R, \theta \in \Theta} \phi(2,x,\theta) \\ &\leqslant e^K \sup_{|x|<\beta R, \theta \in \Theta} u(1,x,\theta) + \delta, \end{aligned}$$

for β large enough.

We now wish to apply the parabolic Harnack inequality up to the boundary of Θ. In order to do this, we use the regularity of $\partial\Theta$ and the Neumann boundary condition to extend the solution u to the solution of a uniformly parabolic equation on a larger domain $\mathbb{R} \times \widetilde{\Theta}$ with $\overline{\Theta} \subset \widetilde{\Theta}$. See e.g. the argument for the proof of Step 2 in [10, Theorem 3.1]. Applying the classical parabolic Harnack inequality in $\mathbb{R} \times \widetilde{\Theta}$ implies, in our context, that we may apply the parabolic Harnack inequality up to the boundary of Θ: there exists a constant $C > 0$ such that

$$e^K \sup_{|x|<\beta R, \theta \in \Theta} u(1,x,\theta) \leqslant C \inf_{|x|<\beta R, \theta \in \Theta} u(2,x,\theta).$$

This gives:

$$\sup_{|x|<R, \theta \in \Theta} u(2,x,\theta) \leqslant C \inf_{|x|<\beta R, \theta \in \Theta} u(2,x,\theta) + \delta.$$

This implies

$$\sup_{\theta \in \Theta} u(t_0,x_0,\theta) \leqslant C \inf_{\theta \in \Theta} u(t_0,x_0,\theta) + \delta.$$

□

3.2 A priori estimates

Lemma 3.2. *For all $\lambda > 0$,*

$$\lambda^2 \inf a - \lambda \|\partial_x a\|_\infty - \|r\|_\infty \leqslant k^\lambda \leqslant \lambda^2 \sup a + \lambda \|\partial_x a\|_\infty + \|r\|_\infty .$$

Proof. For a 1-periodic in x function $g \in \mathcal{C}^{0,\alpha}(\mathbb{R} \times \overline{\Theta})$, we let $\kappa(g)$ be the principal eigenvalue associated to the operator defined by

$$\mathcal{L}u = \partial_x(a\partial_x u) + \nabla_\theta \cdot (\mu \nabla_\theta u) - 2\lambda a \partial_x u + gu,$$

with Neumann boundary conditions on $\mathbb{R} \times \partial\Theta$. By definition, we have

$$k^\lambda = \kappa(\lambda^2 a - \lambda \partial_x a + r).$$

Moreover, if $f_1 \leqslant f_2$ then $\kappa(f_1) \leqslant \kappa(f_2)$. Therefore,

$$\kappa(\lambda^2 \inf a - \lambda \|\partial_x a\|_\infty - \|r\|_\infty) \leqslant k^\lambda \leqslant \kappa(\lambda^2 \sup a + \lambda \|\partial_x a\|_\infty + \|r\|_\infty).$$

Finally, $\varphi \equiv 1$ is an eigenfunction of the operator $\mathcal{L}_g$ when g is constant, which implies:

$$\begin{aligned} k(\lambda^2 \inf a - \lambda \|\partial_x a\|_\infty - \|r\|_\infty) &= \lambda^2 \inf a - \lambda \|\partial_x a\|_\infty - \|r\|_\infty , \\ k(\lambda^2 \sup a + \lambda \|\partial_x a\|_\infty + \|r\|_\infty) &= \lambda^2 \sup a + \lambda \|\partial_x a\|_\infty + \|r\|_\infty . \end{aligned}$$

The conclusion follows. □

3.3 Proof of Theorem 2.3

We define

$$c_{GF} := \inf_{\lambda > 0} \frac{k^\lambda}{\lambda}.$$

Let us show that a solution u of (7) starting from a bounded nonnegative initial condition with support bounded from above, has a spreading speed c, and that c satisfies

$$c = c_{GF}.$$

The proof is cut into two parts: Proposition 3.3 below means that the first requirement of Definition 2.1 is satisfied for all $c \geqslant c_{GF}$; Proposition 3.4 below means that the second requirement of Definition 2.1 is satisfied for all $c \leqslant c_{GF}$.

Proposition 3.3. *Assume that $u_0 \in \mathcal{C}^0(\mathbb{R} \times \overline{\Theta})$ is nonnegative, bounded and has a support bounded from above. Let u be the solution of (7). For each $c' > c_{GF}$,*

$$\lim_{t \to +\infty} \rho(t, c't) = 0.$$

Proof. Let $c' > c_{GF}$ and let $\lambda > 0$ such that $c'' := k^\lambda/\lambda$ satisfies $c_{GF} \leqslant c'' < c'$. Let $\varphi^\lambda > 0$ be a principal eigenfunction of $\mathcal{L}_\lambda$. Let

$$\bar{u}(t,x,\theta) := Ce^{-\lambda(x-c''t)}\varphi^\lambda(x,\theta),$$

for some constant C to be chosen later. Short computations show that $\bar{u}$ solves

$$\partial_t \bar{u} = \partial_x(a\partial_x \bar{u}) + \nabla_\theta \cdot (\mu \nabla_\theta \bar{u}) + r(x,\theta)\bar{u}.$$

Since u_0 is bounded and has a support bounded above, there exists $C > 0$ so large that $u_0 \leqslant \bar{u}(0,\cdot,\cdot)$, we obtain by the parabolic comparison principle: for all $t \geqslant 0$,

$$u(t,\cdot,\cdot) \leqslant \bar{u}(t,\cdot,\cdot). \tag{15}$$

Since φ^λ is continuous and periodic, φ^λ is bounded. Thus for $c' > c''$, $\bar{u}(t,c't,\theta)$ converges to 0 uniformly in θ. With (15), this proves the proposition. □

Proposition 3.4. *Assume that $u_0 \in \mathcal{C}^0(\mathbb{R} \times \overline{\Theta})$ is nonnegative, bounded and has a support bounded from above. Let u be the solution of (7). For each $c'' < c_{GF}$,*

$$\liminf_{t\to+\infty} \rho(t,c''t) > 0.$$

In order to prove the proposition, we first consider the following auxiliary intrinsic growth rate:

$$r^\varepsilon(x,\theta) := r(x,\theta) - \varepsilon$$

and the following auxiliary *local* problem:

$$\begin{cases} \partial_t u^\varepsilon(t,x,\theta) = \partial_x(a\partial_x u^\varepsilon) + \nabla_\theta \cdot (\mu \nabla_\theta u^\varepsilon) + u^\varepsilon\left(r^\varepsilon(x,\theta) - Gu^\varepsilon\right), & t > 1, (x,\theta) \in \mathbb{R}\times\Theta, \\ u^\varepsilon(1,x,\theta) = \dfrac{1}{2}u(1,x,\theta), & (x,\theta) \in \mathbb{R}\times\Theta, \\ \nu \cdot \nabla_\theta u^\varepsilon(t,x,\theta) = 0, & t \geqslant 1, (x,\theta) \in \mathbb{R}\times\partial\Theta, \end{cases} \tag{16}$$

where the constant $G > 0$ is to be chosen in the proof of Lemma 3.5. We note that $0 < u^\varepsilon(1,\cdot,\cdot) < u^\varepsilon(1,\cdot,\cdot)$ thanks to the strong parabolic maximum principle. We will first show that for $G > 0$ well chosen, u spreads at least as fast as u^ε. Then, we will estimate the spreading speed of u^ε. Importantly, we shall remark that u^ε spreads at a speed *independent* of G (the speed, indeed, only depends on the linear problem).

Lemma 3.5. *Let u be the solution of the nonlocal problem (7). Let $\varepsilon > 0$. There exists $G > 0$ such that the solution u^ε of (16) satisfies, for all $t \geqslant 1$, $x \in \mathbb{R}$, $\theta \in \Theta$,*

$$u(t,x,\theta) \geqslant u^\varepsilon(t,x,\theta).$$

Proof. Let us write the first line of the nonlocal problem (7) as

$$\partial_t u(t,x,\theta) - \partial_x(a\partial_x u) - \nabla_\theta \cdot (\mu \nabla_\theta u) = f(t,x,\theta)u$$

with

$$f(t,x,\theta) = r(x,\theta) - \rho(t,x).$$

By the existence theorem of [14], u and ρ are globally bounded. Further, r is bounded, so f is also globally bounded. Therefore, we can apply Theorem 3.1: for each $\delta > 0$, there exists $C > 0$ such that for all $t \geqslant 1$, $x \in \mathbb{R}$, $\theta \in \Theta$,

$$Cu(t,x,\theta) + \delta \geqslant \sup_{\sigma \in \Theta} u(t,x,\sigma).$$

This implies that for each $t \geqslant 1$, $x \in \mathbb{R}$, $\theta \in \Theta$,

$$\rho(t,x) = \int_\Theta u(t,x,\sigma)\,\mathrm{d}\sigma \leqslant |\Theta|\, Cu(t,x,\theta) + |\Theta|\,\delta.$$

We choose δ small enough that $|\Theta|\,\delta < \varepsilon/2$:

$$\rho(t,x) \leqslant |\Theta|\, Cu(t,x,\theta) + \varepsilon/2. \tag{17}$$

Now, we set $G := |\Theta| C$ and we show that for this value of G, the lemma holds. We recall that $u^\varepsilon(1,\cdot,\cdot) < u(1,\cdot,\cdot)$. We assume that there exists a minimal time $t_0 > 1$ such that there exist $x_0 \in \mathbb{R}$ and $\theta_0 \in \Theta$ such that

$$u(t_0,x_0,\theta_0) = u^\varepsilon(t_0,x_0,\theta_0).$$

Then we must have:

$$\left[\partial_t - (\partial_x(a\partial_x) + \nabla_\theta \cdot (\mu \nabla_\theta))\right](u - u^\varepsilon)(t_0,x_0,\theta_0) \leqslant 0.$$

This implies:

$$(r(x_0,\theta_0) - \rho(t_0,x_0))\, u(t_0,x_0,\theta_0) - (r^\varepsilon(x_0,\theta_0) - Gu^\varepsilon(t_0,x_0,\theta_0))\, u^\varepsilon(t_0,x_0,\theta_0) \leqslant 0.$$

Recalling that $u(t_0,x_0,\theta_0) = u^\varepsilon(t_0,x_0,\theta_0) > 0$, we get

$$r(x_0,\theta_0) - \rho(t_0,x_0) \leqslant r^\varepsilon(x_0,\theta_0) - Gu(t_0,x_0,\theta_0).$$

Finally, we note that $r - r^\varepsilon = \varepsilon$. This yields the contact condition:

$$Gu(t_0,x_0,\theta_0) \leqslant \rho(t_0,x_0) - \varepsilon. \tag{18}$$

This contact condition is impossible by virtue of (17) (recall that $G = |\Theta| C$). Therefore, there can be no contact between u and u^ε, so u^ε must remain below u.

□

Proof of Proposition 3.4. Let $k^{\varepsilon,\lambda}$ be the principal eigenvalue of the operator

$$\mathcal{L}^{\varepsilon,\lambda} := \partial_x(a\partial_x) + \nabla_\theta \cdot (\mu \nabla_\theta) - 2\lambda a \partial_x + (r^\varepsilon(x,\theta) + \lambda^2 a + \partial_x a),$$

acting on $\mathcal{C}^2(\mathbb{R}\times\overline{\Theta})$ functions which are 1-periodic in x; that is, $k^{\varepsilon,\lambda}$ is the only value such that there exists $\varphi^{\varepsilon,\lambda}\in\mathcal{C}^2(\mathbb{R}\times\overline{\Theta})$ satisfying

$$\begin{cases} \mathcal{L}^{\varepsilon,\lambda}\varphi^{\varepsilon,\lambda} = k^{\varepsilon,\lambda}\varphi^{\varepsilon,\lambda} & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta\varphi^{\varepsilon,\lambda} = 0 & \text{over } \mathbb{R}\times\partial\Theta, \\ \varphi^{\varepsilon,\lambda} > 0 & \text{in } \mathbb{R}\times\Theta, \\ \varphi^{\varepsilon,\lambda} & \text{1-periodic in } x. \end{cases} \tag{19}$$

Let us denote by

$$c^\varepsilon_{GF} := \inf_{\lambda>0}\frac{k^{\varepsilon,\lambda}}{\lambda}$$

the Freidlin-Gärtner speed corresponding to u^ε. By Section 8 of [42], the solution u^ε of the local problem (16) spreads (in the definition of [42]) at speed c^ε_{GF}. This implies in particular that for all $c'' < c^\varepsilon_{GF}$,

$$\lim_{t\to+\infty}\left(\inf_{\theta\in\Theta} u^\varepsilon(t,c''t,\theta)\right) > 0.$$

Since $r^\varepsilon = r-\varepsilon$, we have $k^{\varepsilon,\lambda} = k^\lambda - \varepsilon$ and:

$$c^\varepsilon_{GF} = \inf_{\lambda>0}\frac{k^{\varepsilon,\lambda}-\varepsilon}{\lambda} = c_{GF} + o_{\varepsilon\to0}(1).$$

Let $c'' < c_{GF}$. There exists $\varepsilon>0$ so small that $c'' < c^\varepsilon_{GF}$. We then have:

$$\liminf_{t\to+\infty}\rho(t,c''t) \geqslant \liminf_{t\to+\infty}\int_\Theta u^\varepsilon(t,c''t,\sigma)\,\mathrm{d}\sigma \geqslant |\Theta|\lim_{t\to+\infty}\left(\inf_{\theta\in\Theta} u^\varepsilon(t,c''t,\theta)\right) > 0,$$

which proves the proposition.

□

4 Behaviour of the spreading speed with respect to the period

This part is devoted to the proof of Proposition 2.11 and Theorems 2.5 and 2.6. For notational convenience, we shall assume throughout that $m=1$. The notations thus simplify:

$$c_L = c_{m,L}, \qquad k^\lambda_L = k^\lambda_{m,L}, \qquad \varphi^\lambda_L = \varphi^\lambda_{m,L}.$$

In Subsection 4.1, we prove that the function $L\mapsto c_L$ is continuous and nondecreasing (Proposition 2.11). In Subsection 4.2, we compute the limit of c_L as $L\to+\infty$ (Theorem 2.5). In Subsection 4.3, we compute the limit of c_L as $L\to0$ (Theorem 2.6).

4.1 Monotony and continuity (Proposition 2.11)

Proof of Proposition 2.11, part 1. Take $L_1 > 0$ such that $k^0_{L_1} > \delta$. Take $L_2 > L_1$. Using Proposition 4.1 below, we have $k^0_L > \delta$ for all $L \in [L_1, L_2]$, so c_L is well defined and positive for all $L \in [L_1, L_2]$. We prove that the function $L \mapsto c_L$ is continuous on $[L_1, L_2]$. We define

$$f : (\lambda, L) \mapsto \frac{k^\lambda_L}{\lambda}.$$

The function $(\lambda, L) \mapsto k^\lambda_L$ is continuous. Hence, as $\lambda \to 0$, we have $f(\lambda, L) \to +\infty$ uniformly in $L \in [L_1, L_2]$. Moreover, by Lemma 3.2, as $\lambda \to +\infty$, we have $f(\lambda, L) \to +\infty$ uniformly in $L \in [L_1, L_2]$. Thus, there exist $\lambda_1 > 0$ and $\lambda_2 > \lambda_1$ such that for all $L \in [L_1, L_2]$,

$$c_L = \min_{\lambda \in [\lambda_1, \lambda_2]} f(\lambda, L).$$

This implies that the function $L \mapsto c_L$ is continuous on (L_1, L_2). □

The second part of Proposition 2.11, i.e. the fact that $L \mapsto c_L$ is nondecreasing, is a consequence of the following proposition.

Proposition 4.1. *For all $\lambda \in \mathbb{R}$, the function $L \mapsto k^\lambda_L$ is nondecreasing on $(0, +\infty)$.*

The proof of the proposition is almost the same as that of [35, Proposition 4.1]. We give an idea of the proof to focus on the assumptions that are needed. For a 1-periodic function f, we denote by $f_L(x, \theta) := f\left(\frac{x}{L}, \theta\right)$ its L-periodic version.

Take functions $q \in \mathcal{C}^{0,\alpha}(\mathbb{R} \times \overline{\Theta})$ and $g \in \mathcal{C}^{0,\alpha}(\mathbb{R} \times \overline{\Theta})$ which are 1-periodic in x. We denote by $\chi[q, g]$ the principal eigenvalue associated to the eigenvalue problem

$$\begin{cases} \partial_x(a_L \partial_x \varphi) + \nabla_\theta \cdot (\mu_L \nabla_\theta \varphi) - q_L \partial_x \varphi g_L \varphi = \chi[q, g]\varphi & \text{in } \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta \varphi = 0 & \text{over } \mathbb{R} \times \partial\Theta, \\ \varphi & \text{is 1-periodic in } x, \\ \varphi > 0 & \text{in } \mathbb{R} \times \Theta. \end{cases}$$

We let $A(x, \theta)$ be the total diffusion matrix in $\mathbb{R}^{1+P}$, that is:

$$A(x, \theta) = \begin{pmatrix} a(x, \theta) & 0 & \cdots & 0 \\ 0 & \mu(x, \theta) & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & \mu(x, \theta) \end{pmatrix}.$$

The main tool of the proof of Proposition 4.1 is the following theorem, which allows one to turn the study of a nonsymmetric operator into the study of a symmetric operator.

Theorem 4.2 (Theorem 2.2 in [35]). *Let $q \in \mathcal{C}^{0,\alpha}(\mathbb{R}\times\overline{\Theta})$ and $g \in \mathcal{C}^{0,\alpha}(\mathbb{R}\times\overline{\Theta})$ be 1-periodic in x. Let*

$$\mathcal{E} := \left\{\beta \in \mathcal{C}^{1,\alpha}(\mathbb{R}\times\overline{\Theta}) \ \ / \ \ \beta \text{ is 1-periodic in } x \text{ and } \nu\cdot\nabla_\theta\beta = 0 \text{ on } \mathbb{R}\times\partial\Theta\right\}.$$

Then:

$$\chi[q,g] = \min_{\beta\in\mathcal{E}} \chi\left[0, g + \nabla_{(x,\theta)}\beta\cdot A\nabla_{(x,\theta)}\beta - q\partial_x\beta + \frac{\partial_x q}{2}\right].$$

The proof of Theorem 4.2 is almost the same as that of [35, Theorem 2.2]. To make it work in our context, the Neumann boundary condition on $\mathbb{R}\times\partial\Theta$, satisfied by the principal eigenfunction and by the elements of $\mathcal{E}$, is central. Using Theorem 4.2, we may conclude in exactly the same way as in the proof of [35, Proposition 4.1] that $L \mapsto k_L^\lambda$ is nondecreasing.

4.2 When the period goes to infinity (Theorem 2.5)

As in the introduction, we let $H(x) = H_m(x)$ be the local-in-x principal eigenvalue, defined by the principal eigenvalue problem

$$\begin{cases} \nabla_\theta\cdot(\mu\nabla_\theta\psi_x) + r(x,\cdot)\psi_x = H(x)\psi_x & \text{in } \Theta, \\ \nu\cdot\nabla_\theta\psi_x = 0 & \text{over } \partial\Theta, \\ \psi_x > 0 & \text{in } \Theta. \end{cases}$$

We set $M = \max_{x\in\mathbb{R}} H(x)$ and we let $j : [M,+\infty) \to \mathbb{R}$ be the function defined by

$$j(k) = \int_0^1 \sqrt{\frac{k - H(x)}{a(x)}}\,\mathrm{d}x, \qquad k \geqslant M.$$

Note that j is a bijection from $[M,+\infty)$ to $[j(M),+\infty)$. We will prove the following proposition.

Proposition 4.3. *Assume that $k_{L_0}^0 > 0$ for some $L_0 > 0$. Assume that a is independent of θ and that μ is independent of x. Then c_L converges as $L \to +\infty$ and*

$$\lim_{L\to+\infty} c_L = \inf_{\lambda\geqslant M} \frac{j^{-1}(\lambda)}{\lambda}.$$

Theorem 2.5 is a consequence of the Proposition 4.3 and of [28, Theorem 2.3], which says that

$$\lim_{L\to+\infty} c^1(a_L, (H_m)_L) = \inf_{\lambda\geqslant M} \frac{j^{-1}(\lambda)}{\lambda}.$$

To prove Proposition 4.3, we first prove the following lemma.

Lemma 4.4. *Let $\lambda > 0$. Let the assumptions of Proposition 4.3 hold. If $\lambda \geqslant j(M)$, then k_L^λ converges as $L \to +\infty$ and*

$$\lim_{L\to+\infty} k_L^\lambda = j^{-1}(\lambda).$$

If $\lambda < j(M)$, then k_L^λ converges as $L \to +\infty$ and

$$\lim_{L\to+\infty} k_L^\lambda = M.$$

Proof. Let $\widetilde{\varphi}_L^\lambda(x,\theta) := \varphi_L^\lambda\left(\frac{x}{L},\theta\right)$ be the 1-periodic version of φ_L^λ. Then $\widetilde{\varphi}_L^\lambda$ solves:

$$\begin{cases} \dfrac{1}{L^2}\partial_x(a\partial_x\widetilde{\varphi}_L^\lambda) + \nabla_\theta\cdot\left(\mu\nabla_\theta\widetilde{\varphi}_L^\lambda\right) - \dfrac{2\lambda a}{L}\partial_x\widetilde{\varphi}_L^\lambda \\ \qquad + \left(r(x,\theta) + \lambda^2 a - \lambda\dfrac{\partial_x a}{L}\right)\widetilde{\varphi}_L^\lambda = k_L^\lambda\widetilde{\varphi}_L^\lambda & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta\widetilde{\varphi}_\lambda = 0 & \text{over } \mathbb{R}\times\partial\Theta, \\ \widetilde{\varphi}_L^\lambda > 0 & \text{in } \mathbb{R}\times\Theta, \\ \widetilde{\varphi}_L^\lambda & \text{is 1-periodic in } x. \end{cases} \tag{20}$$

Therefore, $k_L^\lambda = \overline{k}_L^\lambda + o_{L\to+\infty}(1)$ where $\overline{k}_L^\lambda$ is the principal eigenvalue associated to the same problem but without $-\lambda\frac{\partial_x a}{L}\varphi$:

$$\begin{cases} \dfrac{1}{L^2}\partial_x(a\partial_x\widetilde{\varphi}_L^\lambda) + \nabla_\theta\cdot\left(\mu\nabla_\theta\widetilde{\varphi}_L^\lambda\right) - \dfrac{2\lambda a}{L}\partial_x\widetilde{\varphi}_L^\lambda \\ \qquad + \left(r(x,\theta) + \lambda^2 a\right)\widetilde{\varphi}_L^\lambda = \overline{k}_L^\lambda\widetilde{\varphi}_L^\lambda & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta\widetilde{\varphi}_\lambda = 0 & \text{over } \mathbb{R}\times\partial\Theta, \\ \widetilde{\varphi}_L^\lambda > 0 & \text{in } \mathbb{R}\times\Theta, \\ \widetilde{\varphi}_L^\lambda & \text{is 1-periodic in } x. \end{cases} \tag{21}$$

We now apply [13, Theorem 1.3]. To recover the notations there, we let $\varepsilon = 1/L$, and replace the slow variable by x (instead of y) and the fast variable by θ (instead of z). We rewrite j as

$$j(k) = \int_0^1 \sqrt{\frac{k - (H(x) + \lambda^2 a(x)) + \frac{(2\lambda a(x))^2}{4a(x)}}{a(x)}}\,\mathrm{d}x.$$

Now, [13, Theorem 1.3] says that as $L \to +\infty$ (i.e. $\varepsilon \to 0$),

$$\overline{k}_L^\lambda \to J^{-1}\left(\left|\int_0^1 \frac{2\lambda a(x)}{2a(x)}\right|\right) = j^{-1}(\lambda)$$

if $\lambda \geqslant J(M) = j(M)$, and

$$\overline{k}_L^\lambda \to M$$

otherwise. Hence the same convergence holds for k_L^λ. □

We are now ready to conclude the proof of Proposition 4.3.

Proof of Proposition 4.3. By the persistence assumption that $k^0_{L_0} > 0$, and by Proposition 4.1, there exists $\delta > 0$ such that for each $L \geqslant L_0$: $k^0_L > \delta$. This and Lemma 3.2 imply that for each $L \geqslant L_0$, there exists $\lambda_L > 0$ such that

$$\inf_{\lambda>0} \frac{k^\lambda_L}{\lambda} = \frac{k_L(\lambda_L)}{\lambda_L}.$$

Moreover, there exist $\lambda_- > 0$ and $\lambda_+ > 0$ such that for all $L > 0$, $\lambda_- \leqslant \lambda_L \leqslant \lambda_+$. Thus, there exist an increasing sequence $L_n \to +\infty$ and $\lambda_\infty > 0$ such that, as $n \to +\infty$, $\lambda_{L_n} \to \lambda_\infty$. Since the sequence of functions $\lambda \mapsto k^\lambda_{L_n}$ converges increasingly, as $n \to +\infty$, to

$$\lambda \mapsto \lim_{L\to+\infty} k^\lambda_L,$$

the convergence is locally uniform. We then have,

$$\liminf_{n\to+\infty} c_{L_n} = \liminf_{n\to+\infty} \frac{k_{L_n}(\lambda_{L_n})}{\lambda_{L_n}} = \liminf_{n\to+\infty} \frac{k_{L_n}(\lambda_\infty)}{\lambda_\infty}.$$

Therefore,

$$\liminf_{n\to+\infty} c_{L_n} \geqslant \inf_{\lambda>0} \lim_{L\to+\infty} \frac{k^\lambda_L}{\lambda}.$$

Finally, for all $n \geqslant 1$, and for all $\lambda > 0$, $c_{L_n} \leqslant \frac{k^\lambda_{L_n}}{\lambda}$. Taking the limit $n \to +\infty$, we obtain, for all $\lambda > 0$,

$$\limsup_{n\to+\infty} c_{L_n} \leqslant \lim_{n\to+\infty} \frac{k^\lambda_{L_n}}{\lambda}.$$

With the above, we obtain that c_{L_n} converges for all increasing sequence L_n. Hence c_L also converges and:

$$\lim_{L\to+\infty} c_L = \inf_{\lambda>0} \lim_{n\to+\infty} \frac{k^\lambda_{L_n}}{\lambda}.$$

To conclude, for $\lambda \geqslant j(M)$, we have

$$\lim_{L\to+\infty} k^\lambda_L = j^{-1}(\lambda),$$

and for $\lambda < j(M)$, we have

$$\lim_{L\to+\infty} k^\lambda_L \geqslant M = \lim_{L\to+\infty} k^{j(M)}_L.$$

Thus

$$\lim_{L\to+\infty} c_L = \inf_{\lambda>0} \lim_{L\to+\infty} \frac{k^\lambda_L}{\lambda} = \inf_{\lambda>j(M)} \lim_{L\to+\infty} \frac{k^\lambda_L}{\lambda}.$$

This concludes the proof. □

Proof of Equation (11). Assume for convenience that $a = 1$. On the one hand, we have by Proposition 4.3,

$$\begin{aligned}\lim_{L\to+\infty} c_L &= \inf_{\lambda\geqslant j(M)} \frac{j^{-1}(\lambda)}{\lambda} = \inf_{k\geqslant M} \frac{k}{j(k)} \\ &= \inf_{k\geqslant M} k\left(\int_0^1 \sqrt{k-H(x)}\,\mathrm{d}x\right)^{-1}.\end{aligned}$$

By Jensen inequality, we obtain:

$$\begin{aligned}\lim_{L\to+\infty} c_L &\geqslant \inf_{k\geqslant M} \sqrt{k^2\left(\int_0^1 (k-H(x))\,\mathrm{d}x\right)^{-1}} \\ &= \sqrt{\inf_{k\geqslant M}\left(\frac{k^2}{k-\widetilde{H}^A}\right)},\end{aligned}$$

where $\widetilde{H}^A = \int_0^1 H(x)\,\mathrm{d}x$ is the arithmetic mean of H. But:

$$\begin{aligned}\inf_{k\geqslant M}\left(\frac{k^2}{k-\widetilde{H}^A}\right) &= \inf_{k\geqslant M}\left(2\widetilde{H}^A + (k-\widetilde{H}^A) + \frac{(\widetilde{H}^A)^2}{k-\widetilde{H}^A}\right) \\ &= 2\widetilde{H}^A + \inf_{k\geqslant M-\widetilde{H}^A}\left(k + \frac{(\widetilde{H}^A)^2}{k}\right) \geqslant 4\widetilde{H}^A.\end{aligned}$$

Hence,

$$\lim_{L\to+\infty} c_L \geqslant 2\sqrt{\widetilde{H}^A}.$$

On the other hand, applying Jensen inequality twice,

$$c_H = 2\left(\int_0^1 \frac{\mathrm{d}x}{\sqrt{H(x)}}\right)^{-1} \leqslant 2\int_0^1 \sqrt{H(x)}\,\mathrm{d}x \leqslant 2\sqrt{\int_0^1 H(x)\,\mathrm{d}x} = 2\sqrt{\widetilde{H}^A}.$$

The inequality is strict if H is not constant. The inequality (11) is proved.

□

4.3 When the period goes to zero (Theorem 2.6)

In order to compute the limit of c_L as $L \to 0$, we first compute the limit as $L \to 0$ of k_L^λ. As in the introduction, we define the *homogenised principal eigenvalue* $\widetilde{k}^\lambda$ and the associated homogenised principal eigenfunction $\psi^\lambda \in \mathcal{C}^2(\overline{\Theta})$ by

$$\begin{cases} \nabla_\theta \cdot \left(\tilde{\mu}^A \nabla_\theta \widetilde{\psi}^\lambda\right) + \left(\tilde{r}^A + \lambda^2 \tilde{a}^H\right)\widetilde{\psi}^\lambda = \widetilde{k}^\lambda \widetilde{\psi}^\lambda & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \widetilde{\psi}^\lambda = 0 & \text{over } \partial\Theta, \\ \widetilde{\psi}^\lambda > 0 & \text{in } \Theta. \end{cases}$$

Lemma 4.5. *Fix $\lambda \in \mathbb{R}$. Then, as $L \to 0$,*

$$k_L^\lambda \to \widetilde{k}^\lambda.$$

Proof. Since λ is fixed, we shall omit the superindex λ in the notations. For all $L > 0$, we let $\varphi_L := \varphi_L^\lambda > 0$ and $k_L := k_L^\lambda$ solve

$$\begin{cases} \partial_x \left(a_L \partial_x \varphi_L\right) + \nabla_\theta \cdot \left(\mu_L \nabla_\theta \varphi_L\right) - 2\lambda a_L \partial_x \varphi_L \\ \qquad\qquad + \left(r_L + \lambda^2 a_L - \lambda \partial_x a_L\right) \varphi_L = k_L \varphi_L & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \varphi_L = 0 & \text{over } \partial\Theta, \\ \varphi_L & \text{is } L\text{-periodic in } x, \end{cases} \tag{22}$$

normalised so that

$$\int_{[0,1]\times\Theta} \varphi_L^2 = 1.$$

(Note that we integrate on $[0,1] \times \Theta$, so for $L \neq 1$ we do not integrate exactly on a periodic cell.) We let $\Phi_L(x,\theta) := e^{-\lambda x} \varphi_L(x,\theta)$, so that Φ_L solves

$$\begin{cases} \partial_x \left(a_L \partial_x \Phi_L\right) + \nabla_\theta \cdot \left(\mu_L \nabla_\theta \Phi_L\right) + r_L \Phi_L = k_L^\lambda \Phi_L & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \Phi_L = 0 & \text{over } \partial\Theta. \end{cases} \tag{23}$$

Step 1. Convergence of φ_L to a function $\varphi_{(0)}$ independent of x. First of all, we show that $(\varphi_L)_L$ is bounded in $W_2^1([0,1] \times \Theta)$. For $L > 0$, we note $\widehat{L} := L \times \lceil 1/L \rceil$. We point out that $\widehat{L} \to 1$ as $L \to 0$. We multiply the first line of (22) by φ_L, we integrate on $[0, \widehat{L}] \times \Theta$ and we integrate by parts. Using the L-periodicity in x and $\nu \cdot \nabla_\theta \varphi_L = 0$ on $\mathbb{R} \times \partial\Theta$, we get

$$\begin{aligned} -\int_{[0,\widehat{L}]\times\Theta} a_L \left|\partial_x \varphi_L\right|^2 - \int_{[0,\widehat{L}]\times\Theta} \mu_L \left|\nabla_\theta \varphi_L\right|^2 - 2\lambda \int_{[0,\widehat{L}]\times\Theta} a_L \varphi_L \partial_x \varphi_L \\ + \int_{[0,\widehat{L}]\times\Theta} \left(r_L + \lambda^2 a_L - \lambda \partial_x a_L\right) \varphi_L^2 = k_L \int_{[0,\widehat{L}]\times\Theta} \varphi_L^2. \end{aligned}$$

Thus, replacing $[0, \widehat{L}] \times \Theta$ by $[0,1] \times \Theta$,

$$\begin{aligned} -\int_{[0,1]\times\Theta} a_L \left|\partial_x \varphi_L\right|^2 - \int_{[0,1]\times\Theta} \mu_L \left|\nabla_\theta \varphi_L\right|^2 - 2\lambda \int_{[0,1]\times\Theta} a_L \varphi_L \partial_x \varphi_L \\ + \int_{[0,1]\times\Theta} \left(r_L + \lambda^2 a_L - \lambda \partial_x a_L\right) \varphi_L^2 = k_L \int_{[0,1]\times\Theta} \varphi_L^2 + o_{L\to 0}(1). \end{aligned}$$

Recall the assumption that there exists a constant $\eta > 0$ such that $a_L \geqslant \eta$ and $\mu_L \geqslant \eta$. We get, rearranging the terms:

$$\begin{aligned} \eta \int_{[0,1]\times\Theta} \left|\nabla \varphi_L\right|^2 \leqslant -\lambda \int_{[0,1]\times\Theta} \varphi_L^2 \partial_x a_L \\ - 2\lambda \int_{[0,1]\times\Theta} a_L \varphi_L \partial_x \varphi_L + \int_{[0,1]\times\Theta} \left(r_L + \lambda^2 a_L\right) \varphi_L^2 - k_L \int_{[0,1]\times\Theta} \varphi_L^2 + o_{L\to 0}(1), \end{aligned}$$

with $\nabla\varphi_L = (\partial_x\varphi_L, \nabla_\theta\varphi_L)$. We have:

$$-2\int_{[0,\widehat{L}]\times\Theta} a_L\varphi_L\partial_x\varphi_L - \int_{[0,\widehat{L}]\times\Theta}\varphi_L^2\partial_x a_L = -\int_{[0,\widehat{L}]\times\Theta} a_L\partial_x(\varphi_L^2) - \int_{[0,\widehat{L}]\times\Theta}\varphi_L^2\partial_x a_L$$
$$= \int_{[0,\widehat{L}]\times\Theta}\varphi_L^2\partial_x a_L - \int_{[0,\widehat{L}]\times\Theta}\varphi_L^2\partial_x a_L = 0.$$

We conclude that

$$\int_{[0,1]\times\Theta}|\nabla\varphi_L|^2 \leqslant \frac{1}{\eta}\left(\left(\|r_L\|_\infty + \lambda^2\|a_L\|_\infty\right)\int_{[0,1]\times\Theta}\varphi_L^2 - k_L\int_{[0,1]\times\Theta}\varphi_L^2\right) + o_{L\to 0}(1).$$

Since $(k_L)_{L>0}$ is bounded (see Lemma 3.2) and $\|\varphi_L\|_{L^2([0,1]\times\Theta)} = 1$, the family $(\varphi_L)_L$ is bounded in $W_2^1([0,1]\times\Theta)$. Thus, by a compact injection theorem (here compactness is due to periodicity), there is a sequence $L_n \to 0$ such that (φ_{L_n}) converges in $L^2([0,1]\times\Theta)$ to a function $\varphi_{(0)} \in L^2([0,1]\times\Theta)$. For convenience, we note $\varphi_n := \varphi_{L_n}$, $\Phi_n := \Phi_{L_n}$ and $k_n := k_{L_n}$. Since φ_n is L_n-periodic in x, the limit $\varphi_{(0)}(x,\theta) = \varphi_{(0)}(\theta)$ must be independent of x. We conclude that Φ_n converges in $L^2_{loc}(\mathbb{R}\times\overline{\Theta})$ to the function

$$\Phi_{(0)}(x,\theta) := e^{-\lambda x}\varphi_{(0)}(\theta).$$

Step 2. Apply the oscillating test function method. Since $(k_L)_{L>0}$ is bounded (see Lemma 3.2), there exists $k_{(0)} \in \mathbb{R}$ such that, up to extraction of a subsequence of (L_n),

$$\lim_{n\to+\infty} k_n = k_{(0)}.$$

Now, we show that in the classical sense:

$$\widetilde{a}^H(\theta)\partial_{xx}\Phi_{(0)} + \nabla_\theta\cdot\left(\widetilde{\mu}^A(\theta)\nabla_\theta\Phi_{(0)}\right) + \widetilde{r}^A(\theta)\Phi_{(0)} = k_{(0)}\Phi_{(0)},$$

and that $\nu\cdot\nabla_\theta\Phi_{(0)} = 0$ on $\mathbb{R}\times\partial\Theta$. As a first step, we let $\psi \in W_2^1(\mathbb{R}\times\Theta)$ be a test function such that $e^{-\lambda x}\psi$ is 1-periodic in x (so that $\psi\Phi_1$ and $\psi\partial_x\Phi_1$ are 1-periodic in x), and we show that

$$\int_{[0,1]\times\Theta}\widetilde{a}^H(\partial_x\Phi_{(0)})(\partial_x\psi) - \int_{[0,1]\times\Theta}\widetilde{\mu}^A\nabla_\theta\Phi_{(0)}\cdot\nabla_\theta\psi + \int_{[0,1]\times\Theta}\left(\widetilde{r}^A - k_{(0)}\right)\Phi_{(0)}\psi = 0. \tag{24}$$

To this aim, we apply the oscillating test function method, which is classical in homogenisation theory [4]. We let

$$w(x,\theta) := \int_0^x\left(\frac{\widetilde{a}^H(\theta)}{a(x',\theta)} - 1\right)\mathrm{d}x'.$$

We note that w is 1-periodic in x and solves

$$\partial_x\left[a(x,\theta)(1+\partial_x w(x,\theta))\right] = 0. \tag{25}$$

We set, for $n \geqslant 0$:

$$\psi_n(x,\theta) := \psi(x,\theta) + L_n \partial_x \psi(x,\theta) w\left(\frac{x}{L_n},\theta\right).$$

Since $\nu \cdot \nabla_\theta \Phi_n = 0$ on $\mathbb{R} \times \partial\Theta$, multiplying (23) by ψ_n and integrating by parts on $[0,1] \times \Theta$ gives:

$$-\int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_x \psi_n) - \int_{[0,1]\times\Theta} \mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta \Phi_n \cdot \nabla_\theta \psi + \int_{[0,1]\times\Theta}\left(r\left(\frac{x}{L_n},\theta\right) - k_n\right)\Phi_n \psi_n = o_{L\to 0}(1). \quad (26)$$

As above, the $o_{L\to 0}(1)$ term comes from the fact that the functions which we integrate by parts are L_n-periodic in x and may not be exactly 1-periodic in x.

Now, let us compute the limit as $n \to +\infty$ for each term of Equation (26). First,

$$\begin{aligned}\int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_x \psi_n) &= \int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_x \psi)\left(1 + \partial_x w\left(\frac{x}{L_n},\theta\right)\right) \\ &\quad + L_n \int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_{xx}\psi) w\left(\frac{x}{L_n},\theta\right).\end{aligned}$$

On the one hand,

$$\int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_x \psi)\left(1 + \partial_x w\left(\frac{x}{L_n},\theta\right)\right) = \widetilde{a}^H \int_{[0,1]\times\Theta} \partial_x \Phi_n \partial_x \psi.$$

On the other hand, since Φ^L is bounded in $W_2^1([0,1]\times\Theta)$, the family

$$\left(\int_{[0,1]\times\Theta} a\left(\frac{x}{L},\theta\right)(\partial_x \Phi^L)(\partial_{xx}\psi) w\left(\frac{x}{L},\theta\right)\right)_{0<L<1}$$

is bounded. Thus,

$$\lim_{n\to+\infty} \int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x \Phi_n)(\partial_x \psi_n) = \widetilde{a}^H \int_{[0,1]\times\Theta} \partial_x \Phi_{(0)} \partial_x \psi. \quad (27)$$

Second, an integration by part gives:

$$\int_{[0,1]\times\Theta} \mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta \Phi_n \cdot \nabla_\theta \psi = -\int_{[0,1]\times\Theta} \Phi_n \nabla_\theta \cdot \left(\mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta \psi_n\right).$$

As $n \to +\infty$, the right-hand side goes to

$$-\int_{[0,1]\times\Theta} \Phi_{(0)} \nabla_\theta \cdot \left(\widetilde{\mu}^A \nabla_\theta \psi\right).$$

Thus, by another integration by part:

$$\lim_{n\to+\infty}\int_{[0,1]\times\Theta}\mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta\Phi_n\cdot\nabla_\theta\psi=\int_{[0,1]\times\Theta}\widetilde{\mu}^A(\theta)\,(\nabla_\theta\Phi_{(0)})(\nabla_\theta\psi). \tag{28}$$

Finally,

$$\lim_{n\to+\infty}\int_{[0,1]\times\Theta}\left(r\left(\frac{x}{L_n},\theta\right)-k_{(0)}\right)\Phi_n\psi_n=\int_{[0,1]\times\Theta}\left(\widetilde{r}^A(\theta)-k_{(0)}\right)\Phi_{(0)}\psi. \tag{29}$$

Using Equations (26), (27), (28) and (29), we conclude that the weak formulation (24) holds for all test functions $\psi\in W_2^1(\mathbb{R}\times\Theta)$. Hence, by the notes at the end of [22, Chapter 8], the function $\Phi_{(0)}$ is the unique weak solution of

$$\begin{cases}\widetilde{a}^H\partial_{xx}\Phi_{(0)}+\nabla_\theta\cdot\left(\widetilde{\mu}^A\nabla_\theta\Phi_{(0)}\right)+\widetilde{r}^A\Phi_{(0)}=k_{(0)}\Phi_{(0)} & \text{in } \mathbb{R}\times\Theta,\\ \nu\cdot\nabla_\theta\Phi_{(0)}=0 & \text{over } \mathbb{R}\times\partial\Theta.\end{cases} \tag{30}$$

Step 3. Conclusion. By the regularity of the coefficients of (30) and the uniqueness of the classical solution, we conclude that $\Phi_{(0)}\in\mathcal{C}^2(\mathbb{R}\times\overline{\Theta})$, so (30) is solved in the classical sense. We have also $\Phi_{(0)}(x,\theta)=e^{-\lambda x}\varphi_{(0)}(\theta)$. Therefore $\varphi_{(0)}\in\mathcal{C}^2(\mathbb{R}\times\overline{\Theta})$ solves:

$$\nabla_\theta\cdot\left(\mu\nabla_\theta\varphi_{(0)}\right)+\left(\lambda^2\widetilde{a}^H+\widetilde{r}^A\right)\varphi_{(0)}=k_{(0)}\varphi_{(0)},$$

with $\nu\cdot\nabla_\theta\varphi_{(0)}=\nu\cdot\nabla_\theta\Phi_{(0)}=0$ on $\mathbb{R}\times\partial\Theta$. Finally, since $\varphi_L\to\varphi_{(0)}$ in $L^2(\mathbb{R}\times\Theta)$, we have $\varphi_{(0)}\geqslant 0$. Using the strong comparison principle, we have $\varphi_{(0)}>0$.

Therefore, by the uniqueness of the principal eigenvalue, we have $k_{(0)}=\widetilde{k}$. To conclude, the family $(k_L)_{L>0}$ is bounded (see Lemma 3.2) and $\widetilde{k}$ is the only possible limit of a subsequence as $L\to 0$; hence the whole family converges to $\widetilde{k}$ as $L\to 0$.

□

From Lemma 4.5, we show the first equality in Theorem 2.6.

Proof of Theorem 2.6, part 1. By Lemma 4.5 and the assumption that $\widetilde{k}^0>0$, there exist $\delta>0$ and $L_0>0$ such that for all $L\in(0,L_0)$,

$$k_L^0>\delta.$$

Thus the function $L\mapsto c_L$ is nondecreasing on $(0,+\infty)$ (see Proposition 2.11). Thus

$$\lim_{L\to 0}c_L=\inf_{L>0}c_L.$$

Thus:

$$\lim_{L\to 0}c_L=\inf_{L>0}\left(\inf_{\lambda>0}\frac{k_L^\lambda}{\lambda}\right)=\inf_{\lambda>0}\left(\inf_{L>0}\frac{k_L^\lambda}{\lambda}\right).$$

Since, for each $\lambda > 0$, the function $L \mapsto k_L^\lambda$ is nondecreasing (see Proposition 4.1), we have:

$$\inf_{L>0} \frac{k_L^\lambda}{\lambda} = \frac{\widetilde{k}^\lambda}{\lambda}.$$

Thus:

$$\lim_{L\to 0} c_L = \inf_{\lambda>0} \frac{\widetilde{k}^\lambda}{\lambda}.$$

□

Finally, we show the second equality of Theorem 2.6 by using the Rayleigh formula.

Proof of Theorem 2.6, part 2. For $\psi \in H^1(\Theta)$, we let

$$A_\psi = \int_\Theta \tilde{a}^H \psi^2, \qquad R_\psi = \int_\Theta \left(\tilde{r}^A \psi^2 - \tilde{\mu}^A |\nabla \psi|^2\right).$$

Let us note

$$c_{var} := \sup_{\psi \in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1, R_\psi > 0} 2\sqrt{A_\psi R_\psi}$$

and

$$c_0 := \inf_{\lambda>0} \frac{\widetilde{k}^\lambda}{\lambda}.$$

We will show that $c_0 = c_{var}$.

For $\lambda > 0$, let $\widetilde{k}^\lambda$ be the homogenised principal eigenvalue (defined by (22)). Recall the assumption that for all $L \in (0, L_0)$, $k_{m,L}^0 > \delta$. By Lemma 4.5, therefore, we must have $\widetilde{k}^0 > 0$; hence, the principal eigenfunction $\widetilde{\psi}^0$ for the homogenised eigenvalue problem (12) with $\lambda = 0$ satisfies $R_\psi > 0$. Therefore, the set on which the sup is taken in the definition of c_{var} is nonempty, so c_{var} is well-defined.

By the Rayleigh formula, we have

$$\widetilde{k}^\lambda = \max_{\psi \in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1} \left(R_\psi + \lambda^2 A_\psi\right).$$

Thus

$$\frac{\widetilde{k}^\lambda}{\lambda} = \max_{\psi \in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1} \left(\frac{1}{\lambda} R_\psi + \lambda A_\psi\right).$$

Hence,

$$c_0 = \inf_{\lambda>0} \left[\max_{\psi \in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1} \left(\frac{1}{\lambda} R_\psi + \lambda A_\psi\right)\right]. \tag{31}$$

Moreover, for all $\psi \in H^1(\Theta)$,

$$\min_{\lambda>0} \left(\frac{1}{\lambda} R_\psi + \lambda A_\psi\right) = 2\sqrt{A_\psi |R_\psi|} > 0$$

if $R_\psi > 0$, and

$$\min_{\lambda>0}\left(\frac{1}{\lambda}R_\psi + \lambda A_\psi\right) = -\infty$$

if $R_\psi < 0$. Thus

$$c_{var} = \sup_{\psi\in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1, R_\psi>0}\left[\min_{\lambda>0}\left(\frac{1}{\lambda}R_\psi + \lambda A_\psi\right)\right]. \tag{32}$$

First, we show that $c_{var} \leqslant c_0$. For all ψ_0 such that $\|\psi\|_{L^2(\Theta)} = 1$ and $R_{\psi_0} > 0$, and for all $\lambda_0 > 0$, we have:

$$\min_{\lambda>0}\left(\frac{1}{\lambda}R_{\psi_0} + \lambda A_{\psi_0}\right) \leqslant \max_{\psi\in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1, R_\psi>0}\left(\frac{1}{\lambda_0}R_\psi + \lambda_0 A_\psi\right).$$

By (31) and (32), we obtain: $c_{var} \leqslant c_0$. Second, we show that $c_{var} \geqslant c_0$. For $\psi \in H^1(\Theta)$ such that $R_\psi > 0$, let λ_ψ be the argument that reaches the minimum of

$$\lambda \mapsto \frac{R_\psi}{\lambda} + \lambda A_\psi.$$

We then have:

$$\begin{aligned} c_0 &\leqslant \sup_{\psi\in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1, R_\psi>0}\left(\frac{R_\psi}{\lambda_\psi} + \lambda_\psi A_\psi\right) \\ &= \sup_{\psi\in H^1(\Theta), \|\psi\|_{L^2(\Theta)}=1, R_\psi>0}\min_{\lambda>0}\left(\frac{R_\psi}{\lambda} + \lambda A_\psi\right) = c_{var}. \end{aligned}$$

Hence $c_{var} = c_0$, which concludes. □

5 Behaviour of the spreading speed with respect to the mutation coefficient

This part is devoted to the proofs of Theorem 2.7 (limits of $c_{m,L}$ as $m \to 0$ and $m \to +\infty$), of Theorem 2.8 (optimal mutation coefficient), and of Propositions 2.9 and 2.10, which give various properties of the dependence in the parameter m of the spreading speed. For notational convenience, we shall assume throughout this part that $L = 1$. The notations thus simplify:

$$c_m = c_{m,L}, \qquad k_m^\lambda = k_{m,L}^\lambda, \qquad \varphi_m^\lambda = \varphi_{m,L}^\lambda.$$

We shall also use specific notations for principal eigenvalues for operators without phenotypic variable. If $a \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ and $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ are two 1-periodic functions, we let $\kappa^1(\lambda; a, r)$ be the principal eigenvalue corresponding to the operator

$$\mathcal{L}^{1,\lambda}\phi := \partial_x(a\partial_x\phi) - 2\lambda a\partial_x\phi + \left(r + \lambda^2 a - \lambda\partial_x a\right)\phi$$

acting on 1-periodic functions. That is, $\kappa^1(\lambda;a,r)$ is the only possible value such that there exists a 1-periodic function $\phi \in \mathcal{C}^2(\mathbb{R})$ satisfying

$$\mathcal{L}^{1,\lambda}\phi = \kappa^1(\lambda;a,r)\phi, \qquad \phi > 0.$$

Finally, for a function $f : \mathbb{R}\times\Theta \to \mathbb{R}$, we let

$$\overline{f}(x) := \frac{1}{|\Theta|}\int_\Theta f(x,\theta)\,\mathrm{d}\theta$$

be the arithmetic mean of f in the θ-variable.

In Subsection 5.1, we compute the limit of c_m as $m \to +\infty$. In Subsection 5.2, we compute the limit of c_m as $m \to 0$ and conclude the proof of Theorem 2.7. In Subsection 5.4, we prove Propositions 2.9 and 2.10. Finally, in Subsection 5.3, we prove Theorem 2.8.

5.1 When the mutation coefficient goes to infinity (Theorem 2.7, part (i))

In order to compute the limit of c_m as $m \to +\infty$, we first compute the limit of k_m^λ as $m \to +\infty$.

Lemma 5.1. *Let $\lambda \in \mathbb{R}$. Under the assumptions of Theorem 2.7 (part (i)), as $m \to +\infty$,*

$$k_m^\lambda \to \kappa^1\left(\lambda;a,\overline{r}\right).$$

Proof. For all $m > 0$, we let $\varphi_m > 0$ be the principal eigenfunction associated to k_m^λ such that $\|\varphi_m\|_{L^2([0,1]\times\Theta)} = 1$, i.e. φ_m is positive, 1-periodic in x, and satisfies

$$\begin{cases} \partial_x(a\partial_x\varphi_m) + m\nabla_\theta\cdot(\mu\nabla_\theta\varphi_m) - 2\lambda a\partial_x\varphi + (r+\lambda^2 a - \lambda\partial_x a)\varphi_m = k_m^\lambda\varphi_m & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta\varphi_m = 0 & \text{over } \mathbb{R}\times\partial\Theta. \end{cases} \tag{33}$$

First, we show that $(\varphi_m)_{m>1}$ is bounded in $W_2^1([0,1]\times\Theta)$. Multiplying the first line of (33) by φ_m, integrating on $[0,1]\times\Theta$, and integrating by parts, yields (using that the functions are 1-periodic in x and $\nu\cdot\nabla_\theta\varphi_m = 0$ on $\mathbb{R}\times\partial\Theta$):

$$-\int_{[0,1]\times\Theta} a\left|\partial_x\varphi_m\right|^2 - m\int_{[0,1]\times\Theta}\mu\left|\nabla_\theta\varphi_m\right|^2 - 2\lambda\int_{[0,1]\times\Theta} a\varphi_m\partial_x\varphi_m \\ + \int_{[0,1]\times\Theta}\left(r+\lambda^2 a - \lambda\partial_x a\right)\varphi_m^2 = k_m\int_{[0,1]\times\Theta}\varphi_m^2.$$

Recall the assumption that there exists a constant $\eta > 0$ such that $a \geqslant \eta$ and $\mu \geqslant \eta$. We get, rearranging the terms:

$$\eta\left(\int_{[0,1]\times\Theta}\left|\partial_x\varphi_m\right|^2 + m\int_{[0,1]\times\Theta}\left|\nabla_\theta\varphi_m\right|^2\right) \\ \leqslant -\lambda\int_{[0,1]\times\Theta}\varphi_m^2\partial_x a - 2\lambda\int_{[0,1]\times\Theta} a\varphi_m\partial_x\varphi_m + \int_{[0,1]\times\Theta}\left(r+\lambda^2 a\right)\varphi_m^2 - k_m\int_{[0,1]\times\Theta}\varphi_m^2.$$

An integration by parts gives:

$$-2\int_{[0,1]\times\Theta} a\varphi_m\partial_x\varphi_m - \int_{[0,1]\times\Theta}\varphi_m^2\partial_x a = 0.$$

We conclude that

$$\int_{[0,1]\times\Theta}|\partial_x\varphi_m|^2 + m\int_{[0,1]\times\Theta}|\nabla_\theta\varphi_m|^2 \leqslant \frac{1}{\eta}\left((\|r\|_\infty + \lambda^2\|a\|_\infty)\int_{[0,1]\times\Theta}\varphi_m^2 - k_m\int_{[0,1]\times\Theta}\varphi_m^2\right).$$

Since $(k_m)_{L>0}$ is bounded (see Lemma 3.2) and $\|\varphi_m\|_{L^2([0,1]\times\Theta)} = 1$, the right-hand side of the equation is bounded. Thus the family $(\varphi_m)_{m>1}$ is bounded in $W_2^1([0,1]\times\Theta)$. Thus, by a compact injection theorem, there is a sequence $m_n \to +\infty$ such that φ_{m_n} converges in $L^2([0,1]\times\Theta)$ to a function $\Phi \in L^2([0,1]\times\Theta)$. Moreover,

$$\int_{[0,1]\times\Theta}|\nabla_\theta\varphi_m|^2 \to 0$$

so $\Phi = \Phi(x)$ is independent of θ. To conclude, we let $\psi \in \mathcal{C}^2(\mathbb{R})$ be a nonzero principal eigenfunction of the adjoint of the operator defining $\kappa^1(\lambda; a, \overline{r})$, i.e. ψ is positive, 1-periodic and satisfies

$$\partial_x(a\partial_x\psi) + 2\lambda\partial_x(a\psi) + (\overline{r} + \lambda^2 a - \lambda\partial_x a)\psi.$$

(Under our assumptions, a only depends on x so $a = \overline{a}$.) We see ψ as function of $\mathcal{C}^2(\mathbb{R}\times\Theta)$ with $\nabla_\theta\psi = 0$. Using ψ as a test function in the weak formulation of Equation (33), we have:

$$-\int_{[0,1]\times\Theta} a(\partial_x\varphi_m)(\partial_x\psi) - m\int_{[0,1]\times\Theta}\mu\nabla_\theta\varphi_m\cdot\nabla_\theta\psi - 2\lambda\int_{[0,1]\times\Theta} a\psi\partial_x\varphi_m + \int_{[0,1]\times\Theta}(r + \lambda^2 a - \lambda\partial_x a)\varphi_m\psi = k_m^\lambda\int_{[0,1]\times\Theta}\varphi_m\psi.$$

Recall that $\nabla_\theta\psi = 0$. An integration by parts yields

$$\int_{[0,1]\times\Theta}\varphi_m\partial_x(a\partial_x\psi) + 2\lambda\int_{[0,1]\times\Theta}\partial_x(a\psi)\varphi_m + \int_{[0,1]\times\Theta}(r + \lambda^2 a - \lambda\partial_x a)\varphi_m\psi = k_m^\lambda\int_{[0,1]\times\Theta}\varphi_m\psi.$$

Thus, taking a limit along a subsequence $m_n \to +\infty$ such that $\varphi_{m_n} \to \Phi$ in $L^2([0,1]\times\Theta)$ and $k_{m_n}^\lambda$ converges to some limit k_∞^λ, we obtain:

$$\int_{[0,1]\times\Theta}\Phi\left[\partial_x(a\partial_x\psi) + 2\lambda\partial_x(a\psi) + (r + \lambda^2 a - \lambda\partial_x a)\psi\right] = k_\infty^\lambda\int_{[0,1]\times\Theta}\Phi\psi.$$

Since Φ is independent of θ, the definition of ψ implies:

$$\kappa^1(\lambda; a, \overline{r})\int_{[0,1]\times\Theta}\Phi\psi = k_\infty^\lambda\int_{[0,1]\times\Theta}\Phi\psi.$$

Since $\varphi_m > 0$ for all $m > 0$, we must have $\Phi \geqslant 0$. Since $\|\Phi\|_{L^2([0,1]\times\Theta)} = 1$, Φ is not almost everywhere equal to 0; finally, $\psi > 0$. Therefore $\kappa^1(\lambda; a, \overline{r}) = k_\infty^\lambda$. Thus $\kappa^1(\lambda; a, \overline{r})$ is the only possible limit of a subsequence of k_m^λ as $m \to +\infty$. Since $(k_m^\lambda)_{m>0}$ is bounded (Lemma 3.2), we get that $k_m^\lambda \to \kappa^1(\lambda; a, \overline{r})$ as $m \to +\infty$. □

Proof of the limit $m \to +\infty$ in Theorem 2.7. Since $\kappa^1(0;a,\overline{r}) > 0$, Lemma 5.1 implies that there exist $\delta > 0$ and $\underline{m} > 0$ such that for all $m > \underline{m}$, we have: $k_m^0 > \delta$. Moreover, by Lemma 3.2, for all $m > \underline{m}$ and $\lambda > 0$,

$$k_m^\lambda \geqslant \lambda^2 \inf a - \lambda \|\partial_x a\|_\infty - \|r\|_\infty .$$

Therefore, uniformly in $m > \underline{m}$,

$$\lim_{\lambda \to 0} \frac{k_m^\lambda}{\lambda} = +\infty, \qquad \lim_{\lambda \to +\infty} \frac{k_m^\lambda}{\lambda} = +\infty. \tag{34}$$

By continuity of the function $\lambda \mapsto k_m^\lambda$, for all $m > \underline{m}$, there exists $\lambda_m > 0$ such that:

$$c_m = \inf_{\lambda > 0} \frac{k_m^\lambda}{\lambda} = \frac{k_m^{(\lambda_m)}}{\lambda_m}.$$

By (34), there exist $\lambda_+ > \lambda_- > 0$ such that for all $m > \underline{m}$: $\lambda_- \leqslant \lambda_m \leqslant \lambda_+$. Hence, there exists $\lambda^* > 0$ such that up to extraction of a subsequence $m_n \to +\infty$,

$$\lambda_{m_n} \to \lambda^* \quad \text{as } n \to +\infty.$$

The functions $\lambda \mapsto k_m^\lambda$ $(m > 0)$ and $\lambda \mapsto \kappa^1(\lambda;a,\overline{r})$ are continuous and convex (see the proof of [8, Lemma 3.1] for the concavity of $\lambda \mapsto -\kappa^1(\lambda;a,\overline{r})$; the concavity of $\lambda \mapsto -k_m^\lambda$ works in the same way). Thus

$$\lim_{n \to +\infty} \frac{k_{m_n}^{(\lambda_{m_n})}}{\lambda_{m_n}} = \frac{\kappa^1(\lambda^*;a,\overline{r})}{\lambda^*},$$

so

$$\liminf_{n \to +\infty} c_{m_n} \geqslant c^1(a,\overline{r}).$$

On the other hand, using the continuity of $\lambda \mapsto \kappa^1(\lambda;a,\overline{r})$, the fact that $\kappa^1(0;a,\overline{r}) > 0$ and Lemma 3.2, there exists $\overline{\lambda} > 0$ such that

$$c^1(a,\overline{r}) = \frac{\kappa^1(\overline{\lambda};a,\overline{r})}{\overline{\lambda}}.$$

Therefore,

$$c^1(a,\overline{r}) = \lim_{n \to +\infty} \frac{k_{m_n}^{\overline{\lambda}}}{\overline{\lambda}} \geqslant \limsup_{n \to +\infty} c_{m_n}.$$

We conclude that c_{m_n} converges and

$$\lim_{n \to +\infty} c_{m_n} = c^1(a,\overline{r}).$$

Finally, $(c_m)_{m > \underline{m}}$ is bounded. Since $c^1(a,\overline{r})$ is the only possible limit of a subsequence (c_{m_n}) such that $m_n \to +\infty$, we conclude that the whole family converges to $c^1(a,\overline{r})$.

□

5.2 When the mutation coefficient goes to zero (Theorem 2.7, parts (ii) and (iii))

Here, we compute the limit of c_m as $m \to 0$ (part (ii) of Theorem 2.7) and we show part (iii) of Theorem 2.7.

Lemma 5.2. *Let $\lambda \in \mathbb{R}$. Under the assumptions of Theorem 2.7 (part (ii)), as $m \to 0$,*

$$k_m^\lambda \to \max_{\theta \in \overline{\Theta}} \kappa^1\left(\lambda; a(\cdot), r(\cdot,\theta)\right).$$

With this lemma, we can conclude the proof of the limiting speed as $m \to 0$. The proof is the same as that of the limit $m \to +\infty$, replacing Lemma 5.1 by Lemma 5.2, the limit "$m \to +\infty$" by the limit "$m \to 0$", and $\kappa^1\left(\lambda; a, \overline{r}\right)$ by $\max_{\theta \in \Theta} \kappa^1\left(\lambda; a, r(\cdot,\theta)\right)$. There only remains to prove Lemma 5.2.

Proof of Lemma 5.2. The principal eigenfunction φ_m^λ solves

$$\begin{cases} \partial_x(a\partial_x\varphi_m^\lambda) + m\nabla_\theta \cdot \left(\mu \nabla_\theta \varphi_m^\lambda\right) - 2\lambda a \partial_x \varphi_m^\lambda \\ \qquad + \left(r(x,\theta) + \lambda^2 a - \lambda \partial_x a\right)\varphi_m^\lambda(x,\theta) = k_m^\lambda \varphi_m^\lambda(x,\theta), & (x,\theta) \in \mathbb{R}\times\Theta, \\ \nu \cdot \nabla_\theta \varphi_m^\lambda(x,\theta) = 0, & (x,\theta) \in \mathbb{R}\times\partial\Theta, \\ \varphi_m^\lambda > 0, & (x,\theta) \in \mathbb{R}\times\Theta, \\ \varphi_m^\lambda \text{ 1-periodic in } x. \end{cases}$$

Setting $\varepsilon = m$ and letting $\varphi_\varepsilon = \varphi_m^\lambda$ brings us to the setting of [13, Theorem 1.2]. To get back to the the notations there, we replace the slow variable θ by y, the fast variable x by z, the global eigenvalue k_m^λ by k_ε and the local eigenvalue k^y by $\kappa^1(\lambda; a(\cdot), r(\cdot,\theta))$. The conclusion is then exactly the result of [13, Theorem 1.2]. □

There remains to prove the last statement of Theorem 2.7 about the comparison of the two limits $m \to +\infty$ and $m \to 0$.

Proof of Theorem 2.7, part (iii). It is enough to show that for all $\lambda > 0$,

$$\kappa^1(\lambda; a, \overline{r}) \leqslant \sup_{\theta\in\Theta} \kappa^1(\lambda; a(\cdot,\theta), r(\cdot,\theta)).$$

Since a is assumed to be independent of θ, it is equivalent to show that for all $\lambda > 0$,

$$\kappa^1(\lambda; a, \overline{r}) \leqslant \sup_{\theta\in\Theta} \kappa^1(\lambda; a, r(\cdot,\theta)).$$

By [35, Proposition 2.4], the function $g \in L^\infty([0,1]) \mapsto \kappa^1(\lambda; a, g)$ is convex. Hence, by Jensen inequality, we conclude:

$$\begin{aligned} \kappa^1(\lambda; a, \overline{r}) &= \kappa^1\left(\lambda; a, \frac{1}{|\Theta|}\int_\Theta r(x,\theta)\,\mathrm{d}\theta\right) \\ &\leqslant \frac{1}{|\Theta|}\int_\Theta \kappa^1(\lambda; a, r(\cdot,\theta))\,\mathrm{d}\theta \leqslant \sup_{\theta\in\Theta} \kappa^1(\lambda; a, r(\cdot,\theta)). \end{aligned}$$

□

5.3 The optimal mutation coefficient (Theorem 2.8)

Proof of Theorem 2.8. We assume that a is independent of θ and that μ is independent of x. We also assume that for some $\theta \in \overline{\Theta}$ and $\underline{L} > 0$, $\kappa^1(0; a, r_{\underline{L}}(\cdot,\theta)) > 0$; thus by Lemma 5.2 there exist $\delta > 0$, $\underline{L} > 0$ and $\overline{m} \in (0, +\infty]$ such that for all $m \in (0, \overline{m})$, we have: $k^0_{m,\underline{L}} > \delta$. These assumptions ensure that we can apply Theorems 2.5 and 2.7 (part (ii)). Finally, we assume that (13) holds.

Step 1. Proof that γ is well-defined and that $\gamma_\mu > 0$. On the one hand, for finite $L > 0$, we have by Theorem 2.7:

$$\lim_{m\to 0} c_{m,L} = \max_{\theta\in\overline{\Theta}} c^1(a_L(\cdot), r_L(\cdot,\theta)).$$

Thus, using the monotony in L (Proposition 2.11),

$$\lim_{L\to+\infty} \lim_{m\to 0} c_{m,L} = \max_{\theta\in\overline{\Theta}} \left(\lim_{L\to+\infty} c^1(a_L(\cdot), r_L(\cdot,\theta)) \right). \tag{35}$$

On the other hand, by Theorem 2.5,

$$\lim_{L\to+\infty} c_{m,L} = \left(\inf_{\lambda > j_m(M)} \frac{j_m^{-1}(\lambda)}{\lambda} \right),$$

with

$$j_m(k) := \int_0^1 \sqrt{\frac{k - H_m(y)}{a(y)}}\, \mathrm{d}y$$

(using the notations H_m and M of Theorem 2.5). By the Rayleigh formula,

$$H_m(y) = \sup_{\psi\in H^1(\Theta),\, \|\psi\|_{L^2(\Theta)}=1} \left(\int_\Theta r(y,\sigma)\psi^2(\sigma)\,\mathrm{d}\sigma - m\int_\Theta \mu(\sigma)\,|\nabla\psi|^2(\sigma)\,\mathrm{d}\sigma \right).$$

Let $m_n \to 0$. For fixed $\theta \in \Theta$, we take a sequence $(\psi_n^\theta)_n$, $\psi_n^\theta \in H^1(\Theta)$ with $\|\psi_n^\theta\|_{L^2(\Theta)} = 1$, such that $\psi_n^2 \rightharpoonup \delta_\theta$ in $L^2(\Theta)$ and such that $m_n \left\|\nabla\psi_n^\theta\right\|_\infty^2 \to 0$. We have for all $y \in [0,1]$ and $n \geqslant 1$,

$$H_{m_n}(y) \geqslant \int_\Theta r(y,\sigma)(\psi_n^\theta)^2(\sigma)\,\mathrm{d}\sigma - m_n \int_\Theta \mu(\sigma) \left|\nabla\psi_n^\theta\right|^2(\sigma)\,\mathrm{d}\sigma.$$

As $n \to +\infty$, the right-hand side of the inequality converges to $r(y,\theta)$, uniformly in y. This holds for all $\theta \in \Theta$. Hence

$$\liminf_{n\to+\infty} H_{m_n}(y) \geqslant \sup_{\theta\in\Theta} r(y,\theta) = \max_{\theta\in\overline{\Theta}} r(y,\theta)$$

uniformly in y. Finally, we also have, for all y,

$$H_m(y) \leqslant \max_{\theta\in\overline{\Theta}} r(y,\theta).$$

This proves that as $m \to 0$,

$$H_m(y) \to \max_{\theta \in \overline{\Theta}} r(y, \theta),$$

uniformly in $y \in [0,1]$. Therefore, as $m \to 0$,

$$j_m(k) \to j_0(k) := \int_0^1 \sqrt{\frac{k - \max_{\theta \in \overline{\Theta}} r(y,\theta)}{a(y)}}\, \mathrm{d}y$$

uniformly in $k \in [R_m, R_m']$ with $R_m := \max_{\mathbb{R} \times \overline{\Theta}} r$ and $R_m' > R_m$. We thus get

$$\lim_{m \to 0} \lim_{L \to +\infty} c_{m,L} = \inf_{\lambda \geqslant j_0(M)} \frac{j_0^{-1}(\lambda)}{\lambda},$$

which gives (using [28, Theorem 2.2]):

$$\lim_{m \to 0} \lim_{L \to +\infty} c_{m,L} = \lim_{L \to +\infty} c^1 \left(a_L(\cdot), x \mapsto \max_{\theta \in \overline{\Theta}} r_L(x, \theta) \right).$$

By assumption (13), we have for all $\theta \in \overline{\Theta}$:

$$j_0(k) = \int_0^1 \sqrt{\frac{k - \max_{\theta \in \overline{\Theta}} r(y,\theta)}{a(y)}}\, \mathrm{d}y < \int_0^1 \sqrt{\frac{k - r(y,\theta)}{a(y)}}\, \mathrm{d}y.$$

Therefore, using again [28, Theorem 2.2], we obtain: for all $\theta \in \overline{\Theta}$,

$$\lim_{L \to +\infty} c^1 \left(a_L(\cdot), x \mapsto \max_{\theta \in \overline{\Theta}} r_L(x, \theta) \right) > \lim_{L \to +\infty} c^1 \left(a_L(\cdot), r_L(\cdot, \theta) \right).$$

Thus, with (35), we obtain that the two following limits are well-defined and satisfy:

$$\lim_{m \to 0} \lim_{L \to +\infty} c_{m,L} > \lim_{L \to +\infty} \lim_{m \to 0} c_{m,L}.$$

This implies that γ is well-defined and satisfies: $\gamma > 0$.

Step 2. There exists an optimal mutation coefficient. Let $m_1 > m_0 > 0$ with $m_1 < \overline{m}$. The family of functions $(m \mapsto c_{m,L})_{L > \underline{L}}$ converges increasingly and pointwise to its limit as $L \to +\infty$ (see Proposition 2.11), thus the convergence is uniform on $[m_0, m_1]$. Thus for all $\varepsilon > 0$, there exists $L_0 > \underline{L}$, depending on m_0, m_1 and ε, such that for all $L_1 > L_0$,

$$\sup_{m \in [m_0, m_1]} \left| c_{m,L_1} - \lim_{L \to +\infty} c_{m,L} \right| < \varepsilon. \tag{36}$$

We set:

$$\varepsilon := \frac{1}{2} \left(\lim_{m \to 0} \lim_{L \to +\infty} c_{m,L} - \lim_{m \to \overline{m}, m < \overline{m}} \left(\lim_{L \to +\infty} c_{m,L} \right) \right).$$

By the last point in Proposition 2.9 and by assumption (13) (which implies that there exists $x \in \mathbb{R}$ such that $\theta \mapsto r(x,\theta)$ is not constant), the function

$$m \mapsto \lim_{L\to+\infty} c_{m,L}$$

is strictly decreasing; hence ε exists and is positive. Therefore, for $m_0 > 0$ small enough and $m_1 > m_0$ large enough, Equation (36) implies: for all $m > m_1$, for all $L_1 > L_0$,

$$c_{m_0,L_1} > \lim_{L\to+\infty} c_{m,L} \geqslant c_{m,L_1}.$$

Thus for all $L_1 > L_0$,

$$\sup_{m>0} c_{m,L_1} = \sup_{m\in(0,m_1]} c_{m,L_1}.$$

Now, Proposition 2.11 implies that for $L_1 > L_0$,

$$\lim_{m\to 0} c_{m,L_1} \leqslant \lim_{L\to+\infty} \lim_{m\to 0} c_{m,L} = \lim_{m\to 0} \lim_{L\to+\infty} c_{m,L} - \gamma.$$

Taking $\varepsilon \in (0,\gamma)$ in (36) implies:

$$\sup_{m\in(0,m_1]} c_{m,L_1} = \sup_{m\in[m_0,m_1]} c_{m,L_1}.$$

Also, note that $m \mapsto c_{m,L_1}$ is continuous (this can be proved as the continuity of $L \mapsto c_{m,L}$ for fixed m, see the first part of the proof of Proposition 2.11). Therefore there exists an optimal mutation coefficient $m^*(L_1) \in [m_0, m_1]$. In particular, $m^*(L_1) > 0$.

Step 3. Lower bound for the maximal speed. Let $\varepsilon > 0$. By virtue of Proposition 2.9, there exist $m_1 > 0$ so small that for all $m \in (0, m_1]$,

$$\lim_{L\to+\infty} c_{m,L} \geqslant \lim_{m\to 0} \lim_{L\to+\infty} c_{m,L} - \varepsilon/2.$$

By (36) with ε replaced by $\varepsilon/2$, for all $L_1 \geqslant L_0$, for all $m \in (0, m_1]$,

$$\begin{aligned} c_{m,L_1} &\geqslant \lim_{L\to+\infty} c_{m,L} - \varepsilon/2 \geqslant \lim_{m\to 0} \lim_{L\to+\infty} c_{m,L} - \varepsilon \\ &\geqslant \lim_{L\to+\infty} \lim_{m\to 0} c_{m,L} + \gamma - \varepsilon \\ &\geqslant \lim_{m\to 0} c_{m,L_1} + \gamma - \varepsilon. \end{aligned}$$

This concludes.

□

5.4 Other properties (Propositions 2.9 and 2.10)

Proof of Proposition 2.9. We first prove that

$$m \mapsto \lim_{L\to+\infty} c_{m,L}$$

is nonincreasing (the limit exists thanks to the assumptions and Theorem 2.5). By Proposition 4.3, it is enough to show that for all $k \geqslant M$, $m \mapsto j_m(\lambda)$ is nondecreasing, which is implied by the property that for all $x \in \mathbb{R}$, $m \mapsto H_m(x)$ is nonincreasing . By the Rayleigh formula, we have:

$$H_m(x) = \max_{\phi\in H^1(\Theta),\, \|\phi\|_{L^2(\Theta)}=1} \left(-m\int_\Theta \mu\,|\nabla\phi|^2 + \int_\Theta r(x,\cdot)\phi^2\right).$$

Take $m_1, m_2 \in I$ with $m_1 < m_2$, and let $\phi_2 \in H^1(\Theta)$ with $\phi_2 > 0$ and $\|\phi_2\|_{L^2(\Theta)} = 1$ be the principal eigenfunction associated to the principal eigenvalue $H_{m_2}(x)$. Then:

$$\begin{aligned} H_{m_1}(x) &\geqslant -m_1\int_\Theta \mu\,|\nabla\phi_2|^2 + \int_\Theta r(x,\cdot)\phi_2^2 \\ &\geqslant -m_2\int_\Theta \mu\,|\nabla\phi_2|^2 + \int_\Theta r(x,\cdot)\phi_2^2 = H_{m_2}(x). \end{aligned}$$

Thus for all $x \in \mathbb{R}$, the function $m \mapsto H_m(x)$ is nonincreasing. Moreover, if ϕ_2 is not constant, the second inequality is strict, so the function $m \mapsto H_m(x)$ is strictly decreasing. Hence the function

$$m \mapsto \lim_{L\to+\infty} c_{m,L}$$

is nonincreasing, and strictly decreasing if there exists $x \in \mathbb{R}$ such that $\theta \mapsto r(x,\theta)$ is not constant.

Now, let us prove that

$$m \mapsto \lim_{L\to 0} c_{m,L}$$

is nonincreasing (the limit exists thanks to the assumptions and Theorem 2.6). This comes from the variational formulation in Theorem 2.6, which says:

$$\lim_{L\to 0} c_{m,L} = \sup_{\psi\in H^1(\Theta),\, \|\psi\|_{L^2(\Theta)}=1,\, R_\psi>0} 2\sqrt{A_\psi R_\psi},$$

where, for all $\psi \in H^1(\Theta)$, A_ψ is independent of m and

$$R_\psi := \int_\Theta \left(\widetilde{r}^A\psi^2 - m\widetilde{\mu}^A\,|\nabla\psi|^2\right)$$

is nonincreasing in m. We conclude in the same way as above.

□

Proof of Proposition 2.10. By the Rayleigh formula,

$$k_m^0 = \sup_\phi \left(-\int_{[0,1]\times\Theta} a\,|\nabla_x\phi|^2 - m\int_{[0,1]\times\Theta} \mu\,|\nabla_\theta\phi|^2 + \int_{[0,1]\times\Theta} r\phi^2\right),$$

where the sup is taken on the $\phi \in H^1_{loc}(\mathbb{R}\times\overline{\Theta})$ such that $\|\phi\|_{L^2([0,1]\times\Theta)} = 1$ and ϕ is 1-periodic in x. From this expression, we get that $m \mapsto k_m^0$ is nonincreasing. □

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References

[1] M. Alfaro, H. Berestycki, and G. Raoul. "The effect of climate shift on a species submitted to dispersion, evolution, growth, and nonlocal competition". *SIAM J. Math. Anal.* 49.1 (2017), pp. 562–596.

[2] M. Alfaro, J. Coville, and G. Raoul. "Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypic trait". *Comm. Partial Differential Equations* 38.12 (2013), pp. 2126–2154.

[3] M. Alfaro and G. Peltier. "Populations facing a nonlinear environmental gradient: steady states and pulsating fronts". *Math. Models Methods Appl. Sci.* 32.2 (2022), pp. 209–290.

[4] G. Allaire. "A brief introduction to homogenization and miscellaneous applications". *Mathematical and numerical approaches for multiscale problem*. Vol. 37. ESAIM Proc. EDP Sci., Les Ulis, 2012, pp. 1–49.

[5] H. Berestycki and F. Hamel. "Front propagation in periodic excitable media". *Comm. Pure Appl. Math.* 55.8 (2002), pp. 949–1032.

[6] H. Berestycki, F. Hamel, and G. Nadin. "Asymptotic spreading in heterogeneous diffusive excitable media". *J. Funct. Anal.* 255.9 (2008), pp. 2146–2189.

[7] H. Berestycki, F. Hamel, and N. Nadirashvili. "The speed of propagation for KPP type problems. I. Periodic framework". *J. Eur. Math. Soc. (JEMS)* 7.2 (2005), pp. 173–213.

[8] H. Berestycki, F. Hamel, and L. Roques. "Analysis of the periodically fragmented environment model. II. Biological invasions and pulsating travelling fronts". *J. Math. Pures Appl. (9)* 84.8 (2005), pp. 1101–1146.

[9] H. Berestycki, T. Jin, and L. Silvestre. "Propagation in a non local reaction diffusion equation with spatial and genetic trait structure". *Nonlinearity* 29.4 (2016), pp. 1434–1466.

[10] H. Berestycki and L. Rossi. "Reaction-diffusion equations for population dynamics with forced speed. II. Cylindrical-type domains". *Discrete Contin. Dyn. Syst.* 25.1 (2009), pp. 19–61.

[11] E. Bouin, V. Calvez, N. Meunier, S. Mirrahimi, B. Perthame, G. Raoul, and R. Voituriez. "Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration". *C. R. Math. Acad. Sci. Paris* 350.15-16 (2012), pp. 761–766.

[12] E. Bouin and S. Mirrahimi. "A Hamilton-Jacobi approach for a model of population structured by space and trait". *Commun. Math. Sci.* 13.6 (2015), pp. 1431–1452.

[13] N. Boutillon. "The principal eigenvalue problem for a strongly anisotropic second-order elliptic operator". *arXiv preprint arXiv:2311.12232* (2023).

[14] N. Boutillon and L. Rossi. "Reaction-diffusion model for a population structured in phenotype and space I – Criterion for persistence". *arXiv preprint arXiv:2409.20118* (2024).

[15] N. Champagnat and S. Méléard. "Invasion and adaptive evolution for individual-based spatially structured populations". *J. Math. Biol.* 55.2 (2007), pp. 147–188.

[16] W. Ding, F. Hamel, and X. Liang. "Bistable pulsating fronts in slowly oscillating environments". *arXiv preprint arXiv:2204.09301* (2022).

[17] M. El Smaily, F. Hamel, and L. Roques. "Homogenization and influence of fragmentation in a biological invasion model". *Discrete Contin. Dyn. Syst.* 25.1 (2009), pp. 321–342.

[18] E. C. Elliott and S. J. Cornell. "Dispersal Polymorphism and the Speed of Biological Invasions". *PLOS ONE* 7.7 (2012), e40496.

[19] R. A. Fisher. "The wave of advance of advantageous genes". *Ann. Eugenics* 7.4 (1937), pp. 355–369.

[20] M. Freidlin. "Limit theorems for large deviations and reaction-diffusion equations". *Ann. Probab.* (1985), pp. 639–675.

[21] J. Gärtner and M. I. Freidlin. "The propagation of concentration waves in periodic and random media". *Dokl. Akad. Nauk SSSR* no. 3, (1979), pp. 521–525.

[22] D. Gilbarg and N. S. Trudinger. *Elliptic partial differential equations of second order*. Classics in Mathematics. Reprint of the 1998 edition. Springer-Verlag, Berlin, 2001, pp. xiv+517.

[23] L. Girardin. "Non-cooperative Fisher-KPP systems: traveling waves and long-time behavior". *Nonlinearity* 31.1 (2018), pp. 108–164.

[24] L. Girardin. "Persistence, extinction and spreading properties of non-cooperative Fisher–KPP systems in space-time periodic media". *arXiv preprint arXiv:2305.18857* (2023).

[25] Q. Griette and H. Matano. "Propagation dynamics of solutions to spatially periodic reaction-diffusion systems with hybrid nonlinearity". *arXiv preprint arXiv:2108.10862* (2021).

[26] F. Hamel, F. Lavigne, G. Martin, and L. Roques. "Dynamics of adaptation in an anisotropic phenotype-fitness landscape". *Nonlinear Anal. Real World Appl.* 54 (2020), pp. 103107, 33.

[27] F. Hamel, J. Fayard, and L. Roques. "Spreading speeds in slowly oscillating environments". *Bull. Math. Biol.* 72.5 (2010), pp. 1166–1191.

[28] F. Hamel, G. Nadin, and L. Roques. "A viscosity solution method for the spreading speed formula in slowly varying media". *Indiana Univ. Math. J.* 60.4 (2011), pp. 1229–1247.

[29] F. Hamel and L. Roques. "Fast propagation for KPP equations with slowly decaying initial conditions". *J. Differential Equations* 249.7 (2010), pp. 1726–1745.

[30] P.-E. Jabin. "Small populations corrections for selection-mutation models". *Netw. Heterog. Media* 7.4 (2012), pp. 805–836.

[31] A. N. Kolmogorov, I. G. Petrovsky, and N. S. Piskunov. "Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique". *Bull. Univ. État Moscou* (1937), pp. 1–26.

[32] M. G. Krein and M. A. Rutman. "Linear operators leaving invariant a cone in a Banach space". *Uspehi Matem. Nauk (N. S.)* no. 1(23), (1948), pp. 3–95.

[33] P. Maillard, G. Raoul, and J. Tourniaire. "Spatial dynamics of a population in a heterogeneous environment". *arXiv preprint arXiv:2105.06985* (2021).

[34] A. Morris, L. Börger, and E. Crooks. "Individual Variability in Dispersal and Invasion Speed". *Mathematics* 7.9 (2019), p. 795.

[35] G. Nadin. "The effect of the Schwarz rearrangement on the periodic principal eigenvalue of a nonsymmetric operator". *SIAM J. Math. Anal.* 41.6 (2010), pp. 2388–2406.

[36] G. Peltier. "Accelerating invasions along an environmental gradient". *J. Differential Equations* 268.7 (2020), pp. 3299–3331.

[37] C. Prevost. "Applications des équations aux dérivés partielles aux problèmes de dynamique des populations et traitement numérique". PhD thesis. Orléans, 2004.

[38] L. Roques, N. Boutillon, P. Zamberletti, and J. Papaïx. "Polymorphic population expansion velocity in a heterogeneous environment". *J. Theor. Biol.* (2024), p. 111932.

[39] N. Shigesada and K. Kawasaki. *Biological Invasions: Theory and Practice*. Oxford Series in Ecology and Evolution. Oxford, New York, 1997. 224 pp.

[40] J. G. Skellam. "Random dispersal in theoretical populations". *Biometrika* 38.1 (1951), pp. 196–218.

[41] P. Turchin. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, 1998.

[42] H. F. Weinberger. "On spreading speeds and traveling waves for growth and migration models in a periodic habitat". *J. Math. Biol.* 45.6 (2002), pp. 511–548.

[43] J. Xin. "Front propagation in heterogeneous media". *SIAM Rev.* 42.2 (2000), pp. 161–230.