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Nathanaël Boutillon

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Biostatistiques et processus spatiaux, INRAE

Composition du jury

Nicolas Champagnat Directeur de recherche, INRIA	Rapporteur
Thomas Giletti Professeur, Université Clermont Auvergne	Rapporteur
Matthieu Alfaro Professeur, Université de Rouen Normandie	Examinateur
Vincent Calvez Directeur de recherche, CNRS, Univ. de Brest	Président du jury
Amandine Veber Directrice de recherche, CNRS, Univ. Paris-Cité	Examinatrice
Raphaël Forien Chargé de recherche, INRAE	Co-encadrant de thèse
François Hamel Professeur, Aix-Marseille Université	Co-directeur de thèse
Lionel Roques Directeur de recherche, INRAE	Directeur de thèse
Gaël Raoul Chargé de recherche, École Polytechnique	Membre invité
Luca Rossi Professeur, Sapienza Università di Roma	Membre invité

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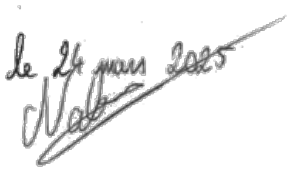

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Liste de publications et participation aux conférences

Liste des publications réalisées dans le cadre du projet de thèse :

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2. L. Roques, N. Boutillon, P. Zamberletti, J. Papaïx, *Polymorphic population expansion velocity in a heterogeneous environment*, Journal of Theoretical Biology (2024), p. 111932.

3. N. Boutillon, L. Rossi, *Reaction–diffusion model for a population structured in phenotype and space: I. Criterion for persistence*, Nonlinearity 38.4 (2025), p. 045019.

4. N. Boutillon, *The principal eigenvalue problem for a strongly anisotropic second-order elliptic operator*, SIAM Journal on Mathematical Analysis 57.4 (2025), pp. 3840–3877.

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Abstract and keywords

The main theme of this thesis is the connection between principal eigenvalues of elliptic operators and the long-time behaviour of variants of the Fisher-KPP equation.

In the first part, we focus closely on different principal eigenvalue problems that have a relevant interpretation from a population dynamics point of view. In three chapters, we focus on the effect of a separation of scales, of the wind, and of heterogeneous diffusion, on the ability of persistence and the spreading speed of the population. Several central proofs of the first part are probabilistic.

In the second part, we are interested in a reaction-diffusion model for a population structured in phenotype and living in a heterogeneous periodic environment. We derive a criterion (involving a generalised principal eigenvalue) for the persistence of the population. Next, we investigate optimisation problems to make persistence as hard or as easy as possible. We are also interested in the spreading speed of the population in different scaling limits. Last, we prove new persistence and spreading results for a simpler equation consisting of only two morphs living in a heterogeneous environment.

In the last part, we focus on the loss of genetic diversity during an invasion. First, we show that a logarithmic delay appears in an equation with nonlocal dispersal. Next, we are interested in experimental data showing a loss of diversity after a population crosses a barrier; we propose some probabilistic models to understand this loss of diversity.

Keywords: Fisher-KPP equations; Elliptic equations; Principal eigenvalue; Long-time behaviour; Population dynamics; Population genetics; Probabilistic interpretation of PDE.

Résumé et mots-clés

Le thème principal de cette thèse est le lien entre des valeurs propres principales d'opérateurs elliptiques et le comportement asymptotique de variantes de l'équation de Fisher-KPP.

Dans la première partie, nous nous concentrons sur des problèmes de valeurs propres principales provenant de la dynamique des populations. Dans trois chapitres, nous étudions l'effet d'une séparation d'échelles, du vent et de la diffusion hétérogène sur la capacité de persistance et sur la vitesse de propagation de la population. Plusieurs preuves centrales de la première partie utilisent des outils probabilistes.

Dans la deuxième partie, nous nous intéressons à un modèle de réaction-diffusion pour une population structurée en phénotype et vivant dans un environnement hétérogène périodique. Nous prouvons un critère (impliquant une valeur propre principale généralisée) pour la persistance de la population. Ensuite, nous étudions des problèmes d'optimisation pour rendre la persistance plus facile ou plus difficile. Nous nous intéressons également à la vitesse de propagation dans différentes limites d'échelle. Enfin, nous prouvons de nouveaux résultats de persistance et de propagation pour une équation plus simple, où l'on considère seulement deux morphes.

Dans la dernière partie, nous nous concentrons sur la perte de diversité génétique pendant une invasion. D'abord, nous montrons qu'un retard logarithmique apparaît dans une équation avec dispersion non-locale. Ensuite, nous nous intéressons à des données expérimentales qui montrent une perte de diversité après qu'une population a passé une barrière ; nous proposons des modèles probabilistes pour comprendre cette perte de diversité.

Mots-clés : Équation de Fisher-KPP ; Équations elliptiques ; Valeurs propres principales ; Comportement en temps long ; Dynamique des populations ; Génétique des populations ; Interprétation probabiliste des EDP.

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Chapter 1

Introduction

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1.1 The Fisher-KPP equation and its variants

The starting point of this thesis is the Fisher-KPP equation, which has been introduced in 1937 in two independent articles by Fisher [94] and Kolmogorov, Petrovsky and Piskunov [143]. For its applications in numerous fields – and especially population dynamics – the Fisher-KPP equation has been widely studied since the founding articles of 1937.

The goal of this section is to provide the reader with an introduction to the standard Fisher-KPP equation, its properties, and to its variants that will be studied throughout the thesis. We shall have a special focus on heterogeneous equations and their connection to principal eigenvalues, and on equations structured in space and phenotype.

1.1.1 The standard Fisher-KPP equation

In its simplest form, the Fisher-KPP equation reads:

$$\partial_t u(t,x) = \Delta u + u(r-u), \qquad t>0,\ x\in\mathbb{R}, \tag{1.1}$$

and is usually supplemented by an initial datum

$$u(0,x) = u_0(x) \in L^\infty(\mathbb{R}), \qquad u_0 \geqslant 0. \tag{1.2}$$

Here, $r>0$ is a constant. The Cauchy problem (1.1)–(1.2) admits a unique bounded solution u and, for all $t>0$, the profile $u(t,\cdot)$ is smooth. See Figure 1.1 for an illustration of a solution u at different times.

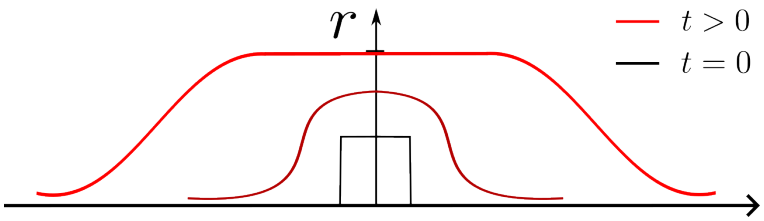


Figure 1.1: Example of the evolution of a solution of the Fisher-KPP equation.

Since $u_0 \geqslant 0$, the comparison principle implies that for all $t\geqslant 0$, $u(t,x)\geqslant 0$. Therefore, we may see the profile $u(t,\cdot)$ as the distribution of a population: $u(t,x)$ represents the density of individuals at time t and position x. The diffusion term Δu of the equation corresponds to movements of individuals. The logistic term $u(r-u)$ corresponds to demography: the linear term ru accounts for growth neglecting interactions, and the nonlinear term $-u^2$ accounts for competition between individuals.

The Fisher-KPP equation can be obtained as a large population limit of (stochastic) individual-based models. In such individual-based models, particles follow Brownian motion (this leads to the diffusion term Δu) and die or give birth at a rate depending on local density (this leads to the logistic term $u(r-u)$). See Subsection 1.2.1 for more details about such individual-based models and such derivations.

Spreading properties.

A fundamental property of the Fisher-KPP equation, which explains why it has raised so much interest in the study of biological invasions, is that its solutions, when started from a

localised distribution, eventually "invade" the environment [14] (this invasion property can be seen on Figure 1.1). More precisely, there exists a constant $c^* > 0$, called the *spreading speed*, such that as soon as u_0 is continuous, nonnegative, not identically equal to 0 and compactly supported, we have: for all $c' \in (0, c^*)$,

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

and for all $c'' > c^*$,

$$u(t, c''t) \to 0 \qquad \text{as } t \to +\infty.$$

In the simple case of Equation (1.1), the spreading speed has an explicit expression: $c^* = 2\sqrt{r}$.

Another interesting feature of Equation (1.1), which is strongly related to spreading, is the existence of travelling waves. Travelling waves, illustrated by Figure 1.2, are self-similar solutions which travel at some speed $c > 0$; namely, they are solutions of the form

$$u(t, x) = U_c(x - ct),$$

where U_c is a profile satisfying

$$0 \leqslant U_c \leqslant 1, \qquad \lim_{x \to -\infty} U_c(x) = r, \qquad \lim_{x \to +\infty} U_c(x) = 0.$$

In their 1937 article, Kolmogorov, Petrovsky and Piskunov proved that such a self-similar solution exists as long as $c \geqslant c^*$; therefore, c^* is not only the spreading speed of a solution that is initially compactly supported, but also the minimal spreading speed of a travelling wave.

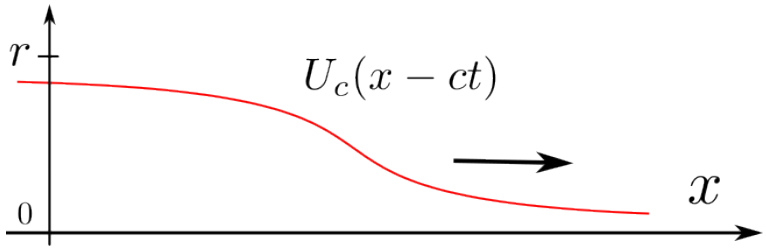


Figure 1.2: Example of a travelling wave.

Further, Kolmogorov, Petrovsky and Piskunov proved that when u_0 is compactly supported, there exists a function $m(t)$ such that $m(t)/t \to 0$ as $t \to +\infty$ and such that, as $t \to +\infty$,

$$u(t, \cdot + ct + m(t)) \to U_{c^*}(\cdot) \qquad \text{uniformly.}$$

This means that up to a correction $m(t)$, the profile of the solution converges to the profile of the travelling wave with minimal speed. It is possible to give very precise properties of the correction m. Although they are much too precise to be relevant for biological interpretation, these properties are very interesting from a mathematical point of view, especially with respect to the methods which were used to prove them. The first results of this kind were proved in 1978 by Bramson [53] and Uchiyama [217]. They proved that as $t \to +\infty$,

$$m(t) = -\frac{3}{2\sqrt{r}} \ln(t) + O(1).$$

Thus m is a logarithmic correction of the position of the solution with initial compact support, with respect to the travelling wave. This logarithmic correction is also called the *Bramson correction*.

Bramson and Uchiyama used different methods, but both were based on probabilistic interpretations of the Fisher-KPP equation. Bramson used a branching Brownian motion representation, which corresponds to *genealogies* of current individuals; much more insight into this fact will be given in Subsection 1.2.2. Uchiyama used a Feynman-Kac representation, which corresponds to following an ancestral lineage of a current individual. The Feynman-Kac representation will be used several times in this thesis, and will be described in Subsection 1.2.3. More recently, the emergence of a logarithmic correction has been proved using PDE methods [120].

Since 1978, numerous extensions have been proved for different extensions of the Fisher-KPP equation: higher dimension [216], heterogeneous equations [121] (see Subsection 1.1.2), nonlocal equations [42, 45, 113, 188, 197] (see Subsection 1.1.4), higher order asymptotics [79, 178], other initial conditions [7, 52, 217]. These proofs use either probabilistic or PDE methods. See Chapter 9 for a review of these works.

A biological insight can be obtained by merely determining whether the correction $m(t)$ is bounded or not; if m is unbounded, we expect that "neutral diversity" is lost along the invasion. The structure of neutral diversity is the object of the next paragraph.

Pulled and pushed spreading.

So far, we have been considering the population as a uniform mass; let us now focus on its inside structure. Consider a travelling wave which is initially decomposed into $n \geqslant 2$ tags. At the initial time, each individual carries a tag, according to their position, so that the tags are organised as on Figure 1.3: there is one tag at the tip of the wave, all others are stacked one behind the other in the "bulk" of the wave. Assume that these tags have no influence on demography or movement; we thus say that we have *neutral diversity* within the wave.

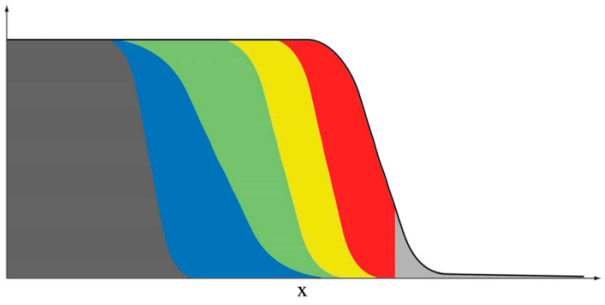


Figure 1.3: Initial distribution of the different tags. Each colour corresponds to a tag. Here, the "light grey" tag is present on the right-hand half of the space.
Source: Roques, Garnier, Hamel, Klein [202].

The main question is the following: *How does the inner structure of the wave evolve as time goes by?* In particular, we would like to know whether the tags which initially are behind will manage, or not, to keep pace with the tip of the wave.

In the case of the standard Fisher-KPP equation (1.1), the tags that are initially located at the tip of the wave lead the invasion, while those that are initially located in the bulk

of the wave are left behind and their proportions near the tip of the wave go to zero [101, 202]. See Figure 1.4, B. The wave is then said to be *pulled* (as the spreading is led by the individuals which are located at the tip of the wave). This phenomenon can be interpreted as a *loss of diversity* during the invasion.

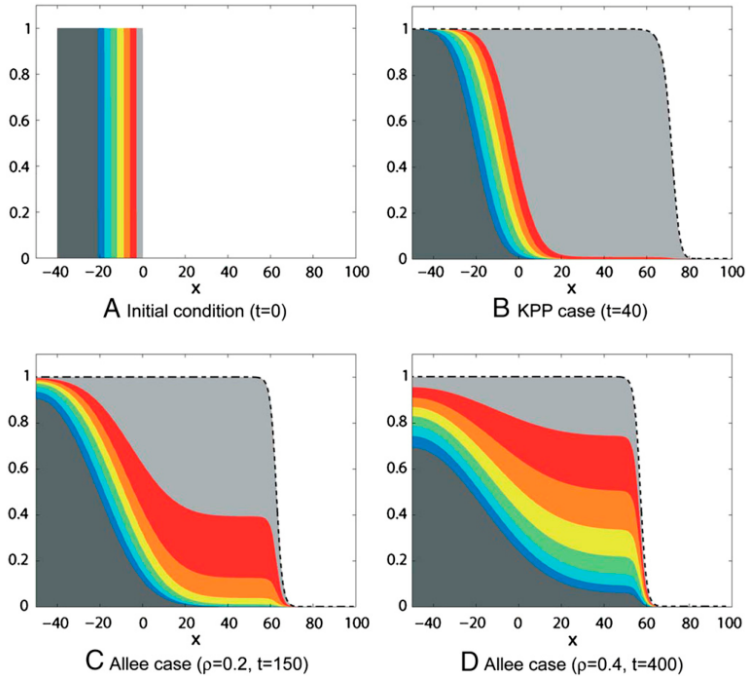


Figure 1.4: Evolution of the inside structure of the waves, with respect to the type of wave. **(A)** Initial condition for the simulation (which differs from the initial condition showed in Figure 1.3 for the analytical results); **(B)** Pulled wave ($B = 0$ and $r = 1$); **(C)** and **(D)** Pushed wave (with $\rho = 0.2$ or $\rho = 0.4$, respectively).
Source: Roques, Garnier, Hamel, Klein [202].

On the other hand, consider, instead of Equation (1.1), the following equation:

$$\partial_t u(t,x) = \Delta u + u(r-u)(u-\rho),$$

where $\rho \in (0, 1/2)$ is a new constant. We obtain a *bistable* equation (the two equilibrium states 0 and 1 are stable), which is used to take into account a *strong Allee effect*. In general, the Allee effect is the positive effect, on the growth rate of the population, of an increase of population size. Such a positive effect can be due, for example, to cooperation between individuals: if the population is too small, one may imagine that individuals cannot defend themselves, or cannot meet each other for reproduction; in either case, the growth rate of the population is negative. In the above equation, ρ is the Allee threshold, below which individuals cannot cooperate, implying that the local growth rate of the population is negative. In such a bistable equation, contrarily to the standard Fisher-KPP equation (1.1), the tags that are initially located at the tip of the wave are caught up by the individuals behind: near the tip of the wave, each tag is represented in a positive proportion [101, 202]. See Figure 1.4, C and D. The wave is then said to be *pushed*, as spreading is led by the individuals that are located in the bulk of the wave. Analogously, this phenomenon can be interpreted as the *conservation of diversity* during the invasion.

Another form of Allee effect is modelled by the following *monostable* equation:

$$\partial_t u(t,x) = \Delta u + u(r-u)(1+Bu),$$

where $B \geqslant 0$ is a new constant. The constant B can be interpreted as the strength of the *weak* Allee effect. This Allee effect is termed "weak" as a lack of cooperation implies a small, yet positive, growth rate. For $B = 0$, we recover Equation (1.1). For $0 \leqslant B \leqslant 2$, the wave is pulled, and diversity is lost (as for the standard Fisher-KPP equation). On the other hand, for $B > 2$, the wave is pushed, and diversity is conserved, as for the bistable equation [101].

The notions of *pulled* and *pushed* waves have been initially defined by Stokes [213] but the definitions which we gave here are those of [101, 202]. Recently, the category of pushed waves has been split into *fully pushed waves* (arising in the monostable equation with $B > B^*$ for some $B^* > 2$) and *semi-pushed waves* (with $2 < B < B^*$) [36]. This distinction arises when the genealogies of the individuals at the tip of the wave are studied more closely.

Let us now explain the connection to the logarithmic correction. The tags that are initially located in the bulk of the wave correspond to a population which is initially compactly supported. If the correction m is bounded, then this population can keep pace with the travelling wave, which is at position c^*t, and no loss of diversity occurs. On the other hand, if $\liminf m = -\infty$ as $t \to -\infty$, then this population *cannot* keep pace with the travelling wave and diversity is lost during the invasion. Indeed, known results about neutral diversity and the logarithmic correction show that diversity is lost when, and only when, there is a logarithmic correction [39, 101, 202].

1.1.2 Heterogeneity and principal eigenvalues

When we see the Fisher-KPP equation (1.1) from a population dynamics point of view, the diffusion term Δu corresponds to movements of individuals and the reaction term $u(r-u)$ corresponds to demography. None of these terms depends on time t, nor on the spatial position x. This means that the behaviour of the individuals is independent of space and time, so the environment that we model is homogeneous in space and time. In general, this is not realistic. Therefore, we may ask the following question: *What happens if we consider a heterogeneous environment?*

In this thesis, we shall consider only heterogeneity in space; this means that at our timescales, the environment does not change much in time. The main tool that we will use to deal with heterogeneity in space is the *principal eigenvalue for elliptic operators*. (If we had considered also heterogeneity in time, we would have focused instead on principal eigenvalues for *parabolic* operators.)

A general form of heterogeneous Fisher-KPP equation is the following:

$$\partial_t u(t,x) = \nabla \cdot (D(x)\nabla u) + \nabla \cdot (b(x)u) + u(r(x)-u), \qquad t > 0,\ x \in \mathbb{R}^N, \tag{1.3}$$

where $N \geqslant 1$ is the spatial dimension, $D(x) \in \mathcal{C}^{2,\alpha}(\mathbb{R}^N)$, $D > 0$, is the diffusion coefficient, $b(x) \in \mathcal{C}^{1,\alpha}(\mathbb{R}^N, \mathbb{R}^N)$ is the transport coefficient and $r(x) \in \mathcal{C}^{0,\alpha}(\mathbb{R}^N)$ is the growth rate (for some $0 < \alpha < 1$). Here and in the sequel, $\mathcal{C}^{k,\alpha}$ denotes the set of functions f such that all partial derivatives of f up to order k are α-Hölder continuous. The heterogeneity in Equation (1.3) corresponds to a situation where the trajectory of particles is not necessarily a Brownian motion, but may depend on their position; the law of a trajectory will be the

law of a solution $(X_t)_{t\geqslant 0}$ to the Itô stochastic differential equation

$$\mathrm{d}X_t = (\nabla D(X_t) - b(X_t))\,\mathrm{d}t + \sqrt{2D(X_t)}\,\mathrm{d}W_t,$$

where $(W_t)_{t\geqslant 0}$ is a standard Brownian motion. Moreover, the net growth rate at position x is $r(x)$, which may be positive or negative. If $r(x) > 0$, then it is understood that the environment is favourable at x. On the other hand, if $r(x) < 0$, then it is understood that the environment is unfavourable at x. If r is uniformly negative, then, as $t \to +\infty$, the solution u converges to 0 uniformly in x. This means that the population gets extinct. Furthermore, if the drift coefficient b is too strong with respect to the growth rate r, the population is washed out from its current position and local extinction occurs. Therefore, contrarily to the homogeneous case, the persistence or extinction of the population is not trivial in the heterogeneous setting with drift.

Thus, we must answer the following question: *When does the population survive?* If it survives, we may also wonder whether the properties of the homogeneous equation also hold for the heterogeneous equation: *Does the population spread? At what speed? Are there travelling waves?*

Equation (1.3) is very general and, without further assumptions on the coefficients, it is really hard to give properties of the solutions. In this thesis, we will always assume that D, b and r are 1-periodic, namely, for all $x \in \mathbb{R}^N$ and for all $h \in \mathbb{Z}^N$, we have

$$D(x+h) = D(x), \qquad b(x+h) = b(x), \qquad r(x+h) = r(x).$$

In this setting, the persistence and spreading properties of Equation (1.3) are described by principal eigenvalues of elliptic operators.

When $b \not\equiv 0$, there are several notions of principal eigenvalues that may differ from one another. The notions of persistence and spreading are also subtler: the population may have a total mass bounded from below by a positive constant, yet get locally extinct. In order to avoid such subtleties, we shall assume here that $b \equiv 0$. In Chapters 3 and 4 (see also Subsection 1.3.2), we shall work in cases where $b \not\equiv 0$. Notably, in Chapter 3, we will define the notions of spreading speed *to the right* and spreading speed *to the left*.

Principal eigenvalues.

Consider the operator $\mathcal{L}_0$ defined by

$$\mathcal{L}_0 : \phi \in \mathcal{C}^2(\mathbb{R}^N) \mapsto \nabla \cdot (D\nabla\phi) + r\phi.$$

The operator $\mathcal{L}_0$ will allow us, in the next paragraph, to find a criterion for *persistence* of the population. In dimension $N = 1$, we will also consider *spreading* properties of the population. The spreading speed will be expressed thanks to a family of operators, based on $\mathcal{L}_0$, which we now define.

Assume $N = 1$. For $\lambda \in \mathbb{R}$, define the function $E_\lambda : x \mapsto e^{\lambda x}$ and consider the operator $\mathcal{L}_\lambda$ defined by

$$\mathcal{L}_\lambda : \phi \in \mathcal{C}^2(\mathbb{R}) \mapsto E_\lambda \mathcal{L}_0 \left(E_{-\lambda}\phi\right).$$

Equivalently, we may write:

$$\mathcal{L}_\lambda : \phi \in \mathcal{C}^2(\mathbb{R}) \mapsto (D\phi')' - (2\lambda D\phi)' + (r + \lambda^2 D + \lambda D')\phi.$$

The operator $\mathcal{L}_\lambda$, $\lambda \in \mathbb{R}$, therefore, is an elliptic operator. We point out that with $\lambda = 0$, we obtain the operator $\mathcal{L}_0$ defined above.

It can be shown that for all $\lambda > 0$, there exists a constant $a > 0$ large enough such that the operator $\mathcal{L}_\lambda - a$ satisfies the strong maximum principle on periodic functions, and $(\mathcal{L}_\lambda - a)^{-1}$ can be defined as an operator $L^2(\mathbb{T}^N) \to H^1(\mathbb{T}^N)$, where $\mathbb{T}^N := \mathbb{R}^N/\mathbb{Z}^N$ is the N-dimensional torus (accounting for the 1-periodicity of the functions that we consider). Since $\mathbb{T}^N$ is compact, the operator $(\mathcal{L}_\lambda - a)^{-1}$ is compact. Under such conditions, the Krein-Rutman theorem can be applied: there exists a unique $k_\lambda \in \mathbb{R}$ and a unique (up to multiplication) 1-periodic $\varphi_\lambda \in \mathcal{C}^2(\mathbb{R}^N)$ such that

$$\mathcal{L}_\lambda \varphi_\lambda = k_\lambda \varphi_\lambda, \qquad \varphi_\lambda > 0.$$

Then, k_λ is called the *principal eigenvalue* of $\mathcal{L}_\lambda$ and φ_λ is called the *principal eigenfunction* of $\mathcal{L}_\lambda$. In Chapters 5 and 6 (see also Subsection 1.4.1), we shall study a situation where the Krein-Rutman theorem cannot be applied, owing to a lack of periodicity. It will then be necessary to use *generalised principal eigenvalues*.

Now that we have defined the principal eigenvalues for the operators $\mathcal{L}_\lambda$, $\lambda \in \mathbb{R}$, we may state the persistence and spreading properties of Equation (1.3).

Persistence.

If $k_0 > 0$, then, for any compactly supported initial datum $u_0 \in L^\infty(\mathbb{R}^N)$ which is nonnegative and not identically equal to 0, we have:

$$\liminf_{t \to +\infty} \sup_{x \in \mathbb{R}^N} u(t,x) > 0.$$

We say that the population persists. On the other hand, if $k_0 \leqslant 0$, then, for the same initial datum, as $t \to +\infty$,

$$u(t,x) \to 0 \qquad \text{uniformly in } x.$$

We say that the population gets extinct. This dichotomy comes from [27] (see also [56] for the same result in bounded domains).

Throughout the thesis, we shall refer to k_0 as the *ability of persistence* of the population. This terminology can be explained as follows. If r is replaced by $r - \kappa$ for a constant $\kappa > 0$, then the population survives as long as $k_0 > \kappa$. Therefore, if k_0 is higher, the population is able to survive to more stringent constant perturbations of the environment; this can be interpreted as the population being better "able to persist".

Spreading.

Let us now focus on the spreading properties; we assume that we work in the 1-dimensional setting, i.e. we set $N = 1$. Recall that k_λ has been defined above as the principal eigenvalue of $\mathcal{L}_\lambda$. We define:

$$c^*_{het} := \inf_{\lambda > 0} \frac{k_\lambda}{\lambda}. \tag{1.4}$$

The function $\lambda \mapsto k_\lambda$ is convex and symmetric. Therefore, by (1.4), $c^*_{het} > 0$ as long as $k_0 > 0$. Under this condition, c^*_{het} is the spreading speed for the heterogeneous Fisher-KPP equation, in the following sense. Let $u_0 \in L^\infty(\mathbb{R})$ be an initial datum which is nonnegative, continuous,

compactly supported and not identically equal to 0. We have: for all $w > c^*_{het}$, as $t \to +\infty$,

$$u(t, wt) \to 0, \qquad u(t, -wt) \to 0,$$

and for all $|w| < c^*_{het}$,

$$\liminf_{t \to +\infty} u(t, wt) > 0.$$

The formula for the spreading speed (1.4) is called the *Freidlin-Gärtner formula* [103]. More general versions (for $b \not\equiv 0$, in higher dimension) are proved in [25, 26, 220].

Note that if there is a drift term $b \not\equiv 0$, the function $\lambda \mapsto k_\lambda$ may not be symmetric and we may have $c^*_{het} \in (-\infty, 0)$ even if $k_0 > 0$. See Chapter 3 for more insight into equations with a possibly strong drift term.

Pulsating travelling waves.

In the heterogeneous setting, the existence of travelling waves cannot be expected, owing to heterogeneity. Instead, in dimension $N = 1$, there exists the notion of *pulsating travelling waves* [209]. Figure 1.5 is an illustration of a pulsating travelling wave.

A pulsating travelling wave with speed $c \in \mathbb{R}$ (again in dimension $N = 1$) is a solution u of (1.3) such that $(t, x) \mapsto u(t, x + ct)$ is periodic in time and has the following limits: for all $c' > c$, $u(t, c't)$ converges to 0, and for all $c'' < c$, the profile $x \mapsto u(t, c''t + x)$ converges locally uniformly, up to a time-dependent shift, to $\phi > 0$ satisfying $(D\phi')' + \phi(r - \phi) = 0$ (i.e. ϕ is a stationary state to (1.3)). If $k_0 \leqslant 0$, then no such ϕ can exist. If $k_0 > 0$ (and $b \equiv 0$), then such a ϕ exists and is unique, and, therefore, is 1-periodic.

Moreover, for all $c \geqslant c^*_{het}$, there exists a pulsating travelling wave with speed c [27]. On the other hand, if there is an advection term $b \not\equiv 0$, then uniqueness of a stationary state may fail, see [29]. If $r \geqslant 0$ and $\int_0^1 b = 0$, then existence and uniqueness of ϕ hold and for all $c \geqslant c^*_{het}$ (which is defined by a formula analogous to (1.4)), there exists a travelling wave with speed c [23, 26].

Last, let us mention that the authors of [121] proved, for a particular case of heterogeneity, that a solution of the heterogeneous Fisher-KPP equation (1.3), when started from a compactly supported initial condition, eventually converges to the pulsating travelling wave up to a logarithmic correction.

1.1.3 Phenotypic structure

In the above subsections, we have been working with the implicit assumption that all individuals are identical; however, the population may well be heterogeneous itself. Typically, individuals with distinct phenotypes may react differently to the same environmental conditions. *How can we take into account the heterogeneity of the population?*

Heterogeneity of the population.

A first way to model the heterogeneity of the population is to assume that there is a finite number of phenotypes: this leads to a system of Fisher-KPP equations, each of them accounting for a given phenotype, competing with the other ones. In this direction, let us mention [109] for homogeneous environments and [110, 115] for heterogeneous environments.

In this thesis, we shall mostly assume that the phenotype is a continuous parameter (but see Chapter 8 and the end of Subsection 1.4.2). We let $\Theta \subset \mathbb{R}^P$ (with $P \in \mathbb{N}$) be the space

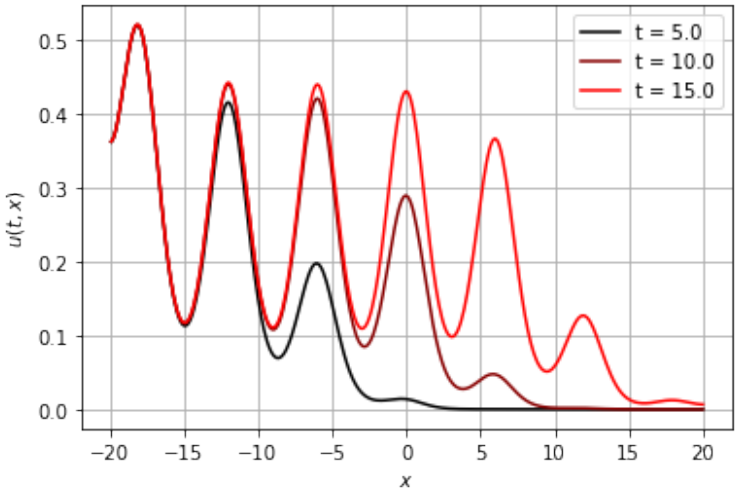


Figure 1.5: Simulation of a pulsating travelling wave, obtained by taking $u_0(x) := \mathbb{1}_{x<-15}$, $D(x) \equiv 1$, $b(x) \equiv 0$ and $r(x) = \cos(\pi x/3)$. To the left, one can see a stationary state appear. The bump to the very left is higher than the others owing to the boundary used for simulations.
The simulation has been obtained using the code of [199].

for the phenotype, and we assume that either Θ is a smooth bounded connected subset of $\mathbb{R}^P$, or $\Theta = \mathbb{R}^P$. In the former case, we let ν be the outward unit normal on $\partial\Theta$. We will consider solutions of the form $u(t,x,\theta)$ ($t > 0$, $x \in \mathbb{R}^N$ and $\theta \in \Theta$) of variants of the standard Fisher-KPP equation. If the environment is homogeneous, the equation is:

$$\begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + u\,(r(\theta) - \rho(t,x))\,, & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \nu \cdot \nabla_\theta u = 0, & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R}^N \times \Theta, \end{cases} \tag{1.5}$$

with

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

Throughout the thesis, when $\Theta = \mathbb{R}^P$, the boundary condition on $\mathbb{R}^N \times \partial\Theta$ must be omitted.

In Equation (1.5), the phenotype is taken into account through the new variable θ. We assume that all individuals located at the same position compete with each other, regardless of their phenotypes. This is translated in the equation by replacing the nonlinear term $-u^2$ by the nonlinear nonlocal term $-\rho u$, where $\rho(t,x)$ is the total population density at (t,x). Finally, we add a term $\Delta_\theta u$, to account for mutations; this modelling means that mutations are small and frequent.

Models similar to (1.5) appeared for the first time in the work of Prévost [194]. Champagnat and Méléard [61] derived variants of (1.5) as large population limits of individual-based models (in their models, the mutations are rarer but larger than in ours). In Subsection 1.2.1, we shall give more details of their derivations. See in particular Figure 1.8 for an illustration of their construction.

Equation (1.5) is studied in [30] in the case $\Theta = \mathbb{R}^P$, under the assumption that $-r$ goes to infinity as $\|\theta\| \to +\infty$. The latter condition allows the authors to define in a standard way

the principal eigenvalue k_0 of the operator

$$\mathcal{L}_0^{phen} := \Delta_x + \Delta_\theta + r(\theta)$$

acting on a Hilbert space. One then has a dichotomy analogous to that for the spatially heterogeneous Fisher-KPP equation (1.3): if $k_0 \leqslant 0$, then the population eventually gets extinct, while if $k_0 > 0$, then the population persists. Moreover, in the latter case, the equation admits a unique positive steady state $V(\theta)$, and any nontrivial solution converges towards V with a spreading speed equal to $c_{phen} := 2\sqrt{k_0}$.

Before moving on to heterogeneous environments, let us mention that a very interesting variant of Equation (1.5) – which we shall not consider in this work – is the *cane-toad equation*, where $\Theta \subset (0, +\infty)$ is unbounded, and $\Delta_x u$ is replaced by $\theta \Delta_x u$. Namely, the diffusion coefficient depends on the phenotype and may be arbitrarily large. In this case, *accelerating* invasions may arise [41], due to the selection, at the tip of the wave, of the fastest individuals. Such an acceleration has been observed in the invasion of the cane-toad in Australia [41].

Heterogeneity of the environment.

Above, we considered a heterogeneous population living in a homogeneous environment. Before that, we considered a homogeneous population living in a heterogeneous environment. In this thesis, we shall thoroughly focus on *heterogeneous populations living in heterogeneous environments*. Namely, in (1.5), we shall replace $r(\theta)$ by $r(x, \theta)$ and obtain

$$\begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \nu \cdot \nabla_\theta u = 0, & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R}^N \times \Theta. \end{cases} \tag{1.6}$$

The environmental heterogeneity here is simpler than in (1.3): it arises only on the reaction term $r(x, \theta)$ but not on the diffusion or mutation term. Further, there are no transport terms. Figure 1.6 is the output of a simulation of Equation (1.6), compared to a simulation of a 2-dimensional Fisher-KPP equations with the same coefficients.

In the literature, the reaction term $r(x, \theta)$ in (1.6) has taken various forms. In [4, 187], the authors studied the case $N = P = 1$ where the population evolves along an environmental gradient, that is:

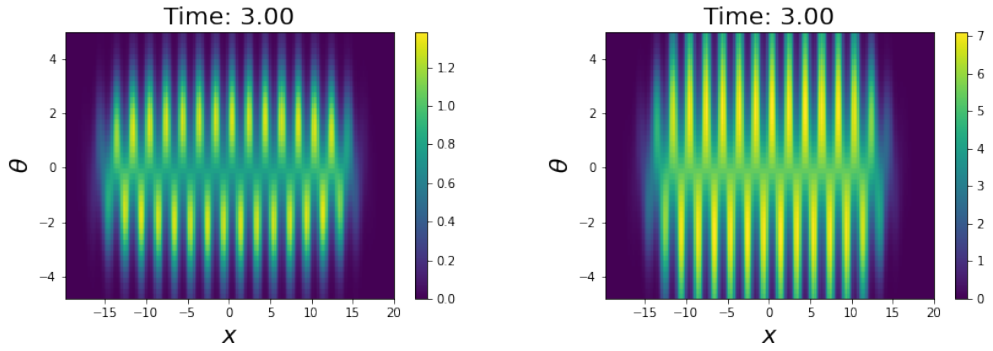
$$r(x,\theta) = R(x - B\theta), \qquad B > 0,$$

with

$$R > 0 \text{ on } (-1,1), \qquad R < 0 \text{ on } \mathbb{R} \setminus [-1,1].$$

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 population to spread. 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 [187], Peltier showed that if the tail of the initial condition is sufficiently heavy, then an accelerating invasion arises, as in the 1-dimensional case [122]. In [4], 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 travelling waves.

Additionally to spatial heterogeneity, the authors of [3] add a heterogeneity in time cor-



(a) **(b)**

Figure 1.6: **(a)** Simulation of Equation (1.6) with $u_0(x,\theta) = e^{-\frac{x^2+\theta^2}{5}}$, $r(x,\theta) = 10 - \frac{1}{2}(y - O(x))^2$ where $O(x) = 3$ if $x \in [0,1/2)$, $O(x) = -3$ if $x \in [1/2,1)$, and O is 1-periodic. **(b)** Simulation of Equation (1.6), with $-\rho u$ replaced by $-u^2$, and with same coefficients. The colour scales in **(a)** and **(b)** are different and range, in both figures, from 0 to $\max u$. *The simulation has been obtained using the code of [199].*

responding to climate change. Their growth rate takes the form $r(x - ct, \theta)$. Different shapes of the favourable space/phenotype zone are studied (confined zone, environmental gradient, or a mixing of the two). In each case, the authors find a criterion for persistence and propagation of the species. The criteria, again, are based on the principal eigenvalue of linear operators.

There have been some works considering the phenotype together with a periodic heterogeneous environment. In [9], Alfaro and Peltier focus on homogeneous environments with a very small periodic perturbation. When the perturbation is sufficiently small, they show the existence of stationary states and pulsating travelling waves. In [44], Bouin and Mirrahimi focus on a situation where evolutionary events (mutations) occur on a much faster timescale than ecological events (movements). In a similar vein, but in the stationary setting, Léculier and Mirrahimi [151] studied the weak mutation limit of the stationary version of a model related to ours. They also give biological properties of the solution; in some cases, they are able to determine if the population at equilibrium is polymorphic or monomorphic.

In Chapters 5, 6 and 7 (see also Subsections 1.4.1 and 1.4.2), we shall consider persistence and spreading properties of a population modelled by (1.6), when r is 1-periodic in space. When $\Theta = \mathbb{R}^P$, we shall make use of *generalised* principal eigenvalues. For a particular form of r, in Chapter 6, we shall give optimisation results of the "ability of persistence" (i.e. of the principal eigenvalue of $\mathcal{L}_0^{phen}$).

1.1.4 Nonlocal variants

A fundamental difference between Equation (1.3) (without phenotype) and Equations (1.5)–(1.6) (with phenotype) is that the former is *local* and the latter are *nonlocal*. An equation on u is said to be *local* when its terms only depend on the value of u in an arbitrarily small neighbourhood of the same point; for example, in Equation (1.3), $\partial_t u(t,x)$, $\Delta u(t,x)$ and $u(r-u)$ only depend on the value of u in an arbitrarily small neighbourhood of (t,x). On the other hand, in Equations (1.5)–(1.6), $\rho(t,x)$ depends on the value of u on $\{(t,x)\} \times \Theta$, and Θ cannot be made arbitrarily small; therefore, Equations (1.5)–(1.6) are nonlocal.

The nonlocality of Equations (1.5)–(1.6) prevents the *comparison principle* to hold. This is a serious difficulty which we shall circumvent by linearising the equation. Thanks to this linearisation, the equation will become local.

Let us now describe two other forms of nonlocal equations which have been studied in the literature, and in which a logarithmic correction is expected to occur, as for the standard Fisher-KPP equation. The first one is related to Equations (1.5)–(1.6), and the second one will be the subject of a more thorough study in Chapter 9.

Another form of nonlocal competition.

In the standard Fisher-KPP equation (1.1), two individuals compete with each other only if they are exactly at the same position (and thus the equation is local). However, we might consider that two individuals that are "quite close" to each other should also be in competition. Assume that two individuals that are at distance $|y|$ exert on each other a competition with strength $\phi(y) = \phi(-y) \geqslant 0$. At time t, the total competition that is exerted on an individual at x is:

$$\phi * u(t,x) := \int_{\mathbb{R}} \phi(y) u(t, x-y) \, \mathrm{d}y.$$

To make sure that everything is well-defined, we assume that the function ϕ belongs to $L^1(\mathbb{R})$ and satisfies $\phi \geqslant 0$. We get the equation:

$$\partial_t u(t,x) = \Delta u + u(1 - \phi * u). \tag{1.7}$$

Equation (1.7) is similar to the standard Fisher-KPP equation (1.1), except that the local competition term $-u^2$ is replaced by a nonlocal competition term $-\phi * u$. It was introduced by Britton in [54].

Similarly to the equation with phenotype (1.6), Equation (1.7) displays a nonlocal competition term which implies a lack of comparison principle. Despite this difficulty, it is possible to prove that travelling waves exist [31, 89, 123]. Moreover, when started from an initial condition with initial compact support, a logarithmic correction appears [42, 188].

However, the travelling waves exhibit a complex behaviour which is not yet fully understood. This complex behaviour is very interesting and is related to the emergence of periodic patterns (see in particular [105]). Let us be more precise about it. Note that $u \equiv 1$ is an equilibrium state of (1.7). For some shapes of the competition kernel ϕ, this equilibrium is unstable, and there exist frequencies $\xi > 0$ such that when started from a perturbation

$$u(0,x) := 1 + \varepsilon \cos(2\pi\xi x)$$

(for some small $\varepsilon > 0$), the perturbation is amplified. In such cases, a periodic pattern with period $1/\xi$ can be expected to appear in the solution. This emergence is made apparent on simulations in [105], see Figure 1.7. In [123], Hamel and Ryzhik show that there exist nonconstant stationary states. A natural question, therefore, is: *when started from a small "random" perturbation, can we determine if such a stationary state emerges, and which one?* In this direction, see [205], where Sasaki shows how some frequencies can be amplified much more than others.

From a modelling point of view, when x is a geographical variable, the emergence of periodic patterns means that clumping of populations is naturally possible. When x is a phenotype variable (i.e., with the notations of Subsection 1.1.3, x is replaced by θ), these

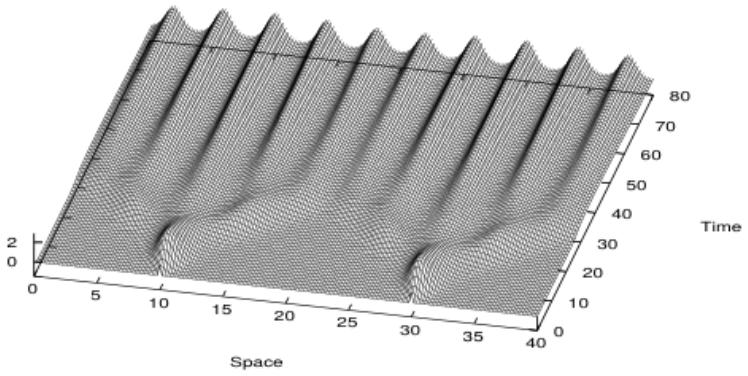


Figure 1.7: Emergence of subpopulations for a well-chosen competition kernel ϕ.
Source: Genieys, Volpert, Auger [105]

periodic patterns are related to *speciation*, as emphasised in the paper by Genieys, Volpert and Auger [105].

Nonlocal dispersal.

When we introduced the standard Fisher-KPP equation, we mentioned that it could be obtained as a large population limit of individual-based models in which particles follow Brownian motion. This means that the individuals of the population that we model make frequent and small movements (with respect to the space and time scales involved). Another possible model is a model where individuals occasionally jump; i.e. they make rare, but large movements. Namely, assume that individuals jump at rate 1. Let $J \in L^1(\mathbb{R})$, with $J \geqslant 0$ and $\int_{\mathbb{R}} J = 1$, be a probability density. For $y \in \mathbb{R}$, let $J(y)\,\mathrm{d}y$ be the probability that an individual makes a jump with size $|y|$ to the right (if $y > 0$) or to the left (if $y < 0$). The evolution of the number of individuals at x owing to these jumps is then:

$$\int_{\mathbb{R}} J(y)u(t,x-y)\,\mathrm{d}y - u(t,x)\int_{\mathbb{R}} J(y)\,\mathrm{d}y.$$

We will use the notation:

$$J * u(t,x) := \int_{\mathbb{R}} J(y)u(t,x-y)\,\mathrm{d}y.$$

The Fisher-KPP equation becomes (removing diffusion and keeping the logistic growth):

$$\partial_t u(t,x) = [J * u(t,x) - u] + u(r-u). \tag{1.8}$$

This equation is nonlocal, owing to the term $J * u(t,x)$. Despite nonlocality, the comparison principle holds. However, the fact that there is no diffusion induces a technical difficulty, as smoothing of solutions no longer holds.

When J decays exponentially, the behaviour of the solutions is analogous to the equations that we saw above: when they start from a compactly supported initial condition, the solutions of (1.8) spread at some speed c^* [113] (independent of the initial condition) and a logarithmic correction emerges. This has been proved mostly with probabilistic methods using branching random walks (instead of branching Brownian motion) [2], and also, in [113,

197], adapting to nonlocal equations the method of [120]. In Chapter 9, we shall prove, with a probabilistic method, that a logarithmic correction holds for a linearised version of (1.8).

Further, as for the local Fisher-KPP equation, there exist travelling waves for all speeds $c \geqslant c^*$ [59, 67, 68, 207]. However, it seems that there is no proof of the convergence to a travelling wave.

On the other hand, when J is integrable but is "fat-tailed" (see [100, 144]), the behaviour is radically different from that of the Fisher-KPP equation. In this case, the invasion may *accelerate*. Namely, for all $w > 0$,

$$\liminf_{t\to+\infty} u(t, wt) > 0.$$

When the invasion accelerates, no travelling wave can exist [102].

1.2 Interactions between PDEs and probability

A central part of this thesis is the use of probabilistic methods to address questions about PDEs. The goal of this section is to present such methods. First, we will see how variants of the Fisher-KPP equation can be derived as large population limits of stochastic models with finite population sizes. Second, we will focus on the McKean-Skorokhod representation of the Fisher-KPP equation, which is based on a branching Brownian motion. As we will see, this representation deals with the genealogies of the individuals modelled by the equation. We will also construct a new representation for the equation with phenotype. Last, we will show that the principal eigenfunction of an elliptic operator can be seen as a quasi-stationary distribution of a killed process. We will then derive the Feynman-Kac formula and use it to better understand the law of the killed process.

The first point to be noted is that for a standard Brownian motion $(B_t)_{t\geqslant 0}$ whose initial law has density $u_0 \geqslant 0$, the density at time $t > 0$ of B_t is $u(t, \cdot)$, where u solves the heat equation:

$$\partial_t u = \frac{1}{2}\Delta u, \qquad u(0, \cdot) = u_0.$$

Throughout Section 1.2, we shall consider the diffusion operator $\frac{1}{2}\Delta$, which is associated with $(B_t)_{t\geqslant 0}$, instead of the operator Δ, which is associated with $(B_{2t})_{t\geqslant 0}$.

For the sake of exposition, we shall only consider elliptic operators without transport terms. If we wished to consider an equation of the form

$$\partial_t u = \frac{1}{2}\Delta u + \nabla \cdot (bu),$$

then the Brownian motion should be replaced by the solution $(X_t)_{t\geqslant 0}$ of the SDE

$$\mathrm{d}X_t = -b(X_t)\,\mathrm{d}t + \mathrm{d}B_t, \qquad X_0 = B_0.$$

For the branching Brownian motion representation and the Feynman-Kac formula, which are processes that see the equation backward in time (i.e. at the initial time, the process corresponds to the individuals at the final time of the equation), we will have to consider instead the process

$$\mathrm{d}X'_t = b(X'_t)\,\mathrm{d}t + \mathrm{d}B_t.$$

As we will only focus on $b = 0$ in this section, the difference will be hidden below (in Chapters 3

and 4, we will consider $b \not\equiv 0$). Yet, it must be kept in mind that the process for the branching Brownian motion representation or for the Feynman-Kac formula do not have the same interpretation as the process constructed to obtain the large population limit.

1.2.1 PDEs as large population limits of stochastic models

In this section, we will see the equations mentioned in the introduction from an individual-based point of view. Namely, we will see these equations as limits of stochastic finite population models. This point of view is helpful to understand how solutions should behave. Further, it will be helpful in Subsection 1.2.2 to understand how branching Brownian motion representations can be constructed.

Logistic growth.

We first forget space and study the simple example of logistic growth:

$$\frac{\mathrm{d}v}{\mathrm{d}t} = v(1-v), \qquad v(0) = v_0 \in (0,1). \tag{1.9}$$

This logistic growth equation can be seen as follows. Consider a population of N individuals, indexed by $\{1,\dots,N\}$. We assume that an individual may be either *full* or *empty*. (This terminology is more concise than the usual one, which deals instead with "real individuals" and "ghost individuals", respectively [156].)

We construct a stochastic process $(Z_t^N)_{t\geqslant 0}$ with values in $[\![1,N]\!]$ counting the number of full individuals. The process Z_t^N takes integer values between 0 and N and is defined in the following way. We start from

$$Z_0^N = \lfloor N v_0 \rfloor$$

with $v_0 \in (0,1)$. Then, at rate N, a *reproduction event* occurs. Upon a reproduction event, we take independently two individuals uniformly at random. If a full individual meets an empty individual – which occurs with probability $\frac{Z_t^N}{N}\left(1-\frac{Z_t^N}{N}\right)$ – then the empty individual becomes full and Z_t^N becomes Z_t^N+1. Otherwise, nothing happens. In the sequel, we shall understand this operation by saying, in both cases, that one of the two individuals involved in the reproduction event is replaced by a copy of the other.

The connection to Equation (1.9) is the following property (see e.g. [167, Theorem 5.6.1]):

For all $T>0$, as $N\to+\infty$, the stochastic process $\left(\frac{Z_t^N}{N}\right)_{0\leqslant t\leqslant T}$ converges in law to the deterministic process $(v(t))_{0\leqslant t\leqslant T}$.

This construction is the forward dynamics of the equation. When we construct the branching Brownian motion representation in Subsection 1.2.2, we will instead consider the backward dynamics.

Now, we add a space and phenotype structure to the population. The point of view is somewhat different, as we do not consider a fixed-size population made up of full and empty individuals. Instead, we only keep track of the full individuals (which, in particular, may be more numerous than N). We will recover an equation similar to the equation with phenotype (1.6). The phenotype structure can be ignored, and then we obtain the standard (heterogeneous) Fisher-KPP equation (1.3).

Add a spatial and a phenotypical variable.

In this paragraph, we introduce a simple version of the model described by Champagnat and Méléard in [61]. The geographical space is a bounded domain $\mathcal{X} \subset \mathbb{R}^N$ with $\mathcal{C}^3$ boundary, and the phenotype space is a bounded domain Θ with $\mathcal{C}^2$ boundary (the latter regularity assumption is not needed in [61] but is needed here). At time t, the population is made up of $N_t \in \mathbb{N}$ individuals. Initially, $N_0 = N$, where N is a scaling parameter. The population is described by the following point measure on $\mathcal{X} \times \Theta$:

$$\mu_t^N := \frac{1}{N} \sum_{i=1}^{N_t} \delta_{(X_t^i, \theta_t^i)},$$

where $X_t^i \in \mathbb{R}$ is the position of the ith individual at time t, and $\theta_t^i \in \Theta$ is the phenotype of the ith individual at time t. Each individual is submitted to the following phenomena:

- Migration: for all $i = 1, \dots, N_t$, X_t^i follows a Brownian motion in $\mathcal{X}$, normally reflected on the boundary $\partial\mathcal{X}$;
- Clonal birth: at rate $b_c(\theta_t^i)$, the individual i gives birth to a clone (i.e. an individual at X_t^i with phenotype θ_t^i);
- Mutations: at rate $b_m(\theta_t^i)$, the individual i gives birth to an individual at X_t^i and with phenotype σ chosen according to the law with density $J(\theta_t^i, \sigma)$ on Θ;
- Death: the individual i dies at a rate

  $$\mu + \frac{1}{N} \sum_{j=1}^{N_t} \mathbb{1}_{\left\| X_t^i - X_t^j \right\| \leqslant \delta},$$

  depending on the local density. Here, $\mu > 0$ is the intrinsic death rate and $\delta > 0$ is the interaction radius.

See Figure 1.8 for an illustration of the population and these four phenomena. Champagnat and Méléard show that the limit as $N \to +\infty$ of the empirical measure μ_t^N has a density u_δ which, as $\delta \to 0$, converges in $L^\infty([0,T], L^1(\mathcal{X} \times \Theta))$ to the unique $u \in L^\infty([0,T], L^1 \cap L^\infty(\mathcal{X} \times \Theta))$ that is a weak solution of

$$\partial_t u(t,x,\theta) = \frac{1}{2} \Delta_x u + \int_\Theta b_m(\sigma) J(\sigma, \theta) u(t,x,\sigma) \, \mathrm{d}\sigma - \mu u + b_c(\theta) u - u \int_\Theta u(t,x,\sigma) \, \mathrm{d}\sigma,$$

with boundary condition $\nu \cdot \nabla u = 0$ on $\partial\mathcal{X} \times \Theta$, where ν is the unit outward normal to $\partial\mathcal{X}$ (since movements in the direction Θ depend on a kernel, they do not need to specify the behaviour on the boundary of Θ). This equation was first studied in [194]. It is akin to our equation with phenotype, except that the geographical space is bounded and that the mutation term differs. The underlying mutation mechanism is a jump process, while for our equation the mutation mechanism is a diffusion process. From the modelling point of view, this means that we consider large timescales (i.e. many generations) with small mutations.

To finish this subsection, it is interesting to mention that the limit of the empirical measure of the particle system depends on the scaling between the different parameters. For example, one may consider rare mutations, or accelerated birth and death. Such scalings are studied by Champagnat, Ferrière and Méléard in [60], for a model structured in phenotype and not

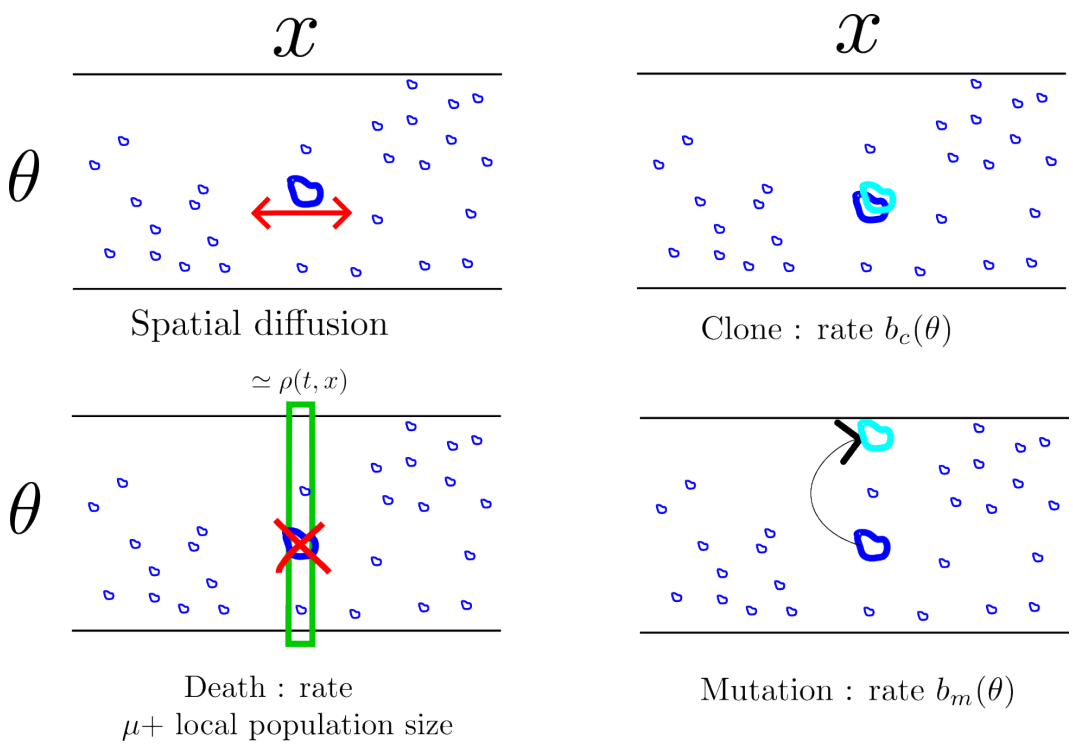


Figure 1.8: An illustration of the individual-based model constructed in [61].

in space. In the limit, depending on the scalings, they can find a deterministic equation, a superprocess, or a jump process. Their numerical simulations give insight into the very different behaviours that can be displayed by the population.

1.2.2 Branching Brownian motion and genealogies of the Fisher-KPP equation

In the previous subsection, we focused on stochastic processes which, under the right rescaling, converge to the solution of the PDE. The "time" of these processes went by in the same direction as the time for the PDE. Now, we will take the backward point of view: we will construct processes that start at the final time of the PDE.

We will first construct the McKean-Skorokhod representation [166, 212], which establishes a connection between a solution of the Fisher-KPP equation and a branching Brownian motion. Notably, it has been used to prove that a logarithmic correction appears [53]. More recently, it has been extended to a wide class of reaction terms [12, 83, 179]. The "voting scheme" leading to the McKean-Skorokhod representation is illustrated on Figure 1.9.

The representation is very surprising, and, without a deeper understanding, it seems hard to extend to other situations. The goal of this subsection is to provide an intuitive explanation of where the representation comes from. In the light of this explanation, we will construct a new representation for the equation (1.5) with phenotype. The representation could be extended to more general reaction terms, as in [12, 83, 179], but for conciseness we will keep to the simple logistic reaction term.

The construction is based on the results of the beginning of the previous subsection. Similar connections can be found in [78] (which also derives stochastic versions of the Fisher-

KPP equation by using other scaling limits), and in the context of spatial Λ-Fleming Viot processes, see in particular [85].

The logistic growth: backward dynamics.

In the beginning of Subsection 1.2.1, we derived the logistic equation (1.9) as the large population limit of a stochastic model. This was the forward approach of the population dynamics hidden in the logistic equation (1.9).

Here, we wish to concentrate on the backward approach. Consider an individual (full or empty) at time t and look at its "ancestral lineages". Recall that a reproduction event involves two individuals, one being replaced by a copy of the other. When the ancestor of the current individual is involved in a reproduction event, either of the following occurs:

- The two individuals involved in the reproduction event are empty; then the resulting individual is empty;
- The two individuals involved in the reproduction event are full; then the resulting individual is a full individual (chosen uniformly at random among the two previous ones);
- Of the two individuals involved in the reproduction event, one is empty and the other is full. Then the resulting individual is full.

When we follow the ancestral lineage of an individual (starting from the present time), we represent reproduction events by a branching. The two resulting branches are the two individuals involved in the reproduction event. The picture that we obtain is a tree, the root of which is the current individual and the leaves of which are the ancestors at time $-t$.

To obtain the type (full or empty) of the current individual, we start from the leaves of the tree, give the individuals there a type sampled according to the *initial distribution* of the population, and go down the branches; see Figure 1.9. Each time two branches merge, the type of the resulting individual is chosen according to the following rules ($\bullet$ stands for "full" and $\emptyset$ stands for "empty"):

$$\begin{aligned} \emptyset + \emptyset &\to \emptyset \\ \bullet + \emptyset &\to \bullet \\ \bullet + \bullet &\to \bullet \end{aligned} \tag{1.10}$$

We point out that if we are able to distinguish two full individuals of types i and j, then the last interaction becomes

$$i + j \to \begin{cases} i & \text{with probability } 1/2, \\ j & \text{with probability } 1/2. \end{cases}$$

This remark will be helpful for the representation of the equation with phenotype.

The above analysis indicates that the solution v of the logistic equation (1.9) satisfies:

$$\begin{aligned} v(t) &= \mathbb{P}\left(\text{the root of the tree is full}\right) = \mathbb{P}\left(\text{there is at least one full leave}\right) \\ &= 1 - \mathbb{E}\left[(1 - v(0))^{N_t}\right], \end{aligned}$$

where N_t stands for the number of leaves in the tree at time t.

The McKean-Skorokhod representation. Let us now consider the spatial version of the logistic equation (1.9):

$$\partial_t u(t,x) = \frac{1}{2}\Delta u + u(1-u), \qquad 0 \leqslant u(0,\cdot) = u_0 \leqslant 1.$$

We consider the backward dynamics described in the previous paragraph, to which we add a spatial structure. Movements are described by Brownian motions.

Namely, fix $t > 0$ and $x \in \mathbb{R}$ and let $((X_s^i)_{1\leqslant i\leqslant N_s})_{0\leqslant s\leqslant t}$ be a branching Brownian motion started from x. More precisely, at time $s = 0$, we have $N_0 = 1$ particle located at x. This particle evolves as a Brownian motion. At rate 1, the particle splits into two independent particles, both starting from the position of the original particle, and following themselves the same rules. The process $(N_s)_{0\leqslant s\leqslant t}$ counts the number of particles.

The initial (i.e. at time t for the branching Brownian motion) type of the individual $1 \leqslant i \leqslant N_t$ is *full* with probability $u_0(X_t^i)$ and *empty* with probability $1-u_0(X_t^i)$. The voting scheme at each branching event follows the rule (1.10), see Figure 1.9. We may interpret this by saying that the individual sampled at (t,x) is not empty if and only if there is a full individual in its ancestral lineage. The McKean-Skorokhod representation tells us that

$$u(t,x) = \mathbb{P}(\text{the root of the tree is full}).$$

In view of the above discussion, this result is very natural.

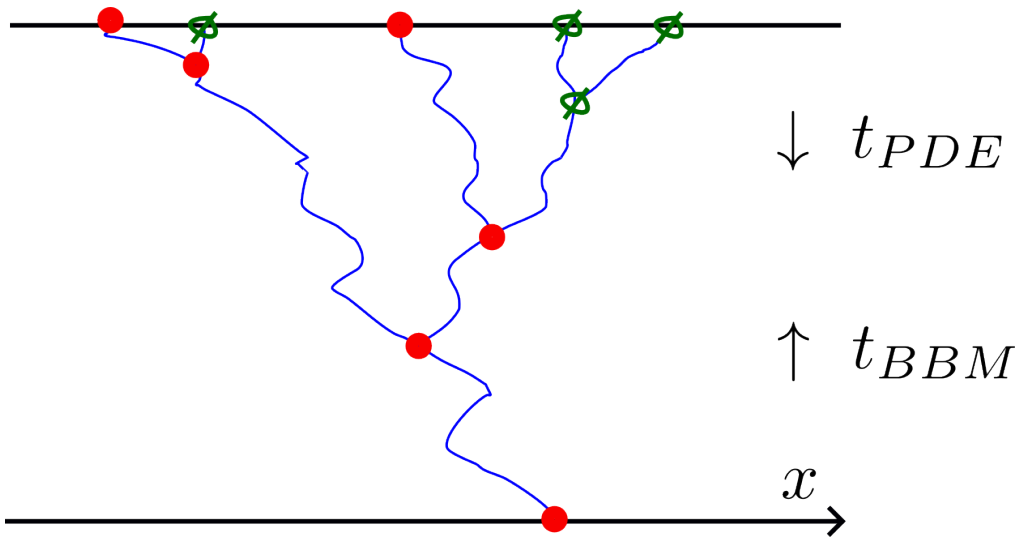


Figure 1.9: A run of the McKean-Skorokhod representation. Red circles are full individuals, and green $\emptyset$-symbols are empty individuals. The branching Brownian motion runs from bottom to top (in the time direction t_{BBM}), and, once the branching Brownian motion is constructed, the voting scheme runs from top to bottom (in the time direction t_{PDE}).

The equation with phenotype: forward approach.

Now, we wish to find a branching Brownian motion representation for the equation with phenotype (1.5) (we take the homogeneous equation with $r(\theta)$, but our construction can be readily extended if $r(\theta)$ is replaced by $r(x,\theta)$). In order to avoid technical complications with the boundary, we assume that the phenotype space is $\Theta = \mathbb{R}^P$ for some $P \in \mathbb{N}$.

As for the standard Fisher-KPP equation, we first consider the nonspatial setting, but still with a phenotype structure:

$$\partial_t v(t,\theta) = \frac{1}{2}\Delta_\theta v + r(\theta)v - \rho(t)v, \qquad v(0,\theta) = v_0(\theta), \tag{1.11}$$

with

$$\rho(t) := \int_{\mathbb{R}^P} v(\theta)\,\mathrm{d}\theta.$$

We assume for the simplicity of the exposition that $0 \leqslant r \leqslant 1$ and $0 \leqslant \rho \leqslant 1$. The assumptions $r \leqslant 1$ and $\rho \leqslant 1$ can be obtained by standard rescaling, as long as r and ρ are bounded above (which holds throughout the thesis). The assumption $r \geqslant 0$ can be removed by adding an additional death term with rate $-\max(-r,0)$. More precisely, we write: $rv = \max(r,0)v - \max(-r,0)v$. Next, the construction below can be adapted without difficulty.

Let us rewrite (1.11) in another way so as to highlight the roles of the different events that we will see below:

$$\partial_t v(t,\theta) = \frac{1}{2}\Delta_\theta v + r(\theta)v(1-\rho) - (1-r(\theta))v\rho. \tag{1.12}$$

This logistic growth equation can be seen as follows. For $N \in \mathbb{N}$, we construct a sequence of stochastic processes $((\xi_t^{k,N})_{t\geqslant 0})_{k\in[\![1,N]\!]}$, each $\xi_t^{k,N}$ ($k \in [\![1,N]\!]$) belonging to $\mathbb{R}^P \cup \{\emptyset\}$, for some "empty type", denoted by $\emptyset$, not belonging to $\mathbb{R}^P$. These stochastic processes are seen as the types of the individuals of the population. The individuals whose type is $\emptyset$ are said to be *empty*, and the individuals whose type belongs to $\mathbb{R}^P$ are said to be *full*.

At the initial time, the types $\xi_0^{k,N}$ are independent and identically distributed, and their law is defined by: for all $k \in [\![1,N]\!]$, for all $A \subset \mathbb{R}^P$,

$$\mathbb{P}\left(\xi_0^{k,N} \in A\right) = \int_A v_0(\theta)\,\mathrm{d}\theta, \qquad \mathbb{P}\left(\xi_0^{k,N} = \emptyset\right) = 1 - \int_{\mathbb{R}^P} v_0(\theta)\,\mathrm{d}\theta. \tag{1.13}$$

Since we assumed that $0 \leqslant \rho \leqslant 1$, these probabilities are well-defined. Next, the time dynamics of $(\xi_t^{k,N})_{t\geqslant 0}$ is a Brownian motion (to account for the term $\frac{1}{2}\Delta_\theta$) that occasionally jumps, at times which we call *reproduction events*.

At rate N, a *reproduction event* occurs. Upon a reproduction event, take independently two individuals uniformly at random among $\{1,\dots,N\}$:

- If the two individuals are empty, then nothing occurs;
- If the two individuals are full, of types θ_1 and θ_2, then the type θ_1 becomes empty with probability $1-r(\theta_1)$ and the type θ_2 independently becomes empty with probability $1-r(\theta_2)$. This yields the $-(1-r(\theta))v\rho$ term appearing in (1.12);
- If a full individual of type θ_1 meets an empty individual, then: either the reproduction fails (i.e. nothing occurs) with probability $1-r(\theta_1)$; or the empty becomes full (with type θ_1), with probability $r(\theta_1)$. This is the $r(\theta)v(1-\rho)$ term in (1.12).

Analogously to the analysis for the standard logistic equation in Subsection 1.2.1, as $N \to +\infty$, we expect the following convergence: for all $T > 0$, for all $A \subset \mathbb{R}^P$,

$$\left(\frac{1}{N}\sum_{i=1}^{N} \mathbb{1}_{\left\{\xi_t^{k,N}\in A\right\}}\right)_{0\leqslant t\leqslant T} \to \left(\int_A v(t,\theta)\,\mathrm{d}\theta\right)_{0\leqslant t\leqslant T} \qquad \text{in law.}$$

We thus have a connection between a stochastic finite population model and the PDE that we study (there are also other natural particle systems whose sequence of empirical measures converges to $v(t,\theta)\,\mathrm{d}\theta$, see e.g. the second particle system constructed in Subsection 1.2.1.) We do not prove convergence, but we will use the genealogies of the finite population to guess what the branching Brownian motion representation should be. Once the representation is constructed, we will prove that it does indeed correspond to the original equation.

Backward dynamics. We have seen the forward approach of the population dynamics hidden in the logistic equation with phenotype (1.12). Now, let us find the backward approach. Consider an individual (full or empty) at time t and look at its "ancestral lineages". Consider a time at which the ancestor is involved in a reproduction event. Recall that each reproduction event involves two individuals. Either of the following occurs:

- The two individuals involved in the reproduction event are empty; then the resulting individual is empty;
- The two individuals involved in the reproduction event are full, of types θ_1 and θ_2; then the resulting individual is of type θ_1 if the first individual is chosen (with probability $1/2$) and did not become empty (with probability $r(\theta_1)$); of type θ_2 if the second individual is chosen (with probability $1/2$) and did not become empty (with probability $r(\theta_2)$); otherwise, the resulting individual is empty;
- Of the two individuals involved in the reproduction event, one is empty and the other is full with type θ_1. Either the reproduction is successful (which occurs with probability $r(\theta_1)$), in which case the resulting individual is of type θ_1. Either the reproduction failed (with probability $1-r(\theta_1)$). In the latter case, the resulting individual is chosen among the full (of type θ_1) or the empty individual, both with probability $1/2$.

The above analysis shows that the voting scheme at a branching event (i.e. a reproduction event) should be:

$$\emptyset + \emptyset \to \emptyset, \tag{1.14}$$

$$\theta_1 + \theta_2 \to \begin{cases} \theta_1 & \text{with probability } \dfrac{r(\theta_1)}{2}, \\ \theta_2 & \text{with probability } \dfrac{r(\theta_2)}{2}, \\ \emptyset & \text{with probability } 1 - \dfrac{r(\theta_1)+r(\theta_2)}{2}, \end{cases} \tag{1.15}$$

and

$$\theta_1 + \emptyset \to \begin{cases} \theta_1 & \text{with probability } \dfrac{1+r(\theta_1)}{2}, \\ \emptyset & \text{with probability } \dfrac{1-r(\theta_1)}{2}. \end{cases} \tag{1.16}$$

Finally, we add a spatial structure to get the branching Brownian motion representation for the equation (1.5) with phenotype, analogous to the standard McKean-Skorokhod representation for the Fisher-KPP equation. We summarise the whole procedure in the following definition. The definition is also illustrated on Figure 1.10.

Definition 1.2.1 (Voting scheme for the equation with phenotype)**.** *Let $t > 0$ and $x \in \mathbb{R}$. Let $0 \leqslant u_0 \leqslant 1$ be an initial condition. The voting scheme for the equation with phenotype is the following procedure.*

(*i*) *Run a branching Brownian motion* $((X_s^i)_{1\leqslant i\leqslant N_s})_{0\leqslant s\leqslant t}$ *in* $\mathbb{R}$*, starting from one particle at* x *and branching at rate* 1*;*

(*ii*) *For* $i\in\{1,\dots,N_t\}$*, label the endpoints* X_t^i *with a type* ξ_0^i *sampled according to* (1.13)*, with* $u_0(X_t^i,\cdot)$ *instead of* $v_0(\cdot)$*;*

(*iii*) *For* $i\in\{1,\dots,N_t\}$*, let the type of* i*, denoted by* $(\xi_t^i)_{t\geqslant 0}$*, follow a Brownian motion (independent of each other), except at some points where it jumps. More precisely, at a branching point of* X *at time* s*, involving* $i\neq j$*, the new type of* i *and* j*,* $\xi_{t-s}^i=\xi_{t-s}^j$*, is chosen according to the rules* (1.14)–(1.16) *where* $\xi_{(t-s)-}^i$ *and/or* $\xi_{(t-s)-}^j$*, if nonempty, play the role of* θ_1 *and/or* θ_2*.*

We denote by $\kappa_t[x]\in\mathbb{R}^P\cup\{\emptyset\}$ *the type of the particle at the bottom of the tree.*

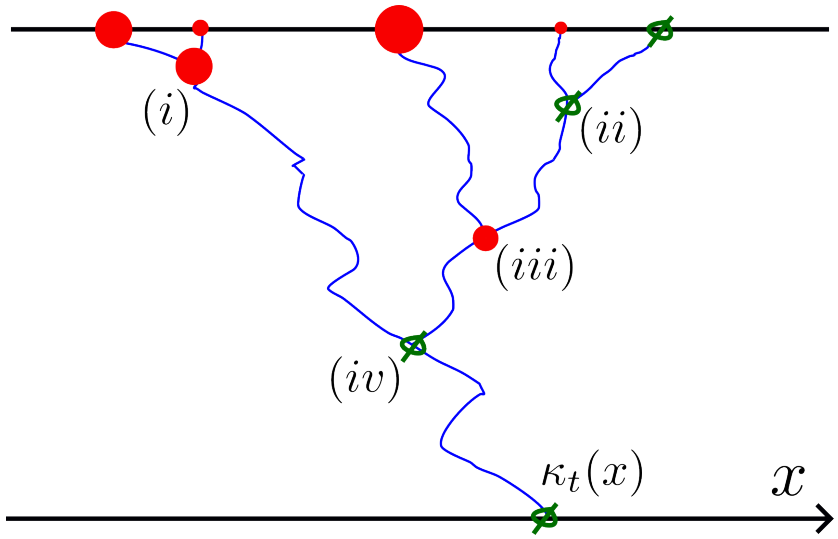


Figure 1.10: A run of the voting scheme for the equation with phenotype. Here, $\kappa_t(x)$ is of type $\emptyset$. Each red circle is a full individual of type θ, and the diameter of the circle is proportional to $r(\theta)$. Examples of branching points: (*i*) Rule (1.15) gives θ_1 or θ_2; (*ii*) Rule (1.16) gives $\emptyset$; (*iii*) Rule (1.16) gives θ_1; note that θ_1 changed substantially between the initial time and the time of branching, owing to mutations; (*iv*) Rule (1.15) gives $\emptyset$.

In Appendix A, we will prove the following theorem, which establishes the correspondence between the process which we have constructed and the equation with phenotype.

Theorem 1.2.2. *Assume that* r *is continuous,* $0\leqslant r\leqslant 1$ *and* $\Theta=\mathbb{R}^P$*. Let* u *solve* (1.5)*. Let* $t\geqslant 0$ *and* $x\in\mathbb{R}$*. Let* $\kappa_t[x]$ *be the result of the voting scheme for the equation with phenotype (Definition 1.2.1). We have, for all* $A\subset\mathbb{R}^P$*,*

$$\int_A u(t,x,\theta)\,\mathrm{d}\theta=\mathbb{P}\left(\kappa_t[x]\in A\right),\qquad \rho(t,x)=\mathbb{P}\left(\kappa_t[x]\neq\emptyset\right).$$

1.2.3 Probabilistic representations of principal eigenvalues

In this subsection, we shall focus on probabilistic representations of elliptic (rather than parabolic) equations. We will first see that the principal eigenfunction of an elliptic operator

can be seen as a quasi-stationary distribution; this fact is developed and used in Chapter 2. Next, we will see the connection to the Feynman-Kac formula, which will be used in Chapter 4 and, in another (nonlocal) context, in Chapter 9.

Connection to a quasi-stationary distribution.

For simplicity, we work in the one-dimensional torus $\mathbb{T} := \mathbb{R}/\mathbb{Z}$. In Chapter 2, we will also work in domains with boundary, and in higher dimension. We consider a solution $(\varphi, k) \in \mathcal{C}^{2,\alpha}(\mathbb{T}) \times \mathbb{R}$ of the following principal eigenvalue problem:

$$\begin{cases} \frac{1}{2}\Delta\varphi - d(w)\varphi(w) = k\varphi(w), & w \in \mathbb{T}, \\ \varphi(w) > 0, & w \in \mathbb{T}, \end{cases}$$

where $d \in \mathcal{C}^{0,1}(\mathbb{T})$ is a Lipschitz-continuous function such that $\inf_{\mathbb{T}} d \geqslant 1$. We normalise φ so that

$$\int_{\mathbb{T}} \varphi = 1.$$

Owing to the Krein-Rutman theorem, the pair (φ, k) is well-defined. Let $m \in L^1(\mathbb{T})$ satisfy

$$m \geqslant 0, \qquad \int_{\mathbb{T}} m = 1.$$

Consider a Brownian motion $(B_t)_{t\geqslant 0}$ on $\mathbb{T}$, such that B_0 follows the law with density m. Our goal is to construct a killed process $(W_t)_{t\geqslant 0}$ based on $(B_t)_{t\geqslant 0}$. Let τ be an exponential clock with rate $(d(B_t))_{t\geqslant 0}$. Namely, let E be an exponential variable with parameter 1, and set:

$$\tau := \inf\left\{ t \geqslant 0 \ / \ \int_0^t d(B_s)\,\mathrm{d}s \geqslant E \right\}.$$

We let $\partial \notin \mathbb{T}$ be a "cemetery state". We define the killed process $(W_t)_{t\geqslant 0}$ by:

$$W_t := \begin{cases} B_t & t < \tau, \\ \partial & t \geqslant \tau. \end{cases}$$

Intuitively, this means that if the particle W is alive at time t, then the probability that it dies on $[t, t + \mathrm{d}t]$ is approximately $d(W_t)\,\mathrm{d}t$. In Chapter 2, we shall give another definition of τ, which is more complicated than the one we gave here, but closer to this intuition and more adapted to the proofs.

We denote by $\mathbb{P}_m$ the joint law of $(\tau, (B_t)_{t\geqslant 0})$ when the distribution of B_0 is m. The following theorem is very useful to get a probabilistic understanding of the principal eigenfunction. The proof comes from [62] and from the remark that φ is a quasi-stationary distribution for the killed process (see also [64, Section 4.4]).

Theorem 1.2.3. *There exist $C, \chi > 0$ such that for all initial distribution m on $\mathbb{T}$, for all $t > 0$, for all measurable $A \subset \mathbb{T}$,*

$$\left| \int_A \varphi(w)\,\mathrm{d}w - \mathbb{P}_m\left(W_t \in A \,|\, \tau > t\right) \right| < Ce^{-\chi t}.$$

We may choose the constants C and χ so that they only depend on $\|d\|_\infty$.

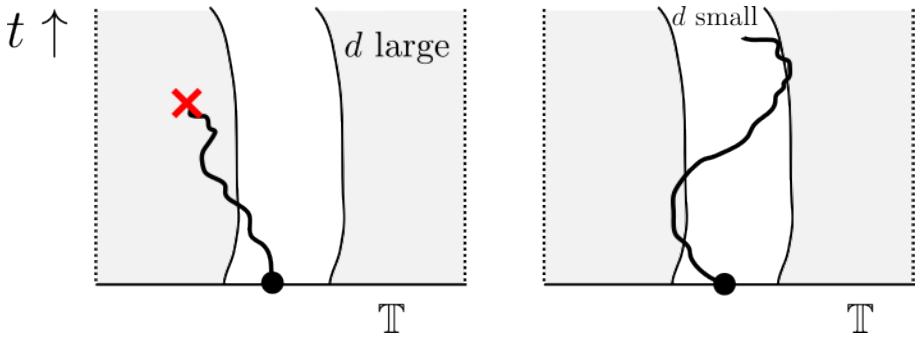


Figure 1.11: *Shaded area:* high death rate. *White area:* low death rate. *Left:* The process $(W_t)_{t\geqslant 0}$ dies at a high rate when it is in the shaded area; *Right:* Conditioned on $\{\tau > t\}$, the process $(W_t)_{t\geqslant 0}$ avoids the shaded area.

Theorem 1.2.3 is stated in a more general context in Chapter 2: the operator $\frac{1}{2}\Delta$ can be replaced by an operator with heterogeneous diffusion and transport terms. The Brownian motion $(B_t)_{t\geqslant 0}$ will be replaced by a stochastic process corresponding to the new operator.

See Figure 1.11 for an illustration of how the killed process $(W_t)_{t\geqslant 0}$ and the process conditioned on not being killed behave.

The Feynman-Kac formula.

Let us now focus on the Feynman-Kac formula and on the light that it can shed on the previous construction. Let $r \in L^\infty(\mathbb{R})$. Let $u(t,x)$ be the bounded solution of the following linear equation on $\mathbb{R}_+ \times \mathbb{R}$:

$$\partial_t u = \frac{1}{2}\Delta u + r(x)u, \qquad u(0,x) = u_0(x),$$

for a nonnegative and bounded initial condition u_0. Let $(B_t)_{t\geqslant 0}$ be a Brownian motion. In Appendix A, we show the following equality, which is commonly known as the *Feynman-Kac formula*:

$$u(t,x) = \mathbb{E}_x\left[u_0(B_t)\exp\left(\int_0^t r(B_u)\,\mathrm{d}u\right)\right],$$

where $\mathbb{E}_x$ means that the Brownian motion starts from x. The Feynman-Kac formula will be used in Chapter 4 to compare the principal eigenvalues of different operators.

An interesting aspect of the Feynman-Kac formula is that it appears in the law of the process $(W_t)_{t\geqslant 0}$ conditioned to survive. Take d as in the previous paragraph and let $r := -d$. Consider an initial condition $u_0 \in \mathcal{C}^2(\mathbb{T})$ and a test function $f \in \mathcal{C}^2(\mathbb{T})$, both nonnegative and with integral 1. Since the killed process W coincides with the Brownian motion B for $t \in [0,\tau]$, we have:

$$\begin{aligned}\mathbb{E}_{u_0}[f(W_t)\,|\,\tau > t] &= \frac{1}{\mathbb{P}_{u_0}(\tau > t)}\mathbb{E}_{u_0}[f(W_t)\,\mathbb{1}_{\{\tau>t\}}] \\ &= \frac{1}{\mathbb{P}_{u_0}(\tau > t)}\mathbb{E}_{u_0}\left[f(B_t)\exp\left(-\int_0^t d(B_s)\,\mathrm{d}s\right)\right].\end{aligned}$$

The last expression is reminiscent of the Feynman-Kac formula. As a consequence of the

above equality, conditioning on $\{\tau > t\}$ is equivalent to replacing the measure $\mathbb{P}_{u_0}$ on $\mathcal{C}([0,T],\mathbb{T})$, which gives the law of $(B_s)_{s\geqslant 0}$, by the measure $\mathbb{P}'_{u_0}$ on $\mathcal{C}([0,T],\mathbb{T})$ defined by

$$\mathbb{P}'_{u_0}(\mathrm{d}w) := \frac{1}{\mathbb{P}_{u_0}(\tau > t)} \exp\left(-\int_0^t d(w(s))\,\mathrm{d}s\right) \mathbb{P}_{u_0}(\mathrm{d}w).$$

Namely, conditioning the process to survive is equivalent to giving more weight to paths w such that $\int_0^t d(w_s)\,\mathrm{d}s$ is small. For example, in view of the connection that we have highlighted, [74, Theorem 1.1] is a result about Feynman-Kac semigroups which, in fact, is similar to our Theorem 1.2.3.

1.3 Properties of principal eigenvalues of elliptic operators

The goal of Sections 1.3, 1.4 and 1.5 is to introduce the main results of this thesis.

First, in Parts I and II, we shall aim at getting insight into the behaviour of biological models inspired by the Fisher-KPP equation. We shall be especially interested in the role of heterogeneity. In Section 1.1, we saw that a central tool to study heterogeneity is the notion of *principal eigenvalue* of elliptic operators. Therefore, we start by presenting, in this section, new results on principal eigenvalues of some elliptic operators which come from biological questions. The chapters presented in this section belong to Part I.

Next, in Section 1.4, we shall focus on equations that model populations structured in phenotype and living in heterogeneous environments. The chapters presented in Section 1.4 belong to Part II.

Last, in Section 1.5, we will study the inner structure of the population during an invasion, notably through experimental data. The chapters presented in Section 1.5 belong to Part III.

1.3.1 The principal eigenvalue problem for a strongly anisotropic second-order elliptic operator

We first present Chapter 2. For the sake of exposition and consistency, we give a simplified version of the results of Chapter 2 and we use different notations: $\theta \in \Theta$ instead of $y \in \mathcal{Y}$ and $x \in \mathbb{T}^N := \mathbb{R}^N/\mathbb{Z}^N$ instead of $z \in \mathcal{Z}$.

Motivations.

The work presented in Chapter 2 is based on the following observation: in the equation with phenotype (1.6), the diffusion in θ corresponds to mutations arising at each birth and death of an individual, and the diffusion in x corresponds to spatial movements of individuals. Therefore, the diffusion in θ should occur on a much slower timescale than the diffusion in x.

In fact, even when the variables x and θ represent phenomena of the same nature, one may have to consider different scales. A first example occurs when x and θ are spatial positions on different scales of spatial heterogeneity: the variable x represents, say, the heterogeneity within a field, while the variable θ represents, say, the heterogeneity within a large region. A second example occurs when the variables x and θ are the coordinates of a phenotype in

a phenotypic landscape, but when mutations according to the θ-direction are much rarer or much smaller than mutations according to the x-direction.

This discussion raises the question: *how do the slow and the fast phenomenon interact?*

The anisotropic eigenvalue problem.

To answer the above question, we wish to study a principal eigenvalue problem with a slow direction (which, in this section, can be thought of as the phenotype) and a fast direction (thought of as the geographical space). With the usual notations, the phenotypic space is $\Theta \subset \mathbb{R}^P$, connected, and has a $\mathcal{C}^{2,\alpha}$ boundary. The geographical space is the torus $\mathbb{T}^N := \mathbb{R}^N/\mathbb{Z}^N$.

For $\varepsilon > 0$, we define two operators acting on $\mathcal{C}^2(\Theta \times \mathbb{T}^N)$:

$$\mathcal{L}^\varepsilon_\theta : \phi \mapsto \varepsilon^2 A \Delta_\theta \phi + \varepsilon B \cdot \nabla_\theta \phi,$$

which differentiates only in the variable $\theta \in \Theta$, and

$$\mathcal{L}_x : \phi \mapsto a \Delta_x \phi + b \cdot \nabla_x \phi,$$

which differentiates only in the variable $x \in \mathbb{T}^N$. The coefficients $A, a \in \mathbb{R}$, $B \in \mathbb{R}^P$ and $b \in \mathbb{R}^N$ are assumed to be constant. More general hypotheses on the coefficients are stated in Chapter 2.

We consider a Lipschitz function $c \in \mathcal{C}^{0,1}(\overline{\Theta} \times \mathbb{T}^N)$. We are interested in the following principal eigenvalue problem:

$$\begin{cases} \mathcal{L}^\varepsilon_\theta \varphi_\varepsilon + \mathcal{L}_x \varphi_\varepsilon + c(\theta, x)\varphi_\varepsilon = k_\varepsilon \varphi_\varepsilon & \text{in } \Theta \times \mathbb{T}^N, \\ \nu \cdot \nabla \varphi_\varepsilon = 0 & \text{on } \partial\Theta \times \mathbb{T}^N, \\ \varphi_\varepsilon > 0 & \text{in } \Theta \times \mathbb{T}^N, \end{cases}$$

with normalisation

$$\int_{\Theta \times \mathbb{T}^N} \varphi_\varepsilon = 1.$$

When $\varepsilon \to 0$, the elliptic operator $\mathcal{L}^\varepsilon_\theta + \mathcal{L}_x + c$ becomes "strongly anisotropic".

For the statement of the results, we will need the following notions. For $\theta_0 \in \overline{\Theta}$, we let $(\psi^{\theta_0}, k^{\theta_0}) \in \mathcal{C}^{2,\alpha}(\mathbb{T}^N) \times \mathbb{R}$ be the solution of the *local* eigenvalue problem:

$$\begin{cases} (\mathcal{L}_x + c(\theta_0, \cdot))\psi^{\theta_0} = k^{\theta_0}\psi^{\theta_0} & \text{in } \mathbb{T}^N, \\ \psi^{\theta_0} > 0 & \text{in } \mathbb{T}^N, \end{cases}$$

with normalisation

$$\int_{\mathbb{T}^N} \psi^{\theta_0} = 1.$$

By the classical Krein-Rutman theory [145], $(\varphi_\varepsilon, k_\varepsilon)$ and $(\psi^{\theta_0}, k^{\theta_0})$ exist and are unique. We extend the function φ_ε from Θ to $\overline{\Theta}$, i.e. we consider $\varphi_\varepsilon \in \mathcal{C}^{2,\alpha}(\overline{\Theta} \times \mathbb{T}^N)$. This is possible by virtue of the regularity assumptions on the coefficients and on $\partial\Theta$.

Behaviour of the principal eigenfunction.

The first theorem below means that the "slices" of the global principal eigenfunction converge, as $\varepsilon \to 0$, to the local principal eigenfunctions. We use the notation

$$\varphi_\varepsilon(\theta_0, \mathbb{T}^N) := \int_{\mathbb{T}^N} \varphi_\varepsilon(\theta_0, x)\,\mathrm{d}x.$$

Theorem 1.3.1. *Let $\beta \in (0, \alpha)$. For all $\theta_0 \in \Theta$, as $\varepsilon \to 0$, we have*

$$\frac{\varphi_\varepsilon(\theta_0, \cdot)}{\varphi_\varepsilon(\theta_0, \mathbb{T}^N)} \to \psi^{\theta_0} \qquad \text{in } \mathcal{C}^{2,\beta}(\mathbb{T}^N).$$

Moreover, the following convergence of measures holds uniformly in $\theta_0 \in \overline{\Theta}$:

$$\frac{\varphi_\varepsilon(\theta_0, x)}{\varphi_\varepsilon(\theta_0, \mathbb{T}^N)}\,\mathrm{d}x \to \psi^{\theta_0}(x)\,\mathrm{d}x \qquad \text{in total variation on } \mathbb{T}^N,$$

namely:

$$\sup_{\theta_0 \in \overline{\Theta}} \left[\sup_{A \subset \mathbb{T}^N, A \text{ measurable}} \int_A \left| \frac{\varphi_\varepsilon(\theta_0, x)}{\varphi_\varepsilon(\theta_0, \mathbb{T}^N)} - \psi^{\theta_0}(x) \right| \mathrm{d}x \right] \to 0.$$

The result is straightforward when c is independent of $\theta \in \Theta$: in this case, indeed, $\varphi_\varepsilon(\theta_0, \cdot)$ is independent of θ_0 and of ε. For the proof in the general case, we will use the probabilistic method described in Subsection 1.2.3. Namely, we will see φ_ε as the quasi-stationary distribution of a killed stochastic process $(\theta_t^\varepsilon, x_t^\varepsilon)_{t \geqslant 0}$. More precisely, we will construct a death time τ for the process $(\theta_t^\varepsilon, x_t^\varepsilon)_{t \geqslant 0}$, such that for all $E \subset \Theta$ and $F \subset \mathbb{T}^N$:

$$\lim_{t \to +\infty} \mathbb{P}\left((\theta_t^\varepsilon, x_t^\varepsilon) \in E \times F \,|\, \tau > t \right) = \int_{E \times F} \varphi_\varepsilon(\theta, x)\,\mathrm{d}\theta\,\mathrm{d}x.$$

As $\varepsilon \to 0$, the process θ_t^ε is slower and slower. This will allow us, in Chapter 2, to forget the dependency in θ_t^ε and to get back to the simple case where the coefficient c is independent of θ.

Once Theorem 1.3.1 is established, a natural question that arises is the behaviour of the principal eigenfunction in the slow direction. The family of principal eigenvalues $(k_\varepsilon)_\varepsilon$ is bounded, so there is a subsequence that converges to some $k_0 \in \mathbb{R}$. The proofs of the following theorems suggest that if Θ is replaced by a torus $\mathbb{R}^P/\mathbb{Z}^P$, then for all $x_0 \in \mathbb{T}^N$, the "slice" $\varphi_\varepsilon(\cdot, x_0)$ concentrates on points $\theta \in \Theta$ such that $k^\theta = k_0$. More precisely, for all $x_0 \in \mathbb{T}^N$, it can be expected that there exists a measure μ^{x_0} on the level set $\Gamma := \left\{ \theta \in \Theta \;/\; k^\theta = k_0 \right\}$, with total mass equal to 1, such that for all $f \in \mathcal{C}^\infty(\Theta)$, along any subsequence such that $k_\varepsilon \to k_0$,

$$\int_\Theta f(\theta) \frac{\varphi_\varepsilon(\theta, x_0)}{\varphi_\varepsilon(\Theta, x_0)}\,\mathrm{d}\theta \to \int_\Gamma f(\theta)\mu^{x_0}(\,\mathrm{d}\theta).$$

See Remark 2.4.5 in Chapter 2 for more details about why this should be true. The proof of this conjecture and its extension to the case where Θ has a nonempty boundary are beyond the scope of this thesis.

Behaviour of the principal eigenvalue.

In two particular cases, we are able to find an exact relation between the limit of k_ε as $\varepsilon \to 0$ and the local eigenvalues k^θ, $\theta \in \overline{\Theta}$. First, let us assume that $B = 0$.

Theorem 1.3.2. *Assume $B = 0$. Then k_ε converges as $\varepsilon \to 0$ and*

$$\lim_{\varepsilon \to 0} k_\varepsilon = \max_{\theta \in \overline{\Theta}} k^\theta.$$

If additionally to $B = 0$, we assume that $b = 0$, the operator $\mathcal{L}_\theta^\varepsilon + \mathcal{L}_x + c$ becomes symmetric. The Rayleigh formula can then be applied directly, and the proof is simpler than in the general case.

Theorem 1.3.2 can be understood from a modelling perspective. When $B = 0$ and $\varepsilon \to 0$, all phenotypes $\theta \in \overline{\Theta}$ are almost independent. Therefore, a population is able to survive if and only if there exists a phenotype which is able to survive by itself. This means that for small $\varepsilon > 0$, the condition $k_\varepsilon > 0$ amounts to the existence of $\theta_0 \in \overline{\Theta}$ such that $k^{\theta_0} > 0$. Thus we expect Theorem 1.3.2 to hold. As we will see now, the independence between phenotypes fails when $B \neq 0$.

How does k_ε behave when $B \neq 0$? It seems that the behaviour is much more complicated. We are unable to give any answer in the context in which we have been working until now, considering that $\Theta \subset \mathbb{R}^P$ has a boundary. Instead, let us assume that Θ is the one-dimensional torus: $\Theta = \mathbb{R}/\mathbb{Z}$. In particular, $B \in \mathbb{R}$ and $A \in \mathbb{R}$. We let

$$M := \max_{\theta \in \Theta} \left(k^\theta - \frac{B^2}{4A} \right).$$

We let $j : [M, +\infty) \to [j(M), +\infty)$ be the bijection defined by

$$j : k \mapsto \int_0^1 \sqrt{\frac{k - k^\theta + \frac{B^2}{4A}}{A}} \, \mathrm{d}\theta.$$

Theorem 1.3.3. *Assume that Θ is the 1-dimensional torus. Then k_ε converges as $\varepsilon \to 0$ and:*

1. *If $|B/2A| \leqslant j(M)$, then*
$$\lim_{\varepsilon \to 0} k_\varepsilon = M;$$
2. *If $|B/2A| \geqslant j(M)$, then*
$$\lim_{\varepsilon \to 0} k_\varepsilon = j^{-1}\left(|B/2A|\right).$$

In the very specific case where all the coefficients are independent of the fast variable x, Theorem 1.3.3 is similar to Proposition 3.2 of [119].

The proof of Theorem 1.3.3 is an adaptation of the proof of Proposition 3.2 of [119], but is more technical due to the interplay between the slow and fast variable. As in [119], the proof hinges on the construction of an explicit viscosity solution of a Hamilton-Jacobi equation that arises naturally after a Hopf-Cole transform of the original eigenproblem. This explicit construction requires us to work in the one-dimensional setting. Next, once the solution is constructed, we need to work in the torus to deduce a result on the principal eigenvalue.

Theorem 1.3.3 shows that when there is a nonzero transport term, even in the particular case where Θ is the 1-dimensional torus, the behaviour of the limiting principal eigenvalue is nontrivial. The study of the limit in the general case (bounded domain; higher dimension), therefore, is left to future work.

In Chapter 2, we shall work in a more general setting, where diffusion may be heterogeneous and the transport terms B and b may be nonconstant. We will see that Theorem 1.3.3 cannot be expected to hold in full generality – some restrictions will be needed: see Equation (2.8).

1.3.2 The q-diffusion operator and the influence of the advection term

Let us now present Chapters 3 and 4. In these chapters, we will work on the heterogeneous Fisher-KPP equation (1.3) in dimension 1. Chapter 3 is a work in collaboration with F. Hamel and L. Roques, and Chapter 4 is a work in collaboration with Y.-J. Kim and L. Roques.

The q-diffusion operator.

In Chapter 4, we will be interested in the following family of heterogeneous Fisher-KPP equations, indexed by a parameter $q \in \mathbb{R}$:

$$\partial_t u(t,x) = \partial_x(D^{1-q}\partial_x(D^q u)) + u(r(x)-u). \tag{1.17}$$

In the field of reaction-diffusion equations, the cases $q=0$ (*Fickian diffusion*) and $q=1$ (*Fokker-Planck diffusion*) are commonly encountered to model heterogeneous diffusions. The initial motivation for Chapter 4 is the following question:

What are the consequences of choosing one or the other in terms of ability of persistence and spreading speed?

In fact, it appeared that considering the whole family of q-diffusion operators allowed one to grasp a better understanding of what Fickian and Fokker-Planck diffusions are compared to one another; as we will see, they are in some sense *symmetric*.

The general q-diffusion operator can emerge as a limit of stochastic processes corresponding to the position of particles modelled by the equation. On the one hand, the Itô integral interpretation of the equation

$$\mathrm{d}X_t = \sqrt{2D(X_t)}\,\mathrm{d}W_t$$

(for a Brownian motion $(W_t)_{t\geqslant 0}$) assumes that the jump $X_{t+\delta t}-X_t$, for a time step δt going to 0, depends on the variance $2D(X_t)$ of the stochastic process at the departure point X_t. This interpretation leads to the Fokker-Planck diffusion ($q=1$). On the other hand, the analysis in [218] indicates that adopting an alternative assumption, where the length of the jump depends on the value of D at an intermediate point $qX_t+(1-q)X_{t+\delta t}$ (for $q\in\mathbb{R}$), leads to the q-diffusion operator. More precisely, X_t being defined, $X_{t+\delta t}$ is implicitly defined, for δt small enough, by

$$X_{t+\delta t}-X_t = \sqrt{2D\left(qX_t+(1-q)X_{t+\delta t}\right)}(W_{t+\delta t}-W_t).$$

Then, Fickian diffusion ($q=0$) is characterised by a dependency on the arrival point. When $q=1/2$, we get the Stratonovich diffusion, which is characterised by a dependency on the midpoint. Alternative constructions of q-diffusions are explored in [6, 180, 193].

The effect of q on the ability of persistence and the spreading speed.

Throughout this subsection, we let $k_\lambda^q[r\,;b\,;D]$ and $c^q[r\,;b\,;D]$ be the principal eigenvalues and spreading speed analogous to those defined in Subsection 1.1.2, but associated with the equation with the q-diffusion operator and a transport term b:

$$\partial_t u = \partial_x(D^{1-q}\partial_x(D^q u)) + \partial_x(bu) + u(r-u).$$

We are indeed in the setting of Subsection 1.1.2, as this equation can be rewritten in the form of Equation (1.3):

$$\partial_t u(t,x) = \partial_x(D\partial_x u) + \partial_x((b+qD')u) + u(r-u).$$

(For the definition of the spreading speed when there is a nonzero advection term, we refer to Chapter 3 or 4.) When D is constant, the equation is independent of q and we will write simply $k_\lambda[r\,;b\,;D]$ and $c[r\,;b\,;D]$, without the superindex q.

A central tool in Chapter 4 is Proposition 4.3.7, which turns the heterogeneous diffusion into a homogeneous diffusion with a drift term depending on q. Thanks to this transformation, we are able to show that there exist a reaction term $R\in\mathcal{C}^{0,\alpha}(\mathbb{R})$ and a transport term $b\in\mathcal{C}^{1,\alpha}(\mathbb{R})$, depending on r and D, which are periodic with a period depending on D, such that

$$c^q[r\,;0\,;D] = \left(\int_0^1 \frac{\mathrm{d}x}{\sqrt{D(x)}}\right)^{-1} \times c\,[R\,;-s_q b\,;1]\,, \qquad \text{with } s_q := \frac{1}{2}-q.$$

This result highlights a symmetry between Fickian diffusion ($q=0$) and Fokker-Planck diffusion ($q=1$), since $s_0=-s_1$. This will lead us, in Chapter 3, to focus on the effect of reversing the direction of the advection in a heterogeneous Fisher-KPP equation with constant diffusion; namely, to compare the principal eigenvalues $k_\lambda[r\,;b\,;1]$ and $k_\lambda[r\,;-b\,;1]$. Before giving the results of Chapter 3, let us go on with Chapter 4.

The main result of Chapter 4 is the following theorem, which shows that for constant r, the spreading speeds for Fickian diffusion ($q=0$) and Fokker-Planck diffusion ($q=1$) coincide. See Figure 1.12 for simulations with Fickian and Fokker-Planck diffusions with constant r.

Theorem 1.3.4. *Assume that $r>0$ is constant. We have the following properties:*

(i) The function $q\mapsto c^q[r\,;0\,;D]$ is symmetric around $1/2$, that is, for all $\tilde{q}\in\mathbb{R}$,

$$c^{1/2-\tilde{q}}[r\,;0\,;D] = c^{1/2+\tilde{q}}[r\,;0\,;D].$$

In particular, $c^0[r\,;0\,;D]=c^1[r\,;0\,;D]$.

(ii) For $q=1/2$, we have the explicit formula:

$$c^{1/2}[r\,;0\,;D] = 2\sqrt{r}\times\left(\int_0^1 \frac{1}{\sqrt{D}}\right)^{-1}.$$

(iii) The maximal speed is reached at $q = 1/2$:

$$c^{1/2}[r\,;0\,;D] = \max_{q\in\mathbb{R}} c^q[r\,;0\,;D].$$

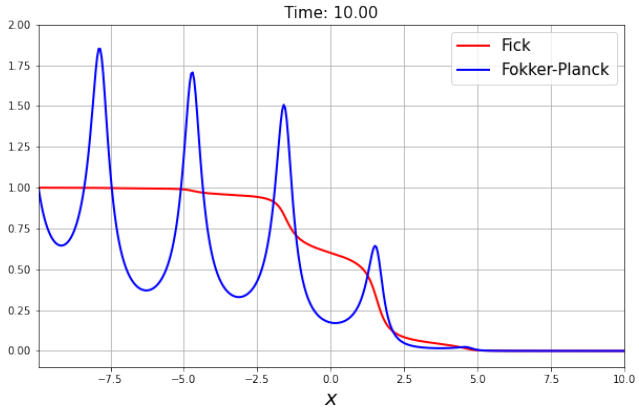


Figure 1.12: Simulations with Fickian and Fokker-Planck diffusion, with constant r. Although the shapes of the waves are different, the spreading speed is the same (as a consequence of Theorem 1.3.4). Here, $D(x) = 0.1 + \cos(x)^2$, $r(x) \equiv 1$, $u_0(x) = \mathbb{1}_{\{x<-8\}}$ and $t = 10$.
The simulation has been obtained using the code of [199].

In Chapter 4, we also consider nonconstant r, and give monotonicity and non-monotonicity properties of $q \mapsto k_0^q[r\,;0\,;D]$ in terms of r and D. The main result about monotonicity is the following.

Theorem 1.3.5. *Let $\kappa : q \mapsto k_0^q[r\,;0\,;D]$. We have:*

(i) If r is a constant, then $\kappa(q) = r$ for all $q \in \mathbb{R}$;

(ii) For this item, assume that D and r are monotonic on $[0,1/2]$, 1-periodic and even (thus D and r are also monotonic on $[1/2,1]$). Under some regularity assumptions, we have:

  (a) κ is monotonic;

  (b) If D and r have the same monotonicity on $[0,1/2]$, then κ is nonincreasing;

  (c) If D and r have opposite monotonicity, then κ is nondecreasing;

(iii) On the other hand, there exist r and D such that κ is not monotonic (and nonconstant);

(iv) Assume that there exists $q \in \mathbb{R}$ such that $k_q^0[r\,;0\,;D] > 0$. Then the function $q \mapsto c^q[r\,;0\,;D]$ is not monotonic.

Item *(ii)* suggests that increasing q (for instance by changing Fickian to Fokker-Planck diffusion) decreases the ability of persistence when r and D are in phase (i.e. when r is large where D is large), and increases the ability of persistence when r and D are out of phase (i.e. when r is large where D is small); see also Figure 1.13, left. This monotonicity is proved by using the Feynman-Kac formula, which we presented in Subsection 1.2.3. In Chapter 4,

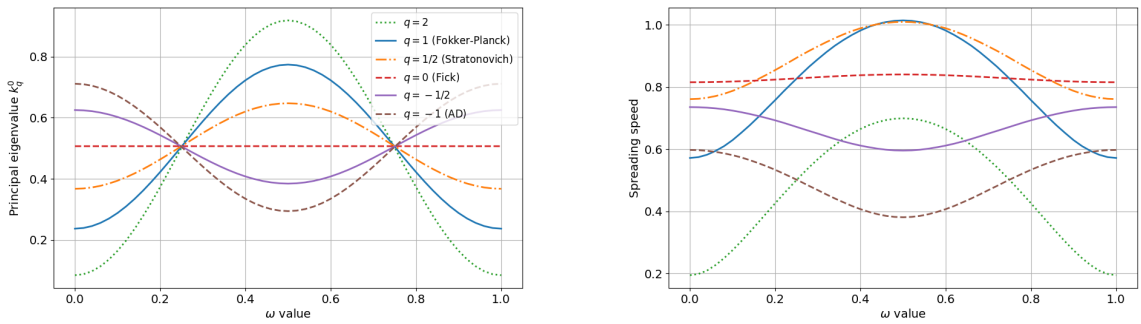


Figure 1.13: *(Left)* Principal eigenvalue $k^q[r\,;0\,;D]$ (denoted by k_q^0 on the figure) and *(Right)* spreading speed $c^q[r\,;0\,;D]$ depending on the phase shift ω between r and D. Here, $r(x)=\cos^2(\pi\,x)$ and $D(x)=0.1+\cos^2(\pi\,(x+\omega))$.

we shall give numerical insights into the effect of the phase shift. We shall also focus on the limit as $q\to\pm\infty$ of $k^q[r\,;0\,;D]$ and $c^q[r\,;0\,;D]$.

Item (ii) suggests that the phase shift between r and D plays an important role in the monotonicity of $q\mapsto k_0^q[r\,;0\,;D]$. From the point of view of ecological modelling, this is significant. Assume that we are able to act on D by positioning barriers to dispersal. If we want to stop the propagation of an invasive species, should the barriers be positioned where the environment is favourable (i.e. where r is large) or where the environment is unfavourable (i.e. where r is small)? Stated differently, is the spreading speed larger when D and r are in phase or when D and r are out of phase? The simulations of Chapter 4 reveal that the best strategy depends on the value of q in a nontrivial way. When $q>0$, the ability of persistence is weaker when D and r are in phase than when D and r are out of phase, and the effect is more pronounced when q increases (see Figure 1.13, left). When $q<0$, the inequalities are reversed. Regarding the spreading speed, it seems that no obvious monotonicity property can be obtained easily (see Figure 1.13, right).

The effect of the direction of the advection term.

Given the symmetry between the Fickian diffusion and the Fokker-Planck diffusion exhibited above, it is natural to consider how, upon a change of direction of the advection term, the ability of persistence and the spreading speed are impacted. It is sufficient, for our purpose, to consider homogeneous diffusion. In Chapter 3, we shall compare the principal eigenvalues $k_\lambda[r\,;b\,;1]$ associated with the equation:

$$\partial_t u=\partial_{xx}u+\partial_x(bu)+u(r-u),$$

and the principal eigenvalues $k_\lambda[r\,;-b\,;1]$ associated with the equation:

$$\partial_t u=\partial_{xx}u-\partial_x(bu)+u(r-u).$$

The main result of Chapter 3 exhibits two classes of pairs $(r\,;b)$ such that the long-time properties are conserved. An illustration of those two classes of pairs is provided by Figure 1.14, (a) and (b). On the other hand, Figure 1.14 (c) provides an example of a pair $(r\,;b)$ such that the long-time properties are *not* conserved upon a change of direction of the advection term (see Proposition 3.2.1 in Chapter 3).

Theorem 1.3.6. *Let $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ and let $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ be two 1-periodic functions. If either one of the following conditions is satisfied, then $k_0[r\,;b\,;1] = k_0[r\,;-b\,;1]$:*

(i) $r(x) = r(-x)$ and $b(x) = b(-x)$ for all $x \in \mathbb{R}$;

(ii) there exist $\beta \in \mathbb{R}$ and $\gamma \in \mathbb{R}$ such that $r = \beta + \gamma b$.

If, additionally to (i) or (ii), we have $\int_0^1 b = 0$, then $c[r\,;b\,;1] = c[r\,;-b\,;1]$.

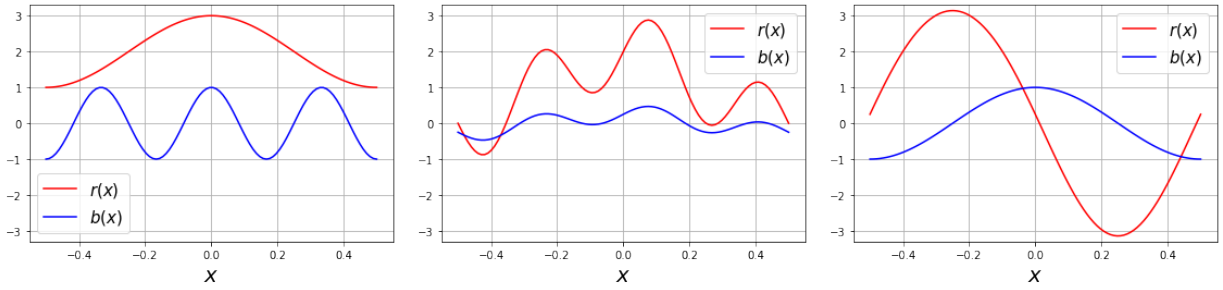


Figure 1.14: **(a)** Condition (i) of Theorem 1.3.6 is satisfied, with $r(x) = \cos(2\pi x)$ and $b(x) = \cos(6\pi x)$; **(b)** Condition (ii) of Theorem 1.3.6 is satisfied, with $r(x) = 1 + \cos(2\pi x) + \sin(6\pi x)$ and $b(x) = \frac{1}{4}(\cos(2\pi x) + \sin(6\pi x))$; **(c)** No condition of Theorem 1.3.6 is satisfied, with $b(x) = \cos(2\pi x)$ and $r(x) = \frac{b(x)^2}{4} + \frac{b'(x)}{2}$. In this situation, we have in fact: $k_0[r\,;b\,;1] \neq k_0[r\,;-b\,;1]$ and $c[r\,;b\,;1] \neq c[r\,;-b\,;1]$, see the proof of Proposition 3.2.1 in Chapter 3.

In particular, item (ii) of the theorem implies that for constant r and for any periodic b with zero integral, we have $k_0[r\,;b\,;1] = k_0[r\,;-b\,;1]$ and $c[r\,;b\,;1] = c[r\,;-b\,;1]$.

The first item of the theorem is due to a straightforward symmetry. The second item is unexpected and much more involved. We will prove it in Chapter 3, by exhibiting an explicit relationship between principal eigenfunctions associated with $k_\lambda[r\,;b\,;1]$ and $k_\lambda[r\,;-b\,;1]$.

In Chapter 3, we will also define the spreading speed even when $\int_0^1 b \neq 0$. In this situation, the spreading speed "to the right", c_+, and the spreading speed "to the left", c_-, may differ (see Figure 3.1 for an intuitive definition of c_+ and c_-). In fact, we will prove that under assumption (i) or (ii) of Theorem 1.3.6, we have: $c_+[r\,;b\,;1] = c_-[r\,;-b\,;1]$.

Connection between the ability of persistence and the spreading speed.

We have been considering independently the effect of various parameters of the model on the ability of persistence and on the spreading speed of the solution. Last, in Chapter 3, we shall compare the joint properties of the ability of persistence and of the spreading speed.

We will see that having a low spreading speed does not imply that the ability of persistence is low. This phenomenon occurs even without the advection term. On the other hand, we will show that the quotient

$$\frac{c[r\,;0\,;1]}{2\sqrt{k[r\,;0\,;1]}}$$

is maximal for constant r. Therefore, if the ability of persistence is low, then the spreading speed must be low as well.

Theorem 1.3.7. *Let r be a 1-periodic function such that $c[r\,;0\,;1]>0$.*

(*i*) *There exists a 1-periodic $\widetilde{r}$ such that $c[r\,;0\,;1]>c[\widetilde{r}\,;0\,;1]$ and $k_0[r\,;0\,;1]<k_0[\widetilde{r}\,;0\,;1]$.*

(*ii*) *If r is constant, then $c[\widetilde{r}\,;0\,;1]<c[r\,;0\,;1]$ for all nonconstant 1-periodic $\widetilde{r}$ such that $k_0[\widetilde{r}\,;0\,;1]\leqslant k_0[r\,;0\,;1]$.*

(*iii*) *If r is nonconstant, then*

$$c[r\,;0\,;1]<2\sqrt{k_0[r\,;0\,;1]}$$

and there exists a constant $\widetilde{r}$ such that $c[r\,;0\,;1]<c[\widetilde{r}\,;0\,;1]$ and $k_0[r\,;0\,;1]>k_0[\widetilde{r}\,;0\,;1]$.

The first two items imply that the relationship between the ability of persistence and the spreading speed is not monotonic. A way to understand this non-monotonicity is to construct an environment with an extremely unfavourable zone, through which individuals will not be able to go, and a very favourable zone, so that the population is yet able to survive. This example is made explicit in Chapter 3, and is illustrated by Figure 1.15. Item (*iii*) is a consequence of item (*ii*).

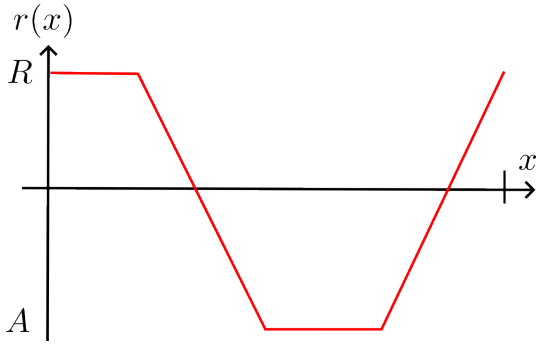


Figure 1.15: Construction which shows that in general, $k_0[r\,;0\,;1]$ is not controlled by $c[r\,;0\,;1]$. The figure illustrates the shape of the periodic pattern of $r(x)$. Here, the maximal value $R>0$ is taken large enough to ensure persistence even for $A=-\infty$; as A goes to $-\infty$, the spreading speed becomes arbitrarily close to 0.

1.4 Reaction-diffusion models for a population structured in phenotype and space

In this section, we will focus on equations that model populations structured in phenotype and living in heterogeneous environments, as Equation (1.6) in Subsection 1.1.3. In Subsection 1.4.1, we will present Chapters 5 and 6, where we give a persistence criterion for the equation and optimise this criterion. Next, in Subsection 1.4.2, we will give an overview of the spreading properties proved in Chapter 7. Last, in the end of Subsection 1.4.2, we will focus on the persistence and spreading properties of a slightly different equation, as in Chapter 8; namely, instead of a population structured in a continuous phenotype, we will consider a population composed of two different phenotypes.

1.4.1 Persistence properties

Chapters 5 and 6 are written in collaboration with L. Rossi. In these chapters, we shall work on the following equation on $u(t,x,\theta)$:

$$\begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), & t>0,\ (x,\theta)\in\mathbb{R}^N\times\Theta, \\ \nu\cdot\nabla_\theta u = 0, & t>0,\ (x,\theta)\in\mathbb{R}^N\times\partial\Theta, \end{cases} \tag{1.18}$$

where

$$\rho(t,x) := \int_\Theta u(t,x,\sigma)\,\mathrm{d}\sigma \tag{1.19}$$

represents the total population at given time and location. We supplement problem (1.18)–(1.19) with an initial condition

$$u(0,x,\theta) = u_0(x,\theta), \qquad (x,\theta)\in\mathbb{R}^N\times\Theta. \tag{1.20}$$

The domain of the spatial variable is the whole space $\mathbb{R}^N$, $N\in\mathbb{N}$. We recall that the domain of the phenotype is denoted by Θ and is either $\mathbb{R}^P$, $P\in\mathbb{N}$, or a smooth bounded domain of $\mathbb{R}^P$. In the latter case we call ν the outward normal to $\partial\Theta$. Any reference to $\partial\Theta$, such as the boundary condition in (1.18), has to be ignored in the case $\Theta=\mathbb{R}^P$.

Equation (1.18) can be seen from an individual-based point of view. See Figure 1.8 for a construction of the individual-based system. See also Figure 1.6, left, for the output of a (deterministic) simulation.

We first state a persistence criterion when the phenotypic space is either $\mathbb{R}^P$ or a $\mathcal{C}^2$ bounded domain in $\mathbb{R}^P$ (Chapter 5). Next, we shall assume that $\Theta=\mathbb{R}^P$ and consider a particular form of heterogeneity, to perform optimisation of eigenvalues (Chapter 6). To keep the notations of the introduction consistent, we will use here $k[r]$ (instead of $\lambda[r]$) for the principal eigenvalue of the linear operator corresponding to r, and $\mathscr{C}$ and $\mathscr{C}_i$ (instead of $\mathcal{C}$ and $\mathcal{C}_i$) for the periodicity cell and the patches of the model of Chapter 6.

We shall refer to r as the *space/phenotype fitness landscape*. To ensure well-posedness of the equation and to state the persistence criterion, we shall make the following assumptions on r:

$$\begin{cases} r\in L^\infty_{loc}(\mathbb{R}^N\times\overline{\Theta}),\ r \text{ is bounded above;} \\ r(x+h,\theta) = r(x,\theta) \ \text{ for all } (x,\theta)\in\mathbb{R}^N\times\Theta \text{ and } h\in\mathbb{Z}^N. \end{cases} \tag{1.21}$$

In the case $\Theta=\mathbb{R}^P$, we will also assume that

$$\limsup_{\|\theta\|\to\infty} r(x,\theta) \leqslant 0, \quad \text{uniformly with respect to } x\in\mathbb{R}^N, \tag{1.22}$$

which means

$$\lim_{R\to+\infty}\left(\sup_{x\in\mathbb{R}^N,\ \|\theta\|\geqslant R} r(x,\theta)\right)\leqslant 0.$$

We point out that, unlike in other mathematical studies in the literature, we do not assume that r converges to $-\infty$ as $\|\theta\|\to+\infty$. This will entail a loss of compactness that we will face using the notion of *generalised principal eigenvalue*.

We prove in Chapter 5 that the Cauchy problem (1.18)–(1.20) is well-posed, in the weak sense. The solution is continuous, and the equation is satisfied almost everywhere. Next, we focus on the long-time behaviour of the solution.

Long-time behaviour of the solution.

We have seen in Subsection 1.1.2 that the long-time behaviour of solutions of the heterogeneous Fisher-KPP equation is characterised by the sign of the principal eigenvalue of the linearised operator around the null state. The same will be true for the equation with phenotype. Let us call $\mathcal{L}[r]$ the linearised operator associated with (1.18), that is:

$$\mathcal{L}[r]\phi := \Delta_x\phi + \Delta_\theta\phi + r(x,\theta)\phi.$$

We emphasise that $\mathcal{L}[r]$ is a local operator.

Definition 1.4.1. *The generalised principal eigenvalue of* $\mathcal{L}[r]$ *is*

$$k[r] := \inf\left\{k \in \mathbb{R} \ / \ \exists \phi > 0,\ \mathcal{L}[r]\phi \leqslant k\phi \text{ in } \mathbb{R}^N \times \Theta,\ \nu \cdot \nabla_\theta \phi \geqslant 0 \text{ on } \mathbb{R}^N \times \partial\Theta\right\}.$$

In the above definition, the functions ϕ is understood to belong to $W^2_{p,loc}(\mathbb{R}^N \times \overline{\Theta})$ for some $p > 1 + N + P$, hence to be $\mathcal{C}^1$ up to the boundary by Morrey's embedding, so the boundary condition holds in the classical sense.

Definition 1.4.1 applies to both cases Θ bounded and $\Theta = \mathbb{R}^P$ (in the latter, the boundary condition is ignored, as usual). We point out that, even in the case of bounded Θ, the domain of the functions ϕ on which the operator acts is not compact, since we do not assume ϕ to be periodic in x. However, despite the lack of compactness, it turns out that $k[r]$ is indeed a *generalised principal eigenvalue* for the operator $\mathcal{L}[r]$ acting on spatially-periodic functions, in the sense that it admits a positive eigenfunction in that space.

Making use of some results concerning the generalised principal eigenvalue, we are able to establish the "standard" extinction/persistence dichotomy for the the long-time behaviour of the solution for our model.

Theorem 1.4.2. *Let* r *satisfy* (1.21)–(1.22) *and let* $k[r]$ *be the generalised principal eigenvalue of* $\mathcal{L}[r]$*. Let* u *be the solution of* (1.18)–(1.20) *with* $u_0 \in \mathcal{C}^0(\mathbb{R}^N \times \overline{\Theta}) \cap L^\infty(\mathbb{R}^N; L^1(\Theta))$ *bounded, nonnegative and not identically equal to* 0*.*

- *If* $k[r] < 0$*, and in addition* u_0 *is compactly supported, then the population gets extinct, in the sense that*

$$\lim_{t\to+\infty} u(t,x,\theta) = 0 \qquad \text{uniformly in } (x,\theta) \in \mathbb{R}^N \times \Theta.$$

- *If* $k[r] > 0$ *then the population persists, in the sense that*

$$\liminf_{t\to+\infty} \left[\sup_{x\in\mathbb{R}^N} \rho(t,x)\right] > 0.$$

We point out that the persistence property in the case $k[r] > 0$ does not provide us with a complete description of the long-time behaviour of the solution; it only ensures that it stays bounded from below away from zero. In particular, we do not know whether the solution converges towards a positive stationary state, as in the case without phenotype (1.3) or in the spatially homogeneous case with phenotype (1.5). For instance, we cannot rule out the possibility that the solution approaches a time-periodic cycle, which is a behaviour observed in some nonlocal reaction-diffusion equations, see e.g. [171] (this phenomenon is also related to the discussion in Subsection 1.1.4 about the emergence of periodic patterns).

In Chapter 5, we shall give first monotonicity properties of $k[r]$ with respect to the period of the environment and with respect to the diffusion coefficient. Next, in Chapter 6, we shall study more thoroughly a particular kind of heterogeneity r. We will be able to give optimisation properties of $k[r]$ with respect to the shape of r. Let us first describe the kind of heterogeneity r that we will consider in Chapter 6. We will call such heterogeneity a *patchwork-like space/phenotype-fitness landscape*.

A patchwork-like space/phenotype-fitness landscape.

From now on, we only work with $\Theta = \mathbb{R}^P$. The starting point to define the function r on which we shall focus in Chapter 6 is the Fisher Geometric Model (FGM). This model is characterised by a fitness function r_0 having a single maximum at $O \in \mathbb{R}^P$ and decaying as the phenotype θ moves away from the optimum O. Typically, one may take as in [214]: $r_0(\theta) = \chi(\|O-\theta\|)$, with $\chi(R) = -a\,|R|^d$, for some $a, d > 0$ and fixed $O \in \mathbb{R}^P$ (in the sequel, we shall consider more general forms of functions χ). The function χ encodes how fitness is affected by the distance of the phenotype θ from the optimum O.

One may also consider situations where the optimum O depends on the environmental conditions. Chapter 6 is devoted to the study of a version of the FGM in which the environment is composed of a patchwork of regions, each one characterised by a fittest optimum O. More precisely, we consider a fitness landscape $r(x,\theta)$ which is periodic in the x variable. We assume that its periodicity cell $\mathscr{C} := [0,1]^N$ is divided into a finite number of patches $\mathscr{C}_1, \dots, \mathscr{C}_K$, which are measurable sets forming a partition of $\mathscr{C}$, and that in each patch $\mathscr{C}_i$ there is an optimal phenotype $O_i \in \mathbb{R}^P$. The space/phenotype-fitness landscape function is then $r : \mathbb{R}^N \times \mathbb{R}^P \to \mathbb{R}$ satisfying

$$r(x,\theta) := \begin{cases} \chi(\|\theta - O_1\|) & \text{if } x \in \mathscr{C}_1, \\ \quad\vdots & \\ \chi(\|\theta - O_K\|) & \text{if } x \in \mathscr{C}_K, \end{cases} \tag{1.23}$$

and extended periodically to all $x \in \mathbb{R}^N$. We will sometimes denote the function r by $r[O_1, \dots, O_K]$ in order to stress its dependence on the optimal phenotypes $O_1, \dots, O_K \in \mathbb{R}^P$ (the patches $\mathscr{C}_i$ being fixed). Jointly with (1.23), we will always assume that $\chi \in L^\infty_{loc}(\mathbb{R}^P)$ satisfies

$$\chi \text{ is decreasing on } [0, +\infty). \tag{1.24}$$

Recall that χ represents the decay of the fitness when the phenotype moves away from the optimum.

Biological interpretation.

The biological situation that one can bear in mind is the following. Consider a crop pathogen living on a patchwork of fields. Each field $\mathscr{C}_i$ is planted with one crop variety i, on which the optimal phenotype for the pathogen is O_i. See Figure 1.16 for a schematic representation. With the above notations, K is the number of varieties, P is the dimension of the phenotypic space, and N is the dimension of the fields (from the point of view of modelling, it is only relevant to consider $N \in \{1, 2\}$). With this biological situation in mind, our problem is seen from an agroecological perspective: one of the goals of agroecology is indeed to use landscape heterogeneity as a tool to protect cultures from pathogens [40, 58]. In view of this application,

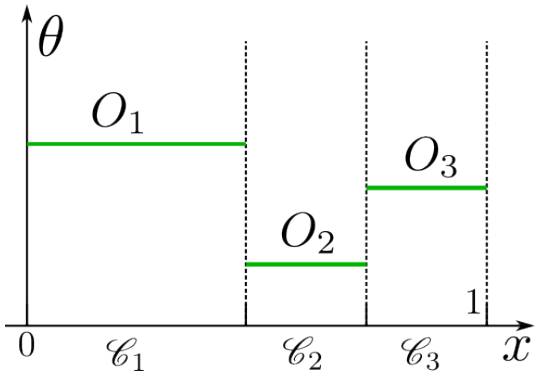


Figure 1.16: Representation of the patchwork landscape (1.23) with $N = P = 1$ and $K = 3$. Here, $\mathscr{C}_1$, $\mathscr{C}_2$, $\mathscr{C}_3$ represent three 1-dimensional fields, each one planted with a different variety, then repeated periodically. On each field $\mathscr{C}_i$, the pathogen has an optimal phenotype $O_i \in \mathbb{R}$.

a very natural question is:

How to arrange the fields $\mathscr{C}_i$ and the corresponding optima O_i so that persistence is as difficult as possible?

Optimisation problems for the persistence of the species reduce to the optimisation of $k[r]$ with respect to the spatial configuration of the fitness landscape. The point of view of modelling can help us understand the results that follow. They are in fact an incarnation of the following ecological intuition:

The more homogeneous is the environment, the easier is the persistence of the species.

"More homogeneous" roughly means that the fluctuations of the landscape function are milder.

In Chapter 6, we devote particular attention to the dependence of the principal eigenvalue $k[r]$ on the size of the periodicity cell, as well as the location of the optima $O_1, \dots, O_K \in \mathbb{R}^P$. For the former, we derive both a homogenisation and a large scale limit, i.e. a rapidly and a slowly varying environment. For the latter, according to the ecological intuition illustrated above, it should hold that the closer the optima $O_1, \dots, O_K$ are to each other, the easier it is for the population to persist. We show in Chapter 6 that this is actually the case in some sense: namely, the configuration maximising k is the one with all points O_i coinciding. However, if one wants to compare two given configurations, then the notion of "being closer to each other" is unclear. At least, one can ask the following.

Question 1. *Given two configurations $O_1, O_2 \dots, O_K$ and $\widehat{O}_1, O_2 \dots, O_K$ satisfying*

$$\left\|\widehat{O}_1 - O_i\right\| \leqslant \|O_1 - O_i\| \quad \text{for all } i = 2, \dots, K,$$

is it true that

$$k[r[\widehat{O}_1, O_2 \dots, O_K]] \geqslant k[r[O_1, O_2 \dots, O_K]] \ ?$$

We are able to answer in the affirmative to this question when the number of patches is not too large, and precisely when $K \leqslant P$ (see Theorem 1.4.5 below).

Given the biological application that we have in mind, our goal would be to minimise $k[r]$ with respect to $O_1,\dots,O_K$. We will show that there is no global minimiser. Questions of minimisation under constraints, therefore, are natural. We will answer the following question if the number of patches is not too large (see Theorem 1.4.6 below).

Question 2. *How to minimise $k[r[O_1,\dots,O_K]]$ among all configurations that satisfy $\|O_i - O_j\| \leqslant D$ for all $i,j = 1,\dots,K$?*

All in all, in the particular cases that we are able to consider, our results will always give an affirmative answer to the following question, which is more ambitious than Question 1.

Question 3. *Given two configurations $O_1, O_2 \dots, O_K$ and $\widehat{O}_1, \widehat{O}_2 \dots, \widehat{O}_K$ satisfying*

$$\left\|\widehat{O}_i - \widehat{O}_j\right\| \leqslant \|O_i - O_j\| \quad \text{for all } i,j = 2,\dots,K,$$

is it true that

$$k[r[\widehat{O}_1, \widehat{O}_2 \dots, \widehat{O}_K]] \geqslant k[r[O_1, O_2 \dots, O_K]] \ ?$$

Varying the positions of the optima.

In this paragraph, we present some monotonicity properties of the principal eigenvalue, always in the patchwork landscape setting (1.23), when the relative positions of the optima $O_1,\dots,O_K$ change, while the function χ and the cells $\mathscr{C}_i$ are fixed. To prove our results, we shall assume that the function χ is decreasing and regular. We shall need an additional assumption which ensures that the (generalised) principal eigenfunction decays exponentially as $\|\theta\| \to +\infty$. This additional assumption is always satisfied if $\chi(R) \to -\infty$ as $R \to +\infty$. In Chapter 6, we will also give examples where $\inf \chi > -\infty$. See Assumption (6.11) and Proposition 6.3.3.

Our first monotonicity result gives a criterion to increase the ability of persistence, measured by the principal eigenvalue $k[r]$, and will be the main tool to prove most other results of Chapter 6. It asserts that a configuration is more favourable than another if it is possible to pass from the latter to the former by a continuous transformation along which the distance between optima never increases. An illustration is given by Figure 1.17.

Theorem 1.4.3. *Let (1.23)–(1.24) and some technical assumptions hold. If $\gamma : [0,1] \to \mathbb{R}^P$ is a $\mathcal{C}^1$ regular curve (i.e. with $\gamma' \neq 0$ on $[0,1]$) such that $s \mapsto \|\gamma(s) - O_i\|$ is nonincreasing for all $i = 2,\dots,K$, then*

$$k[r[\gamma(1), O_2, \dots, O_K] \geqslant k[r[\gamma(0), O_2, \dots, O_K]. \tag{1.25}$$

If, in addition, there exists $j \in \{2,\dots,K\}$ for which

$$\|\gamma(1) - O_j\| < \|\gamma(0) - O_j\|,$$

then the inequality in (1.25) is strict.

Remark 1.4.4. If $s \mapsto \|\gamma(s) - O_i\|$ is constant for all $i = 2,\dots,K$, then applying Theorem 1.4.3 to $s \mapsto \gamma(s)$ and $s \mapsto \gamma(1-s)$ shows that $k[r[\gamma(1), O_2, \dots, O_K] = k[r[\gamma(0), O_2, \dots, O_K]$.

Thanks to Theorem 1.4.3, we are able to answer Question 1 when the number of patches is not too large.

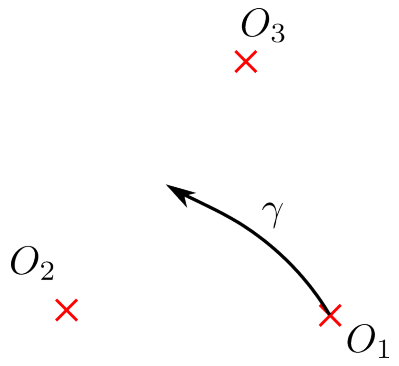


Figure 1.17: Illustration of Theorem 1.4.3. As O_1 follows the path γ_1, the environment becomes more favourable.

Theorem 1.4.5. *Let* (1.23)–(1.24) *and some technical assumptions hold. Assume that* $K \leqslant P$. *Given two configurations* $O_1, O_2 \ldots, O_K$ *and* $\widehat{O}_1, O_2 \ldots, O_K$ *satisfying*

$$\left\|\widehat{O}_1 - O_i\right\| \leqslant \|O_1 - O_i\| \quad \text{for all } i = 2, \ldots, K,$$

we have:

$$k[r[\widehat{O}_1, O_2 \ldots, O_K]] \geqslant k[r[O_1, O_2 \ldots, O_K]]. \tag{1.26}$$

If there exists $i \in \{2, \ldots, K\}$ *for which* $\left\|\widehat{O}_1 - O_i\right\| < \|O_1 - O_i\|$, *then the inequality* (1.26) *is strict. Otherwise, the inequality* (1.26) *is an equality.*

Owing to Theorem 1.4.3, the proof of Theorem 1.4.5 consists in constructing a path from one configuration to another along which the distances of optima decreases, but this is only possible in general if K is not larger than P, see Remark 6.6.6 in Chapter 6.

In Chapter 6, we shall further address Question 3 by focusing on the dependency of the quantity $k[r[O_1, \ldots, O_K]]$ with respect to simultaneous movements of all optima $O_1, \ldots, O_K$. We shall give various kinds of results:

1. Consider a dilatation of the points O_i, i.e., replace O_i by aO_i for some $a \geqslant 0$. We will prove that, under a convexity assumption (see (6.15)) the ability of persistence – measured by the principal eigenvalue $k[r]$ – is nonincreasing in a, and give its limits as $a \to 0$ and $a \to +\infty$;

2. Take $H \in \{1, \ldots, K-1\}$ and $O_{H+1}, \ldots, O_K$. We will prove that the maximum of $(O_1, \ldots, O_H) \mapsto k[r[O_1, \ldots, O_K]]$ is attained by some points $O_1, \ldots, O_H$, all belonging to the convex hull of $\{O_{H+1}, \ldots, O_K\}$;

3. On the other hand, we will prove that the minimum of $(O_1, \ldots, O_H) \mapsto k[r[O_1, \ldots, O_K]]$ is not reached. However, if a constraint is given, then a minimiser can be found, as the following theorem shows.

Theorem 1.4.6. *Let* (1.23)–(1.24) *and some technical assumptions hold. Assume that* $K \leqslant 5$ *and* $K \leqslant P+1$. *Let the sets* $\mathscr{C}_1, \ldots, \mathscr{C}_K$ *be fixed, while* $O_1, \ldots, O_K$ *vary in* $\mathbb{R}^P$. *For a given* $D > 0$, *the solutions of the problem:*

$$\textit{Minimise } k[r[O_1, \ldots, O_K]] \textit{ under the constraint } \|O_i - O_j\| \leqslant D \textit{ for all } i, j = 1, \ldots, K,$$

are the vertices $O_1, \dots, O_K$ of a regular polyhedron of side of length D. Namely:

$$k[r[Q_1, \dots, Q_K]] = \min\Big\{k[r[O_1, \dots, O_K]] \ / \ \|O_i - O_j\| \leqslant D \text{ for all } i \neq j\Big\}$$

if and only if $\|Q_i - Q_j\| = D$ for all $i \neq j$.

1.4.2 Spreading properties

Now, we turn to the spreading properties of the equation with phenotype when the geographical space is one-dimensional and the phenotype space Θ is a bounded domain. In Chapter 7, we shall work with heterogeneous (Fickian) diffusion in space and phenotype; here, for simplicity, we only present our results with homogeneous diffusion. Next, in Chapter 8, we shall study a very simple version of the model, with two morphs (instead of a continuum of phenotypes). Such a simplicity will allow us to get explicit expressions for the spreading speed in some limits, and to get insight into the results through simulations. Chapter 8 is a work in collaboration with L. Roques, P. Zamberletti and J. Papaïx.

Let us first focus on the results of Chapter 7. We consider a mutation coefficient $m > 0$ and a period $L > 0$. 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. The reaction term $r(x, \theta)$ is 1-periodic in $x \in \mathbb{R}$ (recall that the geographical space, here, is one-dimensional), and we denote by

$$r_L(x, \theta) := r\left(\frac{x}{L}, \theta\right)$$

the L-periodic version of r. We write a general version of the initial model (1.6) as:

$$\begin{cases} \partial_t u_{m,L} = \Delta_x u + m\Delta_\theta u + u_{m,L}(r_L(x,\theta) - \rho_{m,L}(t,x)), & t > 0, (x,\theta) \in \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta u_{m,L} = 0, & t > 0, (x,\theta) \in \mathbb{R} \times \partial\Theta, \\ u_{m,L}(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R} \times \Theta, \end{cases} \tag{1.27}$$

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 in the direction x. The initial condition u_0 is independent of m and L. We let $k_{m,L}$ be the principal eigenvalue associated with the linearised evolution operator of (1.27) (in Chapter 7, we will denote it instead by $k^0_{m,L}$, as we will also use $k^\lambda_{m,L}$ to state the Freidlin-Gärtner formula). What we denoted by $k_0[r]$ in Subsection 1.4.1 now corresponds to $k_{1,1}$. In fact, the same criterion for persistence holds for general $m > 0$ and $L > 0$. As we are interested in the spreading of a population, we shall only work with mutation coefficients and periods such that this criterion is satisfied, namely:

$$k_{m,L} > 0.$$

For example, this condition is satisfied for all $m > 0$ and $L > 0$ if $r \geqslant 0$ and $r \not\equiv 0$.

The first result of Chapter 7 is a Freidlin-Gärtner formula adapted to the context of an equation with phenotype (Theorem 7.2.3). Let us focus on the consequences of this new Freidlin-Gärtner formula.

The spreading speed for different scales.

In Chapter 7, we shall be interested in the spreading speed for different scaling limits. This is relevant, since the equation takes into account two phenomena of different nature which, therefore, may take place on different timescales.

The main tools used in this part of Chapter 7 are standard homogenisation techniques and the results of Chapter 2. We will use the notation $c^1(R)$ for the spreading speed of a population not structured in phenotype, living in an environment with periodic intrinsic growth rate $R \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ (see Subsection 7.2.2 in Chapter 7 for more details). The asymptotic results of Chapter 7 read as follows (for simplicity, assume that $r \geqslant 0$, $r \not\equiv 0$, to ensure that persistence always holds and the limits are well-defined):

1. As $L \to +\infty$ and for fixed $m > 0$, the spreading speed $c_{m,L}$ converges and

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

where, for all $x \in \mathbb{R}$, $H_m(x)$ is the principal eigenvalue associated with the *local principal eigenvalue problem*

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

2. As $L \to 0$ and for fixed $m > 0$, the spreading speed $c_{m,L}$ converges and

$$\lim_{L\to 0} c_{m,L} = 2 \max_{\psi\in H^1(\Theta),\ \|\psi\|_{L^2(\Theta)}=1} \sqrt{\int_\Theta \left[\left(\int_0^1 r(x,\theta)\,\mathrm{d}x\right)\psi(\theta)^2 - m\left|\nabla_\theta\psi(\theta)\right|^2\right]\mathrm{d}\theta}.$$

3. As $m \to +\infty$ and for fixed $L > 0$, the spreading speed $c_{m,L}$ converges and

$$\lim_{m\to+\infty} c_{m,L} = c^1\left(x \mapsto \int_\Theta r_L(x,\theta)\,\mathrm{d}\theta\right).$$

4. As $m \to 0$ and for fixed $L > 0$, the spreading speed $c_{m,L}$ converges and

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

This result is represented on Figure 1.18.

Next, using the previous technical mathematical results, we will give several consequences which have a direct biological interpretation and which highlight the effect of mutations on the qualitative behaviour of the population. See Chapter 7 for a more thorough discussion on the modelling and biological implications of these results.

The effect of mutations.

In this paragraph, we assume that no phenotype is best everywhere:

$$\forall \theta \in \overline{\Theta},\ \ \exists (x,\sigma) \in \mathbb{R}\times\overline{\Theta}, \qquad r(x,\sigma) > r(x,\theta). \tag{1.28}$$

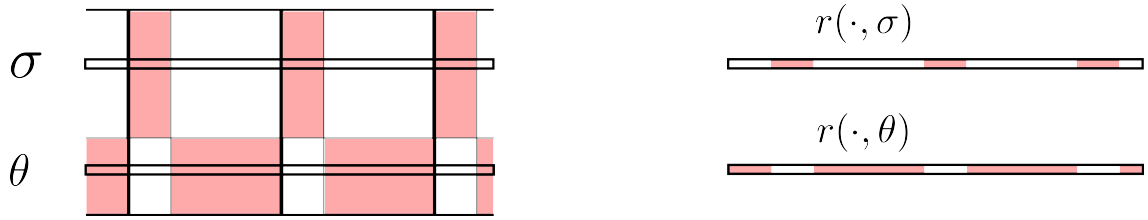


Figure 1.18: When $m \to 0$, $c_{m,L}$ converges to the speed of the phenotype which, if left alone, would go fastest, i.e. to the maximal value taken by $c^1(r(\cdot,\theta))$. For example, on this figure, if the shaded area represents unfavourable zones, the limit of $c_{m,L}$ as $m \to 0$ should be rather close to $c^1(r(\cdot,\sigma))$, i.e. the speed of the phenotype σ when it is left alone.

The following theorem implies that that under assumption (1.28), an "anomalous spreading speed" arises. Namely, for a very large period, vanishingly small mutations have a non-vanishing effect on the spreading speed; this means that the global population spreads faster – even when the different phenotypes are almost independent from one another – than any phenotype taken in isolation. Regarding the phenomenon of "anomalous spreading speeds", see also [82, 169] and Chapter 8 (and in particular Figure 1.19, which is reproduced here). The discrepancy between the spreading speed of the global population and the spreading speed of a single phenotype taken in isolation can be arbitrarily close to

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

The interpretation of the emergence of such an anomalous spreading speed is the fact that at each spatial position, the population is able to exploit the phenotype which is best adapted to the current position. Under assumption (1.28), there are positions where the isolated phenotype is not best, so it cannot spread as fast as the whole population.

To better understand the following theorem, Figure 1.19 can be kept in mind, although it does not deal with the same equation.

Theorem 1.4.7. *Assume that there exist $\underline{L} > 0$ and $\theta \in \overline{\Theta}$ such that the phenotype θ alone survives in a $\underline{L}$-periodic environment (i.e. $k_0[r_{\underline{L}}(\cdot,\theta)\,;0\,;1] > 0$ with the notation of Subsection 1.3.2). Assume that* (1.28) *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

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

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

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

The fact that there is an optimal mutation coefficient $m^*(L) > 0$ suggests 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. We will show that 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. Notably, if there exists

$\theta \in \Theta$ such that $x \mapsto r(x,\theta)$ is not constant, then $m \mapsto \lim_{L\to+\infty} k_{m,L}$ and $m \mapsto \lim_{L\to 0} k_{m,L}$ are strictly decreasing (see Proposition 7.2.9). Notice that, as a consequence of the first limit and Theorem 1.4.7, the optimal mutation rate converges to 0:

$$m^*(L) \underset{L\to+\infty}{\longrightarrow} 0. \tag{1.29}$$

In Chapter 8, which deals with an equation with only two morphs, the optimal mutation coefficient also appears in the simulations (see Figure 1.19) and also converges to 0.

Further, we will see that for the period, there is no trade-off: the larger the period, the higher the speed. This property also holds when the phenotype is not taken into account [173]. Last, we will also prove the counter-intuitive result that *making persistence easier is not equivalent to increasing the spreading speed*. This is connected to the results proved at the end of Chapter 3, see the last paragraph of Subsection 1.3.2.

A population with two morphs.

Let us now turn to Chapter 8, where we shall study a very simple version of the model studied in Chapter 7, with two morphs (i.e. two distinct phenotypes). The simplicity will allow us to get explicit expressions for the spreading speed in some limits, and to get insight into the results through simulations. The system of equations reads as follows:

$$\begin{cases} \partial_t u(t,x) = & D\,\partial_{xx} u + r_L^u(x)\,u - u\,(u+v) + \mu\,(v-u), \\ \partial_t v(t,x) = & D\,\partial_{xx} v + r_L^v(x)\,v - v\,(u+v) + \mu\,(u-v), \end{cases} \qquad t>0,\ x\in\mathbb{R}. \tag{1.30}$$

In this equation, x represents the spatial variable, while $u(t,x)$ and $v(t,x)$ are the population densities of the two morphs. The periodic functions $r_L^u(x)$ and $r_L^v(x)$ are the growth rates of the two morphs, and depend on the spatial position x. Additionally, D is the spatial diffusion coefficient, which is constant in space and shared by both morphs, and μ is a coefficient proportional to the mutation rate. The environment, described by the functions r_L^u and r_L^v, is assumed to be periodic with a period L. Namely,

$$r_L^u(x) = r^u(x/L), \qquad r_L^v(x) = r^v(x/L),$$

where r^u and r^v are 1-periodic functions. One half $[0, L/2)$ of the period cell corresponds to the first patch, and the other half $[L/2, L)$ corresponds to the second patch. We assume that the two morphs have distinct specialisations: one morph has a higher growth rate ($R^+ > 0$) on one of the patches and a lower growth rate ($R^- \leqslant R^+$) on the other patch, while the other morph has the opposite specialisation. In other words:

$$\begin{cases} r_L^u(x) = R^+ \text{ and } r_L^v(x) = R^- \text{ for } x \in [0, L/2), \\ r_L^u(x) = R^- \text{ and } r_L^v(x) = R^+ \text{ for } x \in [L/2, L). \end{cases}$$

In the very particular situation presented here, we are able to give explicit expressions for the ability of persistence and the spreading speed of the system as $L \to 0$, $L \to +\infty$, $\mu \to 0$ and $\mu \to +\infty$. See Tables 1.1 and 1.2.

For the system (1.30), we can approximate the spreading speed, using the Freidlin-Gärtner formula and standard libraries for eigenvalues of matrices. (Such computations would be much harder for the equation with continuous phenotype (1.18), due to the additional dimension). In Figure 1.19, we displayed the simulated spreading speed with two morphs c^{2m}

μ \ L	$L \to 0$	Arbitrary L	$L \to \infty$
$\mu = 0$	$R^+ + R^- > 0$	$k_0^{1m} > 0$	$R^+ > 0$
$\mu \to 0$	$R^+ + R^- > 0$	$k_0^{1m} > 0$	$R^+ > 0$
Arbitrary μ	$R^+ + R^- > 0$	$k_0^{2m} > 0$	$R^+ > \frac{\mu}{1+(\mu/(-R^-))}$ or $R^+ + R^- > 0$
$\mu \to \infty$	$R^+ + R^- > 0$	$R^+ + R^- > 0$	$R^+ + R^- > 0$

Table 1.1: Criterion for persistence. The result remains unchanged whether the limit is taken first in μ or L. Respectively, k_0^{1m} and k_0^{2m} correspond to the principal eigenvalues that determine the persistence condition for a one-morph problem and a two-morph problem. More details are given in Chapter 8.

μ \ L	$L \to 0$	Arbitrary L	$L \to \infty$
$\mu = 0$	$\sqrt{2D(R^+ + R^-)}$	c^{1m}	$c^{1m}(L \to \infty)$, see (8.5)
$\mu \to 0$	$\sqrt{2D(R^+ + R^-)}$	c^{1m}	$\mu \to 0$ then $L \to \infty$: $c^{1m}(L \to \infty)$, see (8.5) $L \to \infty$ then $\mu \to 0$: $2\sqrt{D\,R^+}$
Arbitrary μ	$\sqrt{2D(R^+ + R^-)}$	Fig. 1.19	$\sqrt{2D\left(R^+ + R^- + \sqrt{(R^+ - R^-)^2 + 4\mu^2} - 2\mu\right)}$
$\mu \to \infty$	$\sqrt{2D(R^+ + R^-)}$	$\sqrt{2D(R^+ + R^-)}$	$\sqrt{2D(R^+ + R^-)}$

Table 1.2: Spreading speed c^{2m} of the two-morphs population. Except for the limit $(L, \mu) \to (+\infty, 0)$, the results remain unchanged whether the limit is taken first in μ or L. The notation c^{1m} stands for the spreading speed when there is only one morph. More details are given in Chapter 8.

(y-axis) in terms of the mutation rate μ (x-axis) and the period L of the environment (colour). As in the equation with continuous phenotype, we observe that there is an optimal mutation rate and that there is a discontinuity at $\mu = 0$ of the spreading speed as the period of the environment goes to infinity.

In Figure 1.19, it seems that the optimal mutation rate goes to zero as the period goes to infinity, as is the case for the equation with phenotype, see Equation (1.29) (a similar method can be used to prove this new convergence in the two-morphs setting). Finally, let us point out that the "anomalous spreading speed" is apparent on Figure 1.19, where the spreading speed for finite L and $m = 0$ is much smaller than the spreading speed as $L \to +\infty$ and next $m \to 0$. The notion of "anomalous spreading speed" was discussed more in length above for the equation with continuous phenotype.

1.5 Loss of neutral diversity during an invasion

This section is devoted to the study of the loss of genetic diversity during an invasion. First, we present Chapter 9, where we work on an equation with nonlocal dispersal (see Subsection 1.1.4) and prove that a logarithmic correction appears. The connection between the logarithmic correction and the structure of neutral diversity is explained at the end

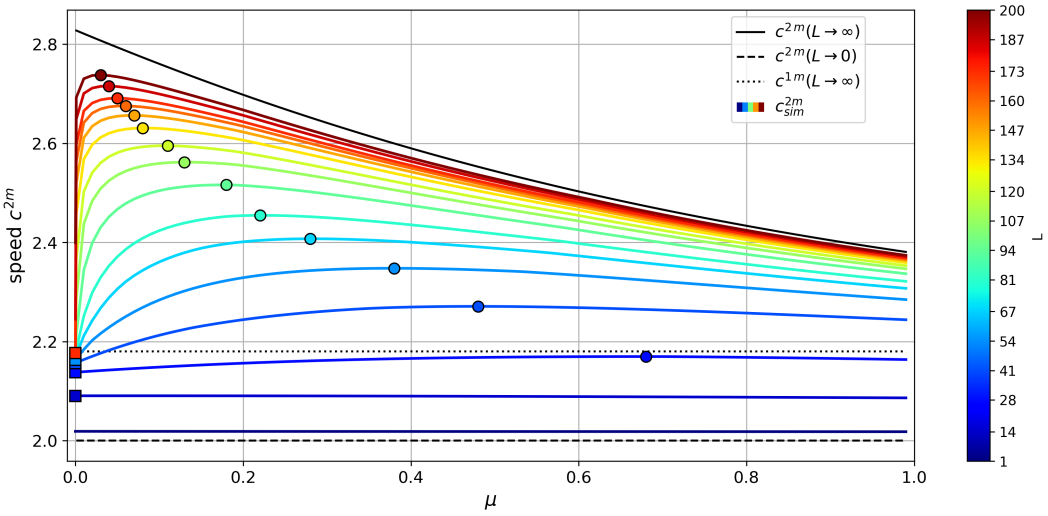


Figure 1.19: Theoretical and simulated speeds in terms of the mutation parameter μ and spatial period L. Here, c^{1m} (resp. c^{2m}) stands for the spreading speed of a population with one morph (resp. with two morphs with reverse specialisation). The circles indicate the maximum values of the simulated speeds c^{2m}_{sim}, for each L. The leftmost points ($\mu = 0$, squares) indicate the values of the simulated speeds c^{1m}_{sim}. The parameter values are $R^+ = 2$, $R^- = 0$, $D = 1$, leading to $c^{1m}(L\to 0) = 2$, $c^{2m}(L\to 0) = 2$, $c^{1m}(L\to\infty) \approx 2.18$, $c^{2m}(L\to\infty) = 2\sqrt{2} \approx 2.83$ as $\mu \to 0$, see Table 1.2.

of Subsection 1.1.1. Next, we present Chapter 10, which deals with probabilistic models designed to analyse the data of an experiment that allows one to *visualise* the loss of neutral diversity during a real invasion.

1.5.1 The logarithmic correction in an equation with nonlocal dispersal

In Chapter 9, we will be concerned with the spreading properties of the solution of the following Fisher-KPP equation with nonlocal dispersal:

$$\begin{cases} \partial_t v(t,x) = [J * v(t,x) - v(t,x)] + v(t,x)(r - v(t,x)) & t > 0, x \in \mathbb{R}, \\ v(0,x) = \mathbb{1}_{(-\infty,0]}(x) & x \in \mathbb{R}, \end{cases} \tag{1.31}$$

where $r > 0$ is a constant and

$$J * v(t,x) := \int_{\mathbb{R}} v(t, x-y) J(\mathrm{d}y).$$

We shall look for the emergence of a logarithmic correction.

Although our primary interest lies in the Cauchy problem (1.31), we shall focus on the *linearised* equation

$$\begin{cases} \partial_t u(t,x) = [J * u(t,x) - u(t,x)] + r u(t,x) & t > 0, x \in \mathbb{R}, \\ u(0,x) = \mathbb{1}_{(-\infty,0]}(x) & x \in \mathbb{R}, \end{cases} \tag{1.32}$$

The behaviour of the linear equation seems simpler to understand. From the study of the solutions of (1.32), we shall deduce a similar (weaker) result on the solutions of (1.31).

In Equations (1.31) and (1.32), J is a measure on $\mathbb{R}$. We assume that J satisfies the assumptions:

$$J((0,+\infty)) > 0, \qquad J(\mathbb{R}) = 1, \tag{1.33}$$

together with the assumption:

$$\text{There exists } L > 0 \text{ such that} \qquad \int_{\mathbb{R}} e^{L|x|} J(\mathrm{d}x) < +\infty. \tag{1.34}$$

Assumption (1.34) means that the dispersal kernel is *thin-tailed*. It means that individuals usually do not move too far away from their origin, and it implies that travelling waves exist. If the tail of J is too heavy, the invasion accelerates [100, 144]. Under mild additional assumptions on the kernel J, there exists a spreading speed c which satisfies the usual spreading properties mentioned in the beginning of Section 1.1, see [157, Theorem 3.2]. In this situation, the expression for c is explicit:

$$c = \inf_{\lambda>0} \frac{M(\lambda)+r-1}{\lambda} \qquad \text{with} \qquad M(\lambda) := \int_{\mathbb{R}} e^{\lambda x} J(\,\mathrm{d}x). \tag{1.35}$$

By [113, Proposition 1.1], under Assumptions (1.33) and (1.34), there exists a unique $\lambda_r > 0$ at which the infimum is reached:

$$c = \frac{M(\lambda_r)+r-1}{\lambda_r}. \tag{1.36}$$

Graham [113] showed that the logarithmic correction also emerges for the nonlocal equation (1.31). He makes an slightly technical assumption on the kernel J, which is not always satisfied (see Chapter 9 for more details). Roquejoffre [197], assuming that J has a compact support, was able to give even more precise asymptotics on the position of the solution, showing that the fluctuations around the position given by Graham converge to 0. The goal of Chapter 9 is to relax their conditions on J and to treat the general case of thin-tailed kernels. A first step towards this goal is to work on the *linear* Cauchy problem and, using the maximum principle, to find an upper bound for the position of the invasion front for the nonlinear Cauchy problem.

The first result of Chapter 9 is a Feynman-Kac formula for Equation (1.32). A kernel J which satisfies the hypotheses (1.33) and (1.34) is a probability law. We consider a sequence $(X_k)_{k\geqslant 1}$ of real independent and identically distributed random variables, following the law J. We will prove that

$$u(t,x) = e^{(r-1)t} \sum_{n=0}^{+\infty} \frac{t^n}{n!} \mathbb{P}\left(S_n \geqslant x\right), \qquad \text{with } S_n := \sum_{k=1}^{n} X_k. \tag{1.37}$$

As we look closely at each term of the sum (1.37), we observe that when x is near the position ct, there is a trade-off between the two factors $\frac{t^n}{n!}$ and $\mathbb{P}\left(S_n \geqslant x\right)$:

- for $t \simeq n$ and $t \gg n$, the factor $\frac{t^n}{n!}$ is large, but the probability $\mathbb{P}\left(S_n \geqslant x\right)$ is small;
- for $t \ll n$, the probability $\mathbb{P}\left(S_n \geqslant x\right)$ is large but the factor $\frac{t^n}{n!}$ is small.

In fact, we shall see in Chapter 9 that for $x = ct + o(\sqrt{t})$, the dominant terms of the sum (1.37) are located around a position $n \simeq \alpha t$ proportional to t. Therefore, when we study $u(t, ct)$,

we will have to deal with probabilities of the form $\mathbb{P}\left(\frac{S_n}{n} \geqslant \frac{c}{\alpha}\right)$, where $\frac{c}{\alpha}$ is a constant. The theory of large deviations provides a useful framework to estimate precisely those very small probabilities as $n \to +\infty$, see Chapter 9. These observations will allow us to prove the main result.

Theorem 1.5.1. *Let J be a kernel which satisfies the hypotheses* (1.33) *and* (1.34). *Let u be a solution of the linear Cauchy problem* (1.32). *Take $\rho \in (0,1)$ and denote by*

$$\sigma^\rho(t) := \sup\{x \in \mathbb{R} \ / \ u(t,x) \geqslant \rho\}$$

the position of the level ρ of u at time t. We have

$$\sigma^\rho(t) = ct - s\ln(t) + O_{t\to+\infty}(1) \qquad \textit{with} \qquad s = \frac{1}{2\lambda_r},$$

where λ_r is defined by (1.36).

Let us point out that we obtain the same result with the local counterpart of the linear Cauchy problem (1.32), i.e. a logarithmic correction with $s = \frac{1}{2\sqrt{r}}$ (here, λ_r plays the role of $\sqrt{r}$ and is the rate of exponential decay of travelling waves [68, Theorem 1.6]):

$$\partial_t z = \partial_{xx} z + rz, \qquad r = f'(0), \tag{1.38}$$

together with the initial condition $z(1,x) = \frac{1}{4\pi} e^{-x^2/4}$. See Chapter 9 for the detailed proof.

Last, using Theorem 1.5.1 and the comparison principle, we will conclude that the logarithmic correction for the nonlinear equation is *at least*

$$-\frac{1}{2\lambda_r}\ln(t) + O_{t\to+\infty}(1).$$

As a consequence, the correction between ct and the actual position of the invasion is unbounded. Therefore, as explained in the end of Subsection 1.1.1, we expect that neutral diversity in Equation (1.31) is lost during an invasion with nonlocal dispersal.

1.5.2 How to analyse the loss of neutral diversity?

Chapter 10 gives an overview of an ongoing work with R. Forien, N. Peeters, L. Roques and S. Vicente. In this work, we are interested in the effect of a barrier on the dynamics of diversity; more precisely, we wish to estimate the strength of a barrier through the measurement of diversity at different positions – see Figure 1.20. The origin of Chapter 10 is an experiment conducted by N. Peeters and S. Vicente.

Description of the experiment. The experiment of N. Peeters and S. Vicente is designed to follow the dynamics of neutral diversity during an invasion of bacteria in a tomato plant. Neutral diversity is artificially created by giving to each bacteria a selectively neutral tag (more precisely, a tag is similar to a "barcode" on the DNA sequence). Their techniques allow them to use $K := 120$ tags, which are assumed to be evenly distributed in the original population.

Once these tags are given, bacteria are inoculated in the soil where the plants grow. After a few days, bacteria have infected most plants. They first entered the root, and then entered

the stem. Once a deterioration of the plants is detected (which means that a large population of bacteria has entered), the plants are dissected and the experimenters can measure the proportions of the different tags in each "compartment" of the plants – in our case, the two compartments are the root and the stem. For each replicate, we know:

- the time of sampling;
- the proportions of each tag in each compartment at the time of sampling;
- the total bacterial load in each compartment at the time of sampling.

Goals. It is hypothesised that bacteria must cross two barriers during the infection of the plant: one barrier between the soil and the root and one barrier between the root and the stem. The questions are:

How do the barriers work? How strong are the barriers? What is the influence of the experimental conditions?

In Chapter 10, we will focus only on the barrier from the soil to the root. On the one hand, we would like to understand how the barrier works. We will consider three categories of models for the barrier:

- The barrier works as a "one-step bottleneck": when sufficiently many bacteria are close to the barrier, all of these bacteria cross the barrier instantly. This is the model provided by the STAMP framework. The name "bottleneck" comes from the metaphor of a population going through a bottleneck and thereby reducing drastically its size;
- The barrier is crossed, at a constant rate, by a single bacteria;
- The population is described by a noisy monostable or bistable Fisher-KPP equation, and the barrier is a zone where the diffusion coefficient is very low.

On the other hand, we would like to know how strong the barrier is. It is expected, indeed, that for different experimental conditions (e.g. temperature), the barrier might be more or less strong. The hope is to be able to address these questions by looking at how neutral diversity is affected by the crossing of a barrier.

In Chapter 10, we will construct and discuss four models for a barrier. Next, we will provide a method to determine, given a set of simulated tag frequency vectors, from which model, and with which parameter, these proportions where simulated. Last, we will apply this method to partial (not released yet) experimental data.

1.6 Perspectives

This thesis raises several open questions and perspectives.

The results of Chapter 2 about strongly anisotropic elliptic operators are still incomplete. We proved the convergence to a local principal eigenfunction of the "slices in the fast direction" of the global principal eigenfunction (i.e. the functions $x \mapsto \varphi_\varepsilon(\theta, x)$ for fixed θ). What about the "slices in the slow direction" of the global principal eigenfunction, i.e. the functions $\theta \mapsto \varphi_\varepsilon(\theta, x)$ for fixed x? Can the ideas in Remark 2.4.5 of Chapter 2 be proved

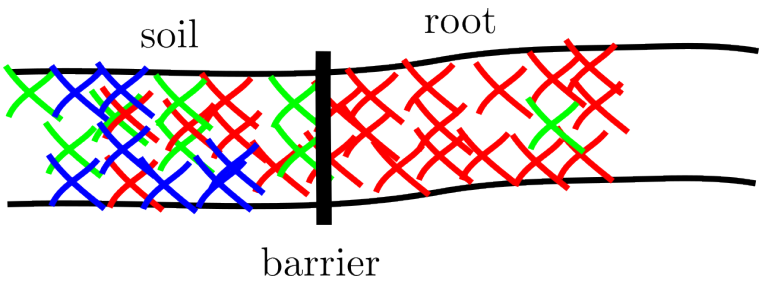


Figure 1.20: A representation of the barrier. Bacteria move from left to right. They are represented by coloured crosses, and their colours correspond to the tags that they carry. Before the barrier, there is a large diversity. After the barrier, diversity is lost, owing to the fact that only the descendants of the very first bacteria that crossed the barrier are present.

and generalised? Next, in two dimensions or more, when the transport term in the slow direction (denoted by B) is nonzero, does the principal eigenvalue converge? What is its limit? Theorem 1.3.3 shows that the problem is complex even in one dimension. At least, owing to Lemma 2.4.4 in Chapter 2, one may conjecture that k_ε converges to

$$\lim_{\varepsilon\to 0} k_\varepsilon = \lim_{\varepsilon\to 0} k_\varepsilon^1[y \mapsto k^y],$$

where $k_\varepsilon^1[y \mapsto k^y]$ is the principal eigenvalue of the operator with only the slow variable and with reaction term replaced by the local principal eigenvalue k^y:

$$\phi \mapsto \varepsilon^2\Delta\phi + \varepsilon B\cdot\nabla\phi + k^y\phi.$$

What is needed to prove such a convergence is the uniqueness of a k_0 such that the equation in Lemma 2.4.4 has a periodic viscosity solution – the current proof only works in dimension 1.

Similarly, in Chapters 3 and 4, we only focus on principal eigenvalue problems in one dimension. The extension to two or more dimensions is complex, and most of our methods fail in the higher-dimensional cases. For example, in Chapter 3, we construct environments which have some very unfavourable portions in some places, to prevent the population to spread; however, in higher dimension, these very unfavourable portions could be bypassed, and thus the spreading speed would be bounded from below by a positive constant.

In Chapter 6, the question of the shapes and relative positions of the patches $\mathscr{C}_i$ is not addressed at all. For example, let the number of patches K and the optima of each patch $O_1,\dots,O_K$ be fixed. Set some volumes $V_1,\dots,V_K > 0$, with $V_1+\dots+V_K = 1$. Is it possible to minimise or maximise the principal eigenvalue among the configurations of patches $(\mathscr{C}_i)_{i=1,\dots,K}$ such that $\mathscr{C}_i \subset [0,1]^N$ and $|\mathscr{C}_i| = V_i$ for all $i = 1,\dots,K$? Assume that the O_i are not all identical. Then the minimisation problem has no solution, as the principal eigenvalue decreases strictly with the period, and the period can always be divided by 2 while still satisfying the constraints of the problem. The maximisation problem, on the other hand, is open. A similar problem of optimal allocation of resources (without phenotype structure) has been extensively studied in the literature, see in particular [27, 147, 155, 165]. We point out that the problem of maximising the principal eigenvalue is different from the problem of maximising the population size at equilibrium, see e.g. [164].

Apart from the shapes of the patches, a number of perspectives regarding the model of Chapters 5–7 are discussed at the end of Subsection 6.3.5 of Chapter 6.

A large part of this thesis is devoted to the study of principal eigenvalues measuring the "ability of persistence". What are the connections to the probability of survival in probabilistic models? For example, consider a branching Brownian motion where a particle X_t branches at rate $a+\max(r(X_t),0)$ and dies at rate $a+\max(-r(X_t),0)$, for some constant $a>0$. As a increases, the probability of extinction increases, even though the net growth rate remains constant equal to $r(X_t)$, and so the associated principal eigenvalue does not change. What are the other important factors to quantify the probability of extinction of such a system?

In Subsection 1.2.2, we constructed a branching Brownian representation for the Fisher-KPP equation with phenotype. Can this representation help us prove or guess new properties of the equation? It would be particularly interesting to extend the representation to more general reaction terms, for example by replacing $u(r-\rho)$ by $u(r-\rho)(1+B\rho)$ for some $B>0$, to model cooperation. Then, for B high enough, the speed is not expected to be determined by a linear operator. The problem becomes very challenging, since the nonlocal nonlinear term must be taken into account. In such cases, can the representation help one to find a spreading speed?

Last, Chapter 10 is an overview of the first results of an ongoing work based on very rich experimental data. How to exploit these data at best?

Part I

Properties of principal eigenvalues of elliptic operators

Chapter 2

A strongly anisotropic elliptic operator

This chapter is based on the article [47]:

N. Boutillon, *The principal eigenvalue problem for a strongly anisotropic second-order elliptic operator*, SIAM Journal on Mathematical Analysis 57.4 (2025), pp. 3840–3877.

Abstract

In this chapter, we consider an elliptic operator in which the second-order term is very small in one direction. In this regime, we study the behaviour of the principal eigenfunction and of the principal eigenvalue. Our first result deals with the limit of the principal eigenfunction and is shown with a representation of the principal eigenfunction as a quasi-stationary distribution. Subsequent results deal with the limit of the principal eigenvalue and are shown using Hamilton-Jacobi equations.

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2.1 Introduction

2.1.1 Presentation of the problem

Let $n \geqslant 1$ and let $\mathcal{Y}$ be either the n-dimensional torus $\mathbb{T}^n = \mathbb{R}^n/\mathbb{Z}^n$, or an open bounded domain in $\mathbb{R}^n$ with $\mathcal{C}^{2,\alpha}$ boundary, for some fixed $\alpha \in (0,1)$. Likewise, let $p \geqslant 1$ and let $\mathcal{Z}$ be either the p-dimensional torus $\mathbb{T}^p = \mathbb{R}^p/\mathbb{Z}^p$, or an open bounded domain in $\mathbb{R}^p$ with $\mathcal{C}^{2,\alpha}$ boundary. We assume that at least $\mathcal{Y}$ or $\mathcal{Z}$ is a torus. Let $\mathcal{W} := \mathcal{Y} \times \mathcal{Z}$. If $\mathcal{Y}$ or $\mathcal{Z}$ is not a torus, the boundary of $\mathcal{W}$ is nonempty, has regularity $\mathcal{C}^{2,\alpha}$, and we let ν be the outward unit normal on $\partial\mathcal{W}$.

Let us focus on the principal eigenvalue problem

$$\begin{cases} \mathcal{L}_y\varphi + \mathcal{L}_z\varphi + c(y,z)\varphi = k\varphi & \text{in } \mathcal{W}, \\ \nu \cdot \nabla\varphi = 0 & \text{on } \partial\mathcal{W}, \\ \varphi > 0 & \text{in } \mathcal{W}, \end{cases} \tag{2.1}$$

where

$$\mathcal{L}_y : \phi \mapsto A\Delta_y\phi + B \cdot \nabla_y\phi$$

differentiates only in the variable $y \in \mathcal{Y}$, and

$$\mathcal{L}_z : \phi \mapsto a\Delta_z\phi + b \cdot \nabla_z\phi$$

differentiates only in the variable $z \in \mathcal{Z}$. Here and below, the boundary condition $\nu \cdot \nabla\varphi = 0$ is required only when $\partial\mathcal{W}$ is nonempty. The coefficients $A, a \in \mathbb{R}$, $B \in \mathbb{R}^n$ and $b \in \mathbb{R}^p$, for now, are assumed to be constant, while $c \in \mathcal{C}^{0,1}(\overline{\mathcal{W}})$ is Lipschitz. More general hypotheses on the coefficients will be stated below.

We are interested in the behaviour of the principal eigenvalue $k \in \mathbb{R}$ and the principal eigenfunction $\varphi \in \mathcal{C}^2(\mathcal{W})$ when the variable y is very slow, in which case the elliptic operator $\mathcal{L}_y + \mathcal{L}_z + c$ becomes "strongly anisotropic". Namely, for $\varepsilon > 0$, we define

$$\mathcal{L}_y^\varepsilon\phi = \varepsilon^2 A\Delta_y\phi + \varepsilon B \cdot \nabla_y\phi,$$

and we consider a solution $(\varphi_\varepsilon, k_\varepsilon) \in \mathcal{C}^2(\mathcal{W}) \times \mathbb{R}$ of the principal eigenvalue problem:

$$\begin{cases} \mathcal{L}_y^\varepsilon\varphi_\varepsilon + \mathcal{L}_z\varphi_\varepsilon + c(y,z)\varphi_\varepsilon = k_\varepsilon\varphi_\varepsilon & \text{in } \mathcal{W}, \\ \nu \cdot \nabla\varphi_\varepsilon = 0 & \text{on } \partial\mathcal{W}, \\ \varphi_\varepsilon > 0 & \text{in } \mathcal{W}. \end{cases} \tag{2.2}$$

Our question is the following: How do φ_ε and k_ε behave as $\varepsilon \to 0$?

For small $\varepsilon > 0$, the eigenvalue problem (2.2) is a two-scale system where the slow variable is y and the fast variable is z. A way to get more insight into what this means is to state the following equivalent problem. With the change of variables $\varphi(y,z) = \widetilde{\varphi}\left(\frac{y}{\varepsilon}, z\right)$, we obtain:

$$\begin{cases} \mathcal{L}_y\widetilde{\varphi}_\varepsilon + \mathcal{L}_z\widetilde{\varphi}_\varepsilon + c\left(\varepsilon y, z\right)\widetilde{\varphi}_\varepsilon = k_\varepsilon\widetilde{\varphi}_\varepsilon & \text{in } \mathcal{W}_\varepsilon, \\ \nu \cdot \nabla\widetilde{\varphi}_\varepsilon = 0 & \text{on } \partial\mathcal{W}_\varepsilon, \\ \widetilde{\varphi}_\varepsilon > 0 & \text{in } \mathcal{W}_\varepsilon, \end{cases} \tag{2.3}$$

where $\mathcal{W}_\varepsilon$ is defined by $\mathcal{W}_\varepsilon := \left\{\left(\frac{y}{\varepsilon}, z\right) \in \mathbb{R}^n \times \mathbb{R}^p \ / \ (y,z) \in \mathcal{W}\right\}$. See Figure 2.1 for the mean-

ing of the two scales: in (2.2), when we see the second-order terms as diffusive movements, the movements along y are very small; in (2.3), the environment along y is very wide.

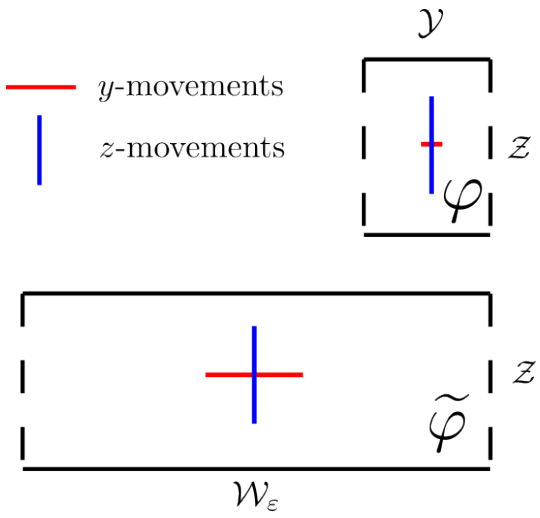

Figure 2.1: The upper part corresponds to (2.2); the lower part corresponds to (2.3). The crosses describe the ability of movements in either direction.

A first motivation for the study of the principal eigenvalue of an elliptic operator $\mathcal{L}$ is its connection to the maximum principle for elliptic equations. If $\mathcal{L}$ acts on functions defined on a bounded and smooth domain $\mathcal{W}$, then the Krein-Rutman theory guarantees the existence and the uniqueness of the principal eigenvalue $k(\mathcal{L})$, and the maximum principle holds for the operator $\mathcal{L}$ if and only if $k(\mathcal{L}) < 0$. Notions of principal eigenvalue, and their connections to the maximum principle, also exist when the domain is non-smooth [21] or when the domain is unbounded [32]. A second motivation arises in quantum mechanics. When $B \equiv 0$ and $b \equiv 0$ we get the Schrödinger operator; then $-c$ is a potential energy and the eigenvalues are energy levels for particles, and it is physically relevant to look for potentials optimising the eigenvalues, see e.g. [125]. Last, principal eigenvalues are often used to describe the long-time behaviour of a particular class of biological models. This is the main motivation for this chapter.

Biological motivations. Consider the Fisher-KPP equation:

$$\partial_t u(t,y) = \Delta u + cu - u^2, \qquad t \geqslant 0, \qquad y \in \mathbb{R},$$

where $u(0,\cdot) \geqslant 0$ is nonzero and has a compact support. Then $u(t,y)$ typically represents a density of individuals at time t and position y, so that $u(t,\cdot)$ is the distribution of a population at time t. In this population dynamics setting, the constant $c > 0$ is the intrinsic growth rate (i.e. the growth rate of the population if the environment has infinite resources); and the $-u^2$ term stands for the competition between individuals. In their articles, Fisher [94] and Kolmogorov, Petrovsky and Piskounov [143] showed that the population eventually invades the environment at a constant velocity $v_{FKPP} = 2\sqrt{c}$, in the following sense. If $v' > v_{FKPP}$, then $u(t, v't) \to 0$, and if $v'' \in (0, v_{FKPP})$, then $u(t, v''t) \to c > 0$.

If the intrinsic growth rate c depends on y (say, if some places are more favourable than

others), then we get the equation

$$\partial_t u(t,y) = \Delta u + c(y)u - u^2, \qquad t \geqslant 0, \qquad y \in \mathbb{R}. \tag{2.4}$$

If the environment is too deleterious, e.g. if $c(y) \ll 0$ for some $y \in \mathbb{R}$, then the population may get extinct. Assume that c is 1-periodic. Then, a classical criterion to know whether the population persists or not depends on the sign of the principal eigenvalue of the symmetric operator

$$\mathcal{L}_{pers} : \phi \mapsto \Delta\phi + c(y)\phi$$

acting on 1-periodic functions on $\mathbb{R}$ [27]. Furthermore, Gärtner and Freidlin [103] showed the so-called Gärtner-Freidlin formula. Let $k(\lambda)$ be the principal eigenvalue associated with the nonsymmetric operator

$$\mathcal{L}_{GF} : \phi \mapsto \Delta\phi - 2\lambda\partial_y\phi + (c(y) + \lambda^2)\phi$$

acting on 1-periodic functions on $\mathbb{R}$. If $k(0) > 0$, then the population spreads at a velocity v_{GF} given by

$$v_{GF} = \inf_{\lambda > 0} \frac{k(\lambda)}{\lambda}.$$

This means that for all $v' > v_{GF}$, $u(t, v't) \to 0$ and for all $v'' < v_{GF}$, $u(t,x)$ converges locally uniformly, on $|x| \leqslant v''t$, to the unique $\phi > 0$ satisfying $\Delta\phi + c\phi - \phi^2 = 0$. The limiting profile ϕ is called the stationary state of the equation and, by uniqueness, is 1-periodic. In the study of the large-time behaviour of populations described by (2.4), we thus need to study operators such as $\mathcal{L}_{pers}$ or $\mathcal{L}_{GF}$, which are similar to (2.1).

If we want to study two distinct phenomena, or a two-dimensional space, we may add a new variable z to the Fisher-KPP equation and get

$$\partial_t u(t,y,z) = \Delta_y u + \Delta_z u + c(y,z)u - u^2 \qquad t \geqslant 0, \qquad y,z \in \mathbb{R}. \tag{2.5}$$

Then the persistence criterion and the Gärtner-Freidlin formula also hold in various cases [26–28, 220].

A typical setting is to consider y as a phenotype and z as a spatial position. Then $c(y,z)$ is the fitness of an individual of phenotype y at position z, and (2.5) becomes

$$\partial_t u(t,y,z) = \Delta_y u + \Delta_z u + c(y,z)u - u \int_{\mathcal{Y}} u(t,y',z)\,\mathrm{d}y'. \tag{2.6}$$

The integral term comes from the fact that the competition occurs between all the individuals located at the same place, regardless of their phenotype. See [61, 194] for the first references about this model. Again, recent works [3, 4, 30] showed in various cases that the long-time behaviour of the solutions is governed by the principal eigenvalue of an elliptic operator.

Let us now explain the relevance of studying eigenvalue problems with a slow variable. In (2.6), the diffusion in y corresponds to mutations arising at each birth and death of an individual, and the diffusion in z corresponds to spatial movements of the individuals. With this model in view, we understand that the diffusion in y occurs on a much slower timescale than the diffusion in z. The initial motivation for this chapter was the study of the spreading speed of a population structured in space and phenotype with such a separation of timescales (see Chapter 7). See also [44] for a study of this slow-fast dynamics from a Hamilton-Jacobi equation point of view.

Even when the variables y and z represent phenomena of the same nature, one may have to consider different scales. A first example occurs when y and z are spatial positions but on different scales of spatial heterogeneity: the variable y represents, say, the heterogeneity within a large region, while the variable z represents, say, the heterogeneity within a field. A second example occurs when both variables y and z are the coordinates of a phenotype in a phenotypic landscape, but when mutations according to the y-direction are much rarer or much smaller than mutations according to the z-direction. See [116] for the study of such an anisotropic phenotypic landscape.

In all these cases, our results can be helpful to understand the interplay between the slow and the fast phenomenon, which are encoded in (2.2) by the small parameter $\varepsilon > 0$.

We point out that different scaling limits (small diffusion and/or large transport term) have been studied in [23, 65, 66, 119]. Although they do not consider anisotropy, the setting in these works is similar, and some results in [65, 119] are reminiscent of ours. Finally, gradient estimates were given in [24] for the solutions of strongly anisotropic elliptic equations such as (2.2).

2.1.2 Main results

General assumptions and notations. Let us describe our general assumptions. We define diffusion coefficients $A \in \mathcal{C}^{2,\alpha}(\overline{\mathcal{Y}}, \mathcal{M}_n(\mathbb{R}))$ and $a \in \mathcal{C}^{2,\alpha}(\overline{\mathcal{Z}}, \mathcal{M}_p(\mathbb{R}))$ (here $\mathcal{M}_q(\mathbb{R})$ is the set of $q \times q$-matrices), transport coefficients $B \in \mathcal{C}^{1,\alpha}(\overline{\mathcal{Y}}, \mathbb{R}^n)$ and $b \in \mathcal{C}^{1,\alpha}(\overline{\mathcal{Z}}, \mathbb{R}^p)$, and a Lipschitz-continuous potential $c \in \mathcal{C}^{0,1}(\overline{\mathcal{W}})$. We assume that A and a are uniformly elliptic on $\overline{\mathcal{W}}$: there exist constants $\overline{A} > \underline{A} > 0$ and $\overline{a} > \underline{a} > 0$ such that for all $(y,z) \in \overline{\mathcal{W}}$, for all $\xi \in \mathbb{R}^n$ and $\xi' \in \mathbb{R}^p$,

$$\underline{A}\,|\xi|^2 \leqslant \xi \cdot (A(y,z)\xi) \leqslant \overline{A}\,|\xi|^2, \qquad \underline{a}\left|\xi'\right|^2 \leqslant \xi' \cdot (a(y,z)\xi') \leqslant \overline{a}\left|\xi'\right|^2.$$

Last, we assume that A and a take their values in symmetric matrices; by the regularity of the coefficients, the solutions of the equations will be of class $\mathcal{C}^2$, so this symmetry assumption comes at no cost.

We let $\mathcal{L}_y^\varepsilon$ be the operator defined by

$$\mathcal{L}_y^\varepsilon : \phi \mapsto \varepsilon^2 \nabla_y \cdot (A \nabla_y \phi) + \varepsilon \nabla_y \cdot (\phi B),$$

and $\mathcal{L}_z$ be the operator defined by

$$\mathcal{L}_z : \phi \mapsto \nabla_z \cdot (a \nabla_z \phi) + \nabla_z \cdot (\phi b).$$

If $\partial\mathcal{W} \neq \emptyset$, we assume that the overall transport term is parallel to $\partial\mathcal{W}$:

$$\begin{pmatrix} B \\ b \end{pmatrix} \cdot \nu = 0 \quad \text{on } \partial\mathcal{W}. \tag{2.7}$$

For clarity, we write out here the variables of the coefficients:

$$A(y),\, a(z),\, B(y),\, b(z),\, c(y,z). \tag{2.8}$$

For $\varepsilon > 0$, we let $(\varphi_\varepsilon, k_\varepsilon) \in \mathcal{C}^{2,\alpha}(\mathcal{W}) \times \mathbb{R}$ be the solution of the *global* eigenvalue problem:

$$\begin{cases} (\mathcal{L}_y^\varepsilon + \mathcal{L}_z + c)\varphi_\varepsilon = k_\varepsilon \varphi_\varepsilon & \text{in } \mathcal{W}, \\ \varphi_\varepsilon > 0 & \text{in } \mathcal{W}, \\ \nu \cdot \mathcal{A}\nabla\varphi_\varepsilon = 0 & \text{on } \partial\mathcal{W}, \\ \int_{\mathcal{W}} \varphi_\varepsilon = 1, \end{cases} \tag{2.9}$$

where, for the statement of the boundary condition, we let $\mathcal{A} := \begin{pmatrix} A & 0 \\ 0 & a \end{pmatrix} \in \mathcal{M}_{n+p}(\mathbb{R})$ be the overall diffusion matrix.

If $\partial\mathcal{Z}$ is nonempty, we let ν_2 be the outward unit normal on $\partial\mathcal{Z}$. For $y_0 \in \overline{\mathcal{Y}}$, we let $(\psi^{y_0}, k^{y_0}) \in \mathcal{C}^{2,\alpha}(\mathcal{Z}) \times \mathbb{R}$ be the solution of the *local* eigenvalue problem:

$$\begin{cases} (\mathcal{L}_z + c(y_0, \cdot))\psi^{y_0} = k^{y_0}\psi^{y_0} & \text{in } \mathcal{Z}, \\ \psi^{y_0} > 0 & \text{in } \mathcal{Z}, \\ \nu_2 \cdot a\nabla\psi^{y_0} = 0 & \text{on } \partial\mathcal{Z}, \\ \int_{\mathcal{Z}} \psi^{y_0} = 1. \end{cases} \tag{2.10}$$

By the classical Krein-Rutman theory [145], $(\varphi_\varepsilon, k_\varepsilon)$ and (ψ^{y_0}, k^{y_0}) are well defined. If $\partial\mathcal{Y}$ is nonempty, we extend the function φ_ε from $\mathcal{Y}$ to $\overline{\mathcal{Y}}$, i.e. we consider $\varphi_\varepsilon \in \mathcal{C}^{2,\alpha}(\overline{\mathcal{Y}} \times \mathcal{Z})$. This is possible by virtue of the regularity assumptions on the coefficients and on $\partial\mathcal{W}$.

Behaviour of the principal eigenfunction. The first theorem means that the "slices" of the global principal eigenfunction converge, as $\varepsilon \to 0$, to the local principal eigenfunctions. We use the notation $\mathcal{Z}' \subset\subset \mathcal{Z}$ to say that $\overline{\mathcal{Z}'} \subset \mathcal{Z}$, and we set

$$\varphi_\varepsilon(y_0, \mathcal{Z}) := \int_{\mathcal{Z}} \varphi_\varepsilon(y_0, z)\,\mathrm{d}z.$$

Theorem 2.1.1. *Let $\beta \in (0, \alpha)$ and let $\mathcal{Z}' \subset\subset \mathcal{Z}$. For all $y_0 \in \mathcal{Y}$, as $\varepsilon \to 0$, we have*

$$\frac{\varphi_\varepsilon(y_0, \cdot)}{\varphi_\varepsilon(y_0, \mathcal{Z})} \to \psi^{y_0} \qquad \text{in } \mathcal{C}^{2,\beta}(\mathcal{Z}').$$

Moreover, the following convergence of measures holds uniformly in $y_0 \in \overline{\mathcal{Y}}$:

$$\frac{\varphi_\varepsilon(y_0, z)}{\varphi_\varepsilon(y_0, \mathcal{Z})}\,\mathrm{d}z \to \psi^{y_0}(z)\,\mathrm{d}z \qquad \text{in total variation on } \mathcal{Z},$$

namely:

$$\sup_{y_0 \in \overline{\mathcal{Y}}} \left[\sup_{A \subset \mathcal{Z},\, A \text{ measurable}} \left| \int_A \left(\frac{\varphi_\varepsilon(y_0, z)}{\varphi_\varepsilon(y_0, \mathcal{Z})} - \psi^{y_0}(z) \right) \mathrm{d}z \right| \right] \to 0.$$

Note that if $\mathcal{Z} = \mathbb{T}^p$, then we may take $\mathcal{Z}' = \mathcal{Z}$ and the convergence holds in $\mathcal{C}^{2,\beta}(\mathcal{Z})$.

The result is straightforward when the coefficients A, B and c are independent of $y \in \mathcal{Y}$: in this case, indeed, $\varphi_\varepsilon = \psi^{y_0}$ is independent of y_0 and of ε. For the proof in the general case, we will use a probabilistic method. We will see φ_ε as the quasi-stationary distribution of a

killed stochastic process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$. Namely, if τ is the death time of $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$, we will have for all $E \subset \mathcal{Y}$ and $F \subset \mathcal{Z}$:

$$\lim_{t\to+\infty} \mathbb{P}\left((Y_t^\varepsilon, Z_t^\varepsilon) \in E \times F \mid \tau > t\right) = \int_{E\times F} \varphi_\varepsilon(y,z)\,\mathrm{d}y\,\mathrm{d}z.$$

As $\varepsilon \to 0$, the process Y_t^ε will be slower and slower. This will allow us to forget the dependence in Y_t^ε and to get back to the simple case where the coefficients are independent of y. See Subsection 2.1.3 for the definition of the process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$.

We will see in the proof of Theorem 2.1.1 why we need Assumption (2.8) on the coefficients. We will go by successive approximations from $(Y_t^\varepsilon, Z_t^\varepsilon)_t$, which corresponds to φ_ε, to a stochastic process corresponding to ψ^{y_0}. For the approximations to be valid, we need a form of independence between $(Y_t^\varepsilon)_t$ and $(Z_t^\varepsilon)_t$; this independence is ensured by Assumption (2.8).

Once Theorem 2.1.1 is established, a natural question that arises is the behaviour of the principal eigenfunction in the slow direction. The family of principal eigenvalues $(k_\varepsilon)_\varepsilon$ is bounded, so there is a subsequence that converges to some $k_0 \in \mathbb{R}$. The proofs of the following theorems suggest that if $\mathcal{Y}$ has empty boundary, then for all $z_0 \in \mathcal{Z}$, there exists a measure μ^{z_0} on the level set $\Gamma := \{y \in \mathcal{Y} \ / \ k^y = k_0\}$, with total mass equal to 1, such that for all $f \in \mathcal{C}^\infty(\mathcal{Y})$, along any subsequence such that $k_\varepsilon \to k_0$,

$$\int_{\mathcal{Y}} f(y) \frac{\varphi_\varepsilon(y,z_0)}{\varphi_\varepsilon(\mathcal{Y},z_0)}\,\mathrm{d}y \to \int_\Gamma f(y)\mu^{z_0}(\mathrm{d}y).$$

See Remark 2.4.5 for more details. The proof of this conjecture and its extension to the case where $\mathcal{Y}$ has a nonempty boundary are beyond the scope of this chapter.

Behaviour of the principal eigenvalue. In two particular cases, we are able to find an exact relation between the limit of k_ε as $\varepsilon \to 0$ and the local eigenvalues k^y, $y \in \overline{\mathcal{Y}}$. First, let us assume that $B \equiv 0$.

Theorem 2.1.2. *Assume $B \equiv 0$. Then k_ε converges as $\varepsilon \to 0$ and*

$$\lim_{\varepsilon\to 0} k_\varepsilon = \max_{y\in\overline{\mathcal{Y}}} k^y.$$

If additionally to $B \equiv 0$, we assume that $b \equiv 0$, the operator $\mathcal{L}_y^\varepsilon + \mathcal{L}_z + c$ becomes symmetric. The Rayleigh formula can then be applied directly, and the proof is simpler than in the general case.

Theorem 2.1.2 can be understood from a modelling perspective. When $B \equiv 0$ and $\varepsilon \to 0$, all "slices" of the environment, $c(y,\cdot)$, $y \in \overline{\mathcal{Y}}$, are almost independent. Therefore, a species is able to survive in the environment if and only if there exists a favourable slice. This means that for small $\varepsilon > 0$, the condition $k_\varepsilon > 0$ amounts to the existence of $y_0 \in \overline{\mathcal{Y}}$ such that $k^{y_0} > 0$. Thus we expect Theorem 2.1.2 to hold. As we will see now, the independence between the slices fails when $B \not\equiv 0$.

Second, we relax the assumption that $B \equiv 0$, and assume instead that $\mathcal{Y}$ is the 1-dimensional torus. In particular, $B(y) \in \mathbb{R}$ and $A(y) \in \mathbb{R}$. We let

$$M := \max_{y\in\mathcal{Y}} \left(k^y - \frac{B(y)^2}{4A(y)}\right).$$

We let $j : [M, +\infty) \to [j(M), +\infty)$ be the bijection defined by

$$j : k \mapsto \int_0^1 \sqrt{\frac{k - k^y + \frac{B(y)^2}{4A(y)}}{A(y)}}\, \mathrm{d}y.$$

Finally, we define

$$\gamma := \int_0^1 \frac{B(y)}{2A(y)}\, \mathrm{d}y.$$

Theorem 2.1.3. *Assume that $\mathcal{Y}$ is the 1-dimensional torus. Then k_ε converges as $\varepsilon \to 0$ and:*

1. *If $|\gamma| \leqslant j(M)$, then*
$$\lim_{\varepsilon \to 0} k_\varepsilon = M;$$
2. *If $|\gamma| \geqslant j(M)$, then*
$$\lim_{\varepsilon \to 0} k_\varepsilon = j^{-1}(|\gamma|).$$

In the very specific case where all the coefficients are independent of the variable z, Theorem 2.1.3 is similar to Proposition 3.2 of [119]. If, moreover, $A = 1$ and B can be written in the form $B(y) = m'(y)$, then $|\gamma| = 0 \leqslant j(M)$ and we get

$$\lim_{\varepsilon \to 0} k_\varepsilon = \max_{y \in \mathcal{Y}} \left(c(y) - \frac{(m'(y))^2}{4} \right).$$

This is analogous to Theorem 1.3 of [65], where $\mathcal{Y}$ is assumed to be a smooth bounded domain in any dimension (contrarily to the setting of our Theorem 2.1.3).

The proof of Theorem 2.1.3 is an adaptation of the proof of Proposition 3.2 of [119], but is more technical due to the interplay between the slow and fast variable. As in [119], the proof hinges on the construction of an explicit viscosity solution to a Hamilton-Jacobi equation that arises naturally after a Hopf-Cole transform of the original eigenproblem. This explicit construction requires us to work in the 1-dimensional setting; once the solution is constructed, we need to work in the periodic setting to deduce a result on the principal eigenvalue.

Theorem 2.1.3 shows that when there is a nonzero transport term, even in the particular case where $\mathcal{Y}$ is the 1-dimensional torus, the behaviour of the limiting principal eigenvalue is nontrivial. The study of the limit in the general case (bounded domain; higher dimension), therefore, is left to a future work. Last, we point out that Theorem 2.1.3 cannot be expected to hold in full generality if we drop Assumption (2.8). Indeed, if A or B are allowed to depend on z, then M, j and γ may not be well-defined.

Layout. In Subsection 2.1.3, we define a stochastic process which will be used in the proof of Theorem 2.1.1 in Section 2.3. Properties of this stochastic process are given in Section 2.2. Finally, in Section 2.4, we show Theorem 2.1.2 and Theorem 2.1.3.

2.1.3 Connection with a killed stochastic process

Let us define a stochastic process which will be at the core of the proof of Theorem 2.1.1. We set $c_m := \|c\|_\infty + \|\nabla \cdot b\|_\infty + \|\nabla \cdot B\|_\infty + 1$ and

$$d(y,z) := c_m - c(y,z) > 0.$$

Introduce a process $(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)_{t\geqslant 0}$. Let $m \in L^1(\mathcal{W})$ satisfy

$$m \geqslant 0, \qquad \int_{\mathcal{W}} m = 1.$$

Let $\widetilde{u}^\varepsilon$ be the solution of the following Cauchy problem:

$$\begin{cases} \partial_t \widetilde{u}^\varepsilon(t,y,z) = \varepsilon^2 \nabla_y \cdot (A \nabla_y \widetilde{u}^\varepsilon) + \varepsilon \nabla_y \cdot (\widetilde{u}^\varepsilon B) + \mathcal{L}_z \widetilde{u}^\varepsilon, & t>0, (y,z) \in \mathcal{W}, \\ \nu \cdot \mathcal{A} \nabla \widetilde{u}^\varepsilon(t,y,z) = 0, & (y,z) \in \partial\mathcal{W}, \\ \widetilde{u}^\varepsilon(0,y,z) = m(y,z), & (y,z) \in \mathcal{W}. \end{cases} \tag{2.11}$$

In particular, thanks to the assumption (2.7), we have for all $t \geqslant 0$,

$$\int_{\mathcal{W}} \widetilde{u}^\varepsilon(t,\cdot) = 1.$$

Using Theorem 7.1 of [206], we construct a Markov process $(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)_{t\geqslant 0}$, with $\widetilde{Y}_t^\varepsilon \in \mathcal{Y}$ and $\widetilde{Z}_t^\varepsilon \in \mathcal{Z}$, with continuous paths, and which has a density at time t given by $\widetilde{u}^\varepsilon(t,\cdot,\cdot)$. Typically, if $a = \sigma^2$ and $A = \Sigma^2$ are constant, we should think of the process $(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)_{t\geqslant 0}$ as a solution of the SDE:

$$\begin{cases} \mathrm{d}\widetilde{Y}_t^\varepsilon = -\varepsilon B(\widetilde{Y}^\varepsilon)\,\mathrm{d}t + \sqrt{2}\varepsilon\,\Sigma\,\mathrm{d}\xi_t^Y, \\ \mathrm{d}\widetilde{Z}_t^\varepsilon = -b(\widetilde{Z}^\varepsilon)\,\mathrm{d}t + \sqrt{2}\,\sigma\,\mathrm{d}\xi_t^Z, \\ \text{reflection on } \partial\mathcal{W}, \end{cases} \tag{2.12}$$

with initial distribution $(\widetilde{Y}_0^\varepsilon, \widetilde{Z}_0^\varepsilon) \sim m$, and where ξ^Y and ξ^Z are independent n-dimensional and p-dimensional Brownian motions respectively.

Kill the process $(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)_{t\geqslant 0}$. Now, we construct a killed process $(Y_t^\varepsilon, Z_t^\varepsilon)$ based on $(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)$. We first need a definition, which will be used several times throughout this chapter. The definition is illustrated by Figure 2.2.

Definition 2.1.4. *Let $(D_t)_{t\geqslant 0}$ be a stochastic process with nonnegative values. Let Π be a Poisson point process on $\mathbb{R}_+ \times \mathbb{R}_+$ with intensity 1, independent of $(D_t)_{t\geqslant 0}$. Define*

$$\tau((D_t)_{t\geqslant 0}) := \inf\left\{ t \geqslant 0 \ / \ \Pi \text{ has a point in } \{(s,y) \ / \ 0 \leqslant s \leqslant t, 0 \leqslant y \leqslant D_t\}\right\}.$$

We say that $\tau((D_t)_{t\geqslant 0})$ is a clock with rate $(D_t)_{t\geqslant 0}$.

Using this definition, we let τ^ε be a clock with rate $(d(\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon))_{t\geqslant 0}$. We let $\partial \notin \mathcal{W}$ be a "cemetery state". We now define the killed process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$ by:

$$(Y_t^\varepsilon, Z_t^\varepsilon) = \begin{cases} (\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon), & t < \tau, \\ \partial, & t \geqslant \tau. \end{cases}$$

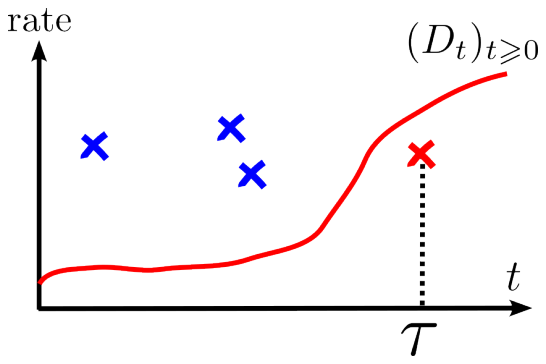

Figure 2.2: The crosses are the points of Π. We are interested in $\tau((D_t)_{t\geqslant 0})$, the first time a cross is under the curve.

We will see τ^ε as a "death time" for the particle, and work conditionally on $\{\tau^\varepsilon > t\}$. See Figure 2.3, left, for a typical trajectory before a death occurs; and see Figure 2.3, right, for the effect of the conditioning on $\{\tau^\varepsilon > t\}$.

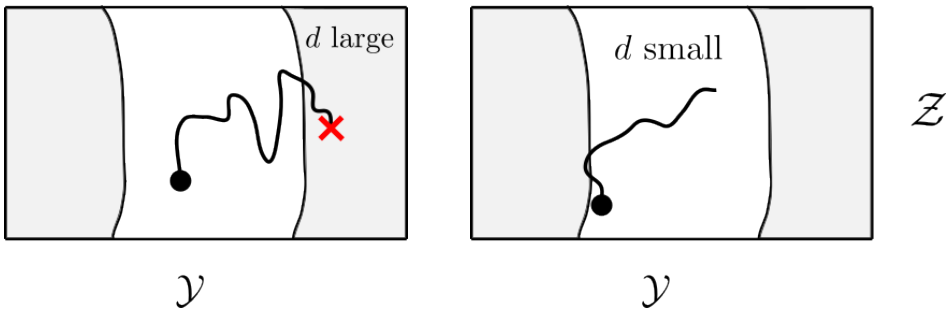

Figure 2.3: *Grey zone:* high death rate. *White zone:* low death rate. *Left:* The process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$ dies at a high rate when it is in the grey zone; *Right:* Conditioned on $\{\tau^\varepsilon > t\}$, the process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$ avoids the grey zone.

We denote by $\mathbb{P}_m$ the joint law of $(\tau, (\widetilde{Y}_t^\varepsilon, \widetilde{Z}_t^\varepsilon)_{t\geqslant 0})$ when the initial condition in (2.11) is m. The following theorem implies that φ_ε is the unique quasi-stationary distribution for the killed process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$. We will use it to find properties of φ_ε by studying the process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$. Let $\|\cdot\|_{TV}$ denote the total variation norm for (signed) measures on $\mathcal{W} = \mathcal{Y} \times \mathcal{Z}$. In particular, for $f : \mathcal{W} \to \mathbb{R}$,

$$\|f(x)\,\mathrm{d}x\|_{TV} := \sup_{A\subset\mathcal{W},\, A \text{ measurable}} \left|\int_{\mathcal{Z}} f\right|.$$

Theorem 2.1.5. *For all $\varepsilon > 0$, there exist $C, \chi > 0$ such that for all initial distribution m on $\mathcal{W}$, and for all $t > 0$,*

$$\|\varphi_\varepsilon(y,z)\,\mathrm{d}y\,\mathrm{d}z - \mathbb{P}_m\left((Y_t^\varepsilon, Z_t^\varepsilon) \in \mathrm{d}y\,\mathrm{d}z \mid \tau > t\right)\|_{TV} < Ce^{-\chi t}.$$

In the next section, we will prove a more general version of Theorem 2.1.5.

2.2 Results about quasi-stationary distributions

2.2.1 General setting

As we will need an equivalent of Theorem 2.1.5 in another setting, we prove a more general version. We proceed to a construction similar to that of $(Y^\varepsilon, Z^\varepsilon)$, but with simpler notations.

Let $\mathcal{Y}$ and $\mathcal{Z}$ be defined as in the introduction and let, for this section, $\mathcal{W} := \mathcal{Y} \times \mathcal{Z}$ or $\mathcal{W} := \mathcal{Z}$. Let q be the dimension of $\mathcal{W}$ (thus either $q = n+p$ or $q = p$). Again, we let ν be the outward unit normal on $\partial\mathcal{W}$. Throughout Section 2.2, we do not treat the variables y and z as separated variables, and we let $w \in \mathcal{W}$ be the generic element of $\mathcal{W}$. Let $\mathcal{A} \in \mathcal{C}^{2,\alpha}(\overline{\mathcal{W}}, \mathcal{M}_q(\mathbb{R}))$ and $\mathcal{B} \in \mathcal{C}^{1,\alpha}(\overline{\mathcal{W}}, \mathbb{R}^q)$. Let Λ be the operator defined by

$$\Lambda u = \nabla \cdot (\mathcal{A}\nabla u) + \nabla \cdot (u\mathcal{B}).$$

When $\mathcal{W} = \mathcal{Y} \times \mathcal{Z}$, we may think of Λ as the operator unifying the $\mathcal{Y}$- and the $\mathcal{Z}$-variables, that is:

$$\mathcal{A} = \begin{pmatrix} A & 0 \\ 0 & a \end{pmatrix}, \qquad \mathcal{B} = \begin{pmatrix} B \\ b \end{pmatrix}.$$

We assume that the transport term is parallel to $\partial\mathcal{W}$:

$$\mathcal{B} \cdot \nu = 0 \quad \text{ on } \partial\mathcal{W}. \tag{2.13}$$

This assumption is a translation of (2.7) in this new framework. We further assume that $\mathcal{A}$ is uniformly elliptic on $\overline{\mathcal{W}}$: there exist $\overline{\mathcal{A}} > \underline{\mathcal{A}} > 0$ such that for all $w \in \overline{\mathcal{W}}$ and $\xi \in \mathbb{R}^q$,

$$\underline{\mathcal{A}}\,|\xi|^2 \leqslant \xi \cdot \mathcal{A}(w)\xi \leqslant \overline{\mathcal{A}}\,|\xi|^2.$$

Last, we assume that $\mathcal{A}$ takes its values in symmetric matrices.

Let $m \in L^1(\mathcal{W})$ satisfy

$$m \geqslant 0, \qquad \int_{\mathcal{W}} m = 1.$$

Let $\widetilde{u}$ be the solution of the following Cauchy problem:

$$\begin{cases} \partial_t \widetilde{u}(t,w) = \Lambda \widetilde{u}, & t > 0,\, w \in \mathcal{W}, \\ \nu \cdot \mathcal{A}\nabla \widetilde{u}(t,w) = 0, & w \in \partial\mathcal{W}, \\ \widetilde{u}(0,w) = m(w), & w \in \mathcal{W}. \end{cases} \tag{2.14}$$

In particular, thanks to the assumption (2.13), we have for all $t \geqslant 0$,

$$\int_{\mathcal{W}} \widetilde{u}(t,\cdot) = 1.$$

Using Theorem 7.1 of [206], we construct a Markov process $(\widetilde{W}_t)_{t\geqslant 0}$, with continuous paths, and which has a density at time t given by $\widetilde{u}$. If $\mathcal{A} = \sigma^2$ is constant, we should think of the process $(\widetilde{W}_t)_{t\geqslant 0}$ as the solution to the SDE

$$\mathrm{d}\widetilde{W}_t = -\mathcal{B}(\widetilde{W}_t)\,\mathrm{d}t + \sqrt{2}\sigma\,\mathrm{d}\xi_t,$$

with reflection on $\partial\mathcal{W}$ and with initial distribution m, and where ξ_t is a standard Brownian

motion in $\mathbb{R}^q$. Let

$$\mathcal{E} := \left\{ f \in \mathcal{C}^2(\overline{\mathcal{W}}) \ / \ \nu \cdot \mathcal{A} \nabla f = 0 \text{ on } \partial\mathcal{W} \right\}.$$

Let Λ^* be the adjoint of Λ, defined on $\mathcal{E}$ by $\Lambda^* : f \in \mathcal{E} \mapsto \nabla \cdot (\mathcal{A}\nabla f) - \mathcal{B} \cdot \nabla f$. The process $(\widetilde{W}_t)_{t \geqslant 0}$ has a semigroup on $\mathcal{C}^0(\mathcal{W})$ with infinitesimal generator Λ^* defined on the domain $\mathcal{E}$. This means that for all $f \in \mathcal{E}$,

$$\frac{\mathbb{E}_{\delta_w}\left[f(\widetilde{W}_t)\right] - f(w)}{t} \to \Lambda^* f(w) \qquad \text{as } t \to 0,$$

uniformly in $w \in \mathcal{W}$, see Chapter 1 of [86]. Here, $\mathbb{E}_{\delta_w}$ corresponds to the expectation when $\widetilde{W}_0 = w$.

Now, we construct a killed process $(W_t)_{t \geqslant 0}$ based on $(\widetilde{W}_t)_{t \geqslant 0}$. We let $d \in \mathcal{C}^{0,1}(\overline{\mathcal{W}})$ be a Lipschitz-continuous function such that $\inf_{\mathcal{W}} d \geqslant 1 + \|\nabla \cdot \mathcal{B}\|_\infty$. We let τ be a clock with rate $(d(\widetilde{W}_t))_{t \geqslant 0}$ (in the sense of Definition 2.1.4). We let $\partial \notin \mathcal{W}$ be a "cemetery state". We define the killed process $(W_t)_{t \geqslant 0}$ by:

$$W_t := \begin{cases} \widetilde{W}_t & t < \tau, \\ \partial & t \geqslant \tau. \end{cases}$$

We denote by $\mathbb{P}_m$ the joint law of $(\tau, (\widetilde{W}_t)_{t \geqslant 0})$ when the initial distribution of $(\widetilde{W}_t)_t$ is m, and by $\mathbb{E}_m$ the corresponding expectation.

Now, we let $(\Phi, k) \in \mathcal{C}^{2,\alpha}(\mathcal{W}) \times \mathbb{R}$ satisfy the following principal eigenvalue problem:

$$\begin{cases} (\Lambda - d(w))\Phi(w) = k\Phi(w), & w \in \mathcal{W}, \\ \Phi(w) > 0, & w \in \mathcal{W}, \\ \nu \cdot \mathcal{A}\nabla\Phi(w) = 0, & w \in \partial\mathcal{W}. \end{cases}$$

We normalise Φ so that

$$\int_{\mathcal{W}} \Phi = 1.$$

The following theorem shows that the principal eigenfunction Φ is a quasi-stationary distribution for the killed process $(W_t)_{t \geqslant 0}$.

Theorem 2.2.1. *There exist $C, \chi > 0$ such that for all initial distribution m on $\mathcal{W}$, and for all $t > 0$,*

$$\|\Phi(w)\,\mathrm{d}w - \mathbb{P}_m\left(W_t \in \mathrm{d}w \mid \tau > t\right)\|_{TV} < Ce^{-\chi t}.$$

Let $\mathcal{B}_M \geqslant \|\mathcal{B}\|_\infty$. We may choose the constants C and χ so that they only depend on $\underline{\mathcal{A}}$, $\overline{\mathcal{A}}$, $\mathcal{B}_M$, $\|d\|_\infty$ and $\mathcal{W}$.

Theorem 2.1.5 is a consequence of Theorem 2.2.1. In Subsections 2.2.2 and 2.2.3, we will prove Theorem 2.2.1.

2.2.2 Properties of the killed stochastic process

Let us now study the law of $(W_t)_{t \geqslant 0}$. We first give the generator of the process; after that, we will give its density.

We denote by $\mathcal{E}^\partial$ the set of functions $f : \mathcal{W} \cup \{\partial\} \to \mathbb{R}$ such that $f_{|\mathcal{W}} \in \mathcal{E}$.

Lemma 2.2.2. *The Markov process $(W_t)_{t\geqslant 0}$ has a semigroup on $\mathcal{C}^0(\mathcal{W})$ with infinitesimal generator $\mathcal{G}$ defined on the domain $\mathcal{E}^\partial$ by:*

$$\begin{aligned}\mathcal{G}f(w) &= (\Lambda^* - d(w))f(w) + d(w)f(\partial), \qquad w \in \mathcal{W},\\ \mathcal{G}f(\partial) &= 0.\end{aligned}$$

In particular, for all $f \in \mathcal{E}^\partial$, the convergence of

$$\frac{1}{h}\left(\mathbb{E}_{\delta_w}\left[f(W_h)\right] - f(w)\right)$$

to $\mathcal{G}f(w)$ as $h \to 0$ is uniform in $w \in \mathcal{W}$.

Proof. Since ∂ is a cemetery state, we have $\mathcal{G}f(\partial) = 0$. Now, let us compute $\mathcal{G}f(w)$ for $w \in \mathcal{W}$. For $h > 0$,

$$\begin{aligned}\mathbb{E}_{\delta_w}\left[f(W_h)\right] &= \mathbb{E}_{\delta_w}\left[f(W_h)\mathbb{1}_{\tau>h}\right] + \mathbb{E}_{\delta_w}\left[f(\partial)\mathbb{1}_{\tau\leqslant h}\right]\\ &= \mathbb{E}_{\delta_w}\left[f(W_h)\mathbb{1}_{\tau>h}\right] + f(\partial)\mathbb{P}_{\delta_w}\left(\tau \leqslant h\right). \qquad (2.15)\end{aligned}$$

First, since d is continuous on $\overline{\mathcal{W}}$, d is also uniformly continuous on $\overline{\mathcal{W}}$; thus

$$\mathbb{P}_{\delta_w}(\tau \leqslant h) = hd(w) + o_{h\to 0}(h),$$

and the $o_{h\to 0}(h)$ is uniform in w. Second,

$$\begin{aligned}\mathbb{E}_{\delta_w}\left[f(W_h)\mathbb{1}_{\tau>h}\right] &= \mathbb{E}_{\delta_w}\left[f(\widetilde{W}_h)\mathbb{1}_{\tau>h}\right]\\ &= \mathbb{E}_{\delta_w}\left[f(\widetilde{W}_h)\right] - \mathbb{E}_{\delta_w}\left[(f(\widetilde{W}_h) - f(w))\mathbb{1}_{\tau\leqslant h}\right] - \mathbb{E}_{\delta_w}\left[f(w)\mathbb{1}_{\tau\leqslant h}\right].\end{aligned}$$

We have $\mathbb{E}_{\delta_w}\left[(f(\widetilde{W}_h) - f(w))\mathbb{1}_{\tau\leqslant h}\right] = O_{h\to 0}(h^2)$ and $\mathbb{E}_{\delta_w}\left[f(w)\mathbb{1}_{\tau\leqslant h}\right] = f(w)\mathbb{P}_{\delta_w}(\tau \leqslant h)$. Therefore, using the fact that Λ^* is the infinitesimal generator of the process $(\widetilde{W}_t)_t$, we have

$$\mathbb{E}_{\delta_w}\left[f(W_h)\mathbb{1}_{\tau>h}\right] = f(w) + h\Lambda^* f(w) - hd(w)f(w) + o_{h\to 0}(h).$$

We get

$$\mathbb{E}_{\delta_w}\left[f(W_h)\right] = f(w) + h(\Lambda^* - d)f(w) + hd(w)f(\partial) + o_{h\to 0}(h).$$

Moreover, the $o_{h\to 0}(h)$ term remains uniform in $w \in \mathcal{W}$. Therefore,

$$\mathcal{G}f = (\Lambda^* - d(w))f(w) - d(w)f(\partial),$$

and the convergence to $\mathcal{G}f$ is uniform on $\mathcal{W}$. □

We are now ready to give the density of $(W_t)_{t\geqslant 0}$. Consider the evolution problem

$$\begin{cases} \partial_t u(t,w) = (\Lambda - d(w))u(t,w), & t > 0, w \in \mathcal{W},\\ u(0,\cdot) = m, & w \in \mathcal{W},\\ \nu \cdot \mathcal{A}\nabla u(w) = 0, & w \in \partial\mathcal{W}. \end{cases} \qquad (2.16)$$

Lemma 2.2.3. *The solution $u(t,\cdot)$ of (2.16) is the density of the law of W_t. Namely, for all $t \geqslant 0$, for all measurable bounded function $f : \mathcal{W} \cup \{\partial\} \to \mathbb{R}$:*

$$\mathbb{E}_m\left[f(W_t)\right] = \mathbb{P}_m\left(\tau < t\right) f(\partial) + \int_{\mathcal{W}} f(w) u(t,w)\,\mathrm{d}w. \tag{2.17}$$

Proof. The law of W_t restricted to $\mathcal{W}$ is absolutely continuous with respect to the law of $\widetilde{W}_t$, which has a density with respect to the Lebesgue measure. For $t > 0$, we let $\zeta(t,\cdot)$ be the density of the law of W_t (restricted to $\mathcal{W}$) with respect to the Lebesgue measure. We show that ζ satisfies (2.16) in a weak sense.

Let u be the solution of the Cauchy Problem (2.16). Let $T > 0$ and $F \in \mathcal{E}$. We have

$$\begin{aligned}\int_{\mathcal{W}} (u(T,w) - u(0,w)) F(w)\,\mathrm{d}w &= \int_0^T \int_{\mathcal{W}} F(w) \partial_t u(t,w)\,\mathrm{d}w\,\mathrm{d}t \\ &= \int_0^T \int_{\mathcal{W}} F(w) \left[(\Lambda - d) u(t,w)\right] \mathrm{d}w\,\mathrm{d}t.\end{aligned}$$

Using the divergence theorem, we obtain:

$$\forall T > 0, \forall F \in \mathcal{E}, \qquad \int_{\mathcal{W}} (u(T,w) - u(0,w)) F(w)\,\mathrm{d}w = \int_0^T \int_{\mathcal{W}} u(t,w)[(\Lambda^* - d)F(w)]\,\mathrm{d}w\,\mathrm{d}t. \tag{2.18}$$

We call (2.18) the weak form of the Cauchy problem (2.16).

We now show that the density ζ satisfies (2.18). Let $F \in \mathcal{E}$ and set $F(\partial) = 0$, so that we can also see F as an element of $\mathcal{E}^\partial$. Let $\mathscr{F}_t = \sigma((W_s), 0 \leqslant s \leqslant t)$ be the σ-field generated by $(W_s)_{s \geqslant 0}$. Then

$$F(W_t) - F(W_0) - \int_0^t (\Lambda^* - d) F(W_s)\,\mathrm{d}s$$

is a $\mathscr{F}_t$-martingale, see e.g. [86, Proposition 4.1.7]. Thus for all $T > 0$,

$$F(W_T) - F(W_0) = \int_0^T \int_{\mathcal{W}} \zeta(t,w)[(\Lambda^* - d)F(w)]\,\mathrm{d}w\,\mathrm{d}t.$$

We obtain:

$$\forall T > 0, \forall F \in \mathcal{E}, \qquad \int_{\mathcal{W}} \left(\zeta(T,w) - \zeta(0,w)\right) F(w)\,\mathrm{d}w = \int_0^T \int_{\mathcal{W}} \zeta(t,w)[(\Lambda^* - d)F(w)]\,\mathrm{d}w\,\mathrm{d}t.$$

This means precisely that ζ satisfies (2.18). It is standard that the weak formulation (2.18) has a unique solution with initial condition m. Therefore, $u = \xi$. □

2.2.3 Proof of Theorem 2.2.1

Before proving Theorem 2.2.1, we give a preliminary result which implies that the principal eigenfunction Φ is a quasi-stationary distribution for the process $(W_t)_{t \geqslant 0}$.

Proposition 2.2.4. *For all measurable set $B \subset \mathcal{W}$, and for all $t > 0$,*

$$\Phi(B) = \mathbb{P}_\Phi\left(W_t \in B \mid \tau > t\right).$$

Proof. Starting from $m = \Phi$, the solution of the system (2.16) is:

$$u(t,w) = e^{kt}\Phi(w).$$

We point out that, due to the positivity of d, we have $k \leqslant 0$; thus $e^{kt} \in (0,1]$. We then apply Lemma 2.2.3 with initial condition Φ and with the test function $f := \mathbb{1}_B$ with $f(\partial) = 0$. We find

$$\mathbb{P}_\Phi(W_t \in B) = \int_B e^{kt}\Phi(w)\,\mathrm{d}w = e^{kt}\mathbb{P}_\Phi(W_0 \in B).$$

Now, we note that $\mathbb{P}_\Phi(\tau > t) = \mathbb{P}_\Phi(W_t \in \mathcal{W})$. Applying again Lemma 2.2.3 with the test function $f = \mathbb{1}_{\mathcal{W}}$, we conclude that

$$\mathbb{P}_\Phi(\tau > t) = e^{kt}.$$

Therefore,

$$\begin{aligned}\mathbb{P}_\Phi(W_t \in B \mid \tau > t) &= \frac{\mathbb{P}_\Phi(W_t \in B, \tau > t)}{\mathbb{P}\tau > t} \\ &= \frac{\mathbb{P}_\Phi(W_t \in B)}{\mathbb{P}\tau > t} \\ &= \mathbb{P}_\Phi(W_0 \in B).\end{aligned}$$

This is the statement of the proposition. □

We are now ready to prove Theorem 2.2.1.

Proof of Theorem 2.2.1. We apply Theorem 1.1 of [63]. It is enough to check that there exists a probability measure μ on $\mathcal{W}$ such that the following two assumptions hold:

1. **Assumption A1.** There exist $t_0 > 0$ and $c_1 > 0$ such that for all $w \in \mathcal{W}$, for all measurable $U \subset \mathcal{W}$,
$$\mathbb{P}_{\delta_w}(W_{t_0} \in U \mid \tau > t_0) \geqslant c_1\mu(U); \tag{2.19}$$
2. **Assumption A2.** There exists $c_2 > 0$ such that for all $t > 0$, for all $w \in \mathcal{W}$,
$$\mathbb{P}_{\delta_w}(\tau > t) \leqslant c_2\mathbb{P}_\mu(\tau > t). \tag{2.20}$$

Here $\mathbb{P}_{\delta_w}$ denotes the law corresponding to the the fundamental solution $\widetilde{u}^{(w)}(t,w')$ associated with (2.14), that is:

$$\begin{cases} \partial_t\widetilde{u}^{(w)}(t,w') = \Lambda\widetilde{u}^{(w)}, & t > 0, w' \in \mathcal{W}, \\ \nu \cdot \mathcal{A}\nabla\widetilde{u}^{(w)}(t,w') = 0, & w' \in \partial\mathcal{W}, \\ \lim\limits_{t\to 0}\widetilde{u}^{(w)}(t,\cdot) = \delta_w. \end{cases}$$

By Proposition 2.2.4, Φ is a quasi-stationary distribution of $(W_t)_{t\geqslant 0}$. If Assumptions A1 and A2 hold, then Φ must be the unique quasi-stationary distribution of $(W_t)_{t\geqslant 0}$ and the exponential convergence to Φ stated in Theorem 2.2.1 must hold.

Step 1. Check that Assumption A1 holds. We let $\mu := \frac{\mathrm{d}w}{|\mathcal{W}|}$ be the uniform law on $\mathcal{W}$. We first check that (2.19) holds with $t_0 := 2$ and for $c_1 > 0$ small enough. Take $\mathcal{B}_M \geqslant \|\mathcal{B}\|_\infty$.

Using the regularity of $\mathcal{W}$, we extend the solution $\widetilde{u}^{(w)}$ by orthogonal reflection with respect to $\partial\mathcal{W}$. We get a function defined on a set $\widetilde{\mathcal{W}}$ containing $\overline{\mathcal{W}}$. The operator Λ is extended to a uniformly elliptic operator $\widetilde{\Lambda}$ on $\widetilde{\mathcal{W}}$. This allows one to apply the parabolic Harnack inequality on the whole $\mathcal{W}$: there exists $C > 0$ depending only on $\underline{\mathcal{A}}$, $\overline{\mathcal{A}}$, $\mathcal{B}_M$ and $\mathcal{W}$ such that for all $t > 0$,

$$\inf_{w' \in \mathcal{W}} \widetilde{u}^{(w)}(t+1, w') \geqslant C \sup_{w' \in \mathcal{W}} \widetilde{u}^{(w)}(t, w').$$

Since we have also, for all $t > 0$,

$$\int_{\mathcal{W}} \widetilde{u}^{(w)}(t, w') \, \mathrm{d}w' = 1,$$

we obtain: for all $t > 0$,

$$\inf_{w' \in \mathcal{W}} \widetilde{u}^{(w)}(t+1, w') \geqslant \eta_1 := \frac{C}{|\mathcal{W}|}.$$

We let $\underline{\tau}$ be a clock independent of $(W_t)_{t \geqslant 0}$, with rate $D := \|d\|_\infty$, and coupled with τ so that $\underline{\tau} \leqslant \tau$ almost surely (this is possible by defining τ and $\underline{\tau}$ with the same Poisson point process taken independent of $(W_t)_{t \geqslant 0}$). We obtain:

$$\begin{aligned}
\mathbb{P}_{\delta_w}(W_2 \in U \mid \tau > 2) &\geqslant \mathbb{P}_{\delta_w}(W_2 \in U, \underline{\tau} > 2) \\
&= \mathbb{P}_{\delta_w}(W_2 \in U) \, e^{-2D} \\
&= e^{-2D} \int_U \widetilde{u}^{(w)}(2, w') \, \mathrm{d}w' \\
&\geqslant \eta_1 e^{-2D} \, |U| = \eta_1 e^{-2D} \, |\mathcal{W}| \, \mu(U).
\end{aligned}$$

Assumption A1 is satisfied with $c_1 := \eta_1 e^{-2D} \, |\mathcal{W}|$.

Step 2. Check that Assumption A2 holds. We let $u^{(w)}(t, w')$ be the fundamental solution associated with (2.16), that is:

$$\begin{cases}
\partial_t u^{(w)}(t, w') = (\Lambda - d(w)) u^{(w)}, & t > 0, w' \in \mathcal{W}, \\
\nu \cdot \mathcal{A} \nabla u^{(w)}(t, w') = 0, & w' \in \partial\mathcal{W}, \\
\lim_{t \to 0} u^{(w)}(t, \cdot) = \delta_w.
\end{cases}$$

Again, we can apply the parabolic Harnack inequality on the whole $\mathcal{W}$: there exists $C' > 0$ depending only on $\underline{\mathcal{A}}$, $\overline{\mathcal{A}}$, $\mathcal{B}_M$, $D := \|d\|_\infty$ and $\mathcal{W}$ such that for all $t > 0$,

$$\inf_{w' \in \mathcal{W}} u^{(w)}(t+1, w') \geqslant C' \sup_{w' \in \mathcal{W}} u^{(w)}(t, w').$$

Since we have also, for all $t > 0$,

$$\int_{\mathcal{W}} u^{(w)}(t, w') \, \mathrm{d}w' \geqslant e^{-Dt},$$

we obtain in particular:

$$\inf_{w' \in \mathcal{W}} u^{(w)}(2, w') \geqslant \eta_2$$

with $\eta_2 := \frac{e^{-2D}}{|\mathcal{W}|}$. We now let $\underline{v}$ be the solution of

$$\begin{cases} \partial_t \underline{v}(t,w') = (\Lambda - d(w))\underline{v}, & t > 2, w' \in \mathcal{W}, \\ \nu \cdot \mathcal{A}\nabla \underline{v}(t,w') = 0, & w' \in \partial\mathcal{W}, \\ \underline{v}(2,w') \equiv \eta_2 & w' \in \mathcal{W}. \end{cases}$$

For all $w \in \mathcal{W}$ and for all $t \geqslant 2$,

$$\mathbb{P}_{\delta_w}(\tau > t) = \int_{\mathcal{W}} u^{(w)}(t,\cdot) \geqslant \int_{\mathcal{W}} \underline{v}(t,\cdot) = \eta_2 \mathbb{P}_\mu(\tau > t-2) \geqslant \eta_2 \mathbb{P}_\mu(\tau > t).$$

Finally, for all $w \in \mathcal{W}$ and for all $t \in [0,2]$, we have $\mathbb{P}_{\delta_w}(\tau > t) \geqslant e^{-2D} \geqslant e^{-2D}\mathbb{P}_\mu(\tau > t)$. Thus Assumption A2 holds with

$$c_2 := \min\left[\eta_2, e^{-2D}\right] > 0.$$

Hence, Assumptions A1 and A2 are satisfied with $\mu = \frac{\mathrm{d}w}{|\mathcal{W}|}$. By Theorem 1.1 of [63], the first part of the theorem is shown. By Theorem 2.1 of [63], the constants C and χ only depend on t_0, c_1 and c_2. We took $t_0 = 2$, and c_1 and c_2 only depend on $\underline{\mathcal{A}}$, $\overline{\mathcal{A}}$, $\mathcal{B}_M$, $\|d\|_\infty$ and $\mathcal{W}$. Thus the constants C and χ only depend on $\underline{\mathcal{A}}$, $\overline{\mathcal{A}}$, $\mathcal{B}_M$, $\|d\|_\infty$ and $\mathcal{W}$. □

2.3 Behaviour of the principal eigenfunction (Theorem 2.1.1)

Throughout Section 2.3, we will abuse notation and denote, for a measurable function $f : \mathcal{W} \to \mathbb{R}$ and for measurable sets $E \subset \mathcal{Y}$ and $F \subset \mathcal{Z}$,

$$f(E,F) = \int_{E\times F} f(y,z)\,\mathrm{d}y\,\mathrm{d}z, \qquad f(\cdot,F) = \int_F f(\cdot,z)\,\mathrm{d}z.$$

Throughout this section, we fix $y_0 \in \overline{\mathcal{Y}}$.

2.3.1 Description of the framework

Recall that in Subsection 2.1.3, we defined a killed process $(Y_t^\varepsilon, Z_t^\varepsilon)_{t\geqslant 0}$ on $\mathcal{W} \cup \{\partial\}$. By Proposition 2.2.4, we have, for all measurable sets $E \subset \mathcal{Y}$ and $F \subset \mathcal{Z}$, for all $t > 0$,

$$\varphi_\varepsilon(E,F) = \mathbb{P}_{\varphi_\varepsilon}\left((Y_t^\varepsilon, Z_t^\varepsilon) \in E \times F \mid \tau^\varepsilon > t\right).$$

With this in view, we understand why Theorem 2.1.1 will be a consequence of the following proposition, the proof of which is the main part of Section 2.3. For $\eta > 0$, we set $V^\eta := B(y_0,\eta) \cap \mathcal{Y}$, where $B(y_0,\eta) \subset \mathbb{R}^n$ is the ball with centre y_0 and radius η.

Proposition 2.3.1. *Let $y_0 \in \overline{\mathcal{Y}}$. For $\varepsilon \in (0,1)$, set $t_\varepsilon := \frac{\ln(1/\varepsilon)}{1+4(\max d - \min d)}$ and $\eta_\varepsilon := \varepsilon^{1/4}$. Let $E^\varepsilon := B\left(y_0, \varepsilon^2\right) \cap \mathcal{Y} \subset V^{\eta_\varepsilon}$. Then, as $\varepsilon \to 0$,*

$$\left\| \mathbb{P}_{\varphi_\varepsilon}\left(Z_{t_\varepsilon}^\varepsilon \in \mathrm{d}z \mid \tau^\varepsilon > t_\varepsilon, Y_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right) - \psi^{y_0}(z)\,\mathrm{d}z \right\|_{TV} \to 0.$$

The convergence holds uniformly in $y_0 \in \overline{\mathcal{Y}}$.

Our goal is to focus on the behaviour of the process when Y_t^ε is close to y_0. Therefore, for $t>0$, $\eta>0$, $\varepsilon>0$, we let

$$T(\eta,\varepsilon;t) := \begin{cases} \inf\left\{s\in[0,t) \mid Y_{t-s}^\varepsilon \notin V^\eta\right\} & \text{if } \left\{s\in[0,t) \mid Y_{t-s}^\varepsilon \notin V^\eta\right\} \neq \emptyset, \\ t & \text{otherwise,} \end{cases}$$

be the time elapsed since Y_t^ε last entered the neighbourhood V^η of y_0 without leaving it. See Figure 2.4. The following lemma is the first step towards the proof of Proposition 2.3.1.

Lemma 2.3.2. *There exist $K>0$, $\chi>0$ and $\chi'>0$, independent of y_0, such that for all $E\subset V^\eta$ and for all $t>0$, $\eta>0$, $\varepsilon>0$,*

$$\begin{aligned} &\left\|\mathbb{P}_{\varphi_\varepsilon}\left(Z_t^\varepsilon \in \mathrm{d}z \mid \tau^\varepsilon > t, Y_t^\varepsilon \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV} \\ &\qquad < K\mathbb{E}_{\varphi_\varepsilon}\left[e^{-\chi T(\eta,\varepsilon;t)} \mid \tau^\varepsilon > t, Y_t^\varepsilon \in E\right] + K\left(e^{\eta\chi' t}-1\right). \end{aligned} \tag{2.21}$$

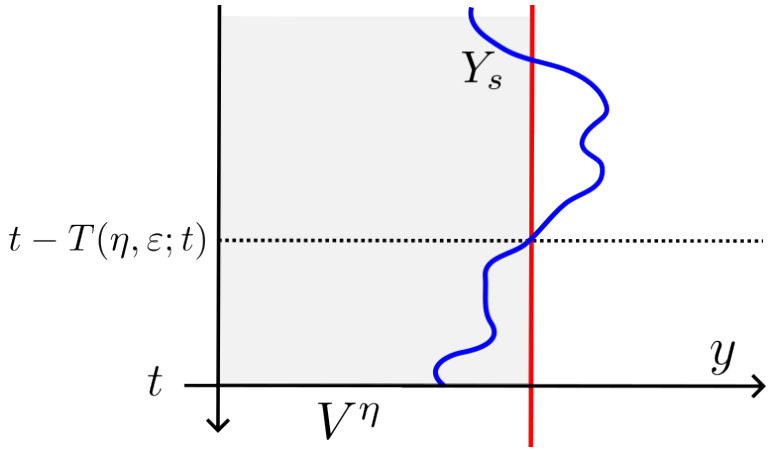

Figure 2.4: Definition of $T(\eta,\varepsilon;t)$.

The proof of Lemma 2.3.2 is based on the observation that if we keep Y_t^ε near y_0, the quasi-stationary distribution for Z_t^ε is approximately ψ^{y_0} (see Proposition 2.2.4). The first term of the right-hand side of (2.21) corresponds to how well the distribution of Z_t^ε conditionally on survival at time t approximates the quasi-stationary distribution ψ^{y_0}. We will see in Subsection 2.3.2 how this term arises. The second term of the right-hand side of (2.21) corresponds to the approximation made when forgetting the role of Y_t^ε. We will see in Subsection 2.3.3 how this term arises. Finally, in Subsection 2.3.4, we will conclude the proof of Proposition 2.3.1 and the proof of Theorem 2.1.1.

2.3.2 Work with a locally frozen death rate

In Subsections 2.3.2 and 2.3.3, we will work with a fixed $\varepsilon>0$. In order to lighten the notations, we will therefore omit the superindex ε. The notations become:

$$\widetilde{Y}=\widetilde{Y}^\varepsilon, \qquad \widetilde{Z}=\widetilde{Z}^\varepsilon, \qquad \tau=\tau^\varepsilon, \qquad T(\eta;t)=T(\eta,\varepsilon;t), \qquad \varphi=\varphi_\varepsilon, \qquad \text{etc.}$$

We should not forget, however, that all these objects do indeed depend on ε.

We call $(\widetilde{Y}_t, \widetilde{Z}_t)_{t\geqslant 0}$ the carrying process; in the sequel, we will construct several processes based on $(\widetilde{Y}_t, \widetilde{Z}_t)_{t\geqslant 0}$ but dying at different stopping times.

Approximate the stopping time τ by another stopping time τ^η. Let $\eta > 0$ and let $V^\eta := B(y_0, \eta) \cap \mathcal{Y}$. We consider a function d^η which approximates d and which, on the neighbouring band $V^\eta \times \mathcal{Z}$, only depends on z:

$$\begin{aligned} d^\eta(y,z) &= d(y,z), && y \notin V^\eta, \\ d^\eta(y,z) &= d(y_0,z), && y \in V^\eta. \end{aligned}$$

See Figure 2.5.

We define a stochastic process $(Y_t^\eta, Z_t^\eta)_{t\geqslant 0}$ exactly as $(Y_t, Z_t)_{t\geqslant 0}$, but which dies at rate d^η instead of dying at rate d. Namely, we let τ^η be a clock with rate $(d^\eta(\widetilde{Y}_t, \widetilde{Z}_t))_{t\geqslant 0}$ and we set

$$(Y_t^\eta, Z_t^\eta) := \begin{cases} (\widetilde{Y}_t, \widetilde{Z}_t), & t < \tau^\eta, \\ \partial, & t \geqslant \tau^\eta. \end{cases}$$

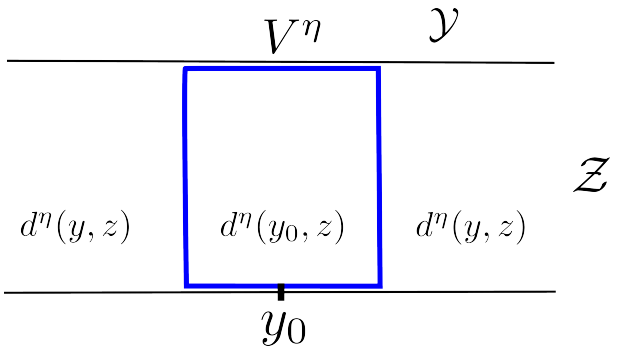

Figure 2.5: In the neighbourhood V^η of y_0, d^η is independent of y, but may still depend on z.

Introduce processes $(\widehat{Y}_s, \widehat{Z}_s)_{s\geqslant 0}$ and $(\widehat{Y}_s^\eta, \widehat{Z}_s^\eta)_{s\geqslant 0}$ living in $V^\eta \times \mathcal{Z} \subset \mathcal{W}$, and their stopping times $\widehat{\tau}$ and $\widehat{\tau}^\eta$. We can bear in mind that between $t - T(\eta; t)$ and t, the coefficients of the SDE analogous to (2.12) satisfied by Z^η are independent of Y^η. To formalise this idea, we consider auxiliary processes $(\widehat{Y}_s, \widehat{Z}_s)_s$ and $(\widehat{Y}_s^\eta, \widehat{Z}_s^\eta)_s$ which behave in a similar way as $(Y_t, Z_t)_t$ and $(Y_t^\eta, Z_t^\eta)_t$, but which die upon reaching $\partial V^\eta \times \mathcal{Z}$.

Namely, we let $\widehat{\tau}_d$ and $\widehat{\tau}_d^\eta$ be two clocks with respective rates $d(\widetilde{Y}_s, \widetilde{Z}_s)$ and $d^\eta(\widetilde{Y}_s, \widetilde{Z}_s)$. We let also:

$$\widehat{\tau}_Y := \inf\left\{u \geqslant 0 \ / \ \widetilde{Y}_u \notin V^\eta\right\}$$

be the first exit time from V^η by $\widetilde{Y}$. Finally, we set $\widehat{\tau} := \widehat{\tau}_d \wedge \widehat{\tau}_Y$ and $\widehat{\tau}^\eta := \widehat{\tau}_d^\eta \wedge \widehat{\tau}_Y$. We now define

$$(\widehat{Y}_s, \widehat{Z}_s) := \begin{cases} (\widetilde{Y}_s, \widetilde{Z}_s), & t < \widehat{\tau}, \\ \partial, & t \geqslant \widehat{\tau}; \end{cases} \qquad (\widehat{Y}_s^\eta, \widehat{Z}_s^\eta) := \begin{cases} (\widetilde{Y}_s^\eta, \widetilde{Z}_s^\eta), & t < \widehat{\tau}^\eta, \\ \partial, & t \geqslant \widehat{\tau}^\eta. \end{cases}$$

Hence $\widehat{\tau}$ and $\widehat{\tau}^\eta$ are the respective death times of the processes $(\widehat{Y}_u, \widehat{Z}_u)_u$ and $(\widehat{Y}_u^\eta, \widehat{Z}_u^\eta)_u$.

We will first compare $(\widehat{Y}_s, \widehat{Z}_s)_s$ and $(Y_t, Z_t)_t$. Then, we will see how to approximate the local principal eigenfunctions ψ^y, $y \in \overline{\mathcal{Y}}$, using the process $(\widehat{Y}^\eta_s, \widehat{Z}^\eta_s)_s$. For this approximation to hold, we need to use the independence of the processes $(\widehat{Y}^\eta_s)_s$ and $(\widehat{Z}^\eta_s)_s$ when started from some $y \in V^\eta$ and $z \in \mathcal{Z}$ respectively; to get the independence, we will use Assumption (2.8). Finally, in the next subsection, we will compare the processes $(\widehat{Y}_s, \widehat{Z}_s)_s$ and $(\widehat{Y}^\eta_s, \widehat{Z}^\eta_s)_s$, and prove Lemma 2.3.2.

For integer k with $0 \leqslant k < t$, we set $I_k := [k, k+1)$. We let $m_k(t)$ be the law of (Y_{t-k}, Z_{t-k}) conditionally on the event $\{T(\eta;t) \in I_k, \tau > t\}$. That is, for $E \subset \mathcal{Y}$ and $F \subset \mathcal{Z}$,

$$m_k(t)\,(E \times F) := \mathbb{P}_\varphi\left((Y_{t-k}, Z_{t-k}) \in E \times F \mid T(\eta;t) \in I_k, \tau > t\right).$$

The following lemma compares the two processes $(\widehat{Y}_s, \widehat{Z}_s)_s$ and $(Y_t, Z_t)_t$.

Lemma 2.3.3. *For all measurable subsets $E \subset V^\eta$ and $F \subset \mathcal{Z}$, for all $t > 0$ and integer k with $0 \leqslant k < t$,*

$$\mathbb{P}_\varphi\left((Y_t, Z_t) \in E \times F \mid \tau > t, T(\eta;t) \in I_k\right) = \mathbb{P}_{m_k(t)}\left((\widehat{Y}_k, \widehat{Z}_k) \in E \times F \mid \widehat{\tau} > k\right).$$

Proof. Let $t_0 := t - k$. We have:

$$\begin{aligned}&\mathbb{P}_\varphi\left((Y_t, Z_t) \in E \times F \mid \tau > t, T(\eta;t) \in I_k\right)\\ &\quad= \mathbb{P}_\varphi\left((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in E \times F \mid \tau > t_0 + k, T(\eta;t) \in I_k\right).\end{aligned}$$

Now, we write:

$$\begin{aligned}&\mathbb{P}_\varphi\left((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in E \times F \mid \tau > t_0 + k, T(\eta;t) \in I_k\right)\\ &\quad= \int_{\mathcal{Y}\times\mathcal{Z}} \mathbb{P}_\varphi\left((\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0}) \in \mathrm{d}y\,\mathrm{d}z, (\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in E \times F \mid \tau > t_0 + k, T(\eta;t) \in I_k\right)\\ &\quad= \int_{\mathcal{Y}\times\mathcal{Z}} m_k(t)(\mathrm{d}y\,\mathrm{d}z)\mathbb{P}_\varphi\left((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in E \times F \mid (\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0}) \in \mathrm{d}y\,\mathrm{d}z, \tau > t_0 + k, T(\eta;t) \in I_k\right),\end{aligned}$$

where we note

$$\begin{aligned}&\mathbb{P}_\varphi\left((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in \cdot \mid (\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0}) \in \mathrm{d}y\,\mathrm{d}z, \tau > t_0 + k, T(\eta;t) \in I_k\right)\\ &\qquad:= \lim_{\varepsilon\to 0} \mathbb{P}_\varphi\left((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in \cdot \mid (\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0}) \in B((y,z),\varepsilon), \tau > t_0 + k, T(\eta;t) \in I_k\right).\end{aligned}$$

The validity of this expression and of the computations follows from the fact that $(\widetilde{Y}_t, \widetilde{Z}_t)$ has a continuous density for all $t \geqslant 0$.

Next, let us rewrite the following events:

$$\{T(\eta;t) \in I_k\} = \left\{\exists u \in [t_0 - 1, t_0], \widetilde{Y}_u \notin V^\eta\right\} \cap \left\{\forall u \in [t_0, t], \widetilde{Y}_u \in V^\eta\right\} =: A_1 \cap A_2,$$

and

$$\{\tau > t_0 + k\} = \{\tau > t_0\} \cap \left\{\tau' > k\right\} =: B_1 \cap B_2,$$

where τ' is a clock with rate $d(\widetilde{Y}_{t_0+t}, \widetilde{Z}_{t_0+t})_{t\geqslant 0}$ (which satisfies $\tau' = \tau - k$ on $\{\tau > k\}$). Now, we use the Markov property, which implies that conditionnally on $(\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0})$, $(\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k})$ is

independent of $(\widetilde{Y}_u, \widetilde{Z}_u)_{u\in[0,t_0]}$, and therefore is independent of A_1 and B_1. We obtain:

$$\mathbb{P}_\varphi\Big((\widetilde{Y}_{t_0+k}, \widetilde{Z}_{t_0+k}) \in E\times F \mid (\widetilde{Y}_{t_0}, \widetilde{Z}_{t_0}) \in \mathrm{d}y\,\mathrm{d}z, \tau > t_0+k, T(\eta;t)\in I_k\Big) \\ = \mathbb{P}_{(y,z)}\Big((\widetilde{Y}'_k, \widetilde{Z}'_k)\in E\times F \mid A_2, B_2\Big),$$

where $(\widetilde{Y}'_t, \widetilde{Z}'_t) := (\widetilde{Y}'_{t_0+t}, \widetilde{Z}'_{t_0+t})$. Gathering everything together, we obtain:

$$\begin{aligned}\mathbb{P}_\varphi\left((Y_t, Z_t)\in E\times F \mid \tau > t, T(\eta;t)\in I_k\right) &= \mathbb{P}_{m_k(t)}\Big((\widetilde{Y}'_k, \widehat{Z}'_k)\in E\times F \mid A_2, B_2\Big)\\ &= \mathbb{P}_{m_k(t)}\Big((\widetilde{Y}_k, \widetilde{Z}_k)\in E\times F \mid \widehat{\tau}_d > k, \widehat{\tau}^Y > k\Big)\\ &= \mathbb{P}_{m_k(t)}\Big((\widehat{Y}_k, \widehat{Z}_k)\in E\times F \mid \widehat{\tau} > k\Big).\end{aligned}$$

□

Introduce a process $(\overline{Z}_s)_{s\geqslant 0}$ living in $\mathcal{Z}$. We consider another auxiliary process $(\overline{Z}_s)_s$ living in $\mathcal{Z}$, which behaves in a similar way as $(Z_t)_{t\geqslant 0}$ and $(\widehat{Z}_s)_{s\geqslant 0}$, but independently of any process in $\mathcal{Y}$. We let $\overline{\tau}$ be a clock with rate $(d(y_0, \overline{Z}_s))_{s\geqslant 0}$. We define

$$\overline{Z}_t := \begin{cases}\widetilde{Z}_t & t < \overline{\tau},\\ \partial & t\geqslant \overline{\tau}.\end{cases}$$

Let us try to understand the behaviour of $(\overline{Z}_s)_{s\geqslant 0}$. In (2.11), if we take the initial condition m independent of y, then the solution $\widetilde{u}^\varepsilon$ remains independent of y (due to (2.8)). In this case, therefore, the density of $\widetilde{Z}_t$ is described by the solution $\widetilde{v}$ of the equation

$$\begin{cases}\partial_t\widetilde{v}(t,z) = \mathcal{L}_z\widetilde{v}, & t\geqslant 0, z\in\mathcal{Z},\\ \nu\cdot a\nabla\widetilde{v} = 0, & z\in\partial\mathcal{Z},\\ \widetilde{v}(0,z) = m(z), & z\in\mathcal{Z}.\end{cases}$$

Taking $\mathcal{W} = \mathcal{Z}$ and $\Lambda = \mathcal{L}_z$, we retrieve the setting of Section 2.2. By Proposition 2.2.4, then, we find that the quasi-stationary distribution of the process $(\overline{Z}_s)_{s\geqslant 0}$ is ψ^{y_0}. Also, note that $(\overline{Z}_s)_s$ and $(\widehat{Z}^\eta_s)_s$ have much the same behaviour. Therefore, in view of Theorem 2.2.1, the following lemma is natural.

Lemma 2.3.4. *There exist $C>0$ and $\chi>0$ such that for all initial distribution m on $\mathcal{W}$ and for all $E\subset V^\eta$,*

$$\Big\|\mathbb{P}_m\Big(\widehat{Z}^\eta_s\in\mathrm{d}z \mid \widehat{\tau}^\eta > s, \widehat{Y}^\eta_s\in E\Big) - \psi^{y_0}(z)\,\mathrm{d}z\Big\|_{TV} \leqslant Ce^{-\chi s}.$$

The constants $C>0$ and $\chi>0$ can be chosen independently of y_0.

Proof. We have, for any initial distribution m on $\mathcal{W}$,

$$\begin{aligned}\mathbb{P}_m\Big(\widehat{Y}^\eta_s\in E, \widehat{Z}^\eta_s\in\cdot \mid \widehat{\tau}^\eta > s\Big) &= \frac{\mathbb{P}_m\Big(\widehat{Y}^\eta_s\in E, \widehat{Z}^\eta_s\in\cdot, \widehat{\tau}^\eta > s\Big)}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\\ &= \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}}\mathbb{P}_{(y,z)}\Big(\widehat{Y}^\eta_s\in E, \widehat{Z}^\eta_s\in\cdot, \widehat{\tau}^\eta > s\Big)\,m(\mathrm{d}y,\mathrm{d}z).\end{aligned}$$

For conciseness, we denoted $\mathbb{P}_{(y,z)}$ instead of $\mathbb{P}_{\delta_{(y,z)}}$. Let $(y,z) \in V^\eta$. The properties of the Cauchy problem (2.14) imply that the processes $(\widetilde{Y}_s)_{s\geqslant 0}$ starting from y and $(\widetilde{Z}_s)_{s\geqslant 0}$ starting from z are independent (this is where we need the restrictions (2.8) on the dependencies of the coefficients). Moreover, the stopping time $\widehat{\tau}_Y^\eta$ is a function of the process $(\widetilde{Y}_s)_{s\geqslant 0}$ only, and the stopping time $\widehat{\tau}_d^\eta$ is a function of the process $(\widetilde{Z}_s^\eta)_{s\geqslant 0}$ only. Therefore, for all $(y,z) \in \mathcal{W}$, for all $s > 0$,

$$\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{Z}_s^\eta \in \cdot, \widehat{\tau}^\eta > s\right) = \mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \cdot, \widehat{\tau}_d^\eta > s\right)\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}_Y^\eta > s\right).$$

We obtain:

$$\begin{aligned}
&\mathbb{P}_m\left(\widehat{Y}_s^\eta \in E, \widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}^\eta > s\right)\\
&\quad= \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}} \mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \cdot, \widehat{\tau}_d^\eta > s\right)\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}_Y^\eta > s\right) m(\mathrm{d}y, \mathrm{d}z)\\
&\quad= \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}} \mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s\right)\mathbb{P}_{(y,z)}\left(\widehat{\tau}_d^\eta > s\right)\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}_Y^\eta > s\right) m(\mathrm{d}y, \mathrm{d}z)\\
&\quad= \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}} \mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s\right)\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}^\eta > s\right) m(\mathrm{d}y, \mathrm{d}z).
\end{aligned}$$

Therefore,

$$\begin{aligned}
&\left\|\mathbb{P}_m\left(\widehat{Y}_s^\eta \in E, \widehat{Z}_s^\eta \in \mathrm{d}z \mid \widehat{\tau}^\eta > s\right) - \mathbb{P}_m\left(\widehat{Y}_s^\eta \in E \mid \widehat{\tau}^\eta > s\right)\psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV}\\
&\quad\leqslant \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}} \left\|\mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \mathrm{d}z' \mid \widehat{\tau}_d^\eta > s\right) - \psi^{y_0}(z')\,\mathrm{d}z'\right\|_{TV}\mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}^\eta > s\right) m(\mathrm{d}y, \mathrm{d}z).
\end{aligned}$$

But, by Theorem 2.2.1 applied to the killed process $(\overline{Z}_s)_{s\geqslant 0}$ (see also the discussion before the statement of Lemma 2.3.4),

$$\begin{aligned}
\left\|\mathbb{P}_{(y,z)}\left(\widehat{Z}_s^\eta \in \mathrm{d}z \mid \widehat{\tau}_d^\eta > s\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV} &= \left\|\mathbb{P}_z\left(\overline{Z}_s \in \mathrm{d}z \mid \overline{\tau} > s\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV}\\
&\leqslant Ce^{-\chi s}.
\end{aligned}$$

Note that the constants C and χ can be chosen independently of y_0, by the second statement in Theorem 2.2.1. Hence

$$\begin{aligned}
&\left\|\mathbb{P}_m\left(\widehat{Y}_s^\eta \in E, \widehat{Z}_s^\eta \in \mathrm{d}z \mid \widehat{\tau}^\eta > s\right) - \mathbb{P}_m\left(\widehat{Y}_s^\eta \in E \mid \widehat{\tau}^\eta > s\right)\psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV}\\
&\quad\leqslant Ce^{-\chi s} \times \frac{1}{\mathbb{P}_m\left(\widehat{\tau}^\eta > s\right)}\int_{\mathcal{W}} \mathbb{P}_{(y,z)}\left(\widehat{Y}_s^\eta \in E, \widehat{\tau}^\eta > s\right) m(\mathrm{d}y, \mathrm{d}z)\\
&\quad= Ce^{-\chi s}\mathbb{P}_m\left(\widehat{Y}_s^\eta \in E \mid \widehat{\tau}^\eta > s\right).
\end{aligned}$$

Dividing both sides by $\mathbb{P}_m\left(\widehat{Y}_s^\eta \in E \mid \widehat{\tau}^\eta > s\right)$, we obtain:

$$\left\|\mathbb{P}_m\left(\widehat{Z}_s^\eta \in \mathrm{d}z \mid \widehat{\tau}^\eta > s, \widehat{Y}_s^\eta \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV} \leqslant Ce^{-\chi s}.$$

Finally, we mentioned that the constants C and χ can be chosen independently of y_0. □

2.3.3 Comparison between $\widehat{\tau}$ and $\widehat{\tau}^\eta$

The processes $(\widehat{Y}_t, \widehat{Z}_t)_{t\geqslant 0}$ and $(\widehat{Y}^\eta_t, \widehat{Z}^\eta_t)_{t\geqslant 0}$, and their respective death times $\widehat{\tau}$ and $\widehat{\tau}^\eta$, are almost the same. The only difference is that the dependence in y of the death rate is removed in the definition of $(\widehat{Y}^\eta_s, \widehat{Z}^\eta_s)$. With this respect, $(\widehat{Y}^\eta_s, \widehat{Z}^\eta_s)$ dies at a rate "frozen" at y_0 while $(\widehat{Y}_s, \widehat{Z}_s)$ dies at a rate depending on the y-coordinate. For small η, the coefficient d does not depend much on $y \in V^\eta$, in the sense that for all $y \in V^\eta$,

$$d(y, \cdot) \simeq d(y_0, \cdot).$$

Therefore, we expect that $\widehat{\tau} \simeq \widehat{\tau}^\eta$. This intuition is made precise in the following lemma, which is the last step before the proof of Lemma 2.3.2.

Lemma 2.3.5. *There exists $\chi' > 0$ such that for all $s > 0$, for all $E \subset V^\eta$, for all probability distribution m on V^η,*

$$\left\| \mathbb{P}_m\left(\widehat{Z}_s \in \cdot \mid \widehat{\tau} > s, \widehat{Y}_s \in E\right) - \mathbb{P}_m\left(\widehat{Z}^\eta_s \in \cdot \mid \widehat{\tau}^\eta > s, \widehat{Y}^\eta_s \in E\right) \right\|_{TV} \leqslant 2\left(e^{\eta\chi' t} - 1\right).$$

The constant χ' can be chosen independently of y_0.

Proof. Recall that $\widehat{\tau} = \widehat{\tau}_d \wedge \widehat{\tau}_Y$ where $\widehat{\tau}_d$ depends on the death rate $d(\widetilde{Y}_t, \widetilde{Z}_t)$, and $\widehat{\tau}_Y$ is the time at which $\widetilde{Y}$ reaches the boundary ∂V^η. Likewise, $\widehat{\tau}^\eta = \widehat{\tau}^\eta_d \wedge \widehat{\tau}_Y$. We therefore decompose:

$$\{\widehat{\tau} > s\} = \{\widehat{\tau}_d > s, \widehat{\tau}_Y > s\}, \qquad \{\widehat{\tau}^\eta > s\} = \left\{\widehat{\tau}^\eta_d > s, \widehat{\tau}_Y > s\right\}.$$

Let $\kappa > 0$ be the Lipschitz constant of d in the y-direction:

$$\kappa := \sup_{z\in\mathcal{Z}} \left(\sup_{y,y'\in\mathcal{Y}, y\neq y'} \frac{|d(y,z) - d(y',z)|}{|y - y'|} \right) < +\infty.$$

On the event $\{\widehat{\tau}_Y > s\}$, we then have, for all $u \in [0, s]$,

$$\left| d(\widehat{Y}_u, \widehat{Z}_u) - d(y_0, \widehat{Z}_u) \right| \leqslant \kappa\eta.$$

For conciseness of notations, denote by $\mathcal{D}$ the event $\mathcal{D} = \left\{\widehat{\tau}_Y > s, \widehat{Y}_s \in E\right\}$. Recall the definition of $\widehat{\tau}_d$ in Subsection 2.3.2, using Definition 2.1.4. We have:

$$\begin{aligned}
\mathbb{P}_m\left(\widehat{\tau}_d > s \mid \mathcal{D}\right) &= \mathbb{E}_m\left[\exp\left(-\int_0^s d(\widetilde{Y}_u, \widetilde{Z}_u)\,\mathrm{d}u\right) \mid \mathcal{D}\right] \\
&\geqslant \mathbb{E}_m\left[\exp\left(-\kappa\eta s - \int_0^s d(y_0, \widetilde{Z}_u)\,\mathrm{d}u\right) \mid \mathcal{D}\right].
\end{aligned}$$

This gives:

$$\begin{aligned}
\mathbb{P}_m\left(\widehat{\tau}_d > s \mid \mathcal{D}\right) &\geqslant e^{-\kappa\eta s}\mathbb{E}_m\left[\exp\left(-\int_0^s d(y_0, \widetilde{Z}_u)\,\mathrm{d}u\right) \mid \mathcal{D}\right] \\
&= e^{-\kappa\eta s}\mathbb{P}_m\left(\widehat{\tau}^\eta_d > s \mid \mathcal{D}\right).
\end{aligned}$$

Likewise, $\mathbb{P}_m\left(\widehat{\tau}^\eta_d > s \mid \mathcal{D}\right) \geqslant e^{-\kappa\eta s}\mathbb{P}_m\left(\widehat{\tau}_d > s \mid \mathcal{D}\right)$. Thus:

$$e^{-\kappa\eta s}\mathbb{P}_m\left(\widehat{\tau}^\eta_d > s \mid \mathcal{D}\right) \leqslant \mathbb{P}_m\left(\widehat{\tau}_d > s \mid \mathcal{D}\right) \leqslant e^{\kappa\eta s}\mathbb{P}_m\left(\widehat{\tau}^\eta_d > s \mid \mathcal{D}\right).$$

Similarly, for all $F \subset \mathcal{Z}$,

$$e^{-\kappa\eta s}\mathbb{P}_m\left(\widehat{Z}_s^\eta \in F, \widehat{\tau}_d^\eta > s \mid \mathcal{D}\right) \leqslant \mathbb{P}_m\left(\widehat{Z}_s \in F, \widehat{\tau}_d > s \mid \mathcal{D}\right) \leqslant e^{\kappa\eta s}\mathbb{P}_m\left(\widehat{Z}_s^\eta \in F, \widehat{\tau}_d^\eta > s \mid \mathcal{D}\right).$$

Therefore, for all $F \subset \mathcal{Z}$,

$$\begin{aligned} e^{-2\kappa\eta s}\mathbb{P}_m\left(\widehat{Z}_s^\eta \in F \mid \widehat{\tau}_d^\eta > s, \mathcal{D}\right) &\leqslant \mathbb{P}_m\left(\widehat{Z}_s \in F \mid \widehat{\tau}_d > s, \mathcal{D}\right) \\ &\leqslant e^{2\kappa\eta s}\mathbb{P}_m\left(\widehat{Z}_s^\eta \in F \mid \widehat{\tau}_d^\eta > s, \mathcal{D}\right). \end{aligned}$$

Since this holds for all $F \subset \mathcal{Z}$, we get:

$$\begin{aligned} &\left\|\mathbb{P}_m\left(\widehat{Z}_s \in \cdot \mid \widehat{\tau}_d > s, \mathcal{D}\right) - \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s, \mathcal{D}\right)\right\|_{TV} \\ &\qquad \leqslant 2\max(e^{2\kappa\eta s} - 1, 1 - e^{-2\kappa\eta s}) = 2\left(e^{2\kappa\eta s} - 1\right). \end{aligned}$$

Finally, note that before their death, the processes $(\widehat{Y}_s, \widehat{Z}_s)_{s\geqslant 0}$ and $(\widehat{Y}_s^\eta, \widehat{Z}_s^\eta)_{s\geqslant 0}$ coincide with $(\widetilde{Y}_s, \widetilde{Z}_s)_{s\geqslant 0}$. In particular, $\left\{\widehat{\tau}_d^\eta > s, \mathcal{D}\right\} = \left\{\widehat{\tau}_d^\eta > s, \widehat{\tau}_Y > s, \widetilde{Y}_s \in E\right\}$. These elements yield

$$\begin{aligned} \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s, \mathcal{D}\right) &= \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s, \widehat{\tau}_Y > s, \widetilde{Y}_s \in E\right) \\ &= \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}_d^\eta > s, \widehat{\tau}_Y > s, \widehat{Y}_s^\eta \in E\right) \\ &= \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}^\eta > s, \widehat{Y}_s^\eta \in E\right). \end{aligned}$$

We obtain: for all $s > 0$,

$$\begin{aligned} &\left\|\mathbb{P}_m\left(\widehat{Z}_s \in \cdot \mid \widehat{\tau} > s, \widehat{Y}_s \in E\right) - \mathbb{P}_m\left(\widehat{Z}_s^\eta \in \cdot \mid \widehat{\tau}^\eta > s, \widehat{Y}_s^\eta \in E\right)\right\|_{TV} \\ &\quad = \left\|\mathbb{P}_m\left(\widehat{Z}_s \in \cdot \mid \widehat{\tau}_d > s, \mathcal{D}\right) - \mathbb{P}_m\left(\widehat{Z}_s \in \cdot \mid \widehat{\tau}_d^\eta > s, \mathcal{D}\right)\right\|_{TV} \\ &\quad \leqslant e^{2\kappa\eta s} - 1. \end{aligned}$$

Thus the lemma holds with $\chi' = 2\kappa$, which is independent of y_0. □

We are ready for end of the proof of Lemma 2.3.2.

Proof of Lemma 2.3.2. Let us decompose the following probability according to the value of $T(\eta;t)$: for all $t > 0$,

$$\begin{aligned} &\mathbb{P}_\varphi(Y_t \in E, Z_t \in \cdot \mid \tau > t) \\ &\quad = \sum_{k=0}^{\lfloor t\rfloor} \mathbb{P}_\varphi(Y_t \in E, T(\eta;t) \in I_k \mid \tau > t)\, \mathbb{P}_\varphi(Z_t \in \cdot \mid \tau > t, Y_t \in E, T(\eta;t) \in I_k) \\ &\quad = \sum_{k=0}^{\lfloor t\rfloor} \mathbb{P}_\varphi(Y_t \in E, T(\eta;t) \in I_k \mid \tau > t)\, \mathbb{P}_{m_k}\left(\widehat{Z}_k \in \cdot \mid \widehat{\tau} > k, \widehat{Y}_k \in E\right), \end{aligned}$$

by Lemma 2.3.3 (using the shortcut $m_k = m_k(t)$). Thus, by the triangle inequality,

$$\begin{aligned} &\|\mathbb{P}_\varphi(Y_t \in E, Z_t \in \mathrm{d}z \mid \tau > t) - \mathbb{P}_\varphi(Y_t \in E \mid \tau > t)\psi^{y_0}(z)\,\mathrm{d}z\|_{TV} \\ &\quad \leqslant \sum_{k=0}^{\lfloor t\rfloor} \mathbb{P}_\varphi(Y_t \in E, T(\eta;t) \in I_k \mid \tau > t) \left\|\mathbb{P}_{m_k}\left(\widehat{Z}_k \in \mathrm{d}z \mid \widehat{\tau} > k, \widehat{Y}_k \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV}. \end{aligned}$$

By the triangle inequality again, and then Lemmas 2.3.5 and 2.3.4, we have for all $k \geqslant 0$:

$$\begin{aligned}
&\left\|\mathbb{P}_{m_k}\left(\widehat{Z}_k \in \mathrm{d}z \mid \widehat{\tau} > k, \widehat{Y}_k \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV} \\
&\quad\leqslant \left\|\mathbb{P}_{m_k}\left(\widehat{Z}_k \in \mathrm{d}z \mid \widehat{\tau} > k, \widehat{Y}_k \in E\right) - \mathbb{P}_m\left(\widehat{Z}_k^\eta \in \mathrm{d}z \mid \widehat{\tau}^\eta > k, \widehat{Y}_k^\eta \in E\right)\right\|_{TV} \\
&\qquad + \left\|\mathbb{P}_m\left(\widehat{Z}_k^\eta \in \mathrm{d}z \mid \widehat{\tau}^\eta > k, \widehat{Y}_k^\eta \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\right\|_{TV} \\
&\quad\leqslant K\left(e^{\chi'\eta k} - 1\right) + Ke^{-\chi k},
\end{aligned}$$

for $K > 0$ large enough. Hence,

$$\begin{aligned}
&\|\mathbb{P}_\varphi\left(Y_t \in E, Z_t \in \mathrm{d}z \mid \tau > t\right) - \mathbb{P}_\varphi(Y_t \in E \mid \tau > t)\psi^{y_0}(z)\,\mathrm{d}z\|_{TV} \\
&\quad\leqslant K\sum_{k=0}^{\lfloor t\rfloor} \mathbb{P}_\varphi\left(Y_t \in E, T(\eta;t) \in I_k \mid \tau > t\right)\left(e^{-\chi k} + e^{\chi'\eta k} - 1\right) \\
&\quad\leqslant K\mathbb{P}_\varphi\left(Y_t \in E \mid \tau > t\right)\sum_{k=0}^{\lfloor t\rfloor} \mathbb{P}_\varphi\left(T(\eta;t) \in I_k \mid \tau > t, Y_t \in E\right) \times e^{-\chi k} \\
&\qquad + K\mathbb{P}_\varphi\left(Y_t \in E \mid \tau > t\right) \times \left(e^{\chi'\eta t} - 1\right).
\end{aligned}$$

This gives, approximating the sum from above by an expectation:

$$\begin{aligned}
&\|\mathbb{P}_\varphi\left(Y_t \in E, Z_t \in \mathrm{d}z \mid \tau > t\right) - \mathbb{P}_\varphi(Y_t \in E \mid \tau > t)\psi^{y_0}(z)\,\mathrm{d}z\|_{TV} \\
&\quad\leqslant K\mathbb{P}_\varphi\left(Y_t \in E \mid \tau > t\right)\mathbb{E}_\varphi\left[e^{-\chi(T(\eta;t)-1)} \mid \tau > t, Y_t \in E\right] \\
&\qquad + K\mathbb{P}_\varphi\left(Y_t \in E \mid \tau > t\right) \times \left(e^{\chi'\eta t} - 1\right).
\end{aligned}$$

Dividing both sides by $\mathbb{P}_\varphi\left(Y_t \in E \mid \tau > t\right)$, we conclude:

$$\begin{aligned}
&\|\mathbb{P}_\varphi\left(Z_t \in \mathrm{d}z \mid \tau > t, Y_t \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\|_{TV} \\
&\quad\leqslant (Ke^{\chi})\mathbb{E}_\varphi\left[e^{-\chi T(\eta;t)} \mid \tau > t, Y_t \in E\right] + K\left(e^{\chi'\eta t} - 1\right).
\end{aligned}$$

Finally, the statements of Lemmas 2.3.4 and 2.3.5 show that the constants K, χ and χ' can be chosen independently of y_0. □

2.3.4 Conclusion of the proof

In Subsections 2.3.2 and 2.3.3, we worked with a fixed $\varepsilon > 0$ and omitted the superindex ε. Here, we will make ε go to zero. Therefore, we need to go back to our former notations: Y^ε, Z^ε, τ^ε, $T(\eta,\varepsilon;t)$, φ_ε, etc. First, we prove Proposition 2.3.1. Then, we will be able to prove Theorem 2.1.1.

Proof of Proposition 2.3.1. Let $\eta > 0$. Recall that $V^\eta = \mathcal{B}(y_0,\eta) \cap \mathcal{Y}$. By Lemma 2.3.2, there exist $K > 0$, $\chi > 0$ and $\chi' > 0$ such that for all $E \subset V^\eta$, for all $t > 0$, $\eta > 0$, $\varepsilon > 0$,

$$\begin{aligned}
&\|\mathbb{P}_{\varphi_\varepsilon}\left(Z_t^\varepsilon \in \mathrm{d}z \mid \tau^\varepsilon > t, Y_t^\varepsilon \in E\right) - \psi^{y_0}(z)\,\mathrm{d}z\|_{TV} \\
&\qquad < K\mathbb{E}_{\varphi_\varepsilon}\left[e^{-\chi T(\eta,\varepsilon;t)} \mid \tau^\varepsilon > t, Y_t^\varepsilon \in E\right] + K\left(e^{\eta\chi' t} - 1\right). \qquad (2.22)
\end{aligned}$$

For $\varepsilon \in (0,1)$ sufficiently small, we let $t_\varepsilon := \frac{\ln(1/\varepsilon)}{1+4(\max d - \min d)}$, $\eta_\varepsilon := \varepsilon^{1/4}$, and $E^\varepsilon := B\left(y_0, \varepsilon^2\right) \cap$

$\mathcal{Y} \subset V^{\eta_\varepsilon}$. For $\varepsilon > 0$ sufficiently small, we have $d(E^\varepsilon, \partial V^{\eta_\varepsilon}) \geqslant \eta_\varepsilon/2$. Further, $\inf_{\varepsilon \in (0,1)} \frac{|E^\varepsilon|}{\varepsilon^2} > 0$. Our goal is to show that as $\varepsilon \to 0$,

$$\mathbb{E}_{\varphi_\varepsilon}\left[e^{-\chi T(\eta_\varepsilon, \varepsilon; t_\varepsilon)} \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right] \to 0, \tag{2.23}$$

$$e^{\eta_\varepsilon \chi' t_\varepsilon} - 1 \to 0. \tag{2.24}$$

With (2.22), we will then be able to conclude. First, we have $t_\varepsilon \eta_\varepsilon \to 0$ as $\varepsilon \to 0$, so (2.24) holds. Second, let us show that (2.23) holds. We have

$$\begin{aligned}
&\mathbb{E}_{\varphi_\varepsilon}\left[e^{-\chi T(\eta_\varepsilon, \varepsilon; t_\varepsilon)} \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right] \\
&\qquad \leqslant e^{-\chi t_\varepsilon} + \mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon, \varepsilon; t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right).
\end{aligned} \tag{2.25}$$

We wish to estimate the very last term. Let $\widetilde{E}^\varepsilon := \{y \in \mathcal{Y} \ / \ d(y, E^\varepsilon) < \eta_\varepsilon/4\}$. Then $E^\varepsilon \subset \widetilde{E}^\varepsilon$ and the triangle inequality implies that for $\varepsilon > 0$ sufficiently small, $d(\widetilde{E}^\varepsilon, \partial V^{\eta_\varepsilon}) \geqslant \eta_\varepsilon/4$. We have, decomposing the above probability according to the value of Y^ε_0,

$$\begin{aligned}
&\mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon, \varepsilon; t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) \\
&\qquad \leqslant \mathbb{P}_{\varphi_\varepsilon}\left(Y^\varepsilon_0 \notin \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) + \mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon, \varepsilon; t_\varepsilon) < t_\varepsilon, Y^\varepsilon_0 \in \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) \\
&\qquad \leqslant \mathbb{P}_{\varphi_\varepsilon}\left(Y^\varepsilon_0 \notin \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) + \mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon, \varepsilon; t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon, Y^\varepsilon_0 \in \widetilde{E}^\varepsilon\right).
\end{aligned} \tag{2.26}$$

Step 1. Estimate the first term of (2.26)**.** First, let us show that the first term on the right-hand side of (2.26) converges to 0 as $\varepsilon \to 0$. Since $d(\widetilde{E}^\varepsilon, \partial V^{\eta_\varepsilon}) \geqslant \eta_\varepsilon/4$ for ε sufficiently small, we have:

$$\mathbb{P}_{\varphi_\varepsilon}\left(Y^\varepsilon_0 \notin \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) \leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\left\|Y^\varepsilon_0 - Y^\varepsilon_{t_\varepsilon}\right\| > \frac{\eta_\varepsilon}{4} \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right).$$

Since the Poisson point process defining τ_ε is independent of the carrying process $(\widetilde{Y}^\varepsilon_t, \widetilde{Z}^\varepsilon_t)_t$, there exist two exponential random variables $\underline{\tau}$ and $\overline{\tau}$, with rates $\max d$ and $\min d$ respectively, independent of $(\widetilde{Y}^\varepsilon_t, \widetilde{Z}^\varepsilon_t)$, and such that

$$\underline{\tau} \leqslant \tau_\varepsilon \leqslant \overline{\tau}. \tag{2.27}$$

Using this comparison, we have:

$$\begin{aligned}
&\mathbb{P}_{\varphi_\varepsilon}\left(\left\|Y^\varepsilon_0 - Y^\varepsilon_{t_\varepsilon}\right\| > \frac{\eta_\varepsilon}{4} \mid \tau^\varepsilon > t_\varepsilon, Y^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) \\
&\qquad \leqslant \frac{1}{\mathbb{P}_{\varphi_\varepsilon}\left(\underline{\tau} > t_\varepsilon, \widetilde{Y}^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right)} \mathbb{P}_{\varphi_\varepsilon}\left(\left\|\widetilde{Y}^\varepsilon_0 - \widetilde{Y}^\varepsilon_{t_\varepsilon}\right\| > \frac{\eta_\varepsilon}{4}, \overline{\tau} > t_\varepsilon, \widetilde{Y}^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) \\
&\qquad \leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\left\|\widetilde{Y}^\varepsilon_0 - \widetilde{Y}^\varepsilon_{t_\varepsilon}\right\| > \frac{\eta_\varepsilon}{4} \mid \widetilde{Y}^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right) e^{(\max d - \min d) t_\varepsilon} \\
&\qquad \leqslant \frac{\mathbb{P}_{\varphi_\varepsilon}\left(\left\|\widetilde{Y}^\varepsilon_0 - \widetilde{Y}^\varepsilon_{t_\varepsilon}\right\| > \frac{\eta_\varepsilon}{4}\right)}{\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}^\varepsilon_{t_\varepsilon} \in E^\varepsilon\right)} e^{(\max d - \min d) t_\varepsilon}.
\end{aligned}$$

On the one hand, there exist constants $C_1, C_2 > 0$, depending only on the diffusion coefficient A, the drift term B and the domain $\mathcal{Y}$ (but not on ε or y_0), such that

$$\mathbb{P}_{\varphi_\varepsilon}\left(\left\|\widetilde{Y}_0^\varepsilon - \widetilde{Y}_{t_\varepsilon}^\varepsilon\right\| > \frac{\eta_\varepsilon}{4}\right) \leqslant C_1 e^{-C_2\eta_\varepsilon^2/\varepsilon^2} = C_1 e^{-C_2/\varepsilon^{3/2}}.$$

On the other hand, let us estimate $\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right)$. The Neumann boundary condition on $\partial\mathcal{Y}$ or $\partial\mathcal{Z}$ (if nonempty) allows us to apply the Harnack inequality up to the boundary to the function $(y,z) \mapsto \varphi_\varepsilon(y/\varepsilon, z)$, which solves an equation that is uniformly elliptic in ε and that has coefficients uniformly bounded in ε (for more details, see the beginning of the proof of Theorem 2.1.1). We obtain that there exists a constant $C_3 \in (0,1)$, depending only on A, B, r, but not on ε or y_0, such that for all $y \in \mathcal{Y}$ (denoting by $\mathcal{Y}[y,\varepsilon]$ the connected component of $\mathcal{Y} \cap B(y,\varepsilon)$ containing y),

$$\inf_{y' \in \mathcal{Y}[y,\varepsilon]} \varphi_\varepsilon(y', \mathcal{Z}) > C_3 \varphi_\varepsilon(y, \mathcal{Z}). \tag{2.28}$$

Let us extend this inequality to any pair of points $y, y' \in \mathcal{Y}$. Since $\mathcal{Y}$ is connected and smooth, $\overline{\mathcal{Y}}$ is path-connected, with paths that can be chosen to be $\mathcal{C}^1$. Hence we can define the geodesic distance $d_{\overline{\mathcal{Y}}}$ on $\overline{\mathcal{Y}}$. By continuity of $d_{\overline{\mathcal{Y}}}$ and compactness of $\overline{\mathcal{Y}}$, the radius $R := \sup_{y,y' \in \overline{\mathcal{Y}}}\{d_{\mathcal{Y}}(y,y')\}$ is finite. Hence, for any $y, y' \in \mathcal{Y}$, there exists a sequence $y = y_1, y_2, \ldots, y_k = y'$, with $k \leqslant R/\varepsilon + 1$, such that $\mathcal{Y}[y_i,\varepsilon] \cap \mathcal{Y}[y_{i+1},\varepsilon]$ is nonempty for all $i = 1, \ldots, k-1$. Therefore, we may apply (2.28) (at most) $\lceil R/\varepsilon \rceil + 1$ times to obtain: for all $\varepsilon > 0$,

$$\inf_{y \in \mathcal{Y}} \varphi_\varepsilon(y, \mathcal{Z}) > C_3^{\lceil R/\varepsilon \rceil + 1} \sup_{y \in \mathcal{Y}} \varphi_\varepsilon(y, \mathcal{Z}).$$

Recalling the normalisation $\varphi_\varepsilon(\mathcal{Y}, \mathcal{Z}) = 1$, we have $\sup_{y \in \mathcal{Y}} \varphi_\varepsilon(y, \mathcal{Z}) \geqslant 1/|\mathcal{Y}|$, so

$$\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_0^\varepsilon \in E^\varepsilon\right) \geqslant |E^\varepsilon| \inf_{y \in \mathcal{Y}} \varphi_\varepsilon(y, \mathcal{Z}) \geqslant \frac{|E^\varepsilon|\, C_3^{\lceil R/\varepsilon \rceil + 1}}{|\mathcal{Y}|},$$

which implies:

$$\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right) \geqslant \left(\inf_{y \in E^\varepsilon} \mathbb{P}_y\left(\widetilde{Y}_1^\varepsilon \in E^\varepsilon\right)\right)^{\lceil t_\varepsilon \rceil} \mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_0^\varepsilon \in E^\varepsilon\right) \geqslant \frac{|E^\varepsilon|\, C_3^{\lceil R/\varepsilon \rceil + 1} (\varepsilon^2 C_4)^{\lceil t_\varepsilon \rceil}}{|\mathcal{Y}|},$$

with

$$C_4 := \inf_{\varepsilon \in (0,1),\, y_0' \in \mathcal{Y}} \left[\frac{1}{\varepsilon^2} \inf_{y \in B(y_0', \varepsilon^2) \cap \mathcal{Y}} \mathbb{P}_y\left(\widetilde{Y}_1^\varepsilon \in B(y_0', \varepsilon^2) \cap \mathcal{Y}\right)\right] > 0,$$

which depends only on the diffusion coefficient A and the drift coefficient B, but not on ε or y_0 (note that as $\varepsilon \to 0$, the term between the brackets converges to $+\infty$ uniformly in y_0', so C_4 is indeed positive). We obtain:

$$\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_0^\varepsilon \notin \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right) \leqslant \frac{|\mathcal{Y}|\, C_1 e^{-C_2/\varepsilon^{3/2}}}{|E^\varepsilon|\, C_3^{\lceil R/\varepsilon \rceil + 1} (\varepsilon^2 C_4)^{\lceil t_\varepsilon \rceil}} e^{(\max d - \min d) t_\varepsilon}.$$

This gives, recalling that $\inf_{\varepsilon\in(0,1)} |E^\varepsilon|/\varepsilon^2 > 0$,

$$\mathbb{P}_{\varphi_\varepsilon}\left(\widetilde{Y}_0^\varepsilon \notin \widetilde{E}^\varepsilon \mid \tau^\varepsilon > t_\varepsilon, \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right) \underset{\varepsilon\to 0}{\longrightarrow} 0. \tag{2.29}$$

Step 2. Estimate the second term of (2.26) **and conclude.** Second, let us show that the second term on the right-hand side of (2.26) converges to 0 as $\varepsilon \to 0$. Define the stopping time

$$\tau_V := \inf\left\{u > 0 \ / \ \widetilde{Y}_u^\varepsilon \in \partial V^{\eta_\varepsilon}\right\}.$$

On the event $\{T(\eta_\varepsilon,\varepsilon;t_\varepsilon) < t_\varepsilon\} \cap \left\{\widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon, \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right\}$, we have $0 < \tau_V < t_\varepsilon$. Therefore,

$$\begin{aligned}
&\mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon,\varepsilon;t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon, \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right)\\
&\quad\leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\tau_V \in (0,t_\varepsilon) \mid \tau^\varepsilon > t_\varepsilon, \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon, \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right)\\
&\quad\leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\tau_V \in (0,t_\varepsilon) \mid \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon, \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right) e^{(\max d - \min d)t_\varepsilon}.
\end{aligned}$$

The last line is obtained by using, as above, the comparison (2.27). Further, since $E^\varepsilon \subset \widetilde{E}^\varepsilon \subset V^{\eta_\varepsilon}$, we have:

$$\mathbb{P}_{\varphi_\varepsilon}\left(\tau_V \in (0,t_\varepsilon) \mid \widetilde{Y}_{t_\varepsilon}^\varepsilon \in E^\varepsilon, \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right) \leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\tau_V \in (0,t_\varepsilon) \mid \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right).$$

Last, recall that $d(\widetilde{E}^\varepsilon, \partial V^\eta) \geqslant \eta_\varepsilon/4$ for $\varepsilon > 0$ sufficiently small. Thus, if $\widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon$, then $\|\widetilde{Y}_{\tau_V}^\varepsilon - \widetilde{Y}_0^\varepsilon\| \geqslant \frac{\eta_\varepsilon}{4}$. Therefore, using the Markov inequality,

$$\begin{aligned}
&\mathbb{P}_{\varphi_\varepsilon}\left(\tau_V \in (0,t_\varepsilon) \mid \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right)\\
&\qquad\leqslant \mathbb{P}_{\varphi_\varepsilon}\left(\sup_{u\in[0,t_\varepsilon]} \|\widetilde{Y}_u^\varepsilon - \widetilde{Y}_0^\varepsilon\| \geqslant \frac{\eta_\varepsilon}{4} \mid \widetilde{Y}_0^\varepsilon \in \widetilde{E}^\varepsilon\right) \leqslant \frac{C'' t_\varepsilon \varepsilon^2}{\eta_\varepsilon^2} = C'' t_\varepsilon \varepsilon^{3/2},
\end{aligned}$$

for some constant $C'' > 0$ depending on the diffusion coefficient A and the drift coefficient B, but not depending on ε or y_0. Combining this with the above, we obtain:

$$\mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon,\varepsilon;t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y_{t_\varepsilon}^\varepsilon \in E^\varepsilon, Y_0^\varepsilon \in \widetilde{E}^\varepsilon\right) \leqslant C'' t_\varepsilon \varepsilon^{3/2} e^{(\max d - \min d)t_\varepsilon},$$

which converges to 0 as $\varepsilon \to 0$. Therefore (2.26) and (2.29) imply that as $\varepsilon \to 0$,

$$\mathbb{P}_{\varphi_\varepsilon}\left(T(\eta_\varepsilon,\varepsilon;t_\varepsilon) < t_\varepsilon \mid \tau^\varepsilon > t_\varepsilon, Y_{t_\varepsilon}^\varepsilon \in E^\varepsilon\right) \to 0.$$

Thus, taking $\varepsilon \to 0$ in Equation (2.25) implies that (2.23) holds. The convergence stated in the proposition follows from (2.22) combined with (2.23)–(2.24). Since the bound of Lemma 2.3.2 is uniform in $y_0 \in \overline{\mathcal{Y}}$, we conclude that the convergence is also uniform in $y_0 \in \overline{\mathcal{Y}}$. □

We are ready to prove Theorem 2.1.1, using Proposition 2.3.1.

Proof of Theorem 2.1.1. For $\varepsilon \in (0,1)$, we set $\eta_\varepsilon := \varepsilon^{1/4}$ and we let $E^\varepsilon := B\left(y_0, \varepsilon^2\right) \cap \mathcal{Y} \subset V^{\eta_\varepsilon}$.

Let us change coordinates. For $\varepsilon \in (0,1)$, we define

$$\mathcal{Y}_\varepsilon := \{y \in \mathbb{R}^n \ / \ y_0 + \varepsilon y \in \mathcal{Y}\}.$$

For all $y \in \mathcal{Y}_\varepsilon$, we set

$$\widetilde{\varphi}_\varepsilon(y,z) := \frac{\varphi_\varepsilon(y_0+\varepsilon y, z)}{\varphi_\varepsilon(y_0,\mathcal{Z})}.$$

We define $\widetilde{A}$, $\widetilde{B}$, $\widetilde{\mathcal{L}}_z$ and $\widetilde{c}$ with the same change of variables (we omit the dependence in ε for the sake of clarity). We let $\widetilde{E}^\varepsilon := B(0,\varepsilon)\cap\mathcal{Y}_\varepsilon$ be the projection of E^ε in this new system of coordinates. First, $\widetilde{\varphi}_\varepsilon$ satisfies

$$\nabla_y\cdot(\widetilde{A}\nabla_y\widetilde{\varphi}_\varepsilon)+\nabla_y\cdot\left(\widetilde{\varphi}_\varepsilon\widetilde{B}\right)+(\widetilde{\mathcal{L}}_z+\widetilde{c})\widetilde{\varphi}_\varepsilon = k_\varepsilon\widetilde{\varphi}_\varepsilon, \qquad y\in\mathcal{Y}_\varepsilon, \qquad z\in\mathcal{Z}.$$

Thanks to this transformation, the diffusion coefficients become uniformly elliptic on the whole domain. Let $U\subset\subset\mathcal{Y}_1$, so that $U\subset\subset\mathcal{Y}_\varepsilon$ for all $\varepsilon\in(0,1)$. Let $\mathcal{Z}'\subset\subset\mathcal{Z}$. For all $\varepsilon>0$, we have $\widetilde{\varphi}_\varepsilon(0,\mathcal{Z})=1$. Therefore, by the Harnack inequality, the family $(\widetilde{\varphi}_\varepsilon)_{\varepsilon\in(0,1)}$ is bounded in $L^\infty(U\times\mathcal{Z}')$. By the interior Schauder inequality ([107, Theorem 6.2]), therefore, the family $(\widetilde{\varphi}_\varepsilon)_{\varepsilon\in(0,1)}$ is bounded in $\mathcal{C}^{2,\alpha}(U\times\mathcal{Z}')$. Hence, taking $\beta\in(0,\alpha)$, up to extraction of a subsequence, there exists a limit $\widetilde{\varphi}_0\in\mathcal{C}^{2,\beta}(U\times\mathcal{Z}')$:

$$\widetilde{\varphi}_\varepsilon\to\widetilde{\varphi}_0 \quad \text{ in } \mathcal{C}^{2,\beta}(U\times\mathcal{Z}').$$

Since $\left|\widetilde{E}^\varepsilon\right|\to 0$, this implies in particular:

$$\frac{1}{\left|\widetilde{E}^\varepsilon\right|}\widetilde{\varphi}_\varepsilon(\widetilde{E}^\varepsilon,\cdot) = \frac{1}{\left|\widetilde{E}^\varepsilon\right|}\int_{\widetilde{E}^\varepsilon}\widetilde{\varphi}_\varepsilon(y,\cdot)\,\mathrm{d}y \to \widetilde{\varphi}_0(0,\cdot) \quad \text{ in } \mathcal{C}^0(\mathcal{Z}'). \tag{2.30}$$

Finally, we note that

$$\frac{1}{\left|\widetilde{E}^\varepsilon\right|}\widetilde{\varphi}_\varepsilon(\widetilde{E}^\varepsilon,\cdot) = \frac{\widetilde{\varphi}_\varepsilon(\widetilde{E}^\varepsilon,\mathcal{Z})}{\left|\widetilde{E}^\varepsilon\right|}\times\frac{\varphi_\varepsilon(E^\varepsilon,\cdot)}{\varphi_\varepsilon(E^\varepsilon,\mathcal{Z})}.$$

On the one hand,

$$\frac{\widetilde{\varphi}_\varepsilon(\widetilde{E}^\varepsilon,\mathcal{Z})}{\left|\widetilde{E}^\varepsilon\right|}\to\widetilde{\varphi}_0(0,\mathcal{Z})=1.$$

On the other hand, using the notations of Proposition 2.3.1,

$$\frac{\varphi_\varepsilon(E^\varepsilon,\cdot)}{\varphi_\varepsilon(E^\varepsilon,\mathcal{Z})} = \frac{\mathbb{P}_{\varphi_\varepsilon}\left(Y^\varepsilon_{t_\varepsilon}\in E^\varepsilon,\, Z^\varepsilon_{t_\varepsilon}\in\cdot\mid\tau^\varepsilon>t_\varepsilon\right)}{\mathbb{P}_{\varphi_\varepsilon}\left(Y^\varepsilon_{t_\varepsilon}\in E^\varepsilon\mid\tau^\varepsilon>t_\varepsilon\right)} = \mathbb{P}_{\varphi_\varepsilon}\left(Z^\varepsilon_{t_\varepsilon}\in\cdot\mid\tau^\varepsilon>t_\varepsilon, Y^\varepsilon_{t_\varepsilon}\in E^\varepsilon\right).$$

Therefore, by Proposition 2.3.1,

$$\frac{\varphi_\varepsilon(E^\varepsilon,\cdot)}{\varphi_\varepsilon(E^\varepsilon,\mathcal{Z})}\,\mathrm{d}z\to\psi^{y_0}(z)\,\mathrm{d}z$$

in total variation on $\mathcal{Z}$. Therefore, we have in total variation on $\mathcal{Z}$ (thus also on $\mathcal{Z}'$):

$$\frac{1}{\left|\widetilde{E}^\varepsilon\right|}\widetilde{\varphi}_\varepsilon(\widetilde{E}^\varepsilon,z)\,\mathrm{d}z\to\psi^{y_0}(z)\,\mathrm{d}z \quad \text{ as } \varepsilon\to 0. \tag{2.31}$$

Note that convergence in $\mathcal{C}^{2,\beta}(\mathcal{Z}')$ of the density implies that the corresponding measure

converges in total variation on $\mathcal{Z}'$. Combining (2.31) with (2.30) yields: for all $z \in \mathcal{Z}'$,

$$\widetilde{\varphi}_0(0,z) = \psi^{y_0}(z).$$

Hence, as $\varepsilon \to 0$,

$$\frac{\varphi_\varepsilon(y_0,\cdot)}{\varphi_\varepsilon(y_0,\mathcal{Z})} \to \psi^{y_0} \quad \text{in } \mathcal{C}^{2,\beta}(\mathcal{Z}').$$

This concludes the first point of the theorem. Finally, the convergence in total variation on $\mathcal{Z}$ is uniform in $y_0 \in \overline{\mathcal{Y}}$, see Proposition 2.3.1. Thus the second point holds. □

2.4 Behaviour of the principal eigenvalue (Theorems 2.1.2 and 2.1.3)

In the previous section, we worked on the principal eigenfunction and proved Theorem 2.1.1 using a probabilistic interpretation. We now use Theorem 2.1.1 to prove results about the principal eigenvalue, in some particular cases. We drop the probabilistic interpretation; the techniques in this part will be based on Hamilton-Jacobi equations.

2.4.1 Preliminary results

We record several lemmas which will be useful for the proof of Theorems 2.1.2 and 2.1.3. The first lemma is basic. The following two lemmas add technical precision on the convergence of φ_ε, and follow from Theorem 2.1.1. The last lemma, which is at the heart of the proof of Theorems 2.1.2 and 2.1.3, makes a connection between the limiting principal eigenvalue and a Hamilton-Jacobi equation. Studying this Hamilton-Jacobi equation will allow us to prove Theorems 2.1.2 and 2.1.3.

Lemma 2.4.1. *For all $\varepsilon > 0$,*

$$|k_\varepsilon| \leqslant \|c\|_\infty .$$

Proof. For $g \in \mathcal{C}^{0,\alpha}(\mathcal{Y}\times\mathcal{Z})$, let $\kappa_\varepsilon(g)$ be the principal eigenvalue associated with the operator

$$\mathcal{L}_g : \phi \mapsto \varepsilon^2 \nabla_y \cdot (A\nabla_y \phi) + \varepsilon \nabla_y \cdot (\phi B) + (\mathcal{L}_z + g)\,\phi,$$

with Neumann boundary conditions on $\partial(\mathcal{Y}\times\mathcal{Z})$. By definition, we have $k_\varepsilon = \kappa_\varepsilon(c)$. Moreover, if $g_1 \leqslant g_2$ then $\kappa_\varepsilon(g_1) \leqslant \kappa_\varepsilon(g_2)$. Therefore,

$$\kappa_\varepsilon(-\|c\|_\infty) \leqslant k_\varepsilon \leqslant \kappa_\varepsilon(\|c\|_\infty).$$

Finally, when g is constant, $\varphi \equiv 1$ is a principal eigenfunction of $\mathcal{L}_g$. Thus:

$$\kappa_\varepsilon(-\|c\|_\infty) = -\|c\|_\infty , \qquad \kappa_\varepsilon(\|c\|_\infty) = \|c\|_\infty .$$

The conclusion follows. □

Lemma 2.4.2. *Let $(y_\varepsilon)_{\varepsilon\in(0,1)}$ be a family of elements of $\overline{\mathcal{Y}}$. For all $\mathcal{Z}' \subset\subset \mathcal{Z}$, the family*

$$\left(\frac{\varphi_\varepsilon(y_\varepsilon,\cdot)}{\varphi_\varepsilon(y_\varepsilon,\mathcal{Z})}\right)_{\varepsilon\in(0,1)}$$

is bounded in $\mathcal{C}^{2,\alpha}(\mathcal{Z}')$.

Proof. Let us change coordinates. For $\varepsilon \in (0,1)$, we define $\mathcal{Y}_\varepsilon := \{y \in \mathbb{R}^n \ / \ y_\varepsilon + \varepsilon y \in \mathcal{Y}\}$. For all $y \in \overline{\mathcal{Y}_\varepsilon}$, we set

$$\widetilde{\varphi}_\varepsilon(y,z) := \frac{\varphi_\varepsilon(y_\varepsilon + \varepsilon y, z)}{\varphi_\varepsilon(y_\varepsilon, \mathcal{Z})},$$

and we define $\widetilde{A}$, $\widetilde{B}$, $\widetilde{\mathcal{L}}_z$ and $\widetilde{c}$ with the same change of coordinates (we omit the dependence in ε for the sake of clarity). We have

$$\nabla_y \cdot (\widetilde{A}\nabla_y \widetilde{\varphi}_\varepsilon) + \nabla_y \cdot \left(\widetilde{\varphi}_\varepsilon \widetilde{B}\right) + (\widetilde{\mathcal{L}}_z + \widetilde{c})\widetilde{\varphi}_\varepsilon = k_\varepsilon \widetilde{\varphi}_\varepsilon, \qquad y \in \mathcal{Y}_\varepsilon \qquad z \in \mathcal{Z}. \tag{2.32}$$

Thanks to this transformation, the diffusion coefficients become uniformly elliptic on the whole domain.

Since $\|\varphi_\varepsilon(y_\varepsilon, \cdot)\|_{\mathcal{C}^{2,\alpha}(\mathcal{Z}')} = \|\widetilde{\varphi}_\varepsilon(0,\cdot)\|_{\mathcal{C}^{2,\alpha}(\mathcal{Z}')}$, it is enough for our scope to show that the family $(\widetilde{\varphi}_\varepsilon(0,\cdot))_{\varepsilon\in(0,1)}$ is bounded in $\mathcal{C}^{2,\alpha}(\mathcal{Z}')$. A slight difficulty arises when y_ε is near the boundary of $\mathcal{Y}_\varepsilon$. We first deal with the particular case where

$$\exists \delta > 0, \ \forall \varepsilon > 0, \qquad d(y_\varepsilon, \partial\mathcal{Y}_\varepsilon) > \delta. \tag{2.33}$$

Case 1. Condition (2.33) **holds.** Let $U := B(0, \delta/2)$. Then for all $\varepsilon \in (0,1)$, we have $d(U, \partial\mathcal{Y}_\varepsilon) > \delta/2$, so we can apply an interior Harnack inequality: the family $(\widetilde{\varphi}_\varepsilon)_{\varepsilon\in(0,1)}$ is bounded in $L^\infty(U \times \mathcal{Z}')$. To conclude, we apply the interior Schauder inequalities ([107, Theorem 6.2]): the family $(\widetilde{\varphi}_\varepsilon)_{\varepsilon\in(0,1)}$ is bounded in $\mathcal{C}^{2,\alpha}(U \times \mathcal{Z}')$. Thus the family $(\widetilde{\varphi}_\varepsilon(0,\cdot))_{\varepsilon\in(0,1)}$ is bounded in $\mathcal{C}^{2,\alpha}(\mathcal{Z}')$.

Case 2. Condition (2.33) **does not hold.** Let $U_\varepsilon := B(0,1) \cap \mathcal{Y}_\varepsilon$ and let

$$I := \{\varepsilon \in (0,1) \ / \ d(y_\varepsilon, \mathcal{Y}_\varepsilon) \leqslant 1\}.$$

By Case 1, there remains to prove that $(\|\widetilde{\varphi}_\varepsilon\|_{\mathcal{C}^{2,\alpha}(U_\varepsilon \times \mathcal{Z}')})_{\varepsilon\in I}$ is bounded. We use the fact that $\widetilde{\varphi}_\varepsilon$ satisfies (2.32) and the boundary condition $\nu \cdot \mathcal{A}\nabla\widetilde{\varphi}_\varepsilon = 0$. There exists a constant $C > 0$ such that for all $\varepsilon \in (0,1)$, the $\mathcal{C}^{2,\alpha}$-norm of $\partial\mathcal{Y}_\varepsilon$ is at most C, i.e. for all $\varepsilon > 0$ and for all $y \in \partial\mathcal{Y}_\varepsilon$, there exists a diffeomorphism Φ which straightens $\partial\mathcal{Y}_\varepsilon$ near y and which satisfies $\|\Phi\|_{\mathcal{C}^{2,\alpha}} \leqslant C$.

Thus we can apply the elliptic Harnack inequality up to the boundary $\partial\mathcal{Y}_\varepsilon$, so there exists a constant C' such that for all $\varepsilon > 0$, we have $\|\widetilde{\varphi}_\varepsilon\|_{L^\infty(U_\varepsilon \times \mathcal{Z})} \leqslant C'$. Then, by boundary Schauder estimates ([107], see the proof of Theorem 6.30 and the comments after the proof of Lemma 6.5), the family $(\|\widetilde{\varphi}_\varepsilon\|_{\mathcal{C}^{2,\alpha}(U_\varepsilon \times \mathcal{Z}')})_{\varepsilon\in I}$ is bounded. Again, we conclude that the family $(\widetilde{\varphi}_\varepsilon(0,\cdot))_{\varepsilon\in(0,1)}$ is bounded in $\mathcal{C}^{2,\alpha}(\mathcal{Z}')$. □

Lemma 2.4.3. *Let* $\varepsilon_n > 0$, $\varepsilon_n \to 0$ *and let* $(y_n)_n$ *be a sequence of elements* $y_n \in \overline{\mathcal{Y}}$ *converging to some* $y_\infty \in \overline{\mathcal{Y}}$. *Let* $z_0 \in \mathcal{Z}$. *Then, up to extraction of a subsequence,*

$$\frac{(\mathcal{L}_z + c)\varphi_{\varepsilon_n}(y_n, z_0)}{\varphi_{\varepsilon_n}(y_n, z_0)} \to k^{y_\infty}.$$

Proof. Take $\mathcal{Z}' \subset\subset \mathcal{Z}$ and $\beta \in (0, \alpha)$. We use the shortcut $\varphi_n := \varphi_{\varepsilon_n}$. Lemma 2.4.2 implies

that $\left(\frac{\varphi_n(y_n,\cdot)}{\varphi_n(y_n,\mathcal{Z})}\right)_{n\geqslant 0}$ is bounded in $\mathcal{C}^{2,\alpha}(\mathcal{Z}')$. Hence up to extraction we must have in $\mathcal{C}^{2,\beta}(\mathcal{Z}')$:

$$\frac{\varphi_n(y_n,\cdot)}{\varphi_n(y_n,\mathcal{Z})} \to \psi \tag{2.34}$$

for some $\psi \in \mathcal{C}^{2,\beta}(\mathcal{Z}')$. Moreover, by Theorem 2.1.1, we have

$$\frac{\varphi_n(y_n,z)}{\varphi_n(y_n,\mathcal{Z})}\,\mathrm{d}z \to \psi^{y_\infty}(z)\,\mathrm{d}z$$

in total variation of measures (we crucially use here that the convergence holds uniformly in y). This implies that (2.34) holds in $\mathcal{C}^{2,\beta}(\mathcal{Z}')$ with $\psi = \psi^{y_\infty}$. To conclude, we write:

$$\frac{(\mathcal{L}_z + c)\varphi_n(y_n,z_0)}{\varphi_n(y_n,z_0)} = \frac{(\mathcal{L}_z + c)\varphi_n(y_n,z_0)}{\varphi_n(y_n,\mathcal{Z})} \times \frac{\varphi_n(y_n,\mathcal{Z})}{\varphi_n(y_n,z_0)}.$$

Thus

$$\lim_{n\to+\infty} \frac{(\mathcal{L}_z + c)\varphi_n(y_n,z_0)}{\varphi_n(y_n,z_0)} = \frac{(\mathcal{L}_z + c)\psi^{y_\infty}(z_0)}{\psi^{y_\infty}(z_0)} = k^{y_\infty}.$$

□

By Lemma 2.4.1, the family $(k_\varepsilon)_{\varepsilon>0}$ is bounded. Thus, there exists a sequence $(\varepsilon_n)_n$ such that $\varepsilon_n \to 0$ and $(k_{\varepsilon_n})_{n\geqslant 0}$ converges to a limit k_0. The following lemma, inspired by Proposition 3.1 in [119], gives a property of k_0. This property is crucial for the proofs of Theorems 2.1.2 and 2.1.3.

Lemma 2.4.4. *Let $k_0 \in \mathbb{R}$ and $\mathcal{Y}' \subset\subset \mathcal{Y}$. If there exists a sequence $(\varepsilon_n)_{n\geqslant 0}$ such that $\varepsilon_n > 0$, $\varepsilon_n \to 0$ and*

$$k_0 = \lim_{n\to+\infty} k_{\varepsilon_n},$$

then the equation

$$-\nabla u(y)\cdot(A(y)\nabla u(y)) - B(y)\cdot\nabla u(y) - k^y + k_0 = 0 \tag{2.35}$$

has a viscosity solution u on $\mathcal{Y}'$, belonging to $\mathcal{C}^{0,\beta}(\mathcal{Y}')$ for all $\beta \in (0,1)$.

Proof. The proof is an adaptation of the proof of [119, Proposition 3.1]. We set:

$$v_n(y,z) := \varepsilon_n \ln\left(\varphi_{\varepsilon_n}(y,z)\right).$$

We use the shortcuts $\varphi_n = \varphi_{\varepsilon_n}$ and $k_n = k_{\varepsilon_n}$. We choose compact subsets $\mathcal{Y}' \subset\subset \mathcal{Y}$ and $\mathcal{Z}' \subset\subset \mathcal{Z}$ and we note $\mathcal{W}' = \mathcal{Y}' \times \mathcal{Z}'$. For convenience, we assume that $0 \in \mathcal{Y}'$ and $0 \in \mathcal{Z}'$. We renormalise φ_ε so that $\varphi_\varepsilon(0,0) = 1$.

Step 1. On $\overline{\mathcal{W}'}$, uniform convergence of the sequence $(v_n)_n$ to a function v. We show that up to extraction, the sequence of restricted functions $(v_{n|\overline{\mathcal{W}'}})_n$ converges uniformly to a function v defined on $\overline{\mathcal{W}'}$. Consider the change of variables $h_n(y,z) := (\varepsilon_n y, z)$ and set $\widetilde{\varphi}_n := \varphi_n \circ h_n$. Then $\widetilde{\varphi}_n$ is a solution of

$$\nabla_y\cdot((A\circ h_n)\nabla_y\widetilde{\varphi}_n) + \nabla_y\cdot(\widetilde{\varphi}_n(B\circ h_n)) + (\mathcal{L}_z\circ h_n + c\circ h_n)\varphi_n = 0.$$

Note that the $\widetilde{\varphi}_n$ are positive, and that the coefficients are bounded uniformly in n. Moreover, the diffusion coefficients $A \circ h_n$ and $a \circ h_n$ are elliptic uniformly in n. By the Harnack inequality (which, if needed, we can apply up to the boundary due to the Neumann boundary condition and the regularity of $\partial\mathcal{W}$), there exists a constant $C_1 > 1$, independent of n, such that for each n, for each $y_0 \in \mathcal{Y}$, for each $(y,z) \in \mathcal{W}$ such that $\|y - y_0\| \leqslant \varepsilon_n$,

$$\frac{1}{C_1}\widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, 0\right) \leqslant \widetilde{\varphi}_n\left(\frac{y}{\varepsilon_n}, z\right) \leqslant C_1 \widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, 0\right). \tag{2.36}$$

Moreover, by an interior estimate on the derivative ([107, Theorem 8.32]), there exists a constant $C_2 > 0$ (independent of n) such that for each n, for each $(y_0, z_0) \in \mathcal{W}'$,

$$\left|\nabla \widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, z_0\right)\right| \leqslant C_2 \sup_{(y,z)\in\mathcal{W},\, \|y-y_0\|\leqslant\varepsilon_n} \widetilde{\varphi}_n\left(\frac{y}{\varepsilon_n}, z\right). \tag{2.37}$$

Using (2.36) and (2.37), we conclude that for all $(y_0, z_0) \in \mathcal{W}'$,

$$|\nabla v_n(y_0, z_0)| = \left|\frac{\nabla \widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, z_0\right)}{\widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, z_0\right)}\right| \leqslant \frac{C_2 \times C_1 \widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, 0\right)}{\frac{1}{C_1}\widetilde{\varphi}_n\left(\frac{y_0}{\varepsilon_n}, 0\right)} = C_1^2 C_2.$$

This estimation being true for each $(y_0, z_0) \in \overline{\mathcal{W}'}$, we conclude that the sequence $(\nabla v_n)_n$ is bounded in $L^\infty(\overline{\mathcal{W}'})$. In particular the sequence $(v_n)_n$ is also bounded in $\mathcal{C}^0(\overline{\mathcal{W}'})$. Thanks to these facts, we infer that the sequence (v_n) is bounded in $W^{1,\infty}(\overline{\mathcal{W}'})$. By Ascoli's theorem, for all $\beta \in (0,1)$, up to extraction, the sequence $(v_{n|\overline{\mathcal{W}'}})_n$ converges in $\mathcal{C}^{0,\beta}(\overline{\mathcal{W}'})$ to a function v defined on $\overline{\mathcal{W}'}$. By a diagonal extraction argument, we get a function v that belongs to $\mathcal{C}^{0,\beta}(\overline{\mathcal{W}'})$ for all $\beta \in (0,1)$.

Now we let

$$u(y) := v(y,0), \qquad u_n(y) := v_n(y,0).$$

Then, u_n converges uniformly to u on $\mathcal{Y}'$, and u belongs to $\mathcal{C}^{0,\beta}(\mathcal{Y}')$ for all $\beta \in (0,1)$.

Step 2. Find an equation satisfied by u_n. We have:

$$\nabla_y v_n = \varepsilon_n \frac{\nabla_y \varphi_n}{\varphi_n},$$

so:

$$\varepsilon_n \nabla_y \cdot (A \nabla_y v_n) = \varepsilon_n^2 \frac{\nabla_y \cdot (A \nabla_y \varphi_n)}{\varphi_n} - \nabla_y v_n \cdot (A \nabla_y v_n).$$

Now, by the definition of φ_n,

$$\begin{aligned}\varepsilon_n^2 \frac{\nabla_y \cdot (A \nabla_y \varphi_n)}{\varphi_n} &= -\varepsilon_n \frac{\nabla_y \cdot (\varphi_n B)}{\varphi_n} - \frac{(\mathcal{L}_z + c)\varphi_n}{\varphi_n} + k_n \\ &= -B \cdot \nabla_y v_n - \varepsilon_n \nabla_y \cdot B - \frac{(\mathcal{L}_z + c)\varphi_n}{\varphi_n} + k_n.\end{aligned}$$

We conclude that

$$-\varepsilon_n \nabla_y \cdot (A\nabla_y v_n) - \nabla_y v_n \cdot (A\nabla_y v_n) - B \cdot \nabla_y v_n - \varepsilon_n \nabla_y \cdot B - \frac{(\mathcal{L}_z + c)\varphi_n}{\varphi_n} + k_n = 0.$$

Recalling that $u_n(y) = v_n(y,0)$, we obtain:

$$-\varepsilon_n \nabla \cdot (A\nabla u_n) - \nabla u_n \cdot (A\nabla u_n) - B \cdot \nabla u_n - \varepsilon_n \nabla \cdot B - \frac{(\mathcal{L}_z + c)\varphi_n(y,0)}{\varphi_n(y,0)} + k_n = 0. \quad (2.38)$$

Step 3. Conclusion. Since u is continuous, we have:

$$u = \left(\limsup_{n\to+\infty}\right)^* u_n,$$

where, as in [69],

$$\left(\limsup_{n\to+\infty}\right)^* u_n(y) := \limsup_{j\to+\infty} \left\{ u_n(y') \ / \ n \geqslant j, y' \in \mathcal{Y}, \left\| y - y' \right\| \leqslant 1/j \right\}.$$

Let us also define the notation

$$J^{2,+}u(y) := \Big\{ (\nabla\varphi(y), \nabla^2\varphi(y)) \in \mathbb{R}^n \times \mathcal{M}_n(\mathbb{R}) \ / \\ \varphi \text{ is } \mathcal{C}^2 \text{ near } y \text{ and } u - \varphi \text{ has a local maximum at } y \Big\}.$$

Let $y \in \mathcal{Y}'$ and $(p, X) \in J^{2,+}u(y)$. By [69, Lemma 6.1], there exist sequences $(y_n)_n$ and $(p_n, X_n) \in J^{2,+}u_n(y_n)$ such that, up to extraction of a subsequence,

$$(y_n, p_n, X_n) \to (y, p, X).$$

Note that the sequence $(X_n)_n$ is bounded and recall that $\varepsilon_n \to 0$, so $\varepsilon_n \operatorname{Tr}(A^T X_n) \to 0$. Further, $\nabla \cdot B$ is globally bounded so $\varepsilon_n \nabla \cdot B(y_n) \to 0$. Moreover, Lemma 2.4.3 yields:

$$\lim_{n\to+\infty} \frac{(\mathcal{L}_z + c)\varphi_n(y_n, 0)}{\varphi_n(y_n, 0)} = k^y.$$

Define $A_d \in \mathcal{C}^{0,\alpha}(\mathcal{Y}, \mathbb{R}^n)$ by $[A_d]_i = \sum_{j=1}^n \partial_i(A_{ij})$ where $[A_d]_i$ is the ith coordinate of the vector A_d and A_{ij} is the coefficient with coordinates i, j of the matrix A. Since A_d is globally bounded, we have $\varepsilon_n A_d \cdot p_n \to 0$.

We have, using the remarks above,

$$\begin{aligned} -p \cdot (A(y)p) - B(y) \cdot p - k^y + k_0 \\ = \lim_{n\to+\infty} \Big[\Big(-\varepsilon_n \Big(\operatorname{Tr}(A^T X_n) + A_d \cdot p_n \Big) - p_n \cdot (Ap_n) - B \cdot p_n - \varepsilon_n \nabla \cdot B \Big)(y_n) \\ - \left(\frac{(\mathcal{L}_z + c)\varphi_n}{\varphi_n} \right)(y_n, 0) + k_n \Big]. \end{aligned}$$

Now, the first line of (2.38) and the fact that $(p_n, X_n) \in J^{2,+}u(y_n)$ imply: for all $n \geqslant 0$,

$$\left(-\varepsilon_n \left(\mathrm{Tr}(A^T X_n) + A_d \cdot p_n\right) - p_n \cdot (Ap_n) - B \cdot p_n - \varepsilon_n \nabla \cdot B\right)(y_n) \\ - \left(\frac{(\mathcal{L}_z + c)\varphi_n}{\varphi_n}\right)(y_n, 0) + k_n \leqslant 0.$$

We obtain, therefore:

$$-p \cdot (Ap) - B \cdot p - k^y + k_0 \leqslant 0.$$

Thus u is a viscosity subsolution of (2.35). Likewise, defining $\liminf_*$ analogously to $\limsup^*$,

$$u(y) = \left(\liminf_{n \to +\infty}\right)_* u_n(y).$$

Thus u is a viscosity supersolution of (2.35). Therefore, u is a viscosity solution of (2.35). □

Remark 2.4.5. The proof of Lemma 2.4.4 suggests that as $\varepsilon \to 0$,

$$\varphi_\varepsilon(y, 0) \simeq e^{u(y)/\varepsilon},$$

where u solves (2.35). Therefore, we expect that

$$\frac{\varphi_\varepsilon(y, 0)}{\varphi_\varepsilon(y, \mathcal{Y})} \to 0$$

everywhere but at points $y_0 \in \overline{\mathcal{Y}}$ such that u is maximal at y_0. If u is of class $\mathcal{C}^1$, then the equation

$$-\nabla u(y) \cdot (A(y) \nabla u(y)) - B(y) \cdot \nabla u(y) - k^y + k_0 = 0$$

holds in the classical sense. If moreover $\mathcal{Y}$ has empty boundary, then all maximum points y_0 of u are interior, so we have $\nabla u(y_0) = 0$ and therefore $k^{y_0} = k_0$. Thus the limit of $\frac{\varphi_\varepsilon(y,0)}{\varphi_\varepsilon(y,\mathcal{Y})}$ should be supported in $\Gamma := \{y \in \mathcal{Y} \ / \ k^y = k_0\}$. Since $\frac{\varphi_\varepsilon(y,0)}{\varphi_\varepsilon(y,\mathcal{Y})}$ has total mass 1, it is natural to expect that there exists a measure μ on Γ, with total mass equal to 1, such that for all $f \in \mathcal{C}^\infty(\mathcal{Y})$,

$$\int_{\mathcal{Y}} f(y) \frac{\varphi_\varepsilon(y, z_0)}{\varphi_\varepsilon(\mathcal{Y}, z_0)} \, \mathrm{d}y \to \int_\Gamma f(y) \mu(\, \mathrm{d}y).$$

This holds also if we replace 0 with any $z_0 \in \mathcal{Z}$.

2.4.2 Main proofs

We first prove Theorem 2.1.2 (where it is assumed that $B \equiv 0$) by studying the Hamilton-Jacobi equation given by Lemma 2.4.4. Next, we prove Theorem 2.1.3 by solving explicitly the Hamilton-Jacobi equation in the periodic 1-dimensional setting.

Proof of Theorem 2.1.2. Assume that $B \equiv 0$. Take $\varepsilon_n \to 0$ such that k_{ε_n} converges to some $k_0 \in \mathbb{R}$. Lemma 2.4.4 then implies that for all $\mathcal{Y}' \subset\subset \mathcal{Y}$, there exists a viscosity solution $u \in \mathcal{C}^{0,\beta}(\mathcal{Y}')$ (for all $\beta \in (0,1)$) of the equation

$$-\nabla u \cdot (A \nabla u) - k^y + k_0 = 0.$$

Starting from this point, the proof is cut into two steps.

Step 1. For all $y \in \mathcal{Y}$, $k_0 \geqslant k^y$. Let $y \in \mathcal{Y}$ and let us show that $k_0 \geqslant k^y$. First, assume that there exists a function ϕ which is $\mathcal{C}^2$ in a neighbourhood of y and such that $u - \phi$ has a local minimum at y. Then, we have $-\nabla\phi \cdot (A\nabla\phi) - k^y + k_0 \geqslant 0$ and, owing to the ellipticity of A, we have $\nabla\phi \cdot (A\nabla\phi) \geqslant 0$. Thus $k_0 \geqslant k^y$.

If there is no such ϕ, we construct a sequence $y_n \to y$ such that y_n is associated with a ϕ_n, and apply the same reasoning at y_n. Namely, we use the $\mathcal{C}^{0,1/2}$-regularity of u to define:

$$a_n := \sup_{y' \in \mathcal{Y}, 0 < \|y'-y\| < 1/n} \frac{|u(y') - u(y)|}{\sqrt{\|y' - y\|}}.$$

We set:

$$b_n := \inf_{y' \in \mathcal{Y}, \|y'-y\| < 1/n} \left(u(y') + 4a_n n^{3/2} \left\| y' - y \right\|^2 \right)$$

and we let

$$\phi_n(y') := b_n - 4a_n n^{3/2} \left\| y' - y \right\|^2.$$

We note that $u(y) \geqslant b_n$ and that $\phi_n(y') \leqslant u(y')$ for $\|y - y'\| \leqslant 1/n$. Moreover, there exists y_n with $\|y_n - y\| \leqslant 1/n$ such that $\phi_n(y_n) = u(y_n)$. Last, for $1/(2n) < \|y' - y\| \leqslant 1/n$,

$$u(y') \geqslant u(y) - a_n \sqrt{\|y' - y\|} \geqslant u(y) - \frac{a_n}{\sqrt{n}},$$

so, using $1/(2n) < \|y' - y\|$,

$$\begin{aligned} u(y') &> u(y) - 4a_n n^{3/2} \left\| y' - y \right\|^2 \\ &\geqslant b_n - 4a_n n^{3/2} \left\| y' - y \right\|^2 = \phi_n(y'). \end{aligned}$$

To summarise, we have: $\|y_n - y\| \leqslant 1/n$, $\phi_n(y_n) = u(y_n)$ and

$$\begin{aligned} &\phi_n(y') \leqslant u(y') && \text{for all } \left\| y' - y \right\| \leqslant 1/n, \\ &\phi_n(y') < u(y') && \text{for all } 1/(2n) < \left\| y' - y \right\| \leqslant 1/n. \end{aligned}$$

Therefore, $\|y_n - y\| \leqslant 1/(2n)$ and $u - \phi_n$ has a local minimum at y_n. Since ϕ_n is $\mathcal{C}^2$, we conclude as above that $k_0 \geqslant k^{y_n}$. We get, using $y_n \to y$ and the continuity of $y \mapsto k^y$, that $k_0 \geqslant k^y$.

Step 2. There exists $y_\infty \in \overline{\mathcal{Y}}$ such that $k_0 = k^{y_\infty}$. Recall that the functions $u_n = \varepsilon_n \ln(\varphi_{\varepsilon_n}(\cdot, 0))$ have been defined in the proof of Lemma 2.4.4. For $n \geqslant 0$, let $y_n \in \overline{\mathcal{Y}}$ satisfy

$$u_n(y_n) = \max_{y \in \overline{\mathcal{Y}}} u_n(y).$$

Since $\overline{\mathcal{Y}}$ is compact, the sequence $(y_n)_n$ converges, up to extraction, to some $y_\infty \in \overline{\mathcal{Y}}$. By Lemma 2.4.3, maybe up to another extraction, we have

$$\frac{(\mathcal{L}_z + c)\varphi_n(y_n, 0)}{\varphi_n(y_n, 0)} \to k^{y_\infty}.$$

If $y_n \in \mathcal{Y}$, then $\nabla u_n(y_n) = 0$. If $y_n \in \partial\mathcal{Y}$, then the condition $\nu \cdot A\nabla u_n = 0$ on $\partial\mathcal{Y}$ implies that $\nabla u_n(y_n) = 0$. In either case, (2.38) implies that for all $n \geqslant 0$,

$$-\varepsilon_n \nabla \cdot (A\nabla u_n)(y_n) - \varepsilon_n \nabla \cdot B - \frac{(\mathcal{L}_z + c)\varphi_n(y_n, 0)}{\varphi_n(y_n, 0)} + k_n = 0.$$

Taking $n \to +\infty$ gives (using the same estimates as in Step 3 of the proof of Lemma 2.4.4): $-k^{y_\infty} + k_0 = 0$. Hence $k_0 = k^{y_\infty}$ so necessarily

$$k_0 = \max_{y \in \overline{\mathcal{Y}}} k^y.$$

Finally, the limit is unique, so the whole family $(k_\varepsilon)_{\varepsilon>0}$ converges to k_0. □

Now, we prove Theorem 2.1.3: we drop the assumption that $B \equiv 0$, but we assume that $\mathcal{Y}$ is the 1-dimensional torus. There are two cases: either $|\gamma| \geqslant j(M)$, either $|\gamma| < j(M)$. We first prove the former.

Proof of Theorem 2.1.3, case $|\gamma| \geqslant j(M)$. The proof is directly inspired from Section 3 of [119]. We assume that $\mathcal{Y}$ is the 1-dimensional torus. Then $\mathcal{Y} \subset\subset \mathcal{Y}$, so we can take $\mathcal{Y}' = \mathcal{Y}$ in Lemma 2.4.4. We first prove that there exists only one k_0 such that (2.35) has a solution on $\mathcal{Y}$, i.e. a 1-periodic viscosity solution defined on $\mathbb{R}$. Then, we make explicit such a solution and conclude.

Step 1. Uniqueness of k_0 such that (2.35) has a periodic solution. We assume that there exist $k_0 \in \mathbb{R}$ and $\hat{k}_0 > k_0$ such that there are periodic viscosity solutions u and $\hat{u}$ to:

$$\begin{aligned} -A(y)(u'(y))^2 - B(y)u'(y) - k^y + k_0 &= 0, \\ -A(y)(\hat{u}'(y))^2 - B(y)\hat{u}'(y) - k^y + \hat{k}_0 &= 0. \end{aligned}$$

Since $k_0 \neq \hat{k}_0$, we must have $u \neq \hat{u}$. Therefore, up to adding a constant to u, we may assume that there exists an interval $U \subset \mathbb{R}$ such that:

$$\begin{cases} u(y) > \hat{u}(y) & \text{at some point } y \in U, \\ u = \hat{u} & \text{on } \partial U. \end{cases} \tag{2.39}$$

But, since $\hat{k}_0 > k_0$, there is a small $\varepsilon > 0$ such that on U:

$$\begin{aligned} &\varepsilon u + A(y)(u'(y))^2 + B(y)u'(y) \\ &\qquad \leqslant \varepsilon\hat{u} + A(y)(\hat{u}'(y))^2 + B(y)\hat{u}'(y) \end{aligned}$$

in the viscosity sense. Now, with the second line of (2.39), we can apply the maximum principle, which implies that $u \leqslant \hat{u}$ in U. We reach a contradiction with the first line of (2.39): this ensures the uniqueness of the limit of k_ε as $\varepsilon \to 0$.

By Lemma 2.4.1, the family $(k_\varepsilon)_{\varepsilon>0}$ is bounded. Hence the whole family $(k_\varepsilon)_\varepsilon$ converges to k_0 as $\varepsilon \to 0$:

$$k_0 = \lim_{\varepsilon \to 0} k_\varepsilon.$$

Let us rewrite (2.35) in the following way:

$$-A\left(u'+\frac{B}{2A}\right)^2-\left(k^y-\frac{B^2}{4A}\right)+k_0=0. \tag{2.40}$$

Step 2. Conclusion. Recall that

$$\gamma=\int_0^1\frac{B(y)}{2A(y)}\,\mathrm{d}y,\qquad j(M)=\int_0^1\sqrt{\frac{M-k^y+\frac{B(y)^2}{4A(y)}}{A(y)}}\,\mathrm{d}y.$$

If $\gamma\geqslant j(M)$, then there exists $k\geqslant M$ such that

$$\int_0^1\frac{B(y)}{2A(y)}\,\mathrm{d}y=j(k)=\int_0^1\sqrt{\frac{k-\left(k^y-\frac{B(y)^2}{4A(y)}\right)}{A(y)}}\,\mathrm{d}y. \tag{2.41}$$

Then, the function

$$\overline{u}(y):=-\int_0^y\frac{B(y')}{2A(y')}\,\mathrm{d}y'+\int_0^y\sqrt{\frac{k-\left(k^{y'}-\frac{B(y')^2}{4A(y')}\right)}{A(y')}}\,\mathrm{d}y'$$

is 1-periodic. Moreover, the function $\overline{u}$ solves (2.40) (with k instead of k_0) and, therefore, solves (2.35). By Lemma 2.4.4 and the uniqueness stated in Step 1, we conclude that k_0 and k must coincide, so that k_0 satisfies (2.41):

$$\int_0^1\frac{B(y)}{2A(y)}\,\mathrm{d}y=j(k_0).$$

This concludes the proof for $\gamma\geqslant j(M)$. If $\gamma\leqslant -j(M)$, then there exists $k\geqslant M$ such that

$$-\int_0^1\frac{B(y)}{2A(y)}\,\mathrm{d}y=j(k)=\int_0^1\sqrt{\frac{k-\left(k^y-\frac{B(y)^2}{4A(y)}\right)}{A(y)}}\,\mathrm{d}y.$$

We conclude in the same way, with the function

$$\overline{u}_{\gamma<0}(y):=\int_0^y\frac{B(y')}{2A(y')}\,\mathrm{d}y'+\int_0^y\sqrt{\frac{k-\left(k^{y'}-\frac{B(y')^2}{4A(y')}\right)}{A(y')}}\,\mathrm{d}y'$$

instead of $\overline{u}$. □

Proof of Theorem 2.1.3, case $|\gamma|\leqslant j(M)$. First, we consider $0\leqslant\gamma<j(M)$, i.e.

$$0\leqslant\int_0^1\frac{B(y)}{2A(y)}\,\mathrm{d}y<\int_0^1\sqrt{\frac{M-k^y+\frac{B(y)^2}{4A(y)}}{A(y)}}\,\mathrm{d}y.$$

We assume for convenience that M is reached at 0, i.e.

$$M = \max_{y\in\mathcal{Y}} \left(k^y - \frac{B(y)^2}{4A(y)} \right) = k^0 - \frac{B(0)^2}{4A(0)}.$$

Since all these functions are 1-periodic, M is also reached at each $y \in \mathbb{Z}$.

Step 1. Construct a viscosity solution of an associated problem. We define a 2-periodic function S by

$$S(y) := \begin{cases} 1, & y \in [0,1), \\ -1, & y \in [1,2). \end{cases}$$

Now, we define v by:

$$v(y) := -\int_0^y \frac{B(y')}{2A(y')}\,\mathrm{d}y' + \int_0^y S(y')\sqrt{\frac{M - \left(k^{y'} - \frac{B(y')^2}{4A(y')}\right)}{A(y')}}\,\mathrm{d}y'.$$

For $y_0 \in \mathbb{R}\setminus\mathbb{Z}$, the function S is continuous at y_0 so v is differentiable at y_0, and satisfies, at $y = y_0$,

$$-A(v')^2 - Bv' - k^y + M = 0. \tag{2.42}$$

For $y_0 \in \mathbb{Z}$, we have

$$M - \left(k^{y_0} - \frac{B(y_0)^2}{4A(y_0)} \right) = 0,$$

so v is also differentiable at y_0 and satisfies (2.42) at $y = y_0$ in the classical sense. In particular, v is a viscosity solution of (2.42).

Step 2. Prove a uniqueness result and conclude. Let $k_0 \in \mathbb{R}$ be a limit of a subsequence of $(k_\varepsilon)_\varepsilon$ and let u be given by Lemma 2.4.4. We have $v(0) = 0$ and $v(1) = j(M) - \gamma > 0$. We add a constant to u in such a way that $u(0) \in (0, v(1))$; Equation (2.35) remains satisfied by u.

We have, by 1-periodicity of u:

$$u(0) > v(0), \qquad u(1) < v(1).$$

We note that

$$y \mapsto v(y) + \gamma y$$

is 2-periodic; therefore, we have $v(y) \to +\infty$ as $y \to -\infty$ and $v(y) \to -\infty$ as $y \to +\infty$. Thanks to these elements, we get the existence of $y_0 < 0$, $y_1 \in (0,1)$ and $y_2 > 1$ such that $u(y_i) = v(y_i)$ for all $i = 1,2,3$. Therefore, there exist two bounded intervals $U := (y_0, y_1)$ and $U' := (y_1, y_2)$ such that:

$$\begin{cases} u(y) > v(y) & \text{at some point } y \in U, \\ v(y) > u(y) & \text{at some point } y \in U', \\ u = v & \text{on } \partial U \text{ and } \partial U'. \end{cases} \tag{2.43}$$

Recall that v is a viscosity solution of (2.42) and that u is a viscosity solution of (2.42) but with k_0 instead of M. Using the same reasoning as in Step 1 of the previous proof (starting from (2.39)), the first and last line of (2.43) imply that $M \leqslant k_0$; the second and last line

of (2.43) imply that $M \geqslant k_0$. Hence, $k_0 = M$.

Finally, the case $-j(M) < \gamma \leqslant 0$ can be proved in the same way, by considering

$$v_{\gamma<0}(y) := \int_0^y \frac{B(y')}{2A(y')}\,\mathrm{d}y' + \int_0^y S(y')\sqrt{\frac{M - \left(k^{y'} - \frac{B(y')^2}{4A(y')}\right)}{A(y')}}\,\mathrm{d}y'$$

instead of v. □

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Chapter 3

The effect of the advection term

This chapter is based on the preprint [48]:

N. Boutillon, F. Hamel, L. Roques, *Periodic KPP equations: new insights into persistence, spreading, and the role of advection*, preprint hal-05005130.

Abstract

We focus on the persistence and spreading properties for a heterogeneous Fisher-KPP equation with advection. After reviewing the different notions of persistence and spreading speeds, we focus on the effect of the direction of the advection term, denoted by b. First, we prove that changing b to $-b$ can have an effect on the spreading speeds and the ability of persistence. Next, we provide a class of relationships between the intrinsic growth term r and the advection term b such that changing b to $-b$ does *n*ot change the spreading speeds and the ability of persistence. We briefly mention the cases of slowly and rapidly varying environments, and bounded domains. Lastly, we show that in general, the spreading speeds are not controlled by the ability of persistence, and conversely. However, when there is no advection term, the spreading speeds are controlled by the ability of persistence, though the converse still does not hold.

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3.1 Introduction

In this chapter, we focus on the persistence and spreading properties of an invasive species living in a heterogeneous periodic environment. We address the following questions:

1. Does the direction of an advection force influence the ability of persistence and the leftward and rightward spreading speeds of the species?

2. Does a better ability of persistence imply higher spreading speeds of the species?

To answer these questions, we work in the formalism of reaction-diffusion equations in a heterogeneous periodic environment, with an advection term:

$$\partial_t u = \partial_{xx} u - \partial_x(b(x)u) + f(x,u), \quad t > 0,\ x \in \mathbb{R}, \tag{3.1}$$

with periodic coefficients in x and unknown function $u(t,x) \geqslant 0$. Equations of this type are commonly considered to model the dynamical properties and propagation phenomena of a population, often assumed to be initially compactly supported, in an unbounded heterogeneous medium [23, 57, 198, 208, 220, 224, 227]. The first objective of this chapter is to analyse the effect of replacing b with $-b$ in the advection term. In particular, a natural question is whether this modification affects the ability of persistence of the population. Due to the periodic nature of the problem, we will see that the answer is not straightforward and cannot be obtained through trivial reasoning. The second objective of this chapter is to study the relationship between the ability of persistence and the spreading speeds of the population, when the initial condition has a compact support.

Before proceeding further, let us clarify the assumptions and precisely define the concepts of persistence and spreading.

Main assumptions.

Throughout this chapter, the function b is assumed to be 1-periodic and of class $\mathcal{C}^{1,\alpha}(\mathbb{R})$, for some $\alpha \in (0,1)$. We assume that the function $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R},\ (x,u) \mapsto f(x,u)$ is of class $\mathcal{C}^{0,\alpha}_{\mathrm{loc}}(\mathbb{R} \times \mathbb{R}_+)$, and that $\frac{\partial f}{\partial u}$ exists and is of class $\mathcal{C}^{0,\alpha}_{\mathrm{loc}}(\mathbb{R} \times \mathbb{R}_+)$. We also assume that f is 1-periodic with respect to x and that

$$f(x,0) = 0 \ \text{ for all } x \in \mathbb{R}. \tag{3.2}$$

We define, for $x \in \mathbb{R}$,

$$r(x) := \frac{\partial f}{\partial u}(x,u)\bigg|_{u=0}. \tag{3.3}$$

The function r is then 1-periodic and of class $\mathcal{C}^{0,\alpha}(\mathbb{R})$. Last, we assume, throughout this chapter, that the following strong variant of the KPP (standing for Kolmogorov-Petrovsky-Piskunov) assumption holds:

$$\forall x \in \mathbb{R},\ u \mapsto \frac{f(x,u)}{u} \text{ is decreasing in } u > 0 \tag{3.4}$$

and

$$\exists M \geqslant 0,\ \forall u \geqslant M,\ \forall x \in \mathbb{R},\ f(x,u) - b'(x)u \leqslant 0. \tag{3.5}$$

These assumptions, together with the other one (3.9) below on the linear instability of the trivial state, will ensure the existence and uniqueness of a positive 1-periodic steady state to (3.1). When we see u as a population density, the coefficient $r(x)$ is interpreted as the intrinsic growth rate of the population. Examples of functions f satisfying the above assumptions include $f(x,u)=r(x)\,u(1-u)$ or $f(x,u)=u(r(x)-\gamma(x)u)$, where r and γ are $\mathcal{C}^{0,\alpha}(\mathbb{R})$ 1-periodic positive functions.

Characterisation of persistence and spreading.

For this kind of reaction-diffusion equation where the KPP assumption is satisfied, it is well-known that the ability of persistence, as well as the asymptotic spreading speeds, for solutions that are initially bounded, continuous, non-negative and compactly supported, can be characterised by principal eigenvalues of elliptic operators with periodicity conditions. Namely, for $\lambda\in\mathbb{R}$, we introduce the operator:

$$\mathcal{L}_\lambda[r;b]\,:\,\psi\mapsto\psi''+(b+2\lambda)\psi'+\left(\lambda^2+\lambda\,b+r\right)\psi, \tag{3.6}$$

acting on 1-periodic $\mathcal{C}^2$ functions. By the Krein-Rutman theorem, for each $\lambda\in\mathbb{R}$, there exists a unique $k_\lambda[r;b]\in\mathbb{R}$ such that there is a 1-periodic function $\psi\in\mathcal{C}^{2,\alpha}(\mathbb{R})$ satisfying

$$\mathcal{L}_\lambda[r;b]\,\psi=k_\lambda[r;b]\,\psi\ \text{ in }\mathbb{R},\quad \psi>0\ \text{ in }\mathbb{R}. \tag{3.7}$$

We say that $k_\lambda[r;b]$ is the principal eigenvalue of $\mathcal{L}_\lambda[r;b]$. We point out that $\mathcal{L}_0[r;b]$ is the adjoint of the operator

$$\mathcal{L}_0[r;b]^*:\psi\mapsto\psi''-(b\psi)'+r\psi,$$

still acting on 1-periodic $\mathcal{C}^2$ functions, and which is obtained from the linearisation of the right-hand side of (3.1) around the trivial state 0. In particular, $\mathcal{L}_0[r;b]$ and $\mathcal{L}_0[r;b]^*$ have the same principal eigenvalue $k_0[r;b]$.

The concept of *persistence* refers to a scenario where, given any function u_0 that is bounded, continuous, non-negative, and not identically equal to zero, the solution u to the Cauchy problem (3.1) with $u(0,\cdot)=u_0$ satisfies

$$\limsup_{t\to+\infty}\|u(t,\cdot)\|_{L^\infty(\mathbb{R})}>0. \tag{3.8}$$

The concept of persistence is directly opposed to the concept of *extinction*, which means that the solution u converges uniformly to 0 at $t\to+\infty$. Actually, due to (3.2) and (3.4), it follows from [27, Theorem 2.1 and Remark 3.1] that, if $k_0[r;b]\leqslant 0$, then any solution u of (3.1) with a bounded continuous non-negative initial condition u_0 goes to extinction as $t\to+\infty$. On the other hand, the condition

$$k_0[r;b]>0, \tag{3.9}$$

together with (3.2) and (3.4)–(3.5), warrants the existence and uniqueness of a positive 1-periodic steady state $p>0$ to (3.1), by [27, Theorem 2.1 and Remark 3.1] and [29, Lemma 3.5, Proposition 6.3 and Theorem 6.5]. Furthermore, when there is no advection ($b=0$), condition (3.9) implies that $u(t,\cdot)\to p$ as $t\to+\infty$ locally uniformly in $\mathbb{R}$, for any continuous non-negative compactly supported initial condition $u_0\not\equiv 0$ (by [27, Theorem 2.6]). In the general case $b\not\equiv 0$, the condition for local convergence to p must be adapted. Namely, if $k_0[r-b'/2-b^2/4;0]>0$, then (3.9) holds and $u(t,\cdot)\to p$ as $t\to+\infty$ locally uniformly in $\mathbb{R}$ (see Proposition 3.6.1 in Section 3.6).

More generally speaking, by [220, Theorems 2.2, 2.3], condition (3.9) implies persistence of the solution u to (3.1), in the sense of (3.8), with any continuous non-negative compactly supported initial condition $u_0 \not\equiv 0$.[1] Moreover, under condition (3.9), there are two *spreading speeds* $c_\pm[r;b] \in \mathbb{R}$, defined by

$$\begin{cases} c_+[r;b] := \inf\Big\{c \in \mathbb{R} \ / \ \forall\, w > c,\, u(t,wt) \to 0 \text{ as } t \to +\infty\Big\}, \\ c_-[r;b] := \inf\Big\{c \in \mathbb{R} \ / \ \forall\, w > c,\, u(t,-wt) \to 0 \text{ as } t \to +\infty\Big\}. \end{cases} \tag{3.10}$$

The two spreading speeds $c_\pm[r;b]$ are independent of u_0, and satisfy $-c_-[r;b] < c_+[r;b]$, and

$$\forall\, w \leqslant w' \in (-c_-[r;b], c_+[r;b]), \qquad \max_{wt \leqslant x \leqslant w't} |u(t,x) - p(x)| \to 0 \text{ as } t \to +\infty.$$

When condition (3.9) is not fulfilled, that is, when $k_0[r;b] \leqslant 0$, then we set $c_\pm[r;b] := -\infty$, which is coherent with (3.10) since $\|u(t,\cdot)\|_{L^\infty(\mathbb{R})} \to 0$ as $t \to +\infty$ in this case.

When the two speeds $c_-[r;b]$ and $c_+[r;b]$ are positive, $c_+[r;b]$ is known as the *rightward spreading speed* and may be interpreted as follows: an observer moving rightwards at a speed greater than $c_+[r;b]$ will observe the population density tend to zero. Conversely, an observer moving rightwards at a nonnegative speed smaller than $c_+[r;b]$ will observe a population density that remains above a positive level. Analogously, $c_-[r;b]$ is called the *leftward spreading speed* and can be interpreted in the same way with "left" instead of "right". The positivity of both speeds $c_-[r;b]$ and $c_+[r;b]$ is guaranteed for instance when $b = 0$ and $k_0[r;0] > 0$ and, more generally speaking, there even holds

$$c_-[r;b] = c_+[r;b] > 0 \quad \text{ when } \int_0^1 b = 0 \text{ and } k_0[r,b] > 0, \tag{3.11}$$

see Proposition 4.3.9 of Chapter 4. We point out that such an equality does not hold for bistable-type equations, for which the leftward and rightward spreading speeds are not equal in general, even without advection term [76].

The concept of spreading speed is somewhat subtle for general periodic advection terms b, as in our setting. In particular, we can have $c_-[r;b] < 0$ or $c_+[r;b] < 0$. Indeed, for instance, if r is equal to a positive constant r_0 and if b is equal to a constant b_0, then

$$c_+[r_0;b_0] = b_0 + 2\sqrt{r_0} \ \text{ and } \ c_-[r_0;b_0] = -b_0 + 2\sqrt{r_0}, \tag{3.12}$$

as immediately follows from [15]. In one of the situations $c_-[r;b] < 0$ or $c_+[r;b] < 0$, it means that a compactly supported initial datum gives rise to a solution to (3.1) which does not propagate to the left (if $c_-[r;b] < 0$) or to the right (if $c_+[r;b] < 0$), see Figure 3.1.

As a matter of fact, the two formulas (3.12) when $r = r_0$ and $b = b_0$ are constant are particular cases of more general so-called Freidlin-Gärtner formulas. More precisely, by [220, Theorems 2.4, 2.5] and [25, Theorem 1.14], the spreading speeds $c_+[r;b]$ and $c_-[r;b]$ are characterised by:

$$c_+[r;b] = \inf_{\lambda > 0} \frac{k_\lambda[r;b]}{\lambda}, \qquad c_-[r;b] = \inf_{\lambda > 0} \frac{k_{-\lambda}[r;b]}{\lambda}, \tag{3.13}$$

where we recall that, for $\lambda \in \mathbb{R}$, $k_\lambda[r;b]$ denotes the principal periodic eigenvalue of the operator $\mathcal{L}_\lambda[r;b]$ given in (3.6)–(3.7). Furthermore, as in the proof of [23, Proposition 5.7],

[1] Persistence then holds even if the initial condition is not compactly supported, by the comparison principle.

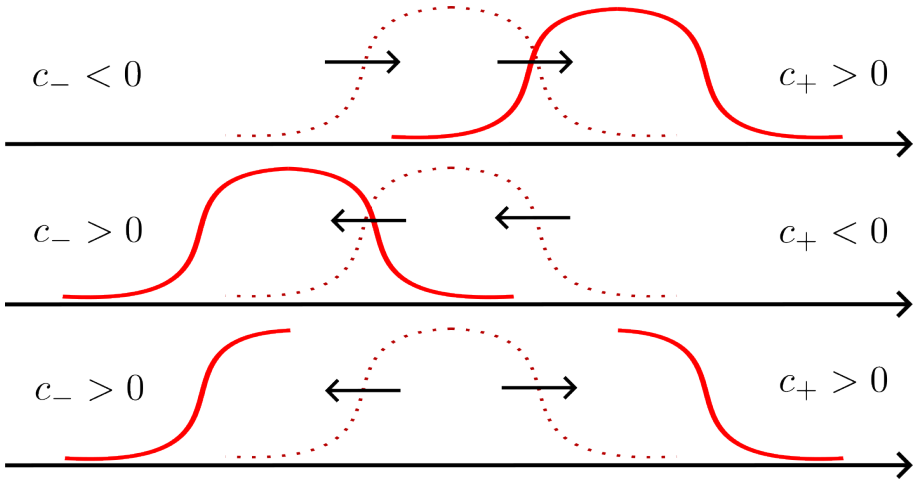

Figure 3.1: Three different situations. In each case, the dotted plot is the initial configuration and the full-line plot is taken at a later time.

the function $\lambda \mapsto k_\lambda[r;b]$ is convex in $\mathbb{R}$, whence continuous in $\mathbb{R}$, and, from (3.7) applied at maximum or minimum points of a principal eigenfunction ψ, it follows that

$$\min_{\mathbb{R}}(\lambda^2+\lambda b+r) \leqslant k_\lambda[r;b] \leqslant \max_{\mathbb{R}}(\lambda^2+\lambda b+r). \tag{3.14}$$

Therefore, $k_{\pm\lambda}[r;b]/\lambda \to +\infty$ as $\lambda \to +\infty$ and, together with (3.9), it follows that both infima in (3.13) are reached. The Freidlin-Gärtner formulas (3.13), which were first obtained in [103] in the case $b=0$, will be central to this chapter, as they imply that studying the principal eigenvalues of the operators $\mathcal{L}_\lambda[r;b]$ is sufficient to study the spreading speeds. We lastly mention that other formulas of the spreading speeds have been given for equations in higher dimensional media [26, 99, 103, 220] or with other types of reactions f [203] .

3.2 Main results

Section 3.2.1 is devoted to the study of the effect of changing b to $-b$ on the ability of persistence, measured by $k_0[r;b]$, and the spreading speeds $c_\pm[r;b]$. Section 3.2.2 is concerned with the link between the ability of persistence and the spreading speeds, and in particular on the non-monotone relationship between these two concepts. Some of the results focus on $c_+[r;b]$ only, but analogous results would also hold true with $c_-[r;b]$.

3.2.1 The influence of inverting the direction of the advection

We start by addressing our first main question, that is, the effect of the direction of the advection term on the long-time dynamics of (3.1). Namely, for fixed 1-periodic functions $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ and $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$, we compare $k_0[r;b]$ with $k_0[r;-b]$, and $c_\pm[r;b]$ with $c_\pm[r;-b]$. Although this problem seems natural, it appears that it has not been investigated until now. We first show that changing b to $-b$ may or may not change the ability of persistence (measured by $k_0[r;\pm b]$) and the spreading speeds. This may occur even if b has zero mean. We next show that, on the contrary, the spreading speeds are not affected by the change of b to $-b$ in the limit of rapidly or slowly oscillating media if b has zero mean. We lastly

investigate the effect of the change of b to $-b$ on the ability of persistence in bounded domains with Dirichlet boundary conditions.

General results.

We first show that in general, changing b to $-b$ really has an influence on the ability of persistence and the spreading speeds in general.

Proposition 3.2.1. *For every 1-periodic function $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ with $b \not\equiv 0$ and $\int_0^1 b = 0$, there exists a 1-periodic function $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that*

$$k_0[r;b] \neq k_0[r;-b], \quad c_+[r;b] \neq c_+[r;-b], \quad \text{and} \quad c_+[r;b] \neq c_-[r;-b].$$

Let us now focus on the preservation of the ability of persistence and the spreading speeds upon a change of direction of the advection term. Our first result in this direction exhibits two classes of pairs $[r;b]$ such that these quantities are left unchanged.

Theorem 3.2.2. *Let $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ and $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ be 1-periodic functions. Assume that*

(i) either there exists $x_0 \in \mathbb{R}$ such that $r(x) = r(x_0 - x)$ and $b(x) = b(x_0 - x)$ for all $x \in \mathbb{R}$,

(ii) or there exist $\beta \in \mathbb{R}$ and $\gamma \in \mathbb{R}$ such that $r = \beta + \gamma b$.

Then

$$k_0[r;b] = k_0[r;-b] \quad \text{and} \quad c_+[r;b] = c_-[r;-b].$$

The first item of Theorem 3.2.2 is due to a straightforward symmetry: letting ψ be a positive principal eigenfunction of (3.7) associated with $\mathcal{L}_\lambda[r;b]$, the evenness of r and b implies that the function $x \mapsto \psi(-x)$ is a positive eigenfunction associated with $\mathcal{L}_{-\lambda}[r;-b]$, which implies that $k_\lambda[r;b] = k_{-\lambda}[r;-b]$ for all $\lambda \in \mathbb{R}$, whence $c_+[r;b] = c_-[r;-b]$ by (3.13).

The second item of Theorem 3.2.2 is unexpected and more involved. It implies in particular that, for constant $r = r_0$ and for any 1-periodic $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$, we have $k_0[r_0;b] = k_0[r_0;-b]$, and $c_+[r_0;b] = c_-[r_0;-b]$. In the proof, under the conditions of item (ii), we will exhibit an explicit relationship between the principal eigenfunctions ϕ^+ and ϕ^- of the operators $\mathcal{L}_0[r;b]$ and $\mathcal{L}_0[r;-b]$, respectively. For example, when b has zero mean, this relationship reads:

$$\phi^-(x) = \Big((\phi^+)'(x) + \gamma\phi^+(x)\Big) \exp\left(\int_0^x b(y)\,\mathrm{d}y\right).$$

The general relationship for 1-periodic functions $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$, which may have nonzero mean, is rather involved. Some remarks about the origin of this relationship are given in Section 3.3 and in Section 3.7. See also Figure 3.2 (top panel) for a numerical illustration of the relationship between ϕ^+ and ϕ^- when item (ii) of Theorem 3.2.2 is satisfied.

When b has zero mean, the leftward and rightward spreading speeds $c_\pm[r;b]$ coincide, see (3.11) when $k_0[r;b] > 0$, while they are both equal to $-\infty$ when $k_0[r;b] \leqslant 0$. Therefore, a consequence of Theorem 3.2.2 is the following corollary.

Corollary 3.2.3. *Let $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ and $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ be 1-periodic functions. Assume that $\int_0^1 b = 0$ and that either (i) or (ii) of Theorem 3.2.2 holds. Then*

$$k_0[r;b] = k_0[r;-b] \quad \text{and} \quad c_+[r;b] = c_+[r;-b] = c_-[r;-b] = c_-[r;b].$$

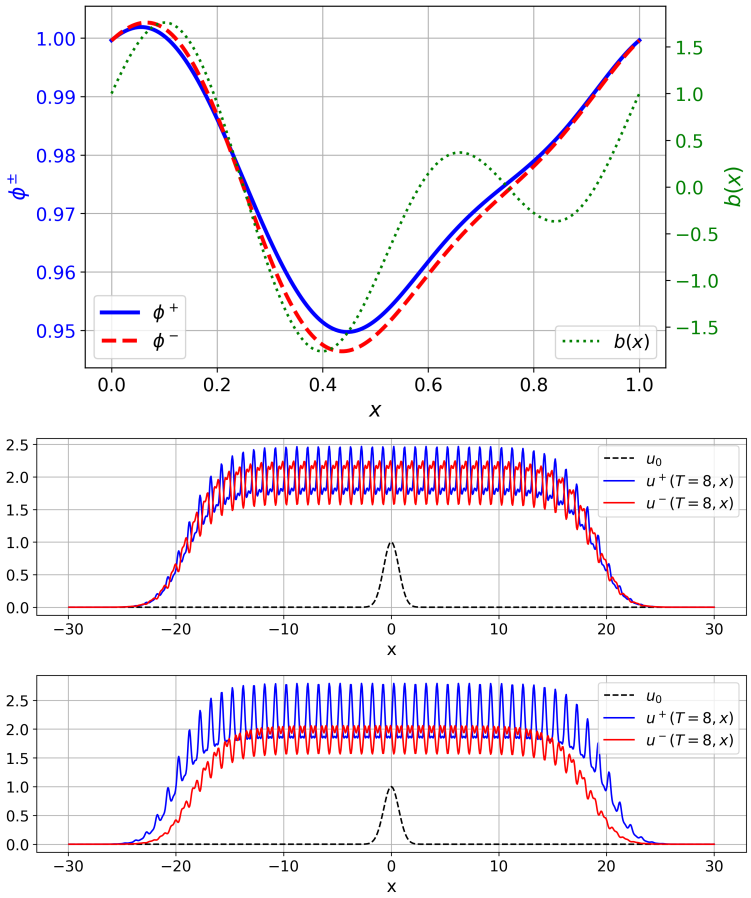

Figure 3.2: The top panel illustrates the nontrivial relationship between ϕ^+ and ϕ^- when item (ii) of Theorem 3.2.2 is satisfied: $b(x) = \cos(2\pi x) + \sin(4\pi x)$ and $r(x) = 2 + b(x)$. The middle panel shows the solutions $u^+ := u[r;b]$ and $u^- := u[r;-b]$ of (3.1) with the same coefficients as in the top panel. The bottom panel shows the solutions $u^+ := u[r;b]$ and $u^- := u[r;-b]$ of (3.1) with $b(x) = \cos(2\pi x) + \sin(4\pi x)$ and $r(x) = 2 + 2\sin(2\pi x)$, not satisfying condition (ii) of Theorem 3.2.2.

In particular, Theorem 3.2.2 and Corollary 3.2.3 imply that, for a constant intrinsic growth term r, the direction of an advection term with zero mean has no influence on the spreading speeds – even this is not at all trivial without any symmetry assumption.

As an illustration of Proposition 3.2.1, Theorem 3.2.2, and Corollary 3.2.3, we numerically computed the values of $k_0[r;b]$, $k_0[r;-b]$, and $c_+[r;b]$, $c_+[r;-b]$ for different coefficients r and b, either satisfying or violating condition (ii) of Theorem 3.2.2. Specifically, we took $b(x) = \cos(2\pi x) + \sin(4\pi x)$. Then, with $r(x) = 2 + b(x)$, we found that $k_0[r;b] = k_0[r;-b] \approx 2.016$ and $c_+[r;b] = c_+[r;-b] \approx 2.819$. In contrast, when $r(x) = 2 + \cos(4\pi x) + \sin(2\pi x)$, condition (ii) was not met, yielding $k_0[r;b] \approx 2.055$ and $k_0[r;-b] \approx 1.976$, while $c_+[r;b] \approx 2.838$ and $c_+[r;-b] \approx 2.799$. In contrast, when $r(x) = 2 + 2\sin(2\pi x)$, condition (ii) was not met, yielding $k_0[r;b] \approx 2.221$ and $k_0[r;-b] \approx 1.892$, while $c_+[r;b] \approx 2.933$ and $c_+[r;-b] \approx 2.745$. The corresponding solutions of the Cauchy problem associated with (3.1), with a compactly supported initial condition u_0, at the fixed time $T = 8$, are depicted in Figure 3.2 (middle and bottom panels). These numerical computations were performed using the Readi2Solve toolbox [199] (see readi2solve.biosp.org).

Slow or fast oscillations.

To state our second result about the effect of the direction of the advection term on the long-time dynamics of (3.1), we vary the spatial period of the underlying medium and we consider rapidly or slowly oscillating media. To do so, we introduce further notations: for fixed 1-periodic functions $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ and $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$, we let, for any $L > 0$,

$$x \mapsto r_L(x) := r\left(\frac{x}{L}\right) \quad \text{and} \quad x \mapsto b_L(x) := b\left(\frac{x}{L}\right)$$

be the L-periodic versions of r and b. The principal eigenvalues $k_\lambda[r_L; b_L]$ are still defined as in (3.7), by the Krein-Rutman theorem, and they are now associated with L-periodic principal eigenfunctions. The spreading speeds $c_\pm[r_L; b_L]$ are defined as in (3.13) but with $k_{\pm\lambda}[r_L; b_L]$ instead of $k_{\pm\lambda}[r; b]$.

The following result shows in particular that, in rapidly oscillating media ($L \to 0$) and in slowly oscillating media ($L \to +\infty$), changing b_L to $-b_L$ does not affect the limiting spreading speeds if b has zero mean.

Proposition 3.2.4. *If* $\displaystyle\int_0^1 r > 0$, *then*

$$\lim_{L\to 0} k_0[r_L; b_L] = \lim_{L\to 0} k_0[r_L; -b_L] = \int_0^1 r > 0$$

and

$$c_+[r_L; b_L] - c_+[r_L; -b_L] \underset{L\to 0}{\longrightarrow} 2\int_0^1 b \quad \text{and} \quad \lim_{L\to 0} c_+[r_L; b_L] = \lim_{L\to 0} c_-[r_L; -b_L]. \tag{3.15}$$

If $\displaystyle\int_0^1 b = 0$ *and* $\max_{\mathbb{R}}(r - b^2/4) > 0$, *then*

$$\lim_{L\to+\infty} k_0[r_L; b_L] = \lim_{L\to+\infty} k_0[r_L; -b_L] = \max_{\mathbb{R}}\left(r - \frac{b^2}{4}\right) > 0$$

and

$$\lim_{L\to+\infty} c_+[r_L; b_L] = \lim_{L\to+\infty} c_+[r_L; -b_L] = \lim_{L\to+\infty} c_-[r_L; b_L] = \lim_{L\to+\infty} c_-[r_L; -b_L].$$

The proof of this proposition is based on more or less explicit computations of the limits as $L \to 0$ or $L \to +\infty$ of the induced quantities, which are partly provided by [81, 117, 119, 126].

Bounded domains and other boundary conditions.

In bounded domains, spreading is no longer possible, but we may still study the ability of persistence. As we only work in the one-dimensional setting, we focus for simplicity on the bounded domain $[-1, 1]$.

For $r \in \mathcal{C}^{0,\alpha}([-1,1])$ and $b \in \mathcal{C}^{1,\alpha}([-1,1])$, we let $k_0^d[r; b]$ be the principal eigenvalue defined

by the Dirichlet eigenproblem

$$\begin{cases} \phi'' + b\phi' + r\phi = k_0^d[r;b]\phi \ \text{ in } [-1,1], \\ \phi(-1) = \phi(1) = 0, \ \ \phi > 0 \text{ in } (-1,1). \end{cases} \tag{3.16}$$

We provide counter-examples to item (ii) of Theorem 3.2.2, showing a strong contrast between the periodic conditions and the Dirichlet boundary condition regarding the effect of the direction of the advection on the ability of persistence.

Proposition 3.2.5. *Let $b(x) := x$. For any $r \in \mathcal{C}^{0,\alpha}([-1,1])$, we have*

$$k_0^d[r;b] = k_0^d[r;-b] - 1.$$

3.2.2 Relationship between the ability of persistence and the spreading speed

We now focus on our second question: *Does a better ability of persistence imply higher spreading speeds of the invasive species?* Although the intuition might suggest that the answer to this question is *yes*, we will construct counter-examples in which increasing the ability of persistence decreases the spreading speeds.

First, we point out that $k_0[r;b] > k_0[\widetilde{r};\widetilde{b}]$ does *not* imply in general that $c_+[r;b] > c_+[\widetilde{r};\widetilde{b}]$ or similarly $c_-[r;b] > c_-[\widetilde{r};\widetilde{b}]$. This is a consequence of Theorem 4.3.10 of Chapter 4, which implies that, for r with $\max_{\mathbb{R}} r > 0$ and b well-chosen,

$$k_0[r;\gamma b] \underset{\gamma\to+\infty}{\longrightarrow} \max_{\mathbb{R}} r > 0 \ \text{ and } \ c_+[r;\gamma b] \underset{\gamma\to+\infty}{\longrightarrow} 0.$$

Therefore, with r_0 constant such that $0 < r_0 < \max_{\mathbb{R}} r$, one has, for all $\gamma > 0$ large enough,

$$k_0[r;\gamma b] > r_0 = k_0[r_0;0] \ \text{ and } \ c_+[r;\gamma b] < 2\sqrt{r_0} = c_+[r_0;0]. \tag{3.17}$$

Second, the converse implication is also wrong: $c_+[r;b] > c_+[\widetilde{r};\widetilde{b}]$ (or similarly $c_-[r;b] > c_-[\widetilde{r};\widetilde{b}]$) does *not* imply in general that $k_0[r;b] > k_0[\widetilde{r};\widetilde{b}]$. Formulas (3.17) provide some counter-examples. But, even more simply, taking constants r_0, $\widetilde{r}_0$, b_0 and $\widetilde{b}_0$ with $0 < r_0 < \widetilde{r}_0$ and $b_0 - \widetilde{b}_0 > 2\sqrt{\widetilde{r}_0} - 2\sqrt{r_0} > 0$, we have:

$$c_+[r_0;b_0] = 2\sqrt{r_0} + b_0 > 2\sqrt{\widetilde{r}_0} + \widetilde{b}_0 = c_+[\widetilde{r}_0;\widetilde{b}_0],$$

but

$$0 < k_0[r_0;b_0] = r_0 < \widetilde{r}_0 = k_0[\widetilde{r}_0,\widetilde{b}_0].$$

Further, note that these examples allow one to make the ratio $|c_+[r;b]|/k_0[r;b]$ arbitrarily large or arbitrarily close to 0. Therefore, neither $k_0[r;b]$ or $c_+[r;b]$ is controlled by the other.

These constructions rely heavily on the fact that we may choose $b \not\equiv 0$. The second one makes use of a disequilibrium between spreading to the right and spreading to the left (indeed, we have $c_+[r_0;b_0] > c_+[\widetilde{r}_0,\widetilde{b}_0]$, but $c_-[r_0;b_0] = -b_0 + 2\sqrt{r_0} < -\widetilde{b}_0 + 2\sqrt{\widetilde{r}_0} = c_-[\widetilde{r}_0;\widetilde{b}_0]$ since $0 < r_0 < \widetilde{r}_0$ and $b_0 > \widetilde{b}_0$). In fact, even if we require "equilibrium", in the sense that

$$c_-[r;b] > c_-[\widetilde{r};\widetilde{b}] \ \text{ and } \ c_+[r;b] > c_+[\widetilde{r};\widetilde{b}],$$

we can have $k_0[r;b] < k_0[\widetilde{r};\widetilde{b}]$. To prove it, we will work with $b \equiv 0$, in which case the spreading speed to the left and the spreading speed to the right coincide, that is,

$$c_+[r;0] = c_-[r,0] > 0,$$

as soon as $k_0[r;0] > 0$, as a particular case of (3.11).

In general, what comparisons can be made when $b \equiv 0$? First, it must be recalled that if $r \leqslant \widetilde{r}$, then $k_0[r;0] \leqslant k_0[\widetilde{r};0]$; and if further $k_0[r;0] > 0$, then $0 < c_+[r;0] \leqslant c_+[\widetilde{r};0]$. This is a consequence of the monotonicity of the eigenvalues $k_\lambda[r;0] = k_{-\lambda}[r;0]$ with respect to r. In the sequel, we will go much beyond this immediate observation. On the one hand, we will show that the spreading speed $c_-[r;0] = c_+[r;0]$ is controlled by the ability of persistence $k_0[r;0]$. Namely, if the ability of persistence is low, then the spreading speed must be low as well. On the other hand, we will see that having a low spreading speed does not imply that the ability of persistence is low.

Theorem 3.2.6. *Let $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ be a 1-periodic function such that $k_0[r;0] > 0$.*

(i) There exists a 1-periodic function $\widetilde{r} \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that

$$0 < k_0[r;0] < k_0[\widetilde{r};0] \quad \text{and} \quad c_+[r;0] > c_+[\widetilde{r};0] > 0.$$

(ii) More generally speaking, for any $M > 0$, there exists a 1-periodic function $\widetilde{r} \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that

$$k_0[\widetilde{r};0] > M \quad \text{and} \quad 0 < c_+[\widetilde{r};0] < \frac{1}{M}. \tag{3.18}$$

(iii) If r is constant, then $0 < c_+[\widetilde{r};0] < c_+[r;0] = 2\sqrt{r}$ for every non-constant 1-periodic $\widetilde{r} \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that $0 < k_0[\widetilde{r};0] \leqslant k_0[r;0] = r$.[2]

(iv) If r is non-constant, then

$$0 < c_+[r;0] < 2\sqrt{k_0[r;0]}$$

and there exists a constant $\widetilde{r} > 0$ such that

$$0 < \widetilde{r} = k_0[\widetilde{r};0] < k_0[r;0] \quad \text{and} \quad 2\sqrt{\widetilde{r}} = c_+[\widetilde{r};0] > c_+[r;0] > 0.$$

On the one hand, items (i) and (iv) imply that the relationship between the ability of persistence and the spreading speed is not monotonous. In the proof of item (i), a way to understand this non-monotonicity is to construct an environment with an extremely unfavourable zone, through which individuals will not be able to go, and a very favourable zone, so that the population is yet able to survive. On the other hand, item (iii) shows that there is still a partial monotonicity if one of the intrinsic growth rates is constant. Lastly, item (iv) shows that the spreading speed is always controlled by the ability of persistence, while the converse is false, from item (ii).

Outline of the chapter. Section 3.3 is devoted to the proof of Theorem 3.2.2, which is our main result about the role of the direction of the advection term. The other results on the role of the direction of the advection term (Propositions 3.2.1, 3.2.4 and 3.2.5) are proved

[2] If $\widetilde{r}$ is a positive constant, then $k_0[\widetilde{r};0] = \widetilde{r} > 0$ and $c_+[\widetilde{r};0] = 2\sqrt{\widetilde{r}}$, hence the pairs $(k_0[r;0], k_0[\widetilde{r};0]) = (r, \widetilde{r})$ and $(c_+[r;0], c_+[\widetilde{r};0]) = (2\sqrt{r}, 2\sqrt{\widetilde{r}})$ are ordered the same way as well.

in Section 3.4. Section 3.5 is devoted to the proof of Theorem 3.2.6 on the monotonicity vs. non-monotonicity relationships between the ability of persistence and the spreading speeds in the case $b=0$. Lastly, Section 3.6 deals with a condition for local persistence at large time and Section 3.7 provides some details on the origin of a crucial change of function used in the proof of Theorem 3.2.2 in Section 3.3.

3.3 A class of pairs $[r;b]$ such that $k_\lambda[r;b]=k_{-\lambda}[r;-b]$ and $c_+[r;b]=c_-[r;-b]$: proof of Theorem 3.2.2

This section is devoted to the proof of Theorem 3.2.2. We first prove item (i), and then item (ii).

Proof of Theorem 3.2.2, item (i). Assume that condition (i) holds. Let $\lambda\in\mathbb{R}$ and let $\psi\in\mathcal{C}^{2,\alpha}(\mathbb{R})$ be a positive, 1-periodic principal eigenfunction associated with $\mathcal{L}_\lambda[r;b]$, i.e.

$$\psi''+(b+2\lambda)\psi'+(r+\lambda b+\lambda^2)\psi=k_\lambda[r;b]\,\psi.$$

Set $\varphi(x):=\psi(x_0-x)$, for all $x\in\mathbb{R}$. Using $r(x)=r(x_0-x)$ and $b(x)=b(x_0-x)$ for all $x\in\mathbb{R}$, we get:

$$\varphi''+(-b-2\lambda)\varphi'+(r+\lambda b+\lambda^2)\varphi=k_\lambda[r;b]\,\varphi.$$

The function $\varphi\in\mathcal{C}^{2,\alpha}(\mathbb{R})$ is 1-periodic and positive; thus, it is a principal eigenfunction for $\mathcal{L}_{-\lambda}[r;-b]$. By uniqueness of the principal eigenvalue, we then have:

$$k_\lambda[r;b]=k_{-\lambda}[r;-b].$$

Taking $\lambda=0$, we obtain $k_0[r;b]=k_0[r;-b]$. Using the Freidlin-Gärtner formulas (3.13), this also gives $c_+[r;b]=c_-[r;-b]$ if $k_0[r;b]=k_0[r;-b]>0$ (otherwise, if $k_0[r;b]=k_0[r;-b]\leqslant 0$, then both $c_+[r;b]$ and $c_-[r;-b]$ are equal to $-\infty$). □

Now, let us prove item (ii), where r can be written $r=\beta+\gamma b$. Our goal is to construct a positive 1-periodic function φ satisfying

$$\varphi''-b\varphi'+(\beta+\gamma b)\varphi=k_0[\beta+\gamma b;b]\,\varphi \tag{3.19}$$

in $\mathbb{R}$. Then, φ is a principal eigenfunction of the operator $\mathcal{L}_0[\beta+\gamma b;-b]$ associated with the eigenvalue $k_0[\beta+\gamma b;b]$. By uniqueness, this means that $k_0[\beta+\gamma b;-b]=k_0[\beta+\gamma b;b]$. The function φ will be obtained as an explicit transformation of a 1-periodic positive solution $\phi\in\mathcal{C}^{2,\alpha}(\mathbb{R})$ of the principal eigenproblem

$$\phi''+b\phi'+(\beta+\gamma b)\phi=k_0[\beta+\gamma b;b]\,\phi \tag{3.20}$$

in $\mathbb{R}$. To construct the function φ, we first prove the following property of any solution $\phi\in\mathcal{C}^2(\mathbb{R})$ of (3.20), even non-periodic.

Lemma 3.3.1. *Let b be a continuous function and let $\gamma\in\mathbb{R}$. Let $\phi\in\mathcal{C}^2(\mathbb{R})$ be positive in $\mathbb{R}$ (we do not require b or ϕ to be periodic) and let $k\in\mathbb{R}$ satisfy*

$$\mathcal{L}_0[\gamma b;b]=k\phi \tag{3.21}$$

in $\mathbb{R}$. Then, either $\phi'+\gamma\phi\equiv 0$ in $\mathbb{R}$, or $\phi'+\gamma\phi$ vanishes at most once in $\mathbb{R}$.

Proof. We consider three separate cases depending on the value of k. Consider first the case $k > \gamma^2$. Assume that there exists $x_0 \in \mathbb{R}$ such that $\phi'(x_0) + \gamma\phi(x_0) = 0$. We have $\phi''(x_0) + b(x_0)(\phi'(x_0) + \gamma\phi(x_0)) = k\phi(x_0)$, which implies that $\phi''(x_0) = k\phi(x_0)$. Thus, recalling that $\phi(x_0) > 0$ and $k > \gamma^2$,

$$(\phi' + \gamma\phi)'(x_0) = \phi''(x_0) + \gamma\phi'(x_0) = k\phi(x_0) + \gamma\phi'(x_0) > \gamma\left(\gamma\phi(x_0) + \phi'(x_0)\right) = 0.$$

Therefore, at each point where the function $\phi' + \gamma\phi$ vanishes, its derivative $(\phi' + \gamma\phi)'$ is positive. As a consequence, $\phi' + \gamma\phi$ can vanish at most once in $\mathbb{R}$.

The same arguments as in the previous paragraph imply that, if $k < \gamma^2$ and if $\phi'(x_0) + \gamma\phi(x_0) = 0$ for some $x_0 \in \mathbb{R}$, then $(\phi' + \gamma\phi)'(x_0) < 0$. This again shows that $\phi' + \gamma\phi$ vanishes at most once in $\mathbb{R}$.

Lastly, consider the case $k = \gamma^2$. Dividing (3.21) by the positive function ϕ, we obtain:

$$\frac{\phi''}{\phi} + b\frac{\phi'}{\phi} + \gamma b = \gamma^2.$$

Setting $w := \frac{\phi'}{\phi} + \gamma$, it follows that $(w - \gamma)' + (w - \gamma)^2 + b(w - \gamma) + \gamma b = \gamma^2$ in $\mathbb{R}$, thus $w' = w(2\gamma - b - w)$ in $\mathbb{R}$. By the Cauchy-Lipschitz theorem, either $w \equiv 0$ in $\mathbb{R}$, or w does not vanish in $\mathbb{R}$. The proof of Lemma 3.3.1 is thereby complete. □

We now turn to the proof of Theorem 3.2.2 with assumption (ii). We first prove the result for the ability of persistence, and then for the spreading speed.

Proof of Theorem 3.2.2, item (ii), for k_0. Assume that there exist $\beta \in \mathbb{R}$ and $\gamma \in \mathbb{R}$ such that $r = \beta + \gamma b$ in $\mathbb{R}$, and let us prove that $k_0[r; b] = k_0[r; -b]$. Without loss of generality, we may assume that $\beta = 0$, since $k_0[\beta + \gamma b; \pm b] = \beta + k_0[\gamma b; \pm b]$. Moreover, if $r = \gamma b$ with $\gamma = 0$, then $k_0[r; b] = k_0[0; b] = 0 = k_0[0; -b] = k_0[r; -b]$, so the result holds.

From now on, we assume that $\beta = 0$ and $\gamma \neq 0$, that is, $r = \gamma b$ with $\gamma \neq 0$. Remember that $\phi \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ is a 1-periodic positive principal eigenfunction of (3.20). The positivity and periodicity of ϕ and the fact that $\gamma \neq 0$ imply that $\phi' + \gamma\phi \not\equiv 0$ in $\mathbb{R}$. Therefore, using Lemma 3.3.1, the function $\phi' + \gamma\phi$ vanishes at most once in $\mathbb{R}$. Hence, by periodicity, the function $\phi' + \gamma\phi$ does not vanish in $\mathbb{R}$, and then has a constant strict sign in $\mathbb{R}$. Thus, the $\mathcal{C}^2(\mathbb{R})$ function g given in $\mathbb{R}$ by

$$g(x) := \int_0^x \frac{\gamma\,\phi'(y) + k_0[\gamma\, b; b]\phi(y)}{\phi'(y) + \gamma\phi(y)}\,\mathrm{d}y$$

is well-defined. Now, set, for $x \in \mathbb{R}$,

$$h(x) := \int_0^x \frac{e^{-g(y)}}{\phi'(y) + \gamma\phi(y)}\,\mathrm{d}y.$$

The function h is of class $\mathcal{C}^2(\mathbb{R})$ and, since h' has a constant strict sign in $\mathbb{R}$ and $h(0) = 0$, we have $h(1) \neq 0$. We then set, for $x \in \mathbb{R}$,

$$\varphi(x) := e^{g(x)}(1 + Ch(x)), \quad \text{with } C := \frac{e^{-g(1)} - 1}{h(1)}, \tag{3.22}$$

whence $\varphi(0) = 1 = \varphi(1)$. The function φ defined is of class $\mathcal{C}^2(\mathbb{R})$. Furthermore, φ is positive

in $[0,1]$ since the function $1+Ch$ is monotone in $\mathbb{R}$ and takes positive values, 1 and $e^{-g(1)}$, at 0 and 1, respectively. We refer to Section 3.7 for the motivation for this expression of φ.

For convenience, we now define the differential operator

$$\mathcal{T} : \mu \mapsto \mu'' - b\mu' + (\gamma b - k_0[\gamma\, b; b])\,\mu$$

acting on $\mathcal{C}^2(\mathbb{R})$ functions μ. Let us first show that $\mathcal{T}[e^g] = 0$ in $\mathbb{R}$. We have

$$\mathcal{T}[e^g] = e^g\Big(g'' + (g')^2 - bg' + \gamma b - k_0[\gamma\, b; b]\Big)$$

in $\mathbb{R}$. Using Equation (3.20), satisfied by ϕ, there holds

$$b = \frac{k_0[\gamma\, b; b]\phi - \phi''}{\phi' + \gamma\phi}$$

in $\mathbb{R}$. Together with the formulas

$$g' = \frac{\gamma\phi' + k_0[\gamma\, b; b]\phi}{\phi' + \gamma\phi} \quad \text{and} \quad g'' = (\gamma^2 - k_0[\gamma\, b; b])\frac{\phi''\phi - (\phi')^2}{(\phi' + \gamma\phi)^2} \tag{3.23}$$

in $\mathbb{R}$, we obtain that $\mathcal{T}[e^g] = 0$ in $\mathbb{R}$.

Let us then show that $\mathcal{T}[\varphi] = 0$ in $\mathbb{R}$. We have

$$\mathcal{T}[\varphi] = \mathcal{T}[e^g(1 + C\,h)] = \mathcal{T}[e^g] + C\,\mathcal{T}[e^g h] = C\,\mathcal{T}[e^g h]$$

since $\mathcal{T}[e^g] = 0$ in $\mathbb{R}$, whence

$$\begin{aligned}
\mathcal{T}[\varphi] &= C\Big([e^g h]'' - b[e^g h]' + (\gamma b - k_0[\gamma\, b; b])e^g h\Big) \\
&= C\, e^g\left[(g'' + (g')^2 - bg' + \gamma b - k_0[\gamma\, b; b])h + h'' + 2h'g' - bh'\right] \\
&= C\,\mathcal{T}[e^g]h + C\, e^g\left[h'' + 2h'g' - bh'\right] \\
&= C\, e^g\left[h'' + 2h'g' - bh'\right],
\end{aligned}$$

again because $\mathcal{T}[e^g] = 0$ in $\mathbb{R}$. Since

$$h' = \frac{e^{-g}}{\phi' + \gamma\phi} \quad \text{and} \quad h'' = e^{-g}\left[\frac{-g'}{\phi' + \gamma\phi} - \frac{\phi'' + \gamma\phi'}{(\phi' + \gamma\phi)^2}\right]$$

in $\mathbb{R}$, together with (3.20) and (3.23), we get $h'' + 2h'g' - bh' = 0$ in $\mathbb{R}$, which entails that

$$\mathcal{T}[\varphi] = 0 \quad \text{in } \mathbb{R}.$$

Let us finally show that the function φ is 1-periodic. Recalling that $\varphi(0) = \varphi(1) = 1$ owing to the definition of C, it is thus sufficient to show that $\varphi'(0) = \varphi'(1)$, by the Cauchy-Lipschitz theorem. On the one hand,

$$\varphi' = e^g\left[g'(1 + Ch) + Ch'\right].$$

On the other hand, since ϕ is 1-periodic, we have

$$g'(0) = g'(1) = \frac{\gamma\phi'(0) + k_0[\gamma b; b]\phi(0)}{\phi'(0) + \gamma\phi(0)}$$

and $h'(1) = e^{-g(1)}h'(0)$. Thus, owing again to the definition of C,

$$\begin{aligned}\varphi'(1) &= e^{g(1)}\left[g'(1)(1+Ch(1)) + Ch'(1)\right] \\ &= g'(0)\,e^{g(1)}(1+Ch(1)) + Ch'(0) = g'(0) + Ch'(0) = \varphi'(0).\end{aligned}$$

Therefore, φ is 1-periodic and, since it is positive in $[0,1]$, it is positive in $\mathbb{R}$.

To conclude, $(\varphi, k_0[\gamma b; b])$ forms a pair consisting of the principal eigenfunction and the principal eigenvalue of the operator $\mathcal{L}_0[\gamma b; -b] : \psi \mapsto \psi'' - b\psi' + \gamma b\psi$, with 1-periodic conditions. By uniqueness of the principal eigenvalue, we deduce that $k_0[\gamma b; -b] = k_0[\gamma b; b]$. Furthermore, by uniqueness of the principal eigenfunction of $\mathcal{L}_0[\gamma b; -b]$ up to multiplication, it follows that φ is equal to the unique principal eigenfunction of $\mathcal{L}_0[\gamma b; -b]$ satisfying the normalisation $\varphi(0) = 1$. □

Proof of Theorem 3.2.2, item (ii), for the speeds. Let $\lambda \in \mathbb{R}$, and let us show that

$$k_\lambda[\beta + \gamma b; b] = k_{-\lambda}[\beta + \gamma b; -b].$$

The eigenvalue $k_\lambda[\beta + \gamma b; b]$ is associated with the operator

$$\begin{aligned}\psi \mapsto \mathcal{L}_\lambda[\beta + \gamma b; b]\psi &= \psi'' + (b + 2\lambda)\psi' + (\beta + \gamma b + \lambda b + \lambda^2)\psi \\ &= \psi'' + (b + 2\lambda)\psi' + (\gamma + \lambda)(b + 2\lambda)\psi + \beta\psi - (\lambda^2 + 2\lambda\gamma)\psi\end{aligned}$$

acting on 1-periodic functions of class $\mathcal{C}^2(\mathbb{R})$. Therefore, we have

$$k_\lambda[\beta + \gamma b; b] = k_0[(\gamma + \lambda)(b + 2\lambda); b + 2\lambda] + \beta - (\lambda^2 + 2\lambda\gamma).$$

We have already proved that if $\widetilde{r} = \widetilde{\gamma}\widetilde{b}$ for some $\widetilde{\gamma} \in \mathbb{R}$, then $k_0[\widetilde{\gamma}\widetilde{b}; \widetilde{b}] = k_0[\widetilde{\gamma}\widetilde{b}; -\widetilde{b}]$. Taking $\widetilde{\gamma} = \gamma + \lambda$ and $\widetilde{b} = b + 2\lambda$, we get

$$k_\lambda[\beta + \gamma b; b] = k_0[(\gamma + \lambda)(b + 2\lambda); -(b + 2\lambda)] + \beta - (\lambda^2 + 2\lambda\gamma).$$

Hence, $k_\lambda[\beta + \gamma b; b]$ is also the principal eigenvalue associated with the operator

$$\begin{aligned}\psi \;\mapsto\; & \psi'' - (b + 2\lambda)\psi' + (\gamma + \lambda)(b + 2\lambda)\psi + \beta\psi - (\lambda^2 + 2\lambda\gamma)\psi \\ &= \psi'' - (b + 2\lambda)\psi' + (\beta + \gamma b + \lambda b + \lambda^2)\psi \\ &= \mathcal{L}_{-\lambda}[\beta + \gamma b; -b]\psi.\end{aligned}$$

As a consequence, $k_\lambda[\beta + \gamma b; b] = k_{-\lambda}[\beta + \gamma b; -b]$ for all $\lambda \in \mathbb{R}$. This implies, using the Freidlin-Gärtner formulas (3.13), that $c_+[\beta + \gamma b; b] = c_-[\beta + \gamma b; -b]$. The proof of Theorem 3.2.2 is thereby complete. □

3.4 Other results on the influence of the direction of the advection term

This section is devoted to the proofs of Propositions 3.2.1, 3.2.4 and 3.2.5.

3.4.1 General effect of the direction of the advection term: proof of Proposition 3.2.1

Proof of Proposition 3.2.1. Let $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ be a 1-periodic function with $b \not\equiv 0$ and $\int_0^1 b = 0$. Let $\lambda \in \mathbb{R}$ and let $\phi > 0$ be a $\mathcal{C}^{2,\alpha}(\mathbb{R})$ principal eigenfunction of $\mathcal{L}_\lambda[r;b]$, where $r \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ is a 1-periodic function that will be chosen later. Consider the transformation $\phi = Fe^{-B/2}$, with $B' = b$. The function $F \in \mathcal{C}^2(\mathbb{R})$ satisfies

$$F'' + 2\lambda F' + \left(r - \frac{b^2}{4} - \frac{b'}{2} + \lambda^2\right) F = k_\lambda[r;b]\, F$$

in $\mathbb{R}$. Furthermore, since ϕ is 1-periodic and positive and since b is 1-periodic with zero mean, the function F is also 1-periodic and positive. The function F is therefore a principal eigenfunction of the operator $\mathcal{L}_\lambda\left[r - \frac{b^2}{4} - \frac{b'}{2}; 0\right]$. Thus, by uniqueness of the principal eigenvalue, we obtain that (see also [173])

$$k_\lambda[r,b] = k_\lambda\left[r - \frac{b^2}{4} - \frac{b'}{2}; 0\right].$$

Similarly, we have

$$k_\lambda[r,-b] = k_\lambda\left[r - \frac{b^2}{4} + \frac{b'}{2}; 0\right].$$

Consider now any positive real number $\eta > 0$ and set

$$r := \frac{b^2}{4} + \frac{b'}{2} + \eta,$$

which is 1-periodic and of class $\mathcal{C}^{0,\alpha}(\mathbb{R})$. Then $k_\lambda[r;b] = k_\lambda[\eta;0] = \lambda^2 + \eta$. Furthermore, since $b \not\equiv 0$ and b has zero mean, the function $b' \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ is not constant, so the principal 1-periodic eigenfunction ψ of the operator $\mathcal{L}_\lambda[b' + \eta; 0]$ (which satisfies

$$\psi'' + 2\lambda\psi' + (b' + \lambda^2 + \eta)\psi = k_\lambda[b' + \eta; 0]\, \psi$$

in $\mathbb{R}$) is not constant. By integrating this equation against $1/\psi$ over $[0,1]$, one gets

$$k_\lambda[b' + \eta; 0] = \int_0^1 \frac{(\psi')^2}{\psi^2} + \lambda^2 + \eta > \lambda^2 + \eta.$$

Thereby, $k_\lambda[r;-b] = k_\lambda[b' + \eta; 0] > \lambda^2 + \eta = k_\lambda[r;b]$. Since this holds for all $\lambda \in \mathbb{R}$, we get in particular that $0 < \eta = k_0[r;b] < k_0[r;-b]$. Moreover, since each infimum in (3.13) is reached at some $\lambda > 0$, we deduce that $c_+[r;b] < c_+[r;-b]$. Last, since b has zero mean, we have $c_+[r;-b] = c_-[r;-b]$ by Proposition 4.3.9 of Chapter 4, so $c_+[r;b] < c_-[r;-b]$. □

3.4.2 Small and large periods: proof of Proposition 3.2.4

We use the results of [81, 119] to compute more or less explicitly the limits as $L \to 0$ and $L \to +\infty$ of $k_0[r_L; b_L]$ and $c_+[r_L; b_L]$. Before that, we extend some results of [81] to the case where there is a nonzero advection term.

Lemma 3.4.1. *Let $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ and $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ be 1-periodic functions, and note*

$$\overline{r} := \int_0^1 r(x)\,\mathrm{d}x \quad \text{and} \quad \overline{b} := \int_0^1 b(x)\,\mathrm{d}x.$$

Then, for every $\lambda \in \mathbb{R}$,

$$k_\lambda[r_L; b_L] \underset{L\to 0}{\longrightarrow} \overline{r} + \lambda\overline{b} + \lambda^2. \tag{3.24}$$

If $\overline{r} > 0$, then

$$c_\pm[r_L; b_L] \underset{L\to 0}{\longrightarrow} \pm\overline{b} + 2\sqrt{\overline{r}}.$$

Proof. We first show that for every $\lambda \in \mathbb{R}$, $k_\lambda[r_L; b_L] \to \overline{r} + \lambda\overline{b} + \lambda^2$ as $L \to 0$. For $L > 0$, let $\phi_L \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ be the positive L-periodic principal eigenfunction of the adjoint of $\mathcal{L}_\lambda[r_L; b_L]$, that is,

$$\phi_L'' - [(b_L + 2\lambda)\phi_L]' + (r_L + \lambda b_L + \lambda^2)\phi_L = k_\lambda[r_L; b_L]\,\phi_L \tag{3.25}$$

in $\mathbb{R}$, with normalisation

$$\int_0^1 \phi_L^2(x)\,\mathrm{d}x = 1. \tag{3.26}$$

By multiplying (3.25) by ϕ_L and integrating by parts over $[0,1]$, we get:

$$-\int_0^1 (\phi_L')^2 + \int_0^1 (b_L + 2\lambda)\phi_L\phi_L' + \int_0^1 (r_L + \lambda b_L + \lambda^2)\phi_L^2 = k_\lambda[r_L; b_L]\int_0^1 \phi_L^2. \tag{3.27}$$

On the other hand, using (3.14) with (r_L, b_L) instead of (r, b), it follows that the family $(k_\lambda[r_L; b_L])_{L>0}$ is bounded. Moreover, by Young's inequality, we have

$$|(b_L + 2\lambda)\phi_L\phi_L'| \leqslant \frac{(\phi_L')^2}{2} + \frac{(b_L + 2\lambda)^2\phi_L^2}{2}.$$

Hence, together with (3.26)–(3.27), we conclude that the family $(\phi_L)_{L>0}$ is bounded in $H^1([0,1])$. Therefore, there exist a sequence $(L_n)_{n\in\mathbb{N}}$ of positive real numbers converging to 0 and a function $\phi \in H^1([0,1])$ such that $\phi_{L_n} \to \phi$ in $\mathcal{C}^{0,\beta}([0,1])$ for all $\beta \in [0, 1/2)$ (by Morrey's inequality), and $\phi_{L_n} \rightharpoonup \phi$ in $H^1([0,1])$ weakly. Last, since each function ϕ_{L_n} is L_n-periodic, we infer that $\phi \equiv C$ is a non-negative constant with $C^2 = 1$, that is, $\phi \equiv 1$ in $[0,1]$.

Now, multiplying (3.25) (with $L = L_n$) by any function $v \in \mathcal{C}_c^1((0,1))$ and integrating by parts over $[0,1]$, we get:

$$-\int_0^1 \phi_{L_n}' v' + \int_0^1 (b_{L_n} + 2\lambda)\phi_{L_n} v' + \int_0^1 (r_{L_n} + \lambda b_{L_n} + \lambda^2)\phi_{L_n} v = k_\lambda[r_{L_n}; b_{L_n}]\int_0^1 \phi_{L_n} v. \tag{3.28}$$

The sequence $(k_\lambda[r_{L_n}; b_{L_n}])_{n\in\mathbb{N}}$ is bounded, so there exists $\kappa \in \mathbb{R}$ such that, up to extraction of a subsequence, $k_\lambda[r_{L_n}; b_{L_n}] \to \kappa$ as $n \to +\infty$. As $n \to +\infty$, we have $r_{L_n} \rightharpoonup \overline{r}$ weakly in $L^2([0,1])$ and $b_{L_n} \rightharpoonup \overline{b}$ weakly in $L^2([0,1])$. Hence, taking the limit $n \to +\infty$ in (3.28) and using the fact that the sequence $(\phi_{L_n})_{n\in\mathbb{N}}$ converges to 1 strongly in (at least) $L^2([0,1])$ and

weakly in $H^1([0,1])$, we infer that

$$\kappa \int_0^1 v = \int_0^1 (\overline{b}+2\lambda)v' + \int_0^1 (\overline{r}+\lambda\overline{b}+\lambda^2)v = (\overline{r}+\lambda\overline{b}+\lambda^2)\int_0^1 v.$$

Since this holds for every $v \in \mathcal{C}^1_c((0,1))$, we obtain that $\kappa = \overline{r}+\lambda\overline{b}+\lambda^2$. This value κ does not depend on any sequence $(L_n)_{n\in\mathbb{N}}$ converging to 0, so we deduce that the whole bounded family $(k_\lambda[r_L;b_L])_{L>0}$ converges to $\overline{r}+\lambda\overline{b}+\lambda^2$ as $L\to 0$, that is, (3.24) is proved.

Let us now show the convergence of $c_+[r_L;b_L]$ as $L\to 0$, assuming that $\overline{r}>0$, that is, $\lim_{L\to 0} k_0[r_L;b_L]>0$. For each $\lambda\in\mathbb{R}$, the function $L\mapsto k_\lambda[r_L;b_L]$ is non-decreasing, by [173, Proposition 4.1].[3] Therefore, $k_0[r_L;b_L]>0$ for all $L>0$, and the functions $L\mapsto c_\pm[r_L;b_L]$ are non-decreasing. Hence

$$\lim_{L\to 0} c_\pm[r_L;b_L] = \inf_{L>0} c_\pm[r_L;b_L] = \inf_{L>0,\lambda>0} \frac{k_{\pm\lambda}[r_L;b_L]}{\lambda} = \inf_{\lambda>0}\Big(\lim_{L\to 0}\frac{k_{\pm\lambda}[r_L;b_L]}{\lambda}\Big).$$

From (3.24), we conclude that

$$\lim_{L\to 0} c_\pm[r_L;b_L] = \inf_{\lambda>0}\left(\frac{\overline{r}}{\lambda}\pm\overline{b}+\lambda\right) = \pm\overline{b}+2\sqrt{\overline{r}},$$

as stated. □

Proof of Proposition 3.2.4, for $L\to 0$. Using Lemma 3.4.1, we note that the limit as $L\to 0$ of $k_0[r_L;\pm b_L]$ is $\overline{r}$ and does not depend on whether we take $+b_L$ or $-b_L$. Replacing b by $-b$ when needed in Lemma 3.4.1, we also obtain the two limits (3.15). □

Proof of Proposition 3.2.4, for $L\to+\infty$. Assume that b has zero mean, that is, $\overline{b}=0$. First, using [119, Proposition 3.2], we have

$$k_0[r_L;\pm b_L] \underset{L\to+\infty}{\longrightarrow} M := \max_{x\in\mathbb{R}}\left(r(x)-\frac{b(x)^2}{4}\right).$$

Hence $k_0[r_L;b_L]$ and $k_0[r_L;-b_L]$ converge to the same limit. Second, assuming $M>0$, both quantities $k_0[r_L;b_L]$ and $k_0[r_L;-b_L]$ are positive for all L large enough, and using [119, Theorem 2.3] we have

$$c_+[r_L;\pm b_L] \underset{L\to+\infty}{\longrightarrow} \min_{\lambda\geqslant j(M),\lambda>0}\frac{j^{-1}(\lambda)}{\lambda},$$

where $j:[M,+\infty)\to[j(M),+\infty)$ is the bijective function defined by

$$j(k) := \int_0^1 \sqrt{k-r(x)+\frac{b(x)^2}{4}}\,\mathrm{d}x.$$

Hence, $\lim_{L\to+\infty} c_+[r_L;b_L] = \lim_{L\to+\infty} c_+[r_L;-b_L]$. Last, by (3.11), $c_+[r_L;\pm b_L] = c_-[r_L;\pm b_L]$ for all L large enough. The conclusion of Proposition 3.2.4 follows. □

[3] The part of the proof of [173, Proposition 4.1] related to the monotonicity of $k_\lambda[r_L;b_L]$ with respect to $L>0$ actually holds for any 1-periodic $b\in\mathcal{C}^{1,\alpha}(\mathbb{R})$, even not divergence-free, that is, here, not constant.

3.4.3 A counter-example to Theorem 3.2.2 in bounded domains: proof of Proposition 3.2.5

Proof of Proposition 3.2.5. Let $\mathcal{L}_0[r;b]$ be the usual operator, but with Dirichlet boundary conditions, see (3.16). Since $b(x)=x$, we have

$$\mathcal{L}_0[r;b]\phi = \phi'' + x\phi' + r\phi = \phi'' - (-x\phi)' + (r-1)\phi$$

for any $\phi \in \mathcal{C}^2([-1,1])$. Using the Dirichlet boundary conditions, we deduce that:

$$\mathcal{L}_0[r;b] = \mathcal{L}_0^*[r;-b] - 1.$$

Since the operators $\mathcal{L}_0[r;-b]$ and $\mathcal{L}_0^*[r;-b]$ (both with Dirichlet boundary conditions) have the same principal eigenvalue, we conclude that $k_0^d[r;b] = k_0^d[r;-b] - 1$. □

3.5 Relationship between the spreading speed and the ability of persistence: proof of Theorem 3.2.6

This section is devoted to the proof of Theorem 3.2.6. Throughout this section, we assume that $b=0$ and, as shortcuts, we then write, for any 1-periodic function $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$,

$$k_\lambda[r] := k_\lambda[r;0], \quad \mathcal{L}_\lambda[r] := \mathcal{L}_\lambda[r;0], \quad \text{and} \quad c_\pm[r] := c_\pm[r;0].$$

Hence, if $k_0[r] > 0$, then $c_-[r] = c_+[r] > 0$, by (3.11).

Proof of Theorem 3.2.6, items (i) and (ii). Since (*ii*) is stronger than (*i*), we directly show (*ii*). Let $M > 0$ be any fixed positive real number. Define

$$R := M + 16\pi^2 > 0.$$

For any $A \in \mathbb{R}$, we then consider the Lipschitz-continuous 1-periodic function $\widetilde{r}^A$ such that

$$\widetilde{r}^A(x) := \begin{cases} R & \text{for } 0 \leqslant x \leqslant 1/4, \\ R + 4(A-R)(x-1/4) & \text{for } 1/4 < x < 1/2, \\ A & \text{for } 1/2 \leqslant x \leqslant 3/4, \\ R + 4(A-R)(1-x) & \text{for } 3/4 < x < 1 \end{cases}$$

(this function is then extended by 1-periodicity in $\mathbb{R}$). For each $\lambda \in \mathbb{R}$, let $k_{\lambda,dir}$ be the principal Dirichlet eigenvalue of

$$\begin{cases} \psi'' + 2\lambda\psi' + (R+\lambda^2)\psi = k_\lambda^d \psi & \text{in } [0,1/4], \\ \psi > 0 & \text{in } (0,1/4), \\ \psi(0) = \psi(1/4) = 0, \end{cases} \tag{3.29}$$

associated with the $\mathcal{C}^\infty([0,1/4])$ principal eigenfunction $\psi : x \mapsto e^{-\lambda x}\sin(4\pi x)$. By uniqueness of the principal eigenvalue, it follows that $k_\lambda^d = R - 16\pi^2$. On the other hand, from [21,

Equation 1.13],

$$k_\lambda^d = \min_{\varphi\in W^{2,1}_{loc}((0,1/4)),\varphi>0 \text{ in } (0,1/4)} \left(\operatorname*{esssup}_{x\in(0,1/4)} \frac{\varphi''(x)+2\lambda\varphi'(x)+(R+\lambda^2)\varphi(x)}{\varphi(x)} \right) \tag{3.30}$$

and the minimum with respect to φ is reached only by the positive multiples of ψ. Hence $k_\lambda^d < k_\lambda[\widetilde{r}^A]$ for each $A\in\mathbb{R}$, since $\widetilde{r}^A = R$ in $[0,1/4]$ and $k_\lambda[\widetilde{r}^A]$ is associated with a positive 1-periodic principal eigenfunction of $\mathcal{L}_\lambda[\widetilde{r}^A]$, whose restriction to $[0,1/4]$ is therefore still positive in $[0,1/4]$. In other words, for every $A\in\mathbb{R}$,

$$k_\lambda[\widetilde{r}^A] > R - 16\pi^2 = M.$$

In particular, $k_0[\widetilde{r}^A] > M > 0$, which is one the two required conclusions of (3.18).

Our goal is now to show that $c_-[\widetilde{r}^A] = c_+[\widetilde{r}^A] < 1/M$ for all $A<0$ negative enough. To do so, for any fixed $\lambda\in\mathbb{R}$, let us first compute the limit of $k_\lambda[\widetilde{r}^A]$ as $A\to-\infty$. If $A_1\leqslant A_2$, then $\widetilde{r}^{A_1}\leqslant\widetilde{r}^{A_2}$ in $\mathbb{R}$, whence $k_\lambda[\widetilde{r}^{A_1}]\leqslant k_\lambda[\widetilde{r}^{A_2}]$. Therefore, there exists a limit

$$\ell := \lim_{A\to-\infty} k_\lambda[\widetilde{r}^A],$$

such that $k_\lambda[\widetilde{r}^0]\geqslant\ell\geqslant R-16\pi^2 = M$. We show in what follows that $\ell = R-16\pi^2$ (as a consequence, ℓ is independent of λ). For $A\leqslant 0$, let $\phi_A>0$ be 1-periodic of class $\mathcal{C}^2(\mathbb{R})$ and satisfy

$$\phi_A'' + 2\lambda\phi_A' + (\widetilde{r}^A+\lambda^2)\phi_A = k_\lambda[\widetilde{r}^A]\phi_A \tag{3.31}$$

with normalisation $\|\phi_A\|_{L^2([0,1])}=1$. Integrating (3.31) against ϕ_A over $[0,1]$, we get:

$$k_\lambda[\widetilde{r}^A] = -\int_0^1 (\phi_A')^2 + \lambda\underbrace{\int_0^1 (\phi_A^2)'}_{=0} + \lambda^2 + \int_0^1 \underbrace{\widetilde{r}^A}_{\leqslant R}\phi_A^2 \leqslant -\int_0^1 (\phi_A')^2 + \lambda^2 + R.$$

Since the family $(k_\lambda[\widetilde{r}^A])_{A\leqslant 0}$ is bounded (it ranges in $[M, k_\lambda[\widetilde{r}^0]]$) and since $\|\phi_A\|_{L^2([0,1])}=1$, we infer that $(\phi_A)_{A\leqslant 0}$ is bounded in $H^1([0,1])$. Therefore, there exist a sequence $(A_n)_{n\in\mathbb{N}}$ of non-positive real numbers diverging to $-\infty$ and a non-negative 1-periodic function $\phi\in H^1_{loc}(\mathbb{R})$ such that $\phi_{A_n}\to\phi$ in $\mathcal{C}^{0,\beta}(\mathbb{R})$ for every $\beta\in[0,1/2)$ and $\phi_{A_n}\rightharpoonup\phi$ weakly in $H^1([0,1])$, as $n\to+\infty$. Furthermore, for any $1/4<a<b<1$, $\widetilde{r}^A\to-\infty$ uniformly in $[a,b]$ as $A\to-\infty$, while

$$\begin{aligned} k_\lambda[\widetilde{r}^A] = -\int_0^1 (\phi_A')^2 + \lambda^2 + \int_0^1 \widetilde{r}^A\phi_A^2 &\leqslant \lambda^2 + R\int_0^a \phi_A^2 + \int_a^b \widetilde{r}^A\phi_A^2 + R\int_b^1 \phi_A^2 \\ &\leqslant \lambda^2 + R + \int_a^b \widetilde{r}^A\phi_A^2 \end{aligned}$$

for every $A\leqslant 0$. Using again the boundedness of the family $(k_\lambda[\widetilde{r}^A])_{A\leqslant 0}$, we get

$$\limsup_{A\to-\infty} \int_a^b |\widetilde{r}^A|\phi_A^2 < +\infty,$$

whence $\int_a^b \phi^2 = 0$. Since this holds for every $1/4<a<b<1$ and $\phi\in H^1_{loc}(\mathbb{R})$ is (at least) continuous, it follows that $\phi=0$ in $[1/4,1]$, and then in $[-3/4,0]$ by 1-periodicity. In par-

ticular, the restriction of ϕ to $[0,1/4]$ belongs to $H^1_0([0,1/4])$. Finally, by integrating (3.31) (with $A=A_n$) against any function $v\in\mathcal{C}^1_c((0,1/4))$ and taking the limit as $n\to+\infty$, we get:

$$-\int_0^{1/4} v'\phi' + 2\lambda\int_0^{1/4} v\phi' + (R+\lambda)^2\int_0^{1/4} v\phi = \ell\int_0^{1/4} v\phi.$$

Therefore, ϕ is a weak $H^1_0([0,1/4])$ and then a strong $H^2([0,1/4])\cap H^1_0([0,1/4])$ and then a $\mathcal{C}^\infty([0,1/4])$ solution of

$$\begin{cases} \phi''+2\lambda\phi'+(R+\lambda^2)\phi=\ell\,\phi & \text{in } [0,1/4],\\ \phi\geqslant 0 & \text{in } [0,1/4],\\ \phi(0)=\phi(1/4)=0. \end{cases}$$

But $\|\phi\|_{L^2([0,1/4])}=\|\phi\|_{L^2([0,1])}=1$ (because $\phi=0$ in $[0,1/4]$), whence $\phi>0$ in $(0,1/4)$ from the strong maximum principle. By uniqueness of the principal eigenvalue of this problem, ℓ is then equal to the principal eigenvalue $k^d_\lambda=R-16\pi^2$ of (3.29), that is, $\ell=R-16\pi^2$. Since $R-16\pi^2$ does not depend on any sequence of the bounded family $(k_\lambda[\widetilde{r}^A])_{A\leqslant 0}$, we conclude that, for every $\lambda\in\mathbb{R}$,

$$k_\lambda[\widetilde{r}^A]\underset{A\to-\infty}{\longrightarrow} R-16\pi^2=M.$$

Lastly, pick any $\lambda_0>M^2$. One then has $(R-16\pi^2)/\lambda_0=M/\lambda_0<1/M$. Thus,

$$\frac{k_{\lambda_0}[\widetilde{r}^A]}{\lambda_0}<\frac{1}{M}$$

for all $A<0$ negative enough, whence

$$0<c_+[\widetilde{r}^A]=c_-[\widetilde{r}^A]\leqslant\frac{k_{\lambda_0}[\widetilde{r}^A]}{\lambda_0}<\frac{1}{M}$$

for all $A<0$ negative enough, by (3.11) and (3.13) (remember also that $k_0[\widetilde{r}^A]>M>0$). Any function $\widetilde{r}:=\widetilde{r}^A$ for $A<0$ negative enough then satisfies (3.18). The proof of items (i)–(ii) of Theorem 3.2.6 is thereby complete. □

Proof of Theorem 3.2.6, item (iii). We assume here that r is constant, whence r is a positive constant (since $0<k_0[r]=r$) and $c_\pm[r]=2\sqrt{r}$. Let $\widetilde{r}\in\mathcal{C}^{0,\alpha}(\mathbb{R})$ be a non-constant 1-periodic function such that

$$0<k_0[\widetilde{r}]\leqslant k_0[r]=r.$$

The quantity $c_-[\widetilde{r}]=c_+[\widetilde{r}]$ is positive by (3.11). Our goal is to show that $c_+[\widetilde{r}]<c_+[r]=2\sqrt{r}$.

First of all, for every $\lambda\in\mathbb{R}$, it follows from [173, Theorem 2.2] that

$$k_\lambda[\widetilde{r}]=\min_{\mu\in\mathcal{C}^1(\mathbb{R}),\,\mu\text{ is 1-periodic}} k_0[\widetilde{r}+\lambda^2+(\mu')^2+2\lambda\mu'] \tag{3.32}$$

Taking $\mu\equiv 0$, we find

$$k_\lambda[\widetilde{r}]\leqslant k_0[\widetilde{r}+\lambda^2]=k_0[\widetilde{r}]+\lambda^2\leqslant k_0[r]+\lambda^2=r+\lambda^2.$$

Together with (3.11) and (3.13), this already shows that $c_+[\widetilde{r}]\leqslant 2\sqrt{r}=c_+[r]$. The goal of the next paragraph is to prove that strict inequality holds.

Consider now any $\lambda > 0$. By the proof of [173, Theorem 2.2] (see in particular [173, Proposition 2.6]), the minimum in (3.32) is actually reached at

$$\mu_m := \frac{1}{2} \ln\Big(\frac{\phi}{\psi}\Big), \tag{3.33}$$

where (ϕ, ψ) is the unique pair (up to multiplication of each function by positive constants) of 1-periodic positive $\mathcal{C}^{2,\alpha}(\mathbb{R})$ functions solving the following pair of adjoint equations (recall that an operator and its adjoint have the same principal eigenvalue):

$$\begin{cases} \phi'' + 2\lambda\phi' + (\widetilde{r} + \lambda^2)\phi &= k_\lambda[\widetilde{r}]\phi, \\ \psi'' - 2\lambda\psi' + (\widetilde{r} + \lambda^2)\psi &= k_\lambda[\widetilde{r}]\psi. \end{cases}$$

If the function μ_m were constant, the functions ϕ and ψ would be identical up to multiplication, and therefore equal without loss of generality. We would then have $-2\lambda\phi' = 2\lambda\phi'$ in $\mathbb{R}$, and ϕ (and ψ) would then be constant, which is impossible since $\widetilde{r}$ is not constant. As a consequence, μ_m is not constant. Further, by [190], the function

$$\nu \mapsto g(\nu) := k_0[\widetilde{r} + \lambda^2 + \nu^2 + 2\lambda\nu]$$

is convex and analytic in the class of continuous 1-periodic functions ν. For any such functions ν and ω with $\omega \not\equiv 0$, and for any $t \in \mathbb{R}$, $g(\nu + t\omega)$ is the principal eigenvalue of the operator $\mathcal{L}_0[\widetilde{r} + \lambda^2 + (\nu + t\omega)^2 + 2\lambda(\nu + t\omega)]$. By integrating the equation satisfied by a corresponding principal 1-periodic eigenfunction φ against $1/\varphi$ over $[0,1]$, it follows that

$$\begin{aligned} g(\nu + t\omega) &= k_0[\widetilde{r} + \lambda^2 + (\nu + t\omega)^2 + 2\lambda(\nu + t\omega)] \\ &\geqslant \int_0^1 \Big(\widetilde{r} + \lambda^2 + (\nu + t\omega)^2 + 2\lambda(\nu + t\omega)\Big), \end{aligned}$$

whence $\liminf_{t\to\pm\infty} g(\nu + t\omega)/t^2 > 0$. Hence, the analytic function $t \mapsto g(\nu + t\omega)$ is convex and not affine, so it is strictly convex. As a consequence, g is strictly convex (in the sense that $g((\nu_1 + \nu_2)/2) < (g(\nu_1) + g(\nu_2))/2$ for any two distinct continuous 1-periodic functions ν_1 and ν_2). Therefore, the minimum in (3.32) is reached only at the function μ_m defined in (3.33), up to additive constants. Since μ_m is not constant, we infer that the function 0 does not minimise (3.32), whence

$$k_\lambda[\widetilde{r}] = k_0[\widetilde{r} + \lambda^2 + (\mu_m')^2 + 2\lambda\mu_m'] < k_0[\widetilde{r} + \lambda^2] = k_0[\widetilde{r}] + \lambda^2.$$

This implies that $k_\lambda[\widetilde{r}] < k_0[r] + \lambda^2$ for every $\lambda > 0$, and we conclude that

$$c_+[\widetilde{r}] = \min_{\lambda>0} \frac{k_\lambda[\widetilde{r}]}{\lambda} < \min_{\lambda>0} \frac{k_0[r] + \lambda^2}{\lambda} = 2\sqrt{k_0[r]} = 2\sqrt{r} = c_+[r].$$

This completes the proof of item (iii) of Theorem 3.2.6. □

Proof of Theorem 3.2.6, item (iv). Item (iv) is a consequence of item (iii) (where the roles of r and $\widetilde{r}$ are reversed). Namely, we assume here that r is non-constant. Since $0 < k_0[r] = k_0[k_0[r]]$, viewing $k_0[r]$ as a constant function and applying (iii) with the pair $(r, k_0[r])$ in place of $(\widetilde{r}, r)$, we get

$$0 < c_+[r] < c_+[k_0[r]] = 2\sqrt{k_0[r]}.$$

This proves the first part of item (iv).

Now, for $\varepsilon > 0$ small enough, we have both

$$k_0[r] > k_0[r] - \varepsilon = k_0[k_0[r] - \varepsilon] > 0$$

and

$$0 < c_+[r] < 2\sqrt{k_0[r] - \varepsilon} = c_+[k_0[r] - \varepsilon].$$

Hence, the second part of item (iv) holds with the positive constant $\widetilde{r} := k_0[r] - \varepsilon$. □

3.6 A condition for local convergence to the positive equilibrium state

We here derive a condition more general than $k_0[r;0] > 0$ in the case $b = 0$, which guarantees local convergence to the 1-periodic positive steady state p as $t \to +\infty$.

Proposition 3.6.1. *If*

$$k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right] > 0, \tag{3.34}$$

then (3.9) *holds and* $u(t,\cdot) \to p$ *as* $t \to +\infty$ *locally uniformly in* $\mathbb{R}$*, for any continuous non-negative compactly supported initial condition* $u_0 \not\equiv 0$*. In particular, if*

$$4\int_0^1 r > \int_0^1 b^2,$$

then (3.34) *holds.*

Proof. As observed in [27] in the case $b = 0$, the important quantity for local extinction or local convergence to a positive stationary state is not the periodic principal eigenvalue $k_0[r;b]$; it is rather the limit of Dirichlet eigenvalues in increasing bounded domains. Namely, for $R > 0$, let $k_0^d(R)$ be the principal eigenvalue of the Dirichlet eigenproblem

$$\begin{cases} \phi'' + b\phi' + r\phi = k_0^d(R)\,\phi & \text{in } [-R,R], \\ \phi > 0 & \text{in } (-R,R), \\ \phi(-R) = \phi(R) = 0, \end{cases} \tag{3.35}$$

associated with $\mathcal{C}^{2,\alpha}([-R,R])$ eigenfunctions ϕ. By [21, Equation 1.13], as in (3.30), there holds

$$k_0^d(R) = \min_{\psi \in W^{2,1}_{loc}((-R,R)), \psi > 0 \text{ in } (-R,R)} \left(\operatorname*{esssup}_{x \in (-R,R)} \frac{\psi''(x) + b(x)\psi'(x) + r(x)\psi(x)}{\psi(x)} \right)$$

for each $R > 0$, and the minimum with respect to ψ is reached only by the positive multiples of the principal eigenfunction ϕ of (3.35). Hence the function $R \mapsto k_0^d(R)$ is non-decreasing, bounded, and $k_0^d(R) < k_0[r;b]$, since $k_0[r;b]$ is associated with a positive 1-periodic principal eigenfunction, whose restriction to $[-R,R]$ is therefore still positive in $[-R,R]$. Thus, there exists a limit

$$k_0^d(\infty) := \lim_{R \to +\infty} k_0^d(R) \ \in \mathbb{R},$$

such that

$$k_0^d(\infty) \leqslant k_0[r;b]. \tag{3.36}$$

Let us prove that

$$k_0^d(\infty) = k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right], \tag{3.37}$$

where, using the notations of the introduction, $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]$ is the periodic principal eigenvalue associated with the operator $\mathcal{T}$ defined by

$$\mathcal{T} : \phi \mapsto \phi'' + \left(r - \frac{b'}{2} - \frac{b^2}{4}\right)\phi.$$

To show (3.37), let, for each $R > 0$, $\phi_R \in \mathcal{C}^{2,\alpha}([-R,R])$ be a positive principal eigenfunction of (3.35), and set $\psi_R = \phi_R e^{B/2}$, with $B' = b$. As in the proof of Proposition 3.2.1, the $\mathcal{C}^{2,\alpha}([-R,R])$ function ψ_R solves $\mathcal{T}\psi_R = k_0^d(R)\,\psi_R$ in $[-R,R]$, with $\psi_R > 0$ in $(-R,R)$ and $\psi_R(\pm R) = 0$. Thus, $k_0^d(R)$ is the Dirichlet principal eigenvalue of $\mathcal{T}$ in $[-R,R]$. Since the operator $\mathcal{T}$ is self-adjoint and has periodic coefficients, it now follows from [27, Lemma 3.6] that $k_0^d(R)$ converges, as $R \to +\infty$, to the periodic principal eigenvalue of $\mathcal{T}$, which is $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]$. To sum up, we have

$$k_0^d(R) \underset{R\to+\infty}{\longrightarrow} k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]. \tag{3.38}$$

Therefore (3.37) holds.

Thus, a comparison between $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]$ and 0 is equivalent to a comparison between $k_0^d(\infty)$ and 0. The proof of local convergence of the solutions u to (3.1) with continuous non-negative compactly supported initial conditions $u_0 \not\equiv 0$ to a stationary state if $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right] > 0$ is the same as the proof of [27, Theorem 2.6] (replacing the notation there λ_1 by our notation $-k_0^d(\infty)$). In particular, the positivity of $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]$ rules out the extinction of these solutions. Notice also that $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right] > 0$ implies directly $k_0[r;b] > 0$, by (3.36) and (3.38).

Lastly, let $\psi \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ be a 1-periodic positive principal eigenfunction of $\mathcal{T}$, that is, $\mathcal{T}\psi = k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right]\psi$ in $\mathbb{R}$. By integrating this equation against $1/\psi$ over $[0,1]$, one gets that

$$k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right] = \int_0^1 \frac{(\psi')^2}{\psi^2} + \int_0^1 \left(r - \frac{b'}{2} - \frac{b^2}{4}\right) \geqslant \int_0^1 r - \frac{1}{4}\int_0^1 b^2.$$

Therefore, if $4\int_0^1 r > \int_0^1 b^2$, then $k_0\left[r - \frac{b'}{2} - \frac{b^2}{4}; 0\right] > 0$. □

3.7 Construction of the principal eigenfunctions in Theorem 3.2.2

In the proof of item (ii) of Theorem 3.2.2, in order to show that $k_0[r;b] = k_0[r;-b]$ when $r = \beta + \gamma b$, $\beta \in \mathbb{R}$, $\gamma \in \mathbb{R}^*$, and $b \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ is 1-periodic, we gave in (3.22) an explicit expression for a principal 1-periodic eigenfunction φ solving (3.19) and associated with $\mathcal{L}_0[r;-b]$, using

a principal 1-periodic eigenfunction ϕ solving (3.20) and associated with $\mathcal{L}_0[r;b]$. As this expression is somewhat complicated, we explain its origin in this subsection. We assume for conciseness that $\beta = 0$, so $r = \gamma b$.

For the moment, we do not consider the periodicity conditions and simply look for the form of the general solution of (3.19) in $\mathbb{R}$, or equivalently, the general solution $\mu \in \mathcal{C}^2(\mathbb{R})$ of $\mathcal{T}[\mu] = 0$ in $\mathbb{R}$, with

$$\mathcal{T} : \mu \mapsto \mu'' - b\mu' + (\gamma b - k_0[\gamma b; b])\mu.$$

We begin with the construction of a particular solution $y_1 \in \mathcal{C}^2(\mathbb{R})$ of $\mathcal{T}[y_1] = 0$ in $\mathbb{R}$, which we seek in the form $y_1 = m\, e^B$, with $B' = b$, $B(0) = 0$, and with a function $m \in \mathcal{C}^2(\mathbb{R})$ to be determined. With this ansatz, we have

$$\mathcal{T}[y_1] = e^B \Big(m'' + bm' + (\gamma b + b' - k_0[\gamma b; b])m \Big).$$

Setting a new operator

$$\widetilde{\mathcal{T}} : \mu \mapsto \mu'' + b\mu' + (\gamma b + b' - k_0[\gamma b; b])\mu,$$

acting on $\mathcal{C}^2(\mathbb{R})$ functions μ, we observe that $\widetilde{\mathcal{T}}[\phi] = b'\phi$. Furthermore, since b is at least of class $\mathcal{C}^1(\mathbb{R})$ and ϕ is at least of class $\mathcal{C}^2(\mathbb{R})$, it follows from (3.20) that ϕ is actually at least of class $\mathcal{C}^3(\mathbb{R})$. Hence, differentiating (3.20), we get $\widetilde{\mathcal{T}}[\phi'] = -\gamma\, b'\, \phi$. As a consequence, by choosing

$$m := \phi' + \gamma\, \phi \ \in \mathcal{C}^2(\mathbb{R}),$$

we have $\mathcal{T}[y_1] = e^B \widetilde{\mathcal{T}}[m] = 0$ in $\mathbb{R}$. Using Lemma 3.3.1, as in the beginning of the proof of item (ii) of Theorem 3.2.2 in Section 3.3, we note that m has a constant strict sign in $\mathbb{R}$. Therefore, since

$$b = \frac{k_0[\gamma b; b]\phi - \phi''}{m}$$

by (3.20), it follows that the solution $y_1 = me^B$ of $\mathcal{T}[y_1] = 0$ can be rewritten as

$$\begin{aligned} y_1(x) &= m(x) \exp\left(\int_0^x b(s)\, \mathrm{d}s \right) \\ &= m(0) \exp\left(\int_0^x \left(b(s) + \frac{m'(s)}{m(s)} \right) \mathrm{d}s \right) = m(0) \exp(g(x)), \end{aligned}$$

with

$$g(x) := \int_0^x \frac{\gamma\, \phi'(s) + k_0[\gamma\, b; b]\phi(s)}{\phi'(s) + \gamma\, \phi(s)}\, \mathrm{d}s.$$

Now, with this particular strictly signed solution $y_1 = m(0)\, e^g$ of $\mathcal{T}[y_1] = 0$ in hand, still forgetting the periodicity properties (actually, the function y_1 is not periodic if the mean of b is not zero), the general solution μ of $\mathcal{T}[\mu] = 0$ in $\mathbb{R}$, can be written from [192, Section 2.2.2] as

$$\mu(x) = y_1(x) \left(C_1 + C_2 \int_0^x \frac{e^{B(z)}}{y_1^2(z)}\, \mathrm{d}z \right),$$

where C_1, C_2 are two constants. Since

$$\frac{e^B}{y_1} = \frac{1}{m} = \frac{1}{\phi' + \gamma\phi} \quad \text{and} \quad y_1 = m(0)\, e^g$$

with $m(0) \neq 0$, up to a modification of the constants C_1 and C_2, we can then write the general solution $\mu \in \mathcal{C}^2(\mathbb{R})$ of $\mathcal{T}[\mu] = 0$ in $\mathbb{R}$ as:

$$\mu(x) = e^{g(x)} \left(C_1 + C_2 \int_0^x \frac{e^{-g(z)}}{\phi'(z) + \gamma\, \phi(z)} \, \mathrm{d}z \right) = e^{g(x)} \Big(C_1 + C_2 h(x) \Big),$$

where

$$h(x) := \int_0^x \frac{e^{-g(z)}}{\phi'(z) + \gamma\, \phi(z)} \, \mathrm{d}z = \int_0^x \frac{e^{-g(z)}}{m(z)} \, \mathrm{d}z.$$

Finally, observing that $h(1) \neq 0$ (because m has a constant strict sign in $\mathbb{R}$), and setting

$$C_1 := 1 \ \text{ and } C_2 := \frac{e^{-g(1)} - 1}{h(1)},$$

we obtain a particular solution μ of $\mathcal{T}[\mu] = 0$ in $\mathbb{R}$, with $\mu(0) = \mu(1) = 1$. Furthermore, the function $C_1 + C_2 h = \mu\, e^{-g}$ is monotone in $\mathbb{R}$, and takes positive values at 0 and 1, whence μ is positive in $[0, 1]$. Lastly, as in the proof of item (ii) of Theorem 3.2.2 in Section 3.3, we can check that $\mu'(0) = \mu'(1)$. As a consequence, with that choice of constants (C_1, C_2), the function $\varphi := \mu \in \mathcal{C}^2(\mathbb{R})$ is a 1-periodic positive solution of (3.19).

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Chapter 4

The effect of the diffusion mechanism

This chapter is based on the preprint [49]:

N. Boutillon, Y.-J. Kim, L. Roques, *Impact of diffusion mechanisms on persistence and spreading*, preprint arxiv:2501.03816.

Abstract

We examine a generalised KPP equation with a "q-diffusion", which is a framework that unifies various standard linear diffusion regimes: Fickian diffusion ($q = 0$), Stratonovich diffusion ($q = 1/2$), Fokker-Planck diffusion ($q = 1$), and nonstandard diffusion regimes for general $q \in \mathbb{R}$. Using both analytical methods and numerical simulations, we explore how the ability of persistence (measured by some principal eigenvalue) and how the asymptotic spreading speed depend on the parameter q and on the phase shift between the growth rate $r(x)$ and the diffusion coefficient $D(x)$.

This chapter underscores the importance of carefully selecting diffusion models in ecological and epidemiological contexts, highlighting their potential implications for persistence, spreading, and control strategies.

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4.1 Introduction

We consider the following reaction-diffusion equations, indexed by a parameter $q \in \mathbb{R}$:

$$\partial_t u(t,x) = \partial_x \left(D(x)^{1-q} \partial_x (D(x)^q u) \right) + f(x,u), \quad t > 0,\ x \in \mathbb{R}. \tag{4.1}$$

Here, the function $x \mapsto D(x)$ is positive and 1-periodic, the function $x \mapsto \partial_u f(x,0)$ is 1-periodic, and f satisfies the KPP condition (we will give the precise definition below). Equivalently, (4.1) can be written:

$$\partial_t u(t,x) = \partial_x \left(D(x) \partial_x u \right) + q \partial_x \left(D'(x) u \right) + f(x,u), \quad t > 0,\ x \in \mathbb{R}. \tag{4.2}$$

Our primary goal is to analyse the persistence and spreading properties of the solutions $u(t,x)$ for varying values of $q \in \mathbb{R}$. In Equation (4.1), the term $\partial_x \left(D(x)^{1-q} \partial_x (D(x)^q u) \right)$ can be referred to as the *"q-diffusion operator"*, and appears in several recent papers [6, 127, 136, 176]. Let us describe why q-diffusion operators have recently raised so much interest.

Since Einstein's seminal work on Brownian motion [80], the parabolic partial differential equation (PDE) $\partial_t u(t,x) = D \partial_{xx} u(t,x)$ with constant diffusion coefficient D has been recognised for its solid physical underpinnings: the solution $u(t,x)$ is typically interpreted as the density of particles undergoing independent Brownian motions. From this starting point, there are several ways to introduce heterogeneity in the movement of particles.

A first way to introduce heterogeneity in the movement of particles in (4.1) is to use the Fokker-Planck equation associated with an Itô stochastic differential equation (SDE), formulated as

$$\mathrm{d}X_t = \sigma(X_t)\, \mathrm{d}W_t. \tag{4.3}$$

Here, $\mathrm{d}W_t$ denotes a forward increment in time of a standard Brownian motion. The SDE (4.3) modifies Brownian motion by incorporating a spatio-temporal variability in the movements of particles, as indicated by the position-dependent random driving force $\sigma(X_t)$. For instance, σ takes lower values in regions where the motion of particles is slower. The associated Fokker-Planck equation describes the dynamics of the transition probability density $u(t,x) = P(X(t) = x | X(0) = x_0)$:

$$\partial_t u(t,x) = \partial_{xx} (D(x)\, u), \quad t > 0, \quad x \in \mathbb{R}, \tag{4.4}$$

where $D(x) = \sigma^2(x)/2$ and $\partial_{xx}(D(x)\, u)$ corresponds to the diffusion term in (4.1) with $q = 1$. The 1-diffusion will be called, throughout this chapter, the *Fokker-Planck diffusion*.

A second standard way to introduce heterogeneity in the movement of particles is to use Fickian diffusion [91]. Fickian diffusion is commonly derived from the physical interplay between particle flux, concentration, and concentration gradient [71, 90]. Particles naturally migrate from regions of higher density to regions of lower density, so this diffusion eventually leads to a homogeneous density of particles. More precisely, Fickian diffusion is derived from Fick's Law, which posits that the particle flux is proportional to the concentration gradient. In this context, the proportionality coefficient $D(x)$ represents the rate at which particles diffuse through a medium, accounting for spatial variations in the medium properties. This construction leads to the following PDE:

$$\partial_t u(t,x) = \partial_x (D(x)\, \partial_x u), \quad t > 0, \quad x \in \mathbb{R}, \tag{4.5}$$

which corresponds to the diffusion term in (4.1) with $q = 0$. The 0-diffusion will be called, throughout this chapter, the *Fickian diffusion*.

Third, Wereide [222] formulated a diffusion law corresponding to the case where $q = 1/2$. This law incorporates the phenomenon of *thermo-diffusion*, where particles migrate not only in response to a concentration gradient but also under the influence of a temperature gradient. Considering the SDE (4.3) but with Stratonovich integration instead of Itô integration, the density $u(t,\cdot)$ of the law of the particle at time t satisfies

$$\partial_t u(t,x) = \partial_x \left(\sqrt{D(x)} \partial_x \left(\sqrt{D(x)}\, u \right) \right), \quad t > 0, \quad x \in \mathbb{R}, \tag{4.6}$$

where $D(x) = \sigma^2(x)/2$ corresponds to the diffusion term in (4.1) with $q = 1/2$. The 1/2-diffusion will be called the *Stratonovich diffusion*. More recently, Kim and Seo [137] developed heterogeneous diffusion equations from reversible kinetic systems and compared various diffusion laws through a theoretical experiment. Notably, they derived the Stratonovich diffusion law as a particular instance of their model.

The Fokker-Planck, Fickian and Stratonovich diffusion laws can also emerge as limits of stochastic processes. The Itô integral interpretation of the equation $\mathrm{d}X_t = \sigma(X_t)\,\mathrm{d}W_t$ assumes that the jump $X_{t+\delta t} - X_t$ (for a time step δt going to 0) depends on the intensity $\sigma(X_t)$ of the stochastic process at the departure point X_t. This interpretation leads to the Fokker-Planck diffusion. The analysis in [218] indicates that adopting an alternative assumption, where the length of the jump depends on the value of σ at an intermediate point $qX_t + (1-q)X_{t+\delta t}$ (for $q \in \mathbb{R}$), leads to the diffusion term $\partial_x \left(D(x)^{1-q} \partial_x (D(x)^q u) \right)$. More precisely, X_t being defined, $X_{t+\delta t}$ is implicitly defined, for δt small enough, by

$$X_{t+\delta t} - X_t = \sigma\left(qX_t + (1-q)X_{t+\delta t}\right)(W_{t+\delta t} - W_t).$$

Then, Fickian diffusion ($q = 0$) is characterised by a dependency on the arrival point and Stratonovich diffusion ($q = 1/2$) is characterised by a dependency on the midpoint. Alternative constructions of q-diffusions have been explored in [180], relying upon jump rates instead of jump lengths, and more recently in [6], where a combination of variable jump rates and jump lengths has been investigated. In [193], the authors focused particularly on the cases $q = 1$ (Fokker-Planck diffusion) and $q = -1$. The latter is interpreted as *attractive dispersal*, i.e. the probability of jumping to one's neighbor depends on the environment at that neighbor. We emphasise that the derivations in these works rely on different factors of random walk systems (length of jumps, waiting time, probability of jumping). The reference point at which this factor is considered (middle point, end point, etc.) depends not only on q but also on the original probabilistic model.

Problematic of this chapter. In the field of reaction-diffusion equations, both Fokker-Planck and Fickian diffusion operators are commonly encountered to model heterogeneous diffusions (for instance [18, 57, 139, 208] use Fickian diffusion and [181, 185] use Fokker-Planck diffusion). There appears to be a preference for the use of Fickian diffusion $\partial_x(D(x)\partial_x u)$, due to its self-adjoint nature, which facilitates mathematical computations.

The above presentation indicates that the Fokker-Planck diffusion operator $\partial_{xx}(D(x)u)$ should be more relevant for the description of Brownian-like individual movements when individuals move differently based on the local information that is accessible to them. Several authors advocate for the use of the Fokker-Planck diffusion in biological systems [124, 193,

200, 215, 218]. In contrast, the Fickian diffusion operator is thought to be more suitable for passive physical phenomena, such as the dilution of a dye in a liquid or the diffusion of heat in a heterogeneous medium. As scientific authors in mathematical ecology often seem to use them interchangeably, depending on the technical constraints related to mathematical proofs or based on the modelling works to which they refer, it seems important to understand the concrete effect related to this choice. For example, as underscored by [19] (refer also to [198]), it is well-established that the formation of patterns in spatially inhomogeneous diffusive systems is significantly more pronounced when diffusion follows the Fokker-Planck law, as opposed to Fick's law.

Reaction-diffusion models predominantly aim at examining the persistence or extinction of populations and their spatial spreading dynamics. In this context, the main goal of our work is to analyse the persistence and spreading dynamics of the model in Equation (4.1), with a focus on the parameter q. Specifically, we investigate whether the assumption of a Fickian or Fokker-Planck diffusion significantly affects the outcomes.

Layout. In Section 4.2, we give our general assumptions and standard properties of equations of the form (4.1) under a KPP assumption. Next, in Section 4.3, we give our main results, along with the main ideas of proofs. We add an analysis of some numerical results. We discuss our results in Section 4.4. Last, Section 4.5 is devoted to the proofs.

4.2 Main assumptions and standard properties

4.2.1 Assumptions

The diffusion coefficient $D(x)$ is assumed to be positive, 1-periodic and of class $\mathcal{C}^{2,\alpha}$ (with $\alpha > 0$). The function $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$ is assumed to be of class $\mathcal{C}^{1,\alpha}$ with respect to (x, u) and $\mathcal{C}^2$ with respect to u. We also assume that f is 1-periodic with respect to x and that $f(x, 0) = 0$ for all $x \in \mathbb{R}$. We define

$$r(x) := \frac{\partial}{\partial u} f(x, u)\bigg|_{u=0}.$$

When u represents a population density, the coefficient $r(x)$ is often interpreted as the intrinsic growth rate of the population.

Furthermore, throughout the chapter, we assume the following, which is a (slightly stronger) variant of the KPP assumption:

$$\forall x \in \mathbb{R},\ u \mapsto \frac{f(x, u)}{u} \text{ is decreasing in } u > 0 \tag{4.7}$$

and, for all $q \in \mathbb{R}$,

$$\exists M_q \geqslant 0,\ \forall u \geqslant M_q,\ \forall x \in \mathbb{R},\ f(x, u) + qD''(x)u \leqslant 0. \tag{4.8}$$

These assumptions, along with the instability assumption (4.9) below, ensure the existence and uniqueness of a positive stationary state to (4.1), i.e. a periodic solution $p > 0$ to

$$\partial_x(D^{1-q}\partial_x(D^q p)) + f(x, p) = 0, \qquad x \in \mathbb{R},$$

see [29]. Examples of functions f satisfying (4.7)–(4.8) for all $q \in \mathbb{R}$ include $f(x,u) = r\,u(1-u)$ or $f(x,u) = u(r(x) - \gamma(x)u)$, where r and γ are $\mathcal{C}^{1,\alpha}$ periodic functions. The regularity assumptions on r and γ (and thus on f) could be relaxed, for example, to L^∞, but it would require us to deal with Sobolev spaces $W^{2,p}$ rather than Hölder spaces $\mathcal{C}^{2,\alpha}$.

4.2.2 Standard persistence and spreading properties

For $q \in \mathbb{R}$, we let $\mathcal{L}_q^0$ be the operator defined by

$$\mathcal{L}_q^0 \psi := \partial_x(D^{1-q}\partial_x(D^q\psi)) + r\psi.$$

For $\lambda \in \mathbb{R}$, we define the operator $\mathcal{L}_q^\lambda$ as follows:

$$\mathcal{L}_q^\lambda \psi(x) := e^{\lambda x}\mathcal{L}_q^0\left(y \mapsto e^{-\lambda y}\psi(y)\right).$$

More explicitly, we have:

$$\mathcal{L}_q^\lambda : \psi \mapsto D\psi'' + \Big((1+q)D' - 2\lambda D\Big)\psi' + \Big(qD'' + \lambda^2 D - (1+q)\lambda D' + r\Big)\psi.$$

We define the principal eigenvalue k_q^λ of $\mathcal{L}_q^\lambda$ as the unique real number for which there exists a 1-periodic function $\varphi > 0$ satisfying

$$\mathcal{L}_q^\lambda \varphi = k_q^\lambda \varphi.$$

For each $q, \lambda \in \mathbb{R}$, the existence and uniqueness of the pair (φ, k_q^λ) (up to multiplication of φ by a constant) is guaranteed by the Krein-Rutman theory. For the sake of explicitness, we will usually use the notations $\mathcal{L}_q^\lambda[r;D]$ and $k_q^\lambda[r;D]$ to insist on the dependency on the coefficients r and D.

We now state two important properties of the principal eigenvalues $k_q^\lambda[r;D]$ ($\lambda \in \mathbb{R}$) to justify why their properties are crucial to the study of the solutions of Equation (4.1).

First, we focus on the persistence of the population. By "persistence", we will refer to the property that starting from any bounded and continuous function u_0 satisfying $u_0 \geqslant 0$ and $u_0 \not\equiv 0$, the solution $u(t,x)$ to the Cauchy problem (4.1) with initial condition $u(0,\cdot) = u_0$ satisfies

$$\liminf_{t\to+\infty} \sup_{x\in\mathbb{R}} u(t,x) > 0.$$

Persistence holds if, and only if

$$k_q^0[r;D] > 0, \tag{4.9}$$

see [27] for $q = 0$, and see Section 3.6 in Chapter 3 for general q. Under condition (4.9), assumptions (4.7)–(4.8) ensure that the solution converges in large time to the unique positive stationary solution p. On the other hand, if $k_q^0[r;D] \leqslant 0$, then, starting from any bounded continuous and nonnegative initial condition u_0 with compact support, the solution converges uniformly to 0. This means, from the point of view of modelling, that the population gets extinct.

In this chapter, we call $k_q^0[r;D]$ the "ability of persistence" for the parameters q, r and D. This terminology comes from the fact that a population described by Equation (4.1) is more resilient to constant perturbations of its growth rate when $k_q^0[r;D]$ is higher. Specifically, if $\kappa > 0$ is a constant, then $k_q^0[r-\kappa;D] = k_q^0[r;D] - \kappa$ becomes negative if $k_q^0[r;D]$ is small. Con-

sequently, a higher value of $k_q^0[r;D]$ increases the likelihood of persistence under a constant random perturbation of r.

Second, let us define the spreading speed (to the right) $c_q^*[r;D]$ by:

$$c_q^*[r;D] = \inf_{\lambda>0} \frac{k_q^\lambda[r;D]}{\lambda} > 0. \tag{4.10}$$

Equation (4.10) is called the *Freidlin-Gärtner formula* for the spreading speed. If $c_q^*[r;D] > 0$, we say that the population spreads to the right. If $u_0 \not\equiv 0$ is continuous, nonnegative and has a compact support, then for each $w \in (0, c_q^*[r;D])$,

$$\liminf_{t\to+\infty} u(t,wt) > 0,$$

and for each $w > c_q^*[r;D]$,

$$\lim_{t\to+\infty} u(t,wt) = 0.$$

This means that if an observer moves to the right at a speed larger than $c_q^*[r;D]$, they will see the solution decay to 0, while if the observer travels at a speed smaller than $c_q^*[r;D]$, they will observe a density that remains bounded from below by a positive constant. More precisely, the solution u converges locally uniformly to the unique stationary state p of Equation (4.1).

We know from [28, 175] that $\lambda \mapsto k_0^\lambda[r;D]$ is strictly convex and reaches its minimum at $\lambda = 0$. Using Proposition 4.3.3 below, we will see that $\lambda \mapsto k_q^\lambda[r;D]$ has the same properties for all $q \in \mathbb{R}$. Thus, if the condition for persistence is satisfied, the condition for spreading is also satisfied. Therefore, we have the following well-known, yet significant, equivalence:

The condition for persistence $k_q^0[r;D] > 0$ is equivalent to
the condition for spreading $c_q^*[r;D] > 0$.

In our context, the existence of a spreading speed and the formula (4.10) follow from [25, 26, 220]. This framework was originally proposed in the work by Gärtner and Freidlin [103] when $q = 0$.

Finally, let us mention that the spreading speed to the left can be defined as well, and the same type of Freidlin-Gärtner formula holds [25, 26]:

$$c_q^{*,left}[r;D] = \inf_{\lambda>0} \frac{k_q^{-\lambda}[r;D]}{\lambda}. \tag{4.11}$$

In our context, the spreading speed to the left and the spreading speed to the right coincide (see Proposition 4.3.9). This is due to the fact that the drift term in (4.2) has zero integral on a period.

4.3 Results

We now state our results. We first prove that in general, the choice of the parameter q of the q-diffusion operator has an influence on the ability of persistence and the spreading speed. Second, we consider a constant reaction term r; then the ability of persistence does not depend on q. Regarding the spreading speed, we prove that there is a symmetry around the Stratonovich diffusion. In particular, the Fickian diffusion and the Fokker-Planck diffusion are symmetric with respect to the Stratonovich diffusion, and thus give the same spreading

speed. Third, we consider general r again and we give monotonicity and non-monotonicity properties of the spreading speed with respect to the parameter q. Last, we provide observations from numerical simulations.

Throughout this section, we work under the assumption that $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ is 1-periodic and $D \in \mathcal{C}^{2,\alpha}(\mathbb{R})$ is 1-periodic and positive.

4.3.1 Different behaviours with respect to q

In our first result, we show that the choice of the value of q may indeed have an impact on the ability of persistence and on the spreading speed. In particular, through appropriate choices of coefficients r and D, the q-diffusion operator can give rise to a higher or lower ability of persistence and spreading speed with respect to Fickian diffusion ($q = 0$).

Theorem 4.3.1. *Consider a nonconstant D and let $q \in \mathbb{R} \setminus \{0\}$.*

(i) There exists r for which $k_q^0[r;D] < k_0^0[r;D]$ and $c_q^*[r;D] < c_0^*[r;D]$;

(ii) There exists r for which $k_q^0[r;D] > k_0^0[r;D]$ and $c_q^*[r;D] > c_0^*[r;D]$.

Consider a nonconstant r and let $q \in \mathbb{R} \setminus \{0\}$.

(iii) There exists D for which $k_q^0[r;D] < k_0^0[r;D]$;

(iv) There exists D for which $k_q^0[r;D] > k_0^0[r;D]$.

Remark 4.3.2. Using the same methodology as in item (i) of the theorem, it can be shown that for every non-constant D and for $|q| > |\tilde{q}|$, there exists a function r such that

$$k_q[r;D] < k_{\tilde{q}}[r;D], \quad c_q^*[r;D] < c_{\tilde{q}}^*[r;D].$$

Our proof does not allow us to obtain other comparisons with general values of q and $\widetilde{q}$.

Let us now describe the main tools that we will use to prove Theorem 4.3.1. The first ingredient for items *(i)* and *(ii)* is the following proposition, which gives a relationship between the eigenvalues $k_q^\lambda[r;D]$ for different values of q.

Proposition 4.3.3. *For all $q \in \mathbb{R}$ and $\lambda \in \mathbb{R}$, we have*

$$k_q^\lambda[r;D] = k_0^\lambda[r - h_q;D],$$

with $h_q := -\dfrac{q}{2}D'' + \dfrac{q^2}{4}\dfrac{(D')^2}{D}$.

This proposition shows that, in terms of persistence and spreading, Equation (4.1) behaves as a Fisher-KPP equation with Fickian diffusion, but where the growth term r is replaced with $r - h_q$. Due to the periodicity of D, the arithmetic mean values of r and $r - h_q$ can be compared: $\langle r - h_q \rangle_A \leqslant \langle r \rangle_A$, and the inequality is strict if D is not constant. Additionally, $\langle r - h_q \rangle_A$ is a decreasing function of q. On the other hand, since D is periodic, there exists x_0 in $[0,1]$ such that $-h_q(x_0) > 0$ and therefore $r(x_0) < r - h_q(x_0)$. With such considerations, we will be able to conclude the first part of items *(i)* and *(ii)* on persistence.

The second ingredient for items *(i)* and *(ii)* is the following proposition, which allows us (in situations of persistence, but close to extinction) to extend a comparison on $k_q^0[r;D]$ to a comparison on $c_q^*[r;D]$.

Proposition 4.3.4. *Let $q, \tilde{q} \in \mathbb{R}$ and r, D be fixed. Assume that $k_q^0[r;D] > k_{\tilde{q}}^0[r;D] > 0$. Then, there exists $\kappa_0 \in (0, k_{\tilde{q}}^0[r;D])$ such that, for all $\kappa \in (\kappa_0, k_{\tilde{q}}^0[r;D])$,*

$$c_q^*[r-\kappa;D] > c_{\tilde{q}}^*[r-\kappa;D] > 0.$$

Finally, for items *(iii)* and *(iv)*, which only deal with a persistence property, we use the following proposition.

Proposition 4.3.5. *Let D and r be fixed. For all $q \in \mathbb{R}$, we have:*

$$\lim_{B\to\infty} k_q^0[r;B\,D] = \int_0^1 r\,\frac{D^{-q}}{\int_0^1 D^{-q}}.$$

On the one hand, Proposition 4.3.5 implies that provided $r > 0$ and B is sufficiently large, diffusion functions of the form $B\,D = B\,r^{1/q}$ lead to a higher ability of persistence for the Fickian diffusion than for other values of q, due to the arithmetic-harmonic mean inequality. The function $Br^{1/q}$ is "in phase" with r for $q > 0$ and is "out of phase" with r for $q < 0$. We will prove (iii) in this way.

To prove the reverse inequality (iv), we will consider functions of the form $D_1 := B\,D$, with B large enough, and for a function D such that $1/D$ is concentrated around the maximum of r if $q > 0$, or D is concentrated around the maximum of r if $q < 0$. Again, (iv) will follow from Proposition 4.3.5.

Since r is fixed in (iii) and (iv), it is not possible in general to choose D such that the population is close to extinction, and to use Proposition 4.3.4 to extend the result on persistence to a result on the spreading speeds, as we did for items (i) and (ii). However, for every non-constant r, it can be stated that there exist pairs (D,κ) (where κ is a constant) such that $c_q^*[r-\kappa;D] < c_0^*[r-\kappa;D]$, and pairs (D,κ) for which $c_q^*[r-\kappa;D] > c_0^*[r-\kappa;D]$.

4.3.2 Constant growth rate r

In this section, we focus on the special case where the growth rate r is constant. The main result of this section is the following theorem, which shows that the spreading speeds for Fickian diffusion ($q = 0$) and Fokker-Planck diffusion ($q = 1$) coincide, as they are, in some sense, symmetric. The center of this symmetry is the Stratonovich diffusion ($q = 1/2$).

Theorem 4.3.6. *Assume that $r > 0$ is constant. We have the following properties:*

(i) The function $q \mapsto c_q^*[r;D]$ is symmetric around $1/2$, that is, for all $\tilde{q} \in \mathbb{R}$,

$$c_{1/2-\tilde{q}}^*[r;D] = c_{1/2+\tilde{q}}^*[r;D].$$

In particular, $c_0^*[r;D] = c_1^*[r;D]$.

(ii) For $q = 1/2$, we have the explicit formula:

$$c_{1/2}^*[r;D] = 2\sqrt{r} \times \left\langle \sqrt{D} \right\rangle_H, \qquad \text{with } \left\langle \sqrt{D} \right\rangle_H := \left(\int_0^1 \frac{1}{\sqrt{D}} \right)^{-1}.$$

(iii) The maximal speed is reached at $q = 1/2$:

$$c_{1/2}^*[r;D] = \max_{q\in\mathbb{R}} c_q^*[r;D].$$

Item (i) of this theorem is somewhat unexpected, and the ideas of its proof are explained below. Item (ii) is also remarkable, because it allows us to establish a connection to previous work on slowly varying media, which we now detail.

For $L > 0$, when $D(x)$ is replaced with $D(x/L)$, we can define the operators $\mathcal{L}_q^\lambda(L)$ analogously to $\mathcal{L}_q^\lambda$; the operator $\mathcal{L}_q^\lambda(L)$ has a principal eigenvalue $k_q^\lambda(L)$, depending on L, and associated with a $L-$periodic principal eigenfunction. The criterion for persistence still holds, and the spreading speed $c_q^*(L)$ is given by the Freidlin-Gärtner formula (4.10), i.e.

$$c_q^*(L) = \inf_{\lambda>0} \frac{k_q^\lambda(L)}{\lambda}.$$

Item (ii) of Theorem 4.3.6 gives an explicit formula for $c_{1/2}^*(1)$; this explicit formula also appears in the context of slowly varying environments. Namely, as a consequence of [119, Theorem 2.3], we have

$$\lim_{L\to+\infty} c_0^*(L) = \inf_{\lambda>0}\left(\frac{r}{\lambda} + \lambda\left\langle\sqrt{D}\right\rangle_H^2\right) = 2\sqrt{r}\times\left\langle\sqrt{D}\right\rangle_H,$$

which is equal to $c_{1/2}^*(1)$. Moreover, in the proof of Theorem 4.3.6 (ii), we will also prove that $c_{1/2}^*(L)$ is in fact independent of L: thereby, for $q = 1/2$ and constant r, the *spreading speed does not depend on the period*. Let us close this discussion about different periods and keep, from now on, $L = 1$.

The proof of item (ii) of Theorem 4.3.6 relies on three key propositions. The first proposition turns the heterogeneous diffusion into a homogeneous diffusion with a drift term depending on q. This transformation uses the space variable change $y = h(x)$, where

$$h(x) := \int_0^x \frac{\mathrm{d}x'}{\sqrt{D(x')}}.$$

Note that $1/h(1) = \left\langle\sqrt{D}\right\rangle_H$.

Proposition 4.3.7. *Let $R(y) := r\left(h^{-1}(y)\right)$, $P(y) := \ln\left(D\left(h^{-1}(y)\right)\right)$ and $s_q := \frac{1}{2} - q$. Let $\widehat{k}_q^\lambda$ be the $h(1)$-periodic principal eigenvalue of the operator $\widehat{\mathcal{L}}_q^\lambda$ defined by*

$$\widehat{\mathcal{L}}_q^\lambda : \Phi \mapsto \partial_{yy}\Phi - \partial_y\left[\left(2\lambda + s_q P'\right)\Phi\right] + \left(R + \lambda s_q P' + \lambda^2\right)\Phi.$$

Then for all $\lambda \in \mathbb{R}$ and $q \in \mathbb{R}$,

$$k_q^\lambda[r; D] = \widehat{k}_q^{\lambda\left\langle\sqrt{D}\right\rangle_H}.$$

As a consequence of Proposition 4.3.7, we have $k_q^0 = \widehat{k}_q^0$ and, using (4.10):

$$c_q^*[r; D] = \left\langle\sqrt{D}\right\rangle_H \times \inf_{\lambda>0} \frac{\widehat{k}_q^\lambda}{\lambda}.$$

This result highlights a symmetry between Fickian diffusion ($q = 0$) and Fokker-Planck diffusion ($q = 1$), since $s_0 = -s_1$. However, demonstrating that $\widehat{k}_0^\lambda = \widehat{k}_1^\lambda$ or, more generally, that $\widehat{k}_{1/2-\tilde{q}}^\lambda = \widehat{k}_{1/2+\tilde{q}}^\lambda$ for $\tilde{q} \in \mathbb{R}$ remains a challenging task. The crucial ingredient is the following result from Chapter 3, which implies that, given a periodic Schrödinger operator with

an advection term and a potential term proportional to the advection term, the principal eigenvalue remains invariant under a sign change of the advection term.

Proposition 4.3.8 (Chapter 3, Theorem 3.2.2)**.** *Let $a \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ and $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ be two 1-periodic functions. Consider the two operators acting on 1-periodic functions:*

$$\mathcal{M}^- : \Phi \mapsto \partial_{yy}\Phi - \partial_y(b\Phi) + a\Phi \text{ and } \mathcal{M}^+ : \Phi \mapsto \partial_{yy}\Phi + \partial_y(b\Phi) + a\Phi.$$

If there exist $\beta \in \mathbb{R}$ and $\gamma \in \mathbb{R}$ such that $a = \beta + \gamma b$, then $\mathcal{M}^-$ and $\mathcal{M}^+$ have the same principal eigenvalue.

In fact, Theorem 2.2 in Chapter 3 deals with the adjoint operators of $\mathcal{M}^-$ and $\mathcal{M}^+$, but the result holds also for $\mathcal{M}^-$ and $\mathcal{M}^+$, since the principal eigenvalue of an operator coincides with the principal eigenvalue of its adjoint.

Last, we will need to use the equality between the spreading speed to the left and the spreading speed to the right. Owing to the nonsymmetric nature of Equation (4.1) with respect to the variable x, this equality is not obvious. We state it in the following proposition.

Proposition 4.3.9. *For all $q \in \mathbb{R}$ and $\lambda \in \mathbb{R}$, $k_q^{-\lambda}[r;D] = k_q^{\lambda}[r;D]$. As a consequence, the spreading speed to the left and the spreading speed to the right coincide:*

$$c_q^*[r;D] = \inf_{\lambda>0} \frac{k_q^{\lambda}[r;D]}{\lambda} = \inf_{\lambda>0} \frac{k_q^{-\lambda}[r;D]}{\lambda} = c_q^{*,left}[r;D].$$

4.3.3 (Non-)monotonicity in q and limiting behaviour as $q \to \pm\infty$

We now go back to the case of general 1-periodic $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ and focus on the dependency of $k_q^0[r;D]$ and $c_q^*[r;D]$ on q. Again, Proposition 4.3.7 will be central in the proofs.

Theorem 4.3.10. (*i*) *Assume that all extremal points of D are non-degenerate (i.e. $D'' \neq 0$ at these points). Let $\underline{\mathcal{A}}$ be the set of points at which D reaches a local minimum and let $\overline{\mathcal{A}}$ be the set of points at which D reaches a local maximum. Then, as $q \to \pm\infty$, the ability of persistence k_q^0 converges to the following limits:*

$$\lim_{q\to+\infty} k_q^0[r;D] = \max_{x\in\underline{\mathcal{A}}} r(x), \qquad \lim_{q\to-\infty} k_q^0[r;D] = \max_{x\in\overline{\mathcal{A}}} r(x);$$

(*ii*) *Assume that D is not constant. Then, as $q \to \pm\infty$, the spreading speed $c_q^*[r;D]$ converges to 0:*

$$\lim_{q\to\pm\infty} c_q^*[r;D] = 0.$$

Let us comment on this theorem. The limit as $q \to \pm\infty$ of $k_q^0[r;D]$ is similar to [66, Theorem 1], which dealt with an eigenvalue problem with Neumann boundary condition (instead of periodic boundary conditions). Our proof share similarities with their proof, but has been adapted to the periodic setting. The second item seems quite surprising, especially when it is compared to the first item: namely, we can have

$$\liminf_{q\to\pm\infty} k_q^0[r;D] > 0$$

but

$$\lim_{q\to\pm\infty} c_q^*[r;D] = 0.$$

The second item highlights a fundamental difference between homogeneous and heterogeneous diffusion, as for constant D, the spreading speed $c_q^*[r;D]$ is independent of q.

The first ingredient of the second item is the *Feynman-Kac formula*. Let $\overline{u}$ be the solution to the *linear adjoint* Cauchy problem

$$\partial_t \overline{u}(t,x) = D(x)\,\partial_{xx}\overline{u} + b(x)\,\partial_x \overline{u} + r(x)\overline{u}, \quad t>0,\ x\in\mathbb{R},$$

with $\overline{u}(0,\cdot) = u_0$ (where $b\in\mathcal{C}^{1,\alpha}(\mathbb{R})$ is also 1-periodic). The Feynman-Kac formula implies that $\overline{u}$ can be expressed in terms of a stochastic process $(X_t)_{t\geqslant 0}$ as:

$$\overline{u}(t,x) = \mathbb{E}_x\left[u_0(X_t)\exp\left(\int_0^t r(X_{t-s})\,\mathrm{d}s\right)\right]. \tag{4.12}$$

The process $(X_t)_{t\geqslant 0}$ under the expectation $\mathbb{E}_x$ is defined by:

$$\mathrm{d}X_t = b(X_t)\,\mathrm{d}t + \sqrt{2D(X_t)}\,\mathrm{d}W_t, \qquad X_0 = x,$$

where $(W_t)_{t\geqslant 0}$ is a standard Brownian motion.

The second ingredient for the proof of the second item of Theorem 4.3.10 is the following proposition, which deals with the exit time of an interval by the process $(X_t)_{t\geqslant 0}$ when the intensity of the drift b goes to infinity. We state the result for general Lipschitz drift term b. This regularity assumption ensures the well-posedness of the equation.

Proposition 4.3.11. *Let $b\in\mathcal{C}^{0,1}(\mathbb{R})$ be a Lipschitz function such that there exists $x_0\in[0,1]$ with $b(x_0)>0$. For $s\in\mathbb{R}$, let $(X_t^s)_{t\geqslant 0}$ be the unique solution of*

$$\mathrm{d}X_t^s = sb(X_t^s)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t, \qquad X_0 = 1.$$

Let $\tau^s := \inf\{t\geqslant 0 \ / \ X_t^s \leqslant 0\}$ be the exit time from $(0,+\infty)$ of $(X_t^s)_{t\geqslant 0}$. Then, for all $a>0$, as $s\to+\infty$,

$$\mathbb{P}\left(\tau^s \leqslant a\right) \to 0.$$

Let us now state our last main result. The simulations in Section 4.3.4 suggest that $q\mapsto k_q^0[r;D]$ is monotonic. In fact, the monotonicity of $q\mapsto k_q^0[r;D]$ depends on the situation and does not hold in general. Finally, the monotonicity of $c_q^*[r;D]$ never holds if spreading can occur.

Theorem 4.3.12. *Let $\kappa : q\mapsto k_q^0[r;D]$. We have:*

(i) If r is a constant, then $\kappa(q) = r$ for all $q\in\mathbb{R}$;

(ii) For this item, assume the following:

- *(a) D and r are monotonic on $[0,1/2]$, 1-periodic and even (thus D and r are also monotonic on $[1/2,1]$);*
- *(b) $D\in\mathcal{C}^3(\mathbb{R})$ and $r\in\mathcal{C}^4(\mathbb{R})$;*
- *(c) $r'\neq 0$ on $(0,1/2)$; $r''(0)\neq 0$ and $r''(1/2)\neq 0$.*

Then κ is monotonic. If D and r have the same monotonicity on $[0,1/2]$, then κ is nonincreasing. If D and r have opposite monotonicity, then κ is nondecreasing;

(iii) On the other hand, there exist r and D such that κ is not monotonic (and nonconstant);

(iv) Assume that there exists $q \in \mathbb{R}$ such that $k_q^0 > 0$. Then the function $q \mapsto c_q^*[r;D]$ is not monotonic.

Item (i) of this theorem is standard. Item (ii) shows, similarly to Proposition 4.3.5 but in greater details, that increasing q (for instance by shifting from Fickian to Fokker-Planck diffusion) enhances the ability of persistence when r and D are in phase, and decreases it when r and D are out of phase. It is proved by using the Feynman-Kac formula. The third item is proved by constructing an explicit counterexample. The fourth item is proved by using Theorem 4.3.10.

4.3.4 Numerical simulations

We use standard matrix methods in Python (SciPy and ARPACK libraries using the eigs function) together with a finite difference approximation to determine the principal eigenvalue $k_q^\lambda[r;D]$ for discrete values of λ. This information is then used in conjunction with the Freidlin-Gärtner formula (4.10) to yield an approximate value of $c_q^*[r;D]$. A Jupyter notebook is available at DOI: 10.17605/OSF.IO/GDQVP. This method is expected to be more reliable than the direct simulation of the solution to (4.1) conducted in previous studies ([139] for $q=0$ and [19] for $q \in [0,1]$) for multiple reasons: (i) it does not require a finite domain approximation since the eigenvalue problem is solved over one period; (ii) it avoids reliance on a finite time approximation to estimate the spreading speed; (iii) it circumvents the challenges posed by nonlinearity (the eigenvalue problem defining $k_q^\lambda[r;D]$ is linear).

Constant r case. In the computations presented in Figure 4.1, we begin by examining the dependency of $c_q^*[r;D]$ on q, where $r \equiv r_0$ is a constant. As expected from the result of Theorem 4.3.6, we find that the speed $q \mapsto c_q^*[r;D]$ is symmetric with respect to $q=1/2$, and is maximal at $q=1/2$. This is also consistent with previous results in [19] for $q \in [0,1]$, where $q \mapsto c_q^*[r;D]$ is close to its maximum and therefore exhibits a parabolic shape. Outside of this range, we observe that $c_q^*[r,D]$ decays, and converges to 0 (we get $c_q^*[r,D] \approx 0.01$ with $q=50$) as $q \to \pm\infty$, which is consistent with the result of Theorem 4.3.10.

Effect of a phase shift between r and D. Next, we explore how $k_q^0[r;D]$ (the principal eigenvalue determining the ability of persistence) and the spreading speed $c_q^*[r;D]$ vary with a phase shift ω between r and D, see Figure 4.2. More precisely, we set $D(x) = C + r(x+\omega)$, for some constant C ensuring $D > 0$, with $\omega \in [0,1]$. Here, $\omega = 0$ means that r and D are "in phase" and $\omega = 1/2$ means that r and D are "out of phase". We consider six values of q: $q=0$ (Fick), $q=1/2$ (Stratonovich), $q=1$ (Fokker-Planck), $q=2$, $q=-1$ (called *attractive dispersal* or AD in [193]), and $q=-1/2$. As expected from Proposition 4.3.5 and Theorem 4.3.10 (i), the effect of the phase shift ω on $k_q^0[r;D]$ (and therefore on $c_q^*[r;D]$) depends strongly on q.

For $q \geqslant 0$, consistently with previous findings ([139] in the Fickian case, see also Theorem 5.1 in [173]), the highest speeds and highest values of k_q^0 are achieved when r and D are out of phase ($\omega = 1/2$). In other terms, $k_q^0[r;D]$ and $c_q^*[r;D]$ tend to increase with $\omega \in (0, 0.5)$.

However, this effect is mild for $q = 0$, as $k_0^0[r; D]$ appears to be almost independent of ω (with only minor numerical variations observed). The amplitude of the effect of ω seems to increase with q. This can be interpreted as follows: when $q > 0$, the term $q\partial_x (D'(x)u)$ in (4.2) causes individuals to concentrate around regions where $D(x)$ is minimal. This concentration can enhance persistence ($k_q^0[r; D]$) if the minimum of $D(x)$ coincides with the maximum of $r(x)$ ($\omega = 1/2$). When q is large, this effect is amplified, as the advection term dominates, further concentrating individuals in favourable regions.

For $q < 0$, such as $q = -1$ and $q = -1/2$, the behaviour changes significantly. In these cases, k_q^0 and c_q^* tend to decrease with $\omega \in (0, 0.5)$. Therefore, the highest speeds and highest values of k_q^0 are achieved when r and D are in phase ($\omega = 0$). This time, the term $q\partial_x (D'(x)u)$ in (4.2) causes individuals to concentrate in regions where $D(x)$ is maximal, allowing them to better exploit $r(x)$ when its maximum coincides with that of D.

Effect of q. We observe that, for each fixed value of ω, the function $q \mapsto k_q^0$ is monotonic (Figure 4.2, left). This behaviour was predicted by Theorem 4.3.12 *(ii)* in the cases $\omega = 0$ and $\omega = 1/2$. Interestingly, and in agreement with the result of Theorem 4.3.12 *(iv)*, this monotonicity property no longer holds for $q \mapsto c_q^*$, even in the cases $\omega = 0$ and $\omega = 1/2$.

Optimisation of the diffusion coefficient. When r and D are in phase ($\omega = 0$), Fickian diffusion results in higher speeds than other diffusion models (Figure 4.2, right). Conversely, when r and D are out of phase ($\omega = 1/2$), Fokker-Planck diffusion leads to the fastest speeds, compared to $q = 0$ and even $q = 1/2$. To gain insight into the specific interactions between r and D that favour either Fickian or Fokker-Planck diffusion relative to each other, we conducted an optimisation procedure. Specifically, we set $r(x) = \cos^2(\pi x)$ and optimised the ratio $c_0^*[r, D]/c_1^*[r, D]$ (respectively, $c_1^*[r, D]/c_0^*[r, D]$) with respect to D. The optimisation is performed using a simulated annealing algorithm, which iteratively modifies the function D. This function is constructed as a smooth, periodic function using cubic splines, based on a vector of four points whose values lie within the range $(0.1, 1)$. These points correspond to the positions $x = 0$, $x = 1/3$, $x = 2/3$, and $x = 1$, with the first and last values necessarily being identical to ensure periodicity. The optimisation process directly operates on this vector of four points to determine the optimal form of D. See Figure 4.3. We observe that the function D maximising the ratio $c_0^*[r, D]/c_1^*[r, D]$ is in phase with r, yielding a ratio of approximately 1.43. Conversely, the function D that maximises the ratio $c_1^*[r, D]/c_0^*[r, D]$ is out of phase with r, resulting in a ratio of approximately 1.15.

4.4 Discussion

General conclusions. The comparative analysis of Fickian, Fokker-Planck and other q-diffusion models in this study shows that the choice between these diffusion models is not merely a matter of mathematical preference, but has profound implications for the understanding of spatial dynamics in heterogeneous environments. Our investigation underscores the sensitivity of both persistence and spreading properties to the diffusion model employed, and that there is no general rule for the comparative behaviour of persistence and spreading speeds for different values of q across all settings. In particular, Theorem 4.3.1 shows that for any $q \neq 0$, suitable configurations of growth rates r and diffusion coefficients D can be found such that the q-diffusion either increases or decreases the ability of persistence and the spreading speed with respect to the traditional Fickian diffusion.

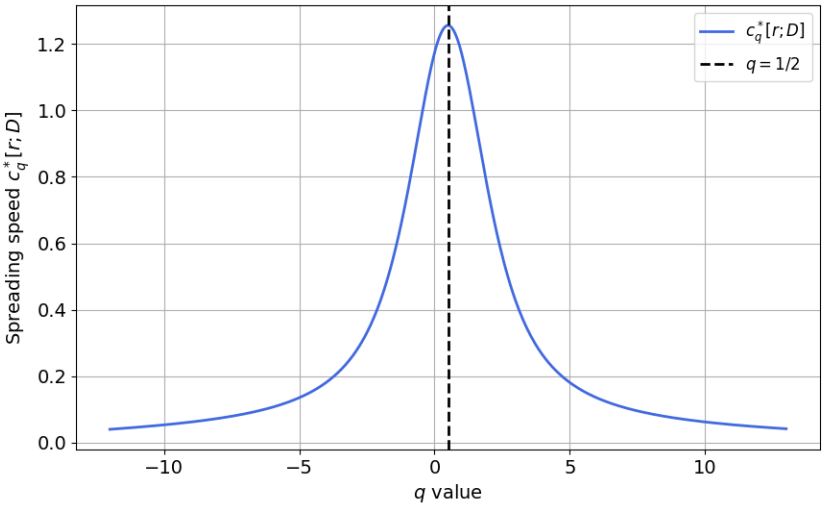

Figure 4.1: Spreading speed $c_q^*[r;D]$ depending on q, with a constant growth term $r \equiv 1$. Here, $D(x) = 0.1 + \cos^2(\pi x)$.

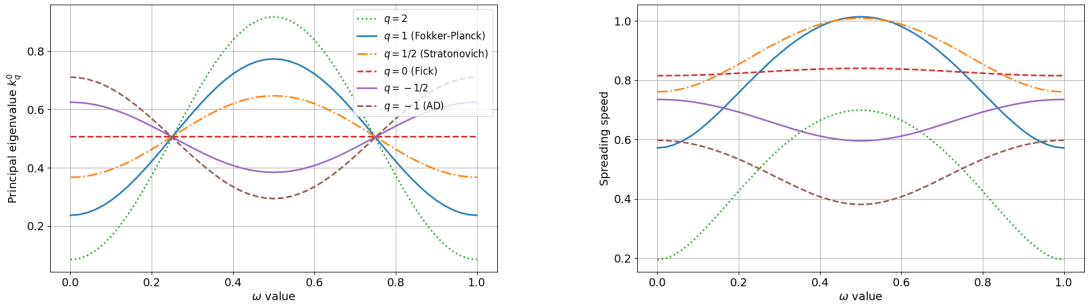

Figure 4.2: Principal eigenvalue k_q^0 and spreading speed $c_q^*[r;D]$ depending on the phase shift ω between r and D. Here, $r(x) = \cos^2(\pi x)$ and $D(x) = 0.1 + \cos^2(\pi(x+\omega))$.

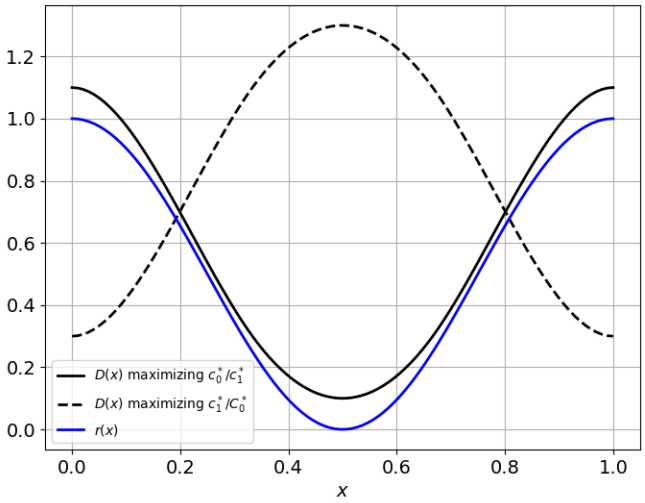

Figure 4.3: Functions D optimising the ratio $c_0^*[r,D]/c_1^*[r,D]$ (respectively, $c_1^*[r,D]/c_0^*[r,D]$) with r fixed to $r(x)=\cos^2(\pi x)$. The optimisation is based on a simulated annealing algorithm. The function D is interpolated from four discrete points using cubic splines.

The case of constant r. A somewhat unexpected finding emerges when the growth rate r is constant. Despite the heterogeneity of D, Fickian ($q=0$) and Fokker-Planck ($q=1$) diffusion models yield equal spreading speeds. This result is a consequence of an underlying symmetry in the function $q\mapsto c_q^*$ around $q=1/2$; Fickian and Fokker-Planck diffusions represent a special case of symmetry. Moreover, the maximal spreading speed is achieved with Stratonovich diffusion ($q=1/2$). We derive an explicit formula for the maximal spreading speed, and we point out that this maximal spreading speed is equal to the already-known limit of the spreading speed for Fickian diffusion as the period of D goes to infinity (in this chapter, the period is mostly kept equal to 1, but the same properties hold for any period, as long as r and D have the same period). Furthermore, we prove that $c_{1/2}^*$ does not depend on the period of D when r is constant.

Although the spreading speeds are equal for Fickian and Fokker-Planck diffusion, it is important to note that the shapes of the solutions can differ significantly. For instance, if $f(x,u)=u(1-u)$ in (4.1), the positive equilibrium solution is $u\equiv 1$ for Fickian diffusion, whereas it is necessarily non-constant with Fokker-Planck diffusion if D is not constant.

Effects of the interactions between r and D. Our analytical results on persistence (Proposition 4.3.5, Theorem 4.3.10 (i), Theorem 4.3.12 (ii)) and numerical findings on persistence and spreading (Figures 4.2 and 4.3) show that, for $q\geqslant 0$, the maximum ability of persistence and the maximum spreading speed are achieved when r and D are out of phase (i.e., r is large where D is small). Biologically, this is relevant and consistent with the existing literature ([139], case $q=0$): organisms tend to remain in favourable environments and leave unfavourable ones. Even when the direction toward a better environment is unknown, because the individuals have access only to very local information, organisms still recognise the necessity of leaving unfavourable areas (this situation could correspond to $q=1/2$ in the case of variable jump length or $q=1$ for variable jump rate, as discussed below).

On the other hand, our results reveal reversed outcomes regarding phase shift effects when $q < 0$. Moreover, the amplitude of speed variation with respect to phase shifts is significantly more pronounced in the Fokker-Planck case ($q = 1$) than in the Fickian case ($q = 0$), highlighting important ecological implications. Specifically, in the context of ecological or epidemiological modelling, the strategic placement of dispersal barriers, which reduce D in regions of high or low r, is likely to have a much stronger impact under Fokker-Planck diffusion than under Fickian diffusion. More precisely, in order to prevent or slow down an invasion, our results indicate that dispersal barriers should be placed where r is small when $q > 0$, where r is large when $q < 0$, and that the position of these barriers will have little effect when q is close to 0.

How to choose q in real-world applications? While this question goes beyond the scope of this chapter and has already been partly addressed in [6, 218], we recall that, as mentioned in the introduction of this chapter, when the q-diffusion is derived from a microscopic probabilistic model, the value of q depends on two factors: the influence of spatial heterogeneity (e.g., the jump rate in [180] or the jump length in [218]) and the chosen reference point. Here, for a jump between X_t and $X_{t+\delta t}$, the reference point is the point Y_t on the line going through X_t and $X_{t+\delta t}$ where the heterogeneity $D(Y_t)$ (or $\sigma(Y_t)$, following the notations in the introduction of this chapter) is evaluated.

Thus, while a middle reference point (i.e. $Y_t = (X_t + X_{t+\delta})/2$) leads to $q = 1/2$ in the construction based on jump length, the same middle reference point leads to $q = 0$ when the construction is based on jump rate [180]. In practice, depending on the physical or biological system under consideration, the most relevant reference point may vary according to the factor being considered. For example, in some biological contexts where individuals have access only to local information, the jump rate should depend on the starting point, leading to $q = 1$; on the other hand, the jump length might depend on the information they gather during their movement and thus depend, e.g., on the midpoint, leading to $q = 1/2$.

In real diffusion phenomena, the effective value of q could be estimated directly from observation data, using a PDE with q-diffusion combined with a statistical estimation procedure, as in [136]. In this case, assuming that the reference point associated with each type of factor is known, estimating the value of q can provide insight into which factor is influenced by spatial heterogeneity. It should be noted that the value of q may also result from a weighted contribution of several factors, each with a different reference point. For example, in [136], the authors find an experimental value of $q \approx 0.25$, which they interpret as a predominant effect of factors leading to $q = 0$, compared to those associated with larger values of q.

Regarding this last point, let us highlight that if $q \in [-1, 1]$, q-diffusion can be obtained as a "convex combination" of the standard models discussed in the introduction of this chapter, where q takes values in $\{-1, 0, 1/2, 1\}$. This can be demonstrated by using convex combinations of Equation (4.2) with $q \in \{-1, 0, 1/2, 1\}$. Consequently, a q-diffusion mechanism can also arise from a combination of several standard q_i-diffusion mechanisms, where $q_i \in \{-1, 0, 1/2, 1\}$. In this chapter, we also consider cases where $q \notin [-1, 1]$, which fall outside the scope of all standard models but yield interesting mathematical properties.

Extensions. While our results are derived in a 1D context, extending this analysis to higher spatial dimensions could unveil additional phenomena that further influence the effects of phase shifts on the spreading speed. A possible extension of q-diffusion operators to higher

dimensions $n \geqslant 2$ could incorporate different types of diffusion along each spatial direction, allowing for direction-dependent exponents q_i. The resulting operator would take the form:

$$\sum_{i=1}^{n} \partial_{x_i} \left(D_i(x_i)^{1-q_i} \partial_{x_i} \left(D_i(x_i)^{q_i} u \right) \right),$$

where $D_i(x_i)$ represents the diffusion coefficient along the i-th direction, and q_i determines the type of diffusion in that direction. In the context of eco-evolutionary models, populations can be structured both in space and phenotypic traits, leading to heterogeneity arising from entirely different mechanisms. This heterogeneity could, for instance, result from environmental variations in space or genomics variations affecting the mutation rate, making the use of such a generalised model potentially relevant.

In summary, this chapter advocates for a paradigm shift in the conventional use of Fickian diffusion in mathematical biology, emphasising the deliberate and informed selection of diffusion models tailored to the unique attributes of the system under study. It underscores the importance of accounting for the interplay between diffusion dynamics and spatial heterogeneity in designing theoretical models, often masked by the homogenising effect of Fickian diffusion.

4.5 Proofs and technical lemmas

4.5.1 Proof of Theorem 4.3.1, persistence

Proof of Theorem 4.3.1, *(i)* and *(ii)*, persistence. We first prove Proposition 4.3.3. We will then use it to prove the persistence part of Theorem 4.3.1, *(i)* and *(ii)*.

Proof of Proposition 4.3.3. Let $\psi > 0$ be a principal eigenfunction associated with $k_0^\lambda[r; D]$. By definition, we have

$$D\psi'' + [D' - 2\lambda D]\psi' + [\lambda^2 D - \lambda D' + r]\psi = k_0^\lambda[r; D]\psi. \tag{4.13}$$

Let $\gamma > 0$ and set

$$\phi := \frac{\psi}{D^\gamma}.$$

Replacing ψ with ϕD^γ in (4.13) and dividing the equation by D^γ, a computation gives

$$D\phi'' + [(1+2\gamma)D' - 2\lambda D]\phi' + \left[\gamma D'' + \gamma^2 \frac{(D')^2}{D} + \lambda^2 D - (1+2\gamma)\lambda D' + r\right]\phi = k_0^\lambda[r; D]\phi.$$

Taking $\gamma = q/2$, we get:

$$\mathcal{L}_q^\lambda \left[r - \frac{q}{2} D'' + \frac{q^2}{4} \frac{(D')^2}{D}; D \right] \phi = k_0^\lambda[r; D]\phi.$$

The uniqueness of the principal eigenvalue implies that

$$k_q^\lambda \left[r - \frac{q}{2} D'' + \frac{q^2}{4} \frac{(D')^2}{D}; D \right] = k_0^\lambda[r; D],$$

which in turn leads to the result of the proposition.

□

Next, we use the result of Proposition 4.3.3 to exhibit a situation where Fickian diffusion ($q = 0$) increases the ability of persistence.

Lemma 4.5.1 (Theorem 4.3.1, *(i)*, persistence)**.** *Assume that D is not constant. Let $r_0 \in \mathbb{R}$ be a constant and, for $q \in \mathbb{R} \setminus \{0\}$, let $h_q := -\frac{q}{2}D'' + \frac{q^2}{4}\frac{(D')^2}{D}$.*
For all $q \in \mathbb{R} \setminus \{0\}$, we have, with $r(x) := r_0 + h_q(x)$,

$$k_q^0[r; D] < k_0^0[r; D].$$

Proof. Using Proposition 4.3.3, we have

$$k_q^0[r; D] = k_0^0[r - h_q; D] = k_0^0[r_0; D]. \tag{4.14}$$

Let

$$\delta := \int_0^1 h_q.$$

Since D is not constant, we have $\delta > 0$. Hence

$$k_0^0[r_0; D] = r_0 < r_0 + \delta = k_0^0[r_0 + \delta; D]. \tag{4.15}$$

Let ψ a principal eigenfunction associated with $k_0^0[r; D]$. By definition, we have

$$(D\psi')' + r\psi = k_0^0[r; D]\psi.$$

Dividing this equation by ψ and integrating by parts, we get:

$$\int_0^1 D\frac{(\psi')^2}{\psi^2} + r_0 + \delta = k_0^0[r; D], \tag{4.16}$$

which implies that $k_0^0[r; D] \geqslant r_0 + \delta$. Using this inequality with (4.14) and (4.15), we get $k_q^0[r; D] < k_0^0[r; D]$.

□

We then use the fact that $-h_q$ takes some positive values to show that the reverse inequality can be true for another choice of r.

Lemma 4.5.2 (Theorem 4.3.1, (ii), persistence)**.** *Assume that D is not constant. For $q \in \mathbb{R} \setminus \{0\}$, let $h_q := -\frac{q}{2}D'' + \frac{q^2}{4}\frac{(D')^2}{D}$.*
For all $q \in \mathbb{R} \setminus \{0\}$, we have, with $r(x) := -ah_q(x)$, and $a > 0$ large enough,

$$k_q^0[r; D] > k_0^0[r; D].$$

Proof. Set $g(a) := k_0^0[-a\,h_q; D]$, for $a \geqslant 0$. It follows from the periodicity of D that there exists x_0 in $[0, 1]$ such that $-h_q(x_0) > 0$. Thus, Proposition 5.2 in [27] also implies that there exists $a_0 > 0$ such that for $a > a_0$, $g(a) > 0$ and g is increasing on $[a_0, +\infty)$. In particular, $g(1 + a) > g(a)$ for $a > a_0$. Coming back to the definition of g, we have $k_0^0[-a\,h_q - h_q; D] >$

$k_0^0[-a\,h_q; D]$ for $a > a_0$. Using Proposition 4.3.3, we get:

$$k_q^0[-a\,h_q; D] > k_0^0[-a\,h_q; D].$$

□

Proof of Theorem 4.3.1, *(iii)* and *(iv)*. As mentioned above, the main ingredient of the proof of *(iii)* and *(iv)* in Theorem 4.3.1 is Proposition 4.3.5. We first prove a variational formula for $k_q^0[r; D]$ as an intermediate step for the proof of Proposition 4.3.5.

Lemma 4.5.3. *We have:*

$$k_q^0[r; D] = \max_{\varphi \in E} \left(-\int_0^1 D^{1-q} |(D^{q/2}\varphi)'|^2 + \int_0^1 r\varphi^2 \right), \tag{4.17}$$

where E is the set of positive 1-periodic $\mathcal{C}^2$ functions φ with $\int_0^1 \varphi^2 = 1$.

Proof. Let $\psi > 0$ be a principal eigenfunction associated with k_q^0. By definition, we have

$$(D^{1-q}(D^q\psi)')' + r\psi = k_q^0\psi.$$

Setting $v = D^q\,\psi$, we get:

$$(D^{1-q}v')' + \frac{r}{D^q}v = \frac{k_q^0}{D^q}v. \tag{4.18}$$

Since the operator $\mathcal{L} : v \mapsto (D^{1-q}v')' + \frac{r}{D^q}v$ is self-adjoint, the operator $\mathcal{T} : \varphi \mapsto D^{q/2}\mathcal{L}\left(D^{q/2}\varphi\right)$ is self-adjoint as well. The principal eigenvalue of $\mathcal{T}$ is precisely k_q^0, and is given by a Rayleigh quotient:

$$k_q^0 = \max_{\phi \in G} \frac{-\int_0^1 D^{1-q}(\phi')^2 + \int_0^1 r D^{-q}\phi^2}{\int_0^1 D^{-q}\phi^2} \tag{4.19}$$

where G is the set of positive smooth 1-periodic functions. Up to multiplication of ϕ by a constant in (4.19), we may assume that $\int_0^1 D^{-q}\phi^2 = 1$, and setting $\varphi = D^{-q/2}\phi$, this concludes the proof of Lemma 4.5.3. □

We are now ready to prove Proposition 4.3.5.

Proof of Proposition 4.3.5. First, we have $k_q^0[r; B\,D] \leqslant \max_{[0,1]} r$. Second, let

$$\langle D^q \rangle_H := \frac{1}{\int_0^1 1/D^q}$$

be the harmonic mean of D^q. Take

$$\varphi = \sqrt{\langle D^q \rangle_H} D^{-q/2}$$

in the variational formula (4.17) of Lemma 4.5.3. This gives

$$\langle D^q \rangle_H \int_0^1 \frac{r}{D^q} \leqslant k_q^0[r; B\,D] \leqslant \max_{[0,1]} r. \tag{4.20}$$

Now, take an arbitrary sequence $B_n \to +\infty$. Let ψ_n be the principal eigenfunction associated with $k_q^0[r; B_n D]$, with the normalisation condition $\|\psi_n\|_{L^2(0,1)} = 1$. By definition, we have

$$(D^{1-q}(D^q\psi_n)')' + \frac{r}{B_n}\psi_n = \frac{k_q^0[r; B_n D]}{B_n}\psi_n. \tag{4.21}$$

Since $k_q^0[r; B_n D]$ is bounded (see (4.20)), standard elliptic estimates and Sobolev injections imply that, up to extraction of a subsequence, the sequence of functions ψ_n converges to a nonnegative function ψ, locally in $W^{2,p}$ for all $1 < p < \infty$. Furthermore, $\|\psi\|_{L^2(0,1)} = 1$, ψ is periodic and satisfies

$$(D^{1-q}(D^q\psi)')' = 0.$$

Thus $\psi \equiv C\, D^{-q}$, for some positive constant C. Since $\|\psi\|_{L^2(0,1)} = 1$, we have $C\|D^{-q}\|_{L^2(0,1)} = 1$, thus $C = \sqrt{\langle D^{2q}\rangle_H}$.

Finally, we set $v_n := D^q\,\psi_n$. We have:

$$B_n\,(D^{1-q}v_n')' + \frac{r}{D^q}v_n = \frac{k_q^0[r; B_n D]}{D^q}v_n. \tag{4.22}$$

We multiply by v_n and integrate by parts. We get:

$$-B_n\int_0^1 D^{1-q}(v_n')^2 + \int_0^1 \frac{r}{D^q}v_n^2 = k_q^0[r; B_n D]\int_0^1 \frac{v_n^2}{D^q}, \tag{4.23}$$

which implies that

$$k_q^0[r; B_n D] \leqslant \frac{\displaystyle\int_0^1 \frac{r}{D^q}v_n^2}{\displaystyle\int_0^1 \frac{v_n^2}{D^q}}.$$

Using (4.20) and passing to the limit $n \to \infty$, we get $v_n \to \sqrt{\langle D^{2q}\rangle_H}$ in $L^2(0,1)$ and

$$\lim_{n\to\infty} k_q^0[r; B_n D] = \langle D^q\rangle_H \int_0^1 \frac{r}{D^q}.$$

The family $(k_q^0[r; B\,D])_{B>0}$ is bounded, and there is only one possible limit to a converging subsequence. Therefore, the whole family converges to the same limit, namely:

$$\lim_{B\to\infty} k_q^0[r; B\,D] = \langle D^q\rangle_H \int_0^1 \frac{r}{D^q}.$$

□

Lemma 4.5.4 (Theorem 4.3.1, *(iii)* and *(iv)*)**.** *Let r be fixed. Assume that r is nonconstant. For all $q \in \mathbb{R}\setminus\{0\}$, there exists a 1-periodic D_0 such that $k_0^0[r; D_0] > k_q^0[r; D_0]$, and there exists a 1-periodic D_1 such that $k_0^0[r; D_1] < k_q^0[r; D_1]$.*

Proof. For all $q \in \mathbb{R}$ and $\kappa \in \mathbb{R}$, we have $k_q[r+\kappa; D] = k_q[r; D] + \kappa$. Therefore, up to replacing r with $r+\kappa$ with κ large enough, we may assume that $r > 0$ without changing the ordering of the eigenvalues.

Consider $D := r^{1/q}$ and let $D_0 = B\,D$. Proposition 4.3.5 implies that

$$\lim_{B\to\infty} k_0^0[r; B\,D] = \int_0^1 r$$

and

$$\lim_{B\to\infty} k_q^0[r; B\,D] = \left(\int_0^1 \frac{1}{r}\right)^{-1}.$$

Jensen's inequality implies that (r being not constant)

$$\int_0^1 r > \left(\int_0^1 \frac{1}{r}\right)^{-1}.$$

Therefore, for B large enough, $k_0^0[r; D_0] > k_q^0[r; D_0]$.

To prove the other inequality, let r_{max} be the maximum of r over $[0,1]$. Assume that the maximum is reached at some point $x_m \in [0,1]$. Take $\varepsilon > 0$ such that $r_{max} - 2\varepsilon > \int_0^1 r$ and choose D such that $D^{-q}/\int_0^1 D^{-q}$ is "close to a Dirac mass at x_m", in the sense that:

$$\int_0^1 r \frac{D^{-q}}{\int_0^1 D^{-q}} > r_{max} - \varepsilon.$$

Proposition 4.3.5 implies that

$$\lim_{B\to\infty} k_0^0[r; B\,D] = \int_0^1 r$$

and

$$\lim_{B\to\infty} k_q^0[r; B\,D] = \int_0^1 r \frac{D^{-q}}{\int_0^1 D^{-q}} > r_{max} - \varepsilon > \int_0^1 r.$$

This concludes the proof of the second inequality in Lemma 4.5.4, with $D_1 = B\,D$ and B large enough.

□

4.5.2 Proof of Theorem 4.3.1, spreading

We now finish the proof of Theorem 4.3.1. Namely, we prove that if q and D are fixed, then there exists r such that $c_q^*[r; D] > c_0^*[r; D]$ and another r such that $c_q^*[r; D] < c_0^*[r; D]$.

We first prove Proposition 4.3.4, which allows us to extend a comparison on the ability of persistence to a comparison on the spreading speed (when the ability of persistence is close to 0). Using the persistence part of Theorem 4.3.1, we will then be able to prove the spreading part.

Proof of Proposition 4.3.4. We first show that $c_{\tilde{q}}^*[r-\kappa; D] \to 0$ as $\kappa \to k_{\tilde{q}}^0[r; D]$. Assume by contradiction that there exist $\delta > 0$ and a sequence $\kappa_n \in (0, k_{\tilde{q}}^0[r; D])$ such that $\kappa_n \to k_{\tilde{q}}^0[r; D]$ as $n \to \infty$ and $c_{\tilde{q}}^*[r-\kappa_n; D] > \delta$ for all n.

From the definition of $k_{\tilde{q}}^\lambda$, by uniqueness, we have $k_{\tilde{q}}^\lambda[r-\kappa_n; D] = k_{\tilde{q}}^\lambda[r; D] - \kappa_n$, and consequently,

$$c_{\tilde{q}}^*[r-\kappa_n; D] = \inf_{\lambda>0}\left(\frac{k_{\tilde{q}}^\lambda[r; D]}{\lambda} - \frac{\kappa_n}{\lambda}\right).$$

Thus,

$$\frac{k^\lambda_{\tilde q}[r;D]}{\lambda} - \frac{\kappa_n}{\lambda} \geqslant c^*_{\tilde q}[r-\kappa_n;D] \geqslant \delta$$

for all $n \geqslant 0$ and $\lambda > 0$. Passing to the limit $n \to \infty$, we get:

$$\forall \lambda \in \mathbb{R}, \qquad \frac{k^\lambda_{\tilde q}[r;D]}{\lambda} - \frac{k^0_{\tilde q}[r;D]}{\lambda} \geqslant \delta. \tag{4.24}$$

We know that the function $\lambda \mapsto k^\lambda_{\tilde q}[r;D]$ is analytic (see e.g. [175]) and that $\lambda = 0$ is a global minimum of this function (using the convexity and Proposition 4.3.9), thus we have $\partial_\lambda k^\lambda_{\tilde q}[r;D]\Big|_{\lambda=0} = 0$. On the other hand, passing to the limit $\lambda \to 0$ in (4.24), we get $\partial_\lambda k^\lambda_{\tilde q}[r;D]\Big|_{\lambda=0} \geqslant \delta$. Thus we get a contradiction. This proves that

$$c^*_{\tilde q}[r-\kappa;D] \to 0 \text{ as } \kappa \to k^0_{\tilde q}[r;D].$$

On the other hand, $k^\lambda_q[r-\kappa;D] = k^\lambda_q[r;D] - \kappa$ is a nonincreasing function of κ and therefore $c^*_q[r-\kappa;D]$ is also a nonincreasing function of κ. Additionally,

$$k^\lambda_q[r - k^0_{\tilde q}[r;D];D] = k^\lambda_q[r;D] - k^0_{\tilde q}[r;D] \geqslant k^0_q[r;D] - k^0_{\tilde q}[r;D] > 0$$

for all $\lambda > 0$. Thus, $c^*_q[r-\kappa;D] \geqslant c^*_q[r - k^0_{\tilde q}[r;D];D] > 0$ for all $\kappa \in [0, k^0_{\tilde q}[r;D]]$. As we have shown that $c^*_{\tilde q}[r-\kappa;D] \to 0$ as $\kappa \to k^0_{\tilde q}[r;D]$, this concludes the proof.

□

Proof of Theorem 4.3.1, (i)–(ii), spreading speed. Let q and D be fixed. Lemma 4.5.1 and Proposition 4.3.4 show the existence of a 1-periodic $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that $c^*_q[r;D] < c^*_0[r;D]$. Conversely, Lemma 4.5.2 and Proposition 4.3.4 show the existence of a 1-periodic $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ such that $c^*_q[r;D] > c^*_0[r;D]$. □

4.5.3 Deformation of space and proof of Theorem 4.3.6

The goal of this section is to prove Theorem 4.3.6. The main ingredients of the proof of Theorem 4.3.6 are Propositions 4.3.7 and 4.3.8. Using a deformation of space, we first prove the following lemma. As a consequence, we will prove Proposition 4.3.7. Next, using Proposition 4.3.8 and Proposition 4.3.9, we will conclude the proof of Theorem 4.3.6.

Lemma 4.5.5. *Let $D \in \mathcal{C}^{2,\alpha}(\mathbb{R})$, $b \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ and $r \in \mathcal{C}^{0,\alpha}(\mathbb{R})$ be 1-periodic functions, with $D > 0$. Consider the diffeomorphism*

$$h(x) := \int_0^x \frac{\mathrm{d}x'}{\sqrt{D(x')}}.$$

Let

$$B(y) := \frac{2b + D'}{2\sqrt{D}}\left(h^{-1}(y)\right).$$

Let $v \geqslant 0$ solve the linear evolution problem

$$\partial_t v = \partial_{xx}(D(x)v) + \partial_x(b(x)v) + r(x)v,$$

with a nonnegative and locally bounded initial condition $v(0,\cdot)$. Let

$$V(t,y) := \sqrt{D(h^{-1}(y))}\, v\left(t, h^{-1}(y)\right)$$

and $R(y) := r\left(h^{-1}(y)\right)$. Then V solves the linear evolution problem

$$\partial_t V = \partial_{yy} V + \partial_y(B(y)V) + R(y)V.$$

Proof of Lemma 4.5.5 when $r \equiv 0$. First, we assume that $r \equiv 0$ and that the initial data $v(0,\cdot)$ is integrable with $\int_0^1 v(0,\cdot) = 1$. These assumptions allow us to understand the lemma from a probabilistic point of view. The proof for general r is much more technical and will be done below.

We use the interpretation of the conservative evolution equation as the Fokker-Planck equation for an Itô diffusion. (Next, we will use linearity to prove the result for initial data that are not integrable.)

By our assumptions, for all $t \geqslant 0$, $v(t,\cdot)$ is the density of the law of a particle satisfying the SDE

$$\mathrm{d}X_t = -b(X_t)\,\mathrm{d}t + \sqrt{2D(X_t)}\,\mathrm{d}W_t$$

with initial law of density $v(0,\cdot)$ (for some Brownian motion $(W_t)_t$). Consider the change of variables $Y_t = h(X_t)$. Then Itô's formula gives

$$\begin{aligned}
\mathrm{d}Y_t &= -h'(X_t) \times b(X_t)\,\mathrm{d}t + h'(X_t)\sqrt{2D(X_t)}\,\mathrm{d}W_t + \frac{1}{2}h''(X_t) \times 2D(X_t)\,\mathrm{d}t \\
&= \left[-\frac{b}{\sqrt{D}} - \frac{D'}{2\sqrt{D}}\right](X_t)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t \\
&= -\frac{2b + D'}{2\sqrt{D}}(X_t)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t.
\end{aligned}$$

The Fokker-Planck equation for this Itô diffusion is precisely:

$$\partial_t V(t,y) = \partial_{yy} V + \partial_y\left(B(y)V\right).$$

This proves the result for $r \equiv 0$ and $\int v(0,\cdot) = 1$. Finally, using the linearity of the equations, we conclude that the result holds for all nonnegative $v(0,\cdot) \in L^1(\mathbb{R})$. Last, using the fact that solving the equation is a local property, the result holds for all nonnegative and locally bounded $v(0,\cdot)$.

□

Proof of Lemma 4.5.5 for general r. When $r \not\equiv 0$, the proof is unfortunately much more technical, because we need to do the explicit computations. For conciseness, let us denote $H := h^{-1}$. Note that $H'(y) = \sqrt{D(H(y))}$. First, we compute:

$$\begin{aligned}
\partial_y V(t,y) &= \sqrt{D(H(y))}H'(y)\partial_y v(t,H(y)) + \frac{H'(y)D'(H(y))}{2\sqrt{D(H(y))}}v(t,H(y)) \\
&= D(H(y))\partial_y v(t,H(y)) + \frac{D'(H(y))}{2}v(t,H(y)).
\end{aligned}$$

Therefore,

$$\begin{aligned}\partial_{yy}V(t,y) &= H'(y)D'(H(y))\partial_y v(t,H(y)) + H'(y)D(H(y))\partial_{yy}v(t,H(y)) \\ &\quad + \frac{H'(y)D'(H(y))}{2}\partial_y v(t,H(y)) + \frac{H'(y)D''(H(y))}{2}v(t,H(y)) \\ &= \frac{3}{2}D'(H(y))\sqrt{D(H(y))}\partial_y v(t,H(y)) + D(H(y))^{3/2}\partial_{yy}v(t,H(y)) \\ &\quad + \sqrt{D(H(y))}\frac{D''(H(y))}{2}v(t,H(y)).\end{aligned}$$

Next, we develop the expression of $\partial_t v$:

$$\partial_t v(t,x) = D\partial_{xx}v(t,x) + (b+2D')\partial_x v(t,x) + (r+D''+b')v(t,x).$$

Now, we can compute:

$$\begin{aligned}\partial_t V(t,y) &= \sqrt{D(H(y))}\partial_t v(t,H(y)) \\ &= D(H(y))^{3/2}\partial_{yy}v(t,H(y)) \\ &\quad + \left(\sqrt{D(H(y))}b + 2D'(H(y))\sqrt{D(H(y))}\right)\partial_y v(t,H(y)) \\ &\quad + \sqrt{D(H(y))}(r(H(y)) + D''(H(y)) + b'(H(y)))v(t,H(y)).\end{aligned}$$

The last expression can be rewritten (each line in the expression below corresponds to a line in the expression above):

$$\begin{aligned}\partial_t V(t,y) &= \partial_{yy}V(t,y) - \frac{3}{2}D'(H(y))\sqrt{D(H(y))}\partial_y v(t,H(y)) - \sqrt{D(H(y))}\frac{D''(H(y))}{2}v \\ &\quad + \left(\sqrt{D(H(y))}b + 2D'(H(y))\sqrt{D(H(y))}\right)\partial_y v(t,H(y)) \\ &\quad + (R(y) + D''(H(y)) + b'(H(y)))V(t,H(y)).\end{aligned} \tag{4.25}$$

The second-order term in (4.25) is $\partial_{yy}V(t,y)$, as required. The first-order term in (4.25) is

$$\begin{aligned}&\left(-\frac{3}{2}D'(H(y))\sqrt{D(H(y))} + \sqrt{D(H(y))}b + 2D'(H(y))\sqrt{D(H(y))}\right)\partial_y v(t,H(y)) \\ &\quad = \left(\frac{1}{2}D'(H(y))\sqrt{D(H(y))} + \sqrt{D(H(y))}b\right)\frac{\partial_y V(t,y) - \frac{D'(H(y))}{2}v(t,H(y))}{D(H(y))} \\ &\quad = B(y)\partial_y V(t,y) - \frac{B(y)D'(H(y))}{2}v(t,H(y)).\end{aligned}$$

We obtain, recalling that $V(t,y) = \sqrt{D(H(y))}v(t,H(y))$,

$$\begin{aligned}\partial_t V(t,y) &= \partial_{yy}V(t,y) + B(y)\partial_y V(t,y) \\ &\quad + \left(-\frac{B(y)D'(H(y))}{2\sqrt{D(H(y))}} + R(y) + \frac{D''(H(y))}{2} + b'(H(y))\right)V(t,H(y)).\end{aligned} \tag{4.26}$$

To compute the zero-order term in (4.26), we first compute:

$$\begin{aligned}B'(y) &= H'(y)\left(\frac{b'(H(y))}{\sqrt{D(H(y))}} - \frac{b(H(y))D'(H(y))}{D(H(y))^{3/2}} + \frac{D''(H(y))}{2\sqrt{D(H(y))}} - \frac{D'(H(y))^2}{4D(H(y))^{3/2}}\right)\\ &= b'(H(y)) - \frac{D'}{2D}b(H(y)) + \frac{D''(H(y))}{2} - \frac{D'(H(y))^2}{4D(H(y))}.\end{aligned}$$

The zero-order term in (4.26) is therefore:

$$\begin{aligned}&\left(-\frac{B(y)D'(H(y))}{2\sqrt{D(H(y))}} + R(y) + \frac{D''(H(y))}{2} + b'(H(y))\right)V(t,y)\\ &\quad= \left(-\frac{bD'(H(y))}{2D(H(y))} - \frac{D'(H(y))^2}{4D(H(y))} + R(y) + \frac{D''(H(y))}{2} + b'(H(y))\right)V(t,y)\\ &\quad= \Big(R(y) + B'(y)\Big)V(t,y).\end{aligned}$$

We conclude that

$$\begin{aligned}\partial_t V &= \partial_{yy}V + B\partial_y V + \Big(R + B'\Big)V\\ &= \partial_{yy}V + \partial_y(BV) + RV,\end{aligned}$$

as stated.

□

Proof of Proposition 4.3.7. In this proof, we write for conciseness $\mathcal{L}_q^\lambda$ instead of $\mathcal{L}_q^\lambda[r;D]$ and k_q^λ instead of $k_q^\lambda[r;D]$.

First, we let $\varphi > 0$ be a principal eigenfunction of the operator $\mathcal{L}_q^\lambda$. We have:

$$(\mathcal{L}_q^\lambda - k_q^\lambda)\varphi = 0.$$

Second, we recall that by the definition of $\mathcal{L}_q^\lambda$, we have, for all $\phi \in \mathcal{C}^{2,\alpha}(\mathbb{R})$,

$$E_\lambda\, \mathcal{L}_q^0(E_{-\lambda}\phi) = \mathcal{L}_q^\lambda \phi \qquad \text{with } E_\lambda(x) := e^{\lambda x}.$$

Therefore,

$$(\mathcal{L}_q^0 - k_q^\lambda)(E_{-\lambda}\varphi) = 0.$$

Now, we rewrite $\mathcal{L}_q^0$ as:

$$\mathcal{L}_q^0\phi = \partial_x\left(D^{1-q}\partial_x\left(D^q\phi\right)\right) + r\phi = \partial_{xx}(D(x)\phi) - (1-q)\partial_x\left(D'\phi\right) + r\phi.$$

The function $(t,x) \mapsto E_{-\lambda}(x)\varphi(x)$ solves:

$$0 = \partial_t(E_{-\lambda}\varphi) = (\mathcal{L}_q^0 - k_q^\lambda)(E_{-\lambda}\varphi).$$

We let $\Phi(y) := \sqrt{D(h^{-1}(y)}E_{-\lambda}(h^{-1}(y))\varphi(h^{-1}(y))$. Then, Lemma 4.5.5 with $v(t,x) = E_{-\lambda}(x)\varphi(x)$

implies that Φ satisfies

$$\partial_{yy}\Phi - s_q\partial_y\left(\frac{D'}{\sqrt{D}}\left(h^{-1}(y)\right)\times\Phi\right) + (R(y)-k_q^\lambda)\Phi = 0,$$

with $s_q := \frac{1}{2} - q$. Setting $P(y) := \ln\left(D\left(h^{-1}(y)\right)\right)$ gives

$$P'(y) = \frac{D'}{h'D}\left(h^{-1}(y)\right) = \frac{D'}{\sqrt{D}}\left(h^{-1}(y)\right).$$

Thus

$$(\widehat{\mathcal{L}}_q^0 - k_q^\lambda)\Phi = \partial_{yy}\Phi - s_q\partial_y\left(P'\Phi\right) + (R(y)-k_q^\lambda)\Phi = 0. \tag{4.27}$$

Now, a short computation shows that

$$E_{\lambda D_H}\widehat{\mathcal{L}}_q^0\left(E_{-\lambda D_H}\phi\right) = \widehat{\mathcal{L}}_q^{\lambda D_H}\phi,$$

where we denote $D_H := \left\langle\sqrt{D}\right\rangle_H$. Therefore, writing $\psi := E_{\lambda D_H}\Phi$ and using (4.27), we obtain:

$$(\widehat{\mathcal{L}}_q^{\lambda D_H} - k_q^\lambda)\psi = 0.$$

Furthermore, we note that

$$\psi(y) = e^{\lambda\left(yD_H - h^{-1}(y)\right)}\varphi(h^{-1}(y)).$$

Hence, since $D_H = 1/h(1)$, we find that ψ is $h(1)$-periodic. Since we also have $\psi > 0$, we conclude that ψ is a principal eigenfunction for $\widehat{\mathcal{L}}_q^{\lambda D_H}$ and that the associated principal eigenvalue is k_q^λ. Therefore, $\widehat{k}_q^{\lambda D_H} = k_q^\lambda$, which is what we wanted to prove. □

We now prove Proposition 4.3.9, which is the last ingredient of Theorem 4.3.6.

Proof of Proposition 4.3.9. The case $q = 0$ is standard (see e.g. [174]). We prove it for the sake of completeness. Let ψ be a principal eigenfunction associated with k_0^λ, and let $\widetilde{\psi}$ be a principal eigenfunction associated with $k_0^{-\lambda}$. We have

$$\begin{aligned}(D\psi')' - 2\lambda D\psi' + [\lambda^2 D - \lambda D' + r]\psi &= k_0^\lambda\psi,\\ (D\widetilde{\psi}')' + 2\lambda D\widetilde{\psi}' + [\lambda^2 D + \lambda D' + r]\widetilde{\psi} &= k_0^{-\lambda}\widetilde{\psi}.\end{aligned}$$

Multiplying the first equation by $\widetilde{\psi}$ and integrating by parts, we get:

$$\int_0^1 [(D\widetilde{\psi}')' + 2\lambda D\widetilde{\psi}' + (\lambda^2 D + \lambda D' + r)\widetilde{\psi}]\psi = k_0^\lambda\int_0^1\widetilde{\psi}\psi.$$

Thus,

$$k_0^{-\lambda}\int_0^1\widetilde{\psi}\psi = k_0^\lambda\int_0^1\widetilde{\psi}\psi,$$

which implies that $k_0^{-\lambda}[r;D] = k_0^\lambda[r;D]$.

Last, for general $q\in\mathbb{R}$, we use Proposition 4.3.3 and get:

$$k_q^{-\lambda}[r;D] = k_0^{-\lambda}[r-h_q;D] = k_0^\lambda[r-h_q;D] = k_q^\lambda[r;D].$$

Using the Freidlin-Gärtner formulas ((4.10) and (4.11)), we obtain that the spreading speed to the left and the spreading speed to the right coincide:

$$c_q^*[r;D] = \inf_{\lambda>0} \frac{k_q^\lambda[r;D]}{\lambda} = \inf_{\lambda>0} \frac{k_q^{-\lambda}[r;D]}{\lambda} = c_q^{*,left}[r;D].$$

□

Proof of Theorem 4.3.6, item (i). By (4.10), it is enough to show that $k^\lambda_{1/2-q} = k^\lambda_{1/2+q}$ for all $\lambda \in \mathbb{R}$ and $q \in \mathbb{R}$. For the simplicity of notations, we note $D_H := \left\langle \sqrt{D} \right\rangle_H$. Using Propositions 4.3.7 and 4.3.9, we have

$$k^\lambda_{1/2-q} = k^{-\lambda}_{1/2-q} = \widehat{k}^{-\lambda D_H}_{1/2-q}, \tag{4.28}$$

where $\widehat{k}^{-\lambda D_H}_{1/2-q}$ is the principal eigenvalue of the operator $\widehat{\mathcal{L}}^{-\lambda D_H}_{1/2-q}$ defined in Proposition 4.3.7, namely (pointing out that $s_{1/2-q} = q$):

$$\widehat{\mathcal{L}}^{-\tilde{\lambda}}_{1/2-q} : \Phi \mapsto \partial_{yy}\Phi - \partial_y\left[\left(-2\tilde{\lambda} + qP'\right)\Phi\right] + \left(R - \tilde{\lambda}qP' + \tilde{\lambda}^2\right)\Phi,$$

with $\tilde{\lambda} := \lambda D_H$. We apply Proposition 4.3.8 with $b(x) := -2\tilde{\lambda} + qP'$ and $a(x) := R - \tilde{\lambda}qP' + \tilde{\lambda}^2$, which can be rewritten:

$$a(x) = (R - \tilde{\lambda}^2) - \tilde{\lambda}b.$$

Here, $R - \tilde{\lambda}^2$ and $\tilde{\lambda}$ are constant. We deduce that $\widehat{k}^{-\lambda D_H}_{1/2-q}$ is also the principal eigenvalue of the operator

$$\Phi \mapsto \partial_{yy}\Phi + \partial_y\left[\left(-2\tilde{\lambda} + qP'\right)\Phi\right] + \left(R - \tilde{\lambda}qP' + \tilde{\lambda}^2\right)\Phi,$$

which is equal to $\widehat{\mathcal{L}}^{\lambda D_H}_{1/2+q}$. In other words, $\widehat{k}^{-\lambda D_H}_{1/2-q} = \widehat{k}^{\lambda D_H}_{1/2+q}$. Substituting into (4.28) and using Proposition 4.3.7 again, we finally obtain:

$$k^\lambda_{1/2-q} = \widehat{k}^{-\lambda D_H}_{1/2-q} = \widehat{k}^{\lambda D_H}_{1/2+q} = k^\lambda_{1/2+q}.$$

□

Proof of Theorem 4.3.6, items (ii) and (iii). We point out that $s_{1/2} = 0$, so $\widehat{k}^\mu_{1/2} = r + \mu^2$. Therefore,

$$\begin{aligned} c^*_{1/2} &= \inf_{\lambda>0} \frac{k^\lambda_{1/2}}{\lambda} = \inf_{\lambda>0} \frac{\widehat{k}^{\lambda\left\langle\sqrt{D}\right\rangle_H}_{1/2}}{\lambda} \\ &= \inf_{\lambda>0} \left(\frac{r}{\lambda} + \lambda\left(\left\langle\sqrt{D}\right\rangle_H\right)^2\right) \\ &= 2\sqrt{r} \times \left\langle\sqrt{D}\right\rangle_H. \end{aligned}$$

Finally, [172, Proposition 2.7] implies that $c^*_q \leqslant c^*_{1/2}$. This proves Theorem 4.3.6, items (*ii*) and (*iii*).

Let us now prove the remark after the statement of Theorem 4.3.6 about the different

periods. Consider the solution to the linearised version of (4.1) in the $L-$periodic setting:

$$\partial_t v = \partial_x(D_L^{1/2}\partial_x(D_L^{1/2}v)) + rv,$$

where $D_L(x) := D(x/L)$ is the $L-$periodic version of D. We denote by $c^*_{1/2}(L)$ the spreading speed of v. Using the change of variables $x' = x/L$, we obtain that $c^*_{1/2}(L) = Lc'$ where c' is the spreading speed of the solution u of

$$\partial_t u = \frac{1}{L^2}\partial_x(D^{1/2}\partial_x(D^{1/2}u)) + ru.$$

The coefficients of this equation are 1-periodic. Hence, by Theorem 4.3.6, item (ii), the spreading speed of u is $c' = 2\sqrt{r} \times \left\langle \sqrt{D}/L \right\rangle_H$, where $\left\langle \sqrt{D}/L \right\rangle_H$ is the harmonic mean of $\sqrt{D}/L$. Therefore,

$$c^*_{1/2}(L) = Lc' = 2\sqrt{r} \times L \left(\int_0^1 \frac{L}{\sqrt{D(x)}} \right)^{-1} = 2\sqrt{r} \times \left\langle \sqrt{D} \right\rangle_H .$$

□

4.5.4 Proof of Theorems 4.3.10 and 4.3.12

Throughout this section, we want to show properties of the principal eigenvalues $k_q^\lambda[r; D]$, with fixed r and D. Using Proposition 4.3.7, this is equivalent to show properties of the principal eigenvalues $\widehat{k}_q^\lambda$. Therefore, we will work on the operators $\widehat{\mathcal{L}}_q^{\tilde{\lambda}}$, with $\tilde{\lambda} = \lambda \left\langle \sqrt{D} \right\rangle_H$, which will be simpler to handle than $\mathcal{L}_q^\lambda$.

Proof of Theorem 4.3.10, item (i). Let us show that the ability of persistence $k_q^0 = \widehat{k}_q^0$ converges to the limit stated in the theorem. We recall that $\widehat{k}_q^0$ is the principal eigenvalue of the operator defined in Proposition 4.3.7; we recall the notations: $R(y) := r(h^{-1}(y))$ and $P(y) := \ln(D(h^{-1}(y))$, where h is the transformation defined before Proposition 4.3.7. We let $\widehat{\mathcal{A}} := \left\{ y \in \mathbb{R} \,/\, h^{-1}(y) \in \overline{\mathcal{A}} \right\}$ be the set of local maxima of P. We want to show that

$$\lim_{q \to -\infty} \widehat{k}_q^0 = \max_{x \in \overline{\mathcal{A}}} r(x).$$

To this aim, we will show that

$$\lim_{q \to -\infty} \widehat{k}_q^0 = \max_{y \in \widehat{\mathcal{A}}} R(y).$$

We consider the adjoint of the problem defining $\widehat{k}_q^0$, namely, we let $\varphi_q > 0$ be a 1-periodic solution of

$$\partial_{yy}\varphi_q + s_q P' \partial_y \varphi_q + R\varphi = \widehat{k}_q^0 \varphi_q. \tag{4.29}$$

We let $\psi_q > 0$ be the 1-periodic function defined by $\psi_q(y) := e^{s_q P(y)/2}\varphi_q(y)$. By computations similar to those of the proof of Proposition 4.3.3, we have:

$$\partial_{yy}\psi_q + \left(R - \frac{(s_q P')^2}{4} - \frac{s_q P''}{2} \right) \psi_q = \widehat{k}_q^0 \psi.$$

Therefore, by the Rayleigh formula, we have:

$$\widehat{k}_q^0 = \max_{\phi\in\mathcal{E}} \left(-\int_0^1 (\phi')^2 + \int_0^1 \left(R - \frac{(s_q P')^2}{4} - \frac{s_q P''}{2} \right) \phi^2 \right),$$

where

$$\mathcal{E} = \left\{ \phi \in H^1_{loc}(\mathbb{R}) \,/\, \|\phi\|_{L^2(0,1)} = 1, \, \phi \text{ is } h(1)\text{-periodic} \right\}.$$

This is analogous to Equation (1.2) in [66]. Moreover, since all critical points of D are non-degenerate, we obtain that all critical points of P are non-degenerate. Last, $s_q \to +\infty$ as $q \to -\infty$. Therefore, the proof of [66, Theorem 1] remains valid in the setting of Equation (4.29) (the proof is simpler in our case since there is no need to deal with the boundary condition). This yields:

$$\lim_{q\to-\infty} \widehat{k}_q^0 = \max_{y\in\widehat{\mathcal{A}}} R(y) = \max_{x\in\overline{\mathcal{A}}} r(x).$$

The case $q \to +\infty$ is the same by replacing P' with $-P'$. □

Before proving item (ii) of Theorem 4.3.10, let us prove Proposition 4.3.11.

Proof of Proposition 4.3.11. We let $b \in \mathcal{C}^{0,1}(\mathbb{R})$ be a function such that $b(x_0) > 0$ for some $x_0 \in [0,1]$. For $s \in \mathbb{R}$, we let $(X_t)_{t\geqslant 0}$ solve

$$\mathrm{d}X_t = sb(X_t)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t, \qquad X_0 = 1.$$

We let $\mathbb{P}_1$ be the law of $(X_t)_{t\geqslant 0}$. Last, we let $\tau := \inf\{t \geqslant 0 \,/\, X_t \leqslant 0\}$ be the exit time from $(0,+\infty)$ of $(X_t)_{t\geqslant 0}$. For clarity, we omit the superindex s in the notations, but the dependency in s should not be forgotten.

As $b(x_0) > 0$, there exists an interval $I \subset (0,1)$ such that $b(x) > 0$ for all $x \in I$. We define the random variables

$$\sigma_- := \inf\{u > 0 \,/\, X_u \leqslant \inf I\}, \qquad \sigma_+ := \sup\{u < \sigma_- \,/\, X_u \geqslant \sup I\},$$

if both infima are well-defined, and $\sigma_\pm = +\infty$ otherwise. Since $X_0 = 1$, we have, conditionally on $\tau < +\infty$: the difference $\sigma_- - \sigma_+$ is finite and is the duration of the first crossing of the interval I, without leaving it, by the process $(X_t)_{t\geqslant 0}$; in particular $\sigma_- - \sigma_+ \leqslant \tau$. Now, we point out that for all $h \geqslant 0$, we have (conditionally on $\tau < +\infty$):

$$X_{\sigma_-} = X_{\sigma_- - h} + s\int_0^h b(X_{\sigma_- - h'})\,\mathrm{d}h' + \sqrt{2}(W_{\sigma_-} - W_{\sigma_- - h}).$$

Moreover, conditionally on $\tau < +\infty$ and $\sigma_- - \sigma_+ > h$, we have $X_u \in I$ for all $u \in [\sigma_- - h, \sigma_-]$, so, owing to the definition of I,

$$X_{\sigma_-} \geqslant X_{\sigma_- - h} + sh\delta + \sqrt{2}(W_{\sigma_-} - W_{\sigma_- - h}).$$

Note that, since $X_0 = 1$, we have almost surely: $\tau \geqslant \sigma_-$ and $\sigma_- \geqslant \sigma_+ \geqslant 0$. Hence, for all

$a > 0$,

$$\begin{aligned}\mathbb{P}_1(\tau \leqslant a) &= \mathbb{P}_1(\tau \leqslant a, \sigma_- - \sigma_+ \leqslant a)\\ &\leqslant \mathbb{P}_1(\sigma_- \leqslant a, \sigma_- - \sigma_+ \leqslant a)\\ &= \mathbb{P}_1(\sigma_- \leqslant a, \exists h \in [0, \sigma_-], X_{\sigma_-} - X_{\sigma_- - h} \leqslant -|I|)\\ &\leqslant \mathbb{P}_1(\exists \sigma \in [0,a], \exists h \in [0,\sigma], X_\sigma - X_{\sigma - h} \leqslant -|I|).\end{aligned}$$

Using the above estimate for X_{σ_-}, this gives:

$$\mathbb{P}_1(\tau \leqslant a) \leqslant \mathbb{P}_1(\exists \sigma \in [0,a], \exists h \in [0,\sigma], \sqrt{2}(W_\sigma - W_{\sigma-h}) \leqslant -sh\delta - |I|),$$

which we rewrite:

$$\mathbb{P}_1(\tau \leqslant a) \leqslant \mathbb{P}_1\left(\exists \sigma \in [0,a], \exists h \in [0,\sigma], \frac{|W_\sigma - W_{\sigma-h}|}{h^{1/4}} \geqslant \frac{1}{\sqrt{2}}\left(sh^{3/4}\delta + h^{-1/4}|I|\right)\right).$$

By virtue of the regularity of Brownian motion, there exists a random constant C, whose law is independent of s, such that almost surely,

$$\sup_{\sigma \in (0,a),\ h \in (0,\sigma)} \frac{|W_\sigma - W_{\sigma-h}|}{h^{1/4}} \leqslant C.$$

Hence

$$\mathbb{P}_1(\tau \leqslant a) \leqslant \mathbb{P}_1\left(\exists h \in [0,a], C \geqslant \frac{1}{\sqrt{2}}\left(sh^{3/4}\delta + h^{-1/4}|I|\right)\right).$$

But, as $s \to +\infty$, we have

$$\inf_{h \in [0,a]} \left(sh^{3/4}\delta + h^{-1/4}|I|\right) \to +\infty.$$

Thus $\mathbb{P}_1(\tau \leqslant a) \to 0$ as $s \to +\infty$.

□

Proof of Theorem 4.3.10, item (ii). Let us show that the spreading speed $c_q^*[r;D]$ converges to 0 as $q \to \pm\infty$. Since the KPP assumption (4.7) holds, the spreading speed is linearly determined; thus, $c_q^*[r;D]$ is also the spreading speed of the level sets of the solution v to the following linear equation:

$$\partial_t v = \mathcal{L}_q^0 v + rv = \partial_{xx}(D(x)v) - (1-q)\partial_x(D'v) + rv, \qquad v(0,x) = \mathbb{1}_{\{x \leqslant 0\}}.$$

Define $h(x) := \int_0^x \mathrm{d}y/\sqrt{D(y)}$ and let

$$V(t,y) := \sqrt{D(h^{-1}(y))}\, v(t, h^{-1}(y)).$$

Using Lemma 4.5.5 and the computations of the proof of Proposition 4.3.7, we have:

$$\partial_t V = \partial_{yy} V - s_q \partial_y(P'V) + RV,$$

with $s_q := 1/2 - q$, $P(y) := \ln(D(h^{-1}(y)))$ and $R(y) := r(h^{-1}(y))$. Define

$$c[V] := \limsup_{t\to+\infty} \frac{1}{t} \sup\{x \in \mathbb{R} \ / \ V(t,x) \geqslant 1/2\}.$$

Then, since $V(t,y) = \sqrt{D(h^{-1}(y))}\, v(t, h^{-1}(y))$ and $\sqrt{D}$ is bounded, and bounded from below by a positive constant, we have: $c[V] = h(1)\, c_q^*[r;D]$. Therefore, proving that $c_q^*[r;D]$ converges to 0 as $q \to \pm\infty$ is equivalent to proving that $c[V]$ converges to 0 as $q \to \pm\infty$.

Let us now consider the adjoint problem:

$$\partial_t V^* = \partial_{yy} V^* + s_q P' \partial_y V^* + R V^*.$$

By the standard Freidlin-Gärtner formula, the spreading speed $c[V^*]$ of the level set $\frac{1}{2}$ of V^* (defined as $c[V]$ but with V^* instead of V) is

$$c[V^*] = \inf_{\lambda>0} \frac{\widehat{k}_q^\lambda[V^*]}{\lambda},$$

where $k_q^\lambda[V^*]$ is the principal eigenvalue of the operator

$$\widehat{\mathcal{L}}_q^\lambda[V^*] : \Phi \mapsto \partial_{yy}\Phi + (s_q P' - 2\lambda)\partial_y \Phi + (R - \lambda s_q P' + \lambda^2)\Phi.$$

We point out that $\widehat{\mathcal{L}}_q^\lambda[V^*] = (\widehat{\mathcal{L}}_q^{-\lambda})^*$ (where $\widehat{\mathcal{L}}_q^{-\lambda}$ is defined in Proposition 4.3.7), so $\widehat{k}_q^\lambda[V^*] = \widehat{k}_q^{-\lambda}$. Owing to Proposition 4.3.9 (which can also be applied with $\widehat{k}_q^\lambda$ instead of k_q^λ), we have: $\widehat{k}_q^{-\lambda} = \widehat{k}_q^\lambda$, so $\widehat{k}_q^\lambda[V^*] = k_q^\lambda$. We conclude that $c[V] = c[V^*]$.

Hence, we wish to prove that $c[V^*]$ converges to 0 as $q \to \pm\infty$. To this aim, we will prove that for all $\gamma > 0$, for $|q|$ large enough, we have: $V^*(t, \gamma t) \to 0$ as $t \to +\infty$. For the remaining of the proof, we fix $\gamma > 0$. For conciseness, we note $s = s_q$ and consider $q \to -\infty$, so $s \to +\infty$.

First, we estimate $V^*(t, \gamma t)$. By the Feynman-Kac formula (4.12), we have:

$$V^*(t,y) = \mathbb{E}_y \left[\mathbb{1}_{\{X_t \leqslant 0\}} \exp\left(\int_0^t R(X_{t-s})\, \mathrm{d}s \right) \right],$$

where $\mathbb{E}_y$ is the expectation corresponding to the probability $\mathbb{P}_y$, which is the law of a solution $(X_t)_{t\geqslant 0}$ to

$$\mathrm{d}X_t = sP'(X_t)\, \mathrm{d}t + \sqrt{2}\, \mathrm{d}W_t, \qquad X_0 = y,$$

for a standard Brownian motion $(W_t)_{t\geqslant 0}$ (we do not make it explicit in the notations that V^* and the law of X depend on s, but this should not be forgotten). Letting $r_m := \max r$, we obtain:

$$V^*(t,y) \leqslant e^{r_m t}\, \mathbb{P}_y(X_t \leqslant 0). \tag{4.30}$$

We will prove that for all $\gamma > 0$, for s large enough, $e^{r_m t} \mathbb{P}_{\gamma t}(X_t \leqslant 0) \to 0$ as $t \to +\infty$. Using (4.30), we will then be able to conclude.

We define, for $i \in \mathbb{Z}$, the random variable

$$\tau_i := \inf\{u \geqslant 0 \ / \ X_u = i\}$$

if the infimum is well-defined, and $\tau_i := +\infty$ otherwise. For $0 \leqslant i \leqslant \lfloor \gamma t \rfloor - 1$, when $X_0 = \gamma t > 1$

and conditionally on $X_t \leqslant 0$, the difference $\tau_i - \tau_{i+1}$ is positive almost surely and corresponds to the time spent by the particle X_t to cross the interval $[i, i+1]$ for the first time (from right to left). We point out that, using the Markov inequality, we have:

$$\mathbb{P}_{\gamma t}(X_t \leqslant 0) \leqslant \mathbb{P}_{\gamma t}(\tau_0 \leqslant t) \leqslant e^t \mathbb{E}_{\gamma t}[e^{-\tau_0}].$$

Moreover, the $\tau_i - \tau_{i+1}$ are independent and have the same law. Hence, for $\gamma t > 2$,

$$\begin{aligned}
\mathbb{E}_{\gamma t}[e^{-\tau_0}] &\leqslant \mathbb{E}_{\gamma t}\left[\exp\left(-\sum_{i=0}^{\lfloor \gamma t \rfloor - 1}(\tau_i - \tau_{i+1})\right)\right] = \left(\mathbb{E}_{\gamma t}\left[e^{-(\tau_0 - \tau_1)}\right]\right)^{\lfloor \gamma t \rfloor} \\
&\leqslant \left(\mathbb{E}_{\gamma t}\left[e^{-(\tau_0 - \tau_1)}\right]\right)^{\gamma t/2} \\
&= \left(\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right]\right)^{\gamma t/2}.
\end{aligned}$$

On the last line, contrarily to the previous lines, the expectation is taken for a process starting from 1 (as indicated by the index "1" on the expectation symbol). The above computations show that:

$$e^{r_m t}\, \mathbb{P}_{\gamma t}(X_t \leqslant 0) \leqslant \exp\left[t\left(r_m + 1 + \frac{\gamma}{2}\ln\left(\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right]\right)\right)\right]. \tag{4.31}$$

Our goal is now to show that, for s large enough, we have $r_m + 1 + \frac{\gamma}{2}\ln\left(\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right]\right) < 0$. We will prove the stronger result that $\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right]$ converges to 0 as $s \to +\infty$. We point out that $\mathbb{P}_1(\tau_1 = 0) = 1$. Hence we may write:

$$\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right] = \mathbb{E}_1\left[e^{-\tau_0}\right] = \int_0^1 \mathbb{P}_1(e^{-\tau_0} \geqslant u)\,\mathrm{d}u = \int_0^1 \mathbb{P}_1(\tau_0 \leqslant -\ln(u))\,\mathrm{d}u.$$

Since D is periodic and nonconstant, P' changes sign, so in particular there exists $x_0 \in [0,1]$ such that $P'(x_0) > 0$. Therefore, we may apply Proposition 4.3.11 with $b = P'$. We get: for all $a > 0$,

$$\mathbb{P}_1(\tau_0 \leqslant a) \to 0 \qquad \text{as} \qquad s \to +\infty.$$

Therefore, $\mathbb{E}_1\left[e^{-(\tau_0 - \tau_1)}\right] \to 0$ as $s \to +\infty$. Owing to (4.31), we obtain that for s large enough, $e^{r_m t}\, \mathbb{P}_{\gamma t}(X_t \leqslant 0) \to 0$ as $t \to +\infty$. Owing to (4.30), therefore, we have:

$$V^*(t, \gamma t) \to 0 \qquad \text{as } t \to +\infty.$$

This implies that $c[V] = c[V^*] \leqslant \gamma$ for s large enough, i.e. for $-q$ large enough. Since γ is arbitrary, we get: $c[V] \to 0$ as $q \to -\infty$, and thus $c_q^*[r; D] \to 0$ as $q \to -\infty$.

The same argument holds for $q \to +\infty$, by considering $-P'$ instead of P'. □

We now show the monotonicity properties of Theorem 4.3.12.

Proof of Theorem 4.3.12, item (i). By definition of $\kappa(q)$, there exists $\psi > 0$ such that

$$\partial_x(D\partial_x\psi) + q\partial_x(D'\psi) + (r - \kappa(q))\psi = 0.$$

Recall that r is constant. Integrating the equation on $[0,1]$ gives, using the periodicity:

$$(r - \kappa(q))\int_0^1 \psi = 0.$$

Since $\psi > 0$, we have $r = \kappa(q)$.

□

Proof of Theorem 4.3.12, item (ii). We let r and D satisfy the assumptions of item (ii), namely: $D \in \mathcal{C}^3(\mathbb{R})$ and $r \in \mathcal{C}^4(\mathbb{R})$ are 1-periodic and even on $\mathbb{R}$, and monotonic on $[0,1/2]$; $r' \neq 0$ on $(0,1/2)$; $r''(0) \neq 0$ and $r''(1/2) \neq 0$.

For convenience, we assume that r and D are nonincreasing on $[0,1/2]$ (the other cases are proved in an analogous way). Therefore, we have:

$$r'(x) < 0 \text{ on } (0,1/2), \qquad r'(x) > 0 \text{ on } (1/2,1), \qquad r'(0) = r'(1/2) = 0.$$

Further, we have $r''(0) < 0$ and $r''(1/2) > 0$.

Let us prove that $q \mapsto \kappa(q) = k_q^0[r;D]$ is nonincreasing. This is equivalent to proving that $q \mapsto \widehat{k}_q^0$ is nonincreasing, where $\widehat{k}_q^0$ is defined in Proposition 4.3.7 as the principal eigenvalue of the operator

$$\widehat{\mathcal{L}}_q^0 : \Phi \mapsto \partial_{yy}\Phi - s_q \partial_y(P'\Phi) + R\Phi,$$

with $P(y) = \ln(D(h^{-1}(y))$, $R(y) = r(h^{-1}(y))$ and $s_q = \frac{1}{2} - q$, where h is defined before Proposition 4.3.7. To avoid confusions, we rescale space by a constant in such a way that $h(0) = 0$ and $h(1) = 1$; since D is even and 1-periodic, this implies also that $h(1/2) = 1/2$. Then R and P are still even and 1-periodic.

We let $q^1 > q^2$ and denote $s^1 := s_{q^1}$ and $s^2 := s_{q^2}$, so $s^1 < s^2$. We define two processes X^1 and X^2 by:

$$\begin{aligned} \mathrm{d}X_t^1 &= s^1 P'(X_t^1)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t^1, \qquad & X_0^1 &= 0, \\ \mathrm{d}X_t^2 &= s^2 P'(X_t^2)\,\mathrm{d}t + \sqrt{2}\,\mathrm{d}W_t^2, \qquad & X_0^2 &= 0, \end{aligned}$$

where $(W_t^1)_{t\geqslant 0}$ and $(W_t^2)_{t\geqslant 0}$ are two standard Brownian motions. In the following, we will couple the processes $(R(X_t^i))_{t\geqslant 0}$. First, let us establish a connection between the processes $(R(X_t^i))_{t\geqslant 0}$ and the principal eigenvalues $\widehat{k}_{q_i}^0$.

Step 1. Use the Feynman-Kac formula. We now establish a connection between the processes $(R(X_t^i))_{t\geqslant 0}$ and the principal eigenvalues $\widehat{k}_{q_i}^0$ by using the Feynman-Kac formula (4.12). We work with the adjoint problem. We point out that the principal eigenvalue of $(\widehat{\mathcal{L}}_q^0)^*$ is equal to the principal eigenvalue of $\widehat{\mathcal{L}}_q^0$, which is precisely $\widehat{k}_q^0$. Therefore, for $i = 1,2$, we have

$$\left[(\widehat{\mathcal{L}}_{q^i}^0)^* - \widehat{k}_{q^i}^0\right]\varphi_i^* = \partial_{xx}\varphi_i^* + s^i P' \partial_x \varphi_i^* + (R - \widehat{k}_{q^i}^0)\varphi_i^* = 0,$$

where φ_i^* is the principal eigenfunction of $(\widehat{\mathcal{L}}_{q^i}^0)^*$ such that $\varphi_i^*(0) = 1$. By the Feynman-Kac formula (4.12) (applied to the stationary function $\overline{u}(t,x) = \varphi_i^*(x)$), therefore, we have, for all $t \geqslant 0$,

$$\varphi_i^*(x) = \mathbb{E}_x\left[\varphi_i^*(X_t^i)\exp\left(\int_0^t (R(X_{t-s}^i) - \widehat{k}_{q^i}^0)\,\mathrm{d}s\right)\right].$$

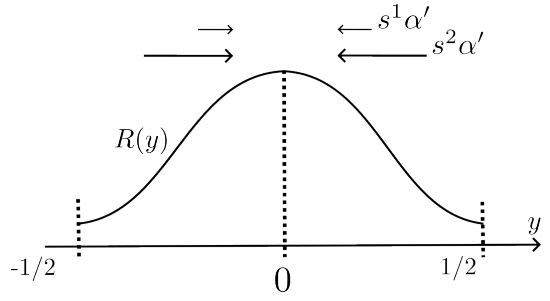

Figure 4.4: The processes X^1 and X^2 are submitted to a drift bringing them to the center, where R is larger. The process X^2 is submitted to a stronger drift than X^1, which is what we want to exploit in the proof.

Since $0 < \varphi_i^* < +\infty$, there is a constant $C > 1$ such that, for $i = 1, 2$, for all $t \geqslant 0$,

$$\frac{1}{C}\exp\left(-\widehat{k}^0_{q^i}t\right)\mathbb{E}_x\left[\exp\left(\int_0^t R(X^i_{t-s})\,\mathrm{d}s\right)\right] \leqslant \varphi_i^*(x) \leqslant C\exp\left(-\widehat{k}^0_{q^i}t\right)\mathbb{E}_x\left[\exp\left(\int_0^t R(X^i_{t-s})\,\mathrm{d}s\right)\right].$$

Therefore, for $i = 1, 2$,

$$0 < \liminf_{t\to+\infty}\exp\left(-\widehat{k}^0_{q^i}t\right)\mathbb{E}_x\left[\exp\left(\int_0^t R(X^i_{t-s})\,\mathrm{d}s\right)\right] \leqslant \limsup_{t\to+\infty}\exp\left(-\widehat{k}^0_{q^i}t\right)\mathbb{E}_x\left[\exp\left(\int_0^t R(X^i_{t-s})\,\mathrm{d}s\right)\right] < +\infty.$$

Hence, to prove that $\widehat{k}^0_{q^1} \leqslant \widehat{k}^0_{q^2}$, it is sufficient to prove that

$$\mathbb{E}_x\left[\exp\left(\int_0^t R(X^1_{t-s})\,\mathrm{d}s\right)\right] \leqslant \mathbb{E}_x\left[\exp\left(\int_0^t R(X^2_{t-s})\,\mathrm{d}s\right)\right].$$

The goal of the following step is to prove this inequality. We will construct a process $(Y^2_t)_{t\geqslant 0}$ such that: $(Y^2_t)_{t\geqslant 0} = (R(X^2_t))_{t\geqslant 0}$ in law, and such that almost surely, for all $t \geqslant 0$, $R(X^1_t) \leqslant Y^2_t$.

Step 2. Write an equation for the process $(R(X^1_t))_{t\geqslant 0}$. For $x \in \mathbb{R}$, we let $\{x\}$ be analogous to the fractional part of x, but belonging to $(-1/2, 1/2]$ instead of $[0, 1)$, namely, $\{x\}$ is the unique real number such that:

$$\{x\} \in (-1/2, 1/2], \qquad x - \{x\} \in \mathbb{Z}.$$

We define the sign function sgn by: $sgn(x) = 1$ if $x \geqslant 0$ and $sgn(x) = -1$ if $x < 0$. By our symmetry assumptions on r and D, we have $r(x) = r(|\{x\}|)$, so

$$R(x) = R(|\{x\}|), \qquad R'(x) = sgn(\{x\})R'(|\{x\}|),$$

and $D(x) = D(|\{x\}|)$, so

$$P'(x) = sgn(\{x\})P'(|\{x\}|).$$

Now, we set $Y_t^1 := R(X_t^1)$. Applying Itô's formula, we have:

$$\mathrm{d}Y_t^1 = \left[s^1 R'(X_t^1)P'(X_t^1) + R''(X_t^1)\right]\mathrm{d}t + \sqrt{2}\,R'(X_t^1)\,\mathrm{d}W_t^1.$$

By our above remarks, we get:

$$\mathrm{d}Y_t^1 = \left[s^1 R'(\left|\left\{X_t^1\right\}\right|)P'(\left|\left\{X_t^1\right\}\right|) + R''(\left|\left\{X_t^1\right\}\right|)\right]\mathrm{d}t + \sqrt{2}\,sgn(\left\{X_t^1\right\})R'(\left|\left\{X_t^1\right\}\right|)\,\mathrm{d}W_t^1.$$

By our monotonicity assumptions on R, the function $x \mapsto R(x)$ is a bijection from $[0,1/2]$ to $[R(1/2), R(0)]$. Therefore, since $x \mapsto |\{x\}|$ takes its values in $[0,1/2]$, we can write:

$$\left|\left\{X_t^1\right\}\right| = R^{-1}(Y_t^1).$$

We obtain that Y_t^1 satisfies

$$\mathrm{d}Y_t^1 = \left[s^1 b(Y_t^1) + B(Y_t^1)\right]\mathrm{d}t + \sigma(Y_t^1)\,\mathrm{d}\overline{W}_t, \tag{4.32}$$

where

$$\overline{W}_t := \int_0^t sgn(\left\{X_t^1\right\})\,\mathrm{d}W_t^1$$

and, for $y \in [R(1/2), R(0)]$,

$$b(y) := R'(R^{-1}(y))P'(R^{-1}(y)), \qquad B(y) := R''(R^{-1}(y)), \qquad \sigma(y) := \sqrt{2}\,R'(R^{-1}(y)).$$

Last, $(\overline{W}_t)_{t\geqslant 0}$ is a martingale with increasing process

$$\left\langle \overline{W} \right\rangle_t = \int_0^t sgn(\left\{X_t^1\right\})^2\,\mathrm{d}t = t,$$

so $(\overline{W}_t)_{t\geqslant 0}$ is a Brownian motion.

Step 3. Regularity of the coefficients of (4.32)**.** We prove that b, B and σ^2 are Lipschitz. We will see in Step 4 that these conditions ensure the existence and uniqueness of a solution to (4.32).

First, $R(y) = r(h^{-1}(y))$, so $R \in \mathcal{C}^4(\mathbb{R})$, and

$$R'(y) = \frac{r'(h^{-1}(y))}{h'(h^{-1}(y))} = \sqrt{D(h^{-1}(y))}\,r'(h^{-1}(y))$$

is nonzero on $(0,1/2)$. Moreover,

$$R''(y) = \frac{1}{h'(h^{-1}(y))}\left(\frac{D'(h^{-1}(y))\,r'(h^{-1}(y))}{2\sqrt{D(h^{-1}(y))}} + \sqrt{D(h^{-1}(y))}\,r''(h^{-1}(y))\right).$$

Since $D'(0) = D'(1/2) = 0$, we have, at $y = 0$ and at $y = 1/2$:

$$R''(y) = \frac{1}{h'(h^{-1}(y))} \sqrt{D(h^{-1}(y))}\, r''(h^{-1}(y)),$$

which, by our assumptions on r, is nonzero. Further, R shares the same monotonicity properties as r. Hence, properties (a), (b) and (c) of the statement also hold with R instead of r.

Second, we have:

$$b'(y) = \frac{R''(R^{-1}(y))}{R'(R^{-1}(y))} P'(R^{-1}(y)) + P''(R^{-1}(y)).$$

Since R and P are of class $\mathcal{C}^2$, R'' and P'' are bounded. Further, $R'(0) = R'(1/2) = 0$ and R' is nonzero on $(0, 1/2)$. Since $R''(0) \neq 0$ and $P'(0) = 0$, we have, for $x \to 0$:

$$\left| \frac{R''(x)}{R'(x)} P'(x) \right| \leqslant \frac{R''(0)}{R''(0)x + O(x^2)}\ O(x),$$

which is bounded. Hence b' is bounded near 0. Likewise, b' is bounded near $1/2$. Therefore, b' is bounded on $[0, 1/2]$ so b is Lipschitz.

Third, we have

$$B'(y) = \frac{R'''(R^{-1}(y))}{R'(R^{-1}(y))}.$$

The function R''' is bounded on $[0, 1/2]$ and R' is nonzero on $(0, 1/2)$. Moreover, owing to $R \in \mathcal{C}^4(\mathbb{R})$, we have, as $x \to 0$, $R'''(x) = O(x)$ and $R'(x) = R''(0)x + O(x^2)$. Since $R''(0) \neq 0$, R'''/R' is bounded near 0. Likewise, R'''/R' is bounded near $1/2$. This implies that B' is bounded on $[0, 1/2]$, so B is Lipschitz.

Last, we have:

$$(\sigma^2)'(y) = 2\sigma(y)\sigma'(y) = \frac{4R'(R^{-1}(y))R''(R^{-1}(y))}{R'(R^{-1}(y))} = 4R''(R^{-1}(y)),$$

which is bounded. Therefore, σ^2 is Lipschitz.

Step 4. Conclusion. By Step 3, $s^1 b + B$ and σ^2 are Lipschitz on $[R(1/2), R(0)]$. We extend the functions b, B and σ^2 to Lipschitz functions on $\mathbb{R}$, with $b \geqslant 0$. Then, using [195, Theorem IX.3.5.(ii)] (with $\rho(x) := |x|$), we conclude that pathwise uniqueness holds for Equation (4.32).

Now, let us consider the following equation:

$$\mathrm{d}Y_t^2 = \left[s^2 b(Y_t^2) + B(Y_t^2) \right] \mathrm{d}t + \sigma(Y_t^2)\, \mathrm{d}W_t. \tag{4.33}$$

As for (4.32), pathwise uniqueness holds for (4.33). Further, doing the same computations as in Step 2, there exists a Brownian motion $(\overline{W}')_{t \geqslant 0}$ (constructed as $(\overline{W}_t)_{t \geqslant 0}$ with $(W^2)_{t \geqslant 0}$ instead of $(W^1)_{t \geqslant 0}$) such that $(R(X_t^2))_{t \geqslant 0}$ solves (4.33) with $W = \overline{W}'$.

Hence, Equation (4.33) has a solution; owing to pathwise uniqueness, it follows from [195] (see Theorem IX.1.7 and the associated Remark 2) that this solution is strong, and, therefore, that there exists a (unique) solution $(Y_t^2)_{t \geqslant 0}$ to (4.33) carried by the Brownian motion $W = \overline{W}$

defined in Step 2. By uniqueness in law, we have:

$$(Y_t^2)_{t\geqslant 0} = (R(X_t^2))_{t\geqslant 0} \qquad \text{in law.}$$

We point out that the processes $(Y_t^1)_{t\geqslant 0}$ and $(Y_t^2)_{t\geqslant 0}$ are carried by the same Brownian motion, which allows us to compare them. We have indeed, on $\mathbb{R}$,

$$s^1 b + B \leqslant s^2 b + B.$$

Hence, the comparison result stated in [195, Theorem IX.3.7], implies that almost surely,

$$\forall t \geqslant 0, \qquad Y_t^1 \leqslant Y_t^2.$$

Therefore,

$$\mathbb{E}\left[\exp\left(\int_0^t Y_t^1 \,\mathrm{d}y\right)\right] \leqslant \mathbb{E}\left[\exp\left(\int_0^t Y_t^2 \,\mathrm{d}y\right)\right].$$

Recalling Step 1, this concludes the proof.

□

Proof of Theorem 4.3.12, item (iii). Let D be nonconstant and, on $[0,1)$, have exactly one local minimum at $\underline{x} \in [0,1)$ and one local maximum at $\overline{x} \in [0,1)$. We let $\varepsilon > 0$ and define

$$r_\varepsilon(x) := \begin{cases} 1 & x \in (\underline{x}-\varepsilon, \underline{x}+\varepsilon) \cup (\overline{x}-\varepsilon, \overline{x}+\varepsilon), \\ 0 & \text{otherwise.} \end{cases}$$

By Theorem 4.3.10, we have for all $\varepsilon > 0$,

$$\lim_{q\to-\infty} k_q^0[r_\varepsilon, D] = \lim_{q\to+\infty} k_q^0[r_\varepsilon, D] = 1.$$

Thus, for all $\varepsilon > 0$, $q \mapsto k_q^0[r_\varepsilon, D]$ cannot be monotonic unless it is constant. But $r_\varepsilon \to 0$ in $L^2([0,1])$ as $\varepsilon \to 0$. Therefore, for all $q \in \mathbb{R}$, $k_q^0[r_\varepsilon, D] \to 0$ as $\varepsilon \to 0$. Hence, for $\varepsilon > 0$ small enough, $q \mapsto k_q^0[r_\varepsilon, D]$ is not monotonic.

□

Proof of Theorem 4.3.12, item (iv). By Theorem 4.3.10, we have:

$$\lim_{q\to-\infty} c_q^*[r; D] = \lim_{q\to+\infty} c_q^*[r; D] = 0.$$

On the other hand, for $q \in \mathbb{R}$ such that $k_q^0[r; D] > 0$, we have $c_q^*[r; D] > 0$. This proves that $q \mapsto c_q^*[r; D]$ cannot be monotonic. □

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Part II

Reaction-diffusion models for a population structured in phenotype and space

Chapter 5

Persistence of a structured population

This chapter is based on the article [51]:

N. Boutillon, L. Rossi, *Reaction–diffusion model for a population structured in phenotype and space: I. Criterion for persistence*, Nonlinearity 38.4 (2025), p. 045019.

Abstract

We consider a reaction-diffusion model for a population structured in phenotype. We assume that the population lives in a heterogeneous periodic environment, so that a given phenotypic trait may be more or less fit according to the spatial location. The model features spatial mobility of individuals as well as mutation.

We first prove the well-posedness of the model. Next, we derive a criterion for the persistence of the population which involves the *generalised principal eigenvalue* associated with the linearised elliptic operator. This notion allows us to handle the possible lack of coercivity of the operator. We then obtain a monotonicity result for the generalised principal eigenvalue, in terms of the frequency of spatial fluctuations of the environment and in terms of the spatial diffusivity. We deduce that the more heterogeneous is the environment, or the higher is the mobility of individuals, the harder is the persistence for the species.

This chapter lays the mathematical foundation to investigate some other optimisation problems for the environment to make persistence as hard or as easy as possible, which will be addressed in Chapter 6.

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5.1 Introduction

5.1.1 Presentation of the model

We consider a model of population dynamics which takes into account both the spatial heterogeneity of the environment and the phenotypic structure of the population. This amounts to a reaction-diffusion equation with a nonlocal reaction term of the Fisher-KPP type.

More precisely, let $u(t,x,\theta)$ denote the density at time t of a population structured in space (x-variable) and in phenotype (θ-variable). The domain of the spatial variable is the whole space $\mathbb{R}^N$, $N \in \mathbb{N}$, and the domain of the phenotype, denoted by Θ, is either $\mathbb{R}^P$, $P \in \mathbb{N}$, or a smooth bounded domain of $\mathbb{R}^P$. In the latter case we call ν the outward normal to $\partial\Theta$.

The dynamic of the density is governed by the system

$$\begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), & t>0,\ (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \nu \cdot \nabla_\theta u = 0, & t>0,\ (x,\theta) \in \mathbb{R}^N \times \partial\Theta, \end{cases} \tag{5.1}$$

with

$$\rho(t,x) := \int_\Theta u(t,x,\sigma)\,\mathrm{d}\sigma \tag{5.2}$$

representing the total population at given time and location. We supplement problem (5.1)–(5.2) with an initial condition

$$u(0,x,\theta) = u_0(x,\theta), \qquad (x,\theta) \in \mathbb{R}^N \times \Theta. \tag{5.3}$$

The quantity $r(x,\theta)$ corresponds to the fitness of an individual of phenotype θ at location x, in the absence of competition. We refer to r as the *space/phenotype fitness landscape*. We will assume in the sequel that r is periodic in the spatial variable x. The term $\rho(t,x)u(t,x,\theta)$, which is nonlocal in the θ variable, is the competition faced by individuals of phenotype θ located at x. Throughout this chapter, any reference to $\partial\Theta$, such as the boundary condition in (5.1), has to be ignored in the case $\Theta = \mathbb{R}^P$.

The first question that we address in this chapter is the well-posedness of the problem, which is not covered by the existing literature under the generality of our assumptions. We will derive it by first showing that solutions remain bounded, despite the equation lacks the comparison principle.

The next two fundamental questions on the model are:

1. *When does the population survive or get extinct?*
2. *How to optimise the chances of persistence/extinction?*

In Section 5.2.3, we shall answer the first question by giving a persistence criterion based on the *generalised principal eigenvalue* of the linearised operator. Using this criterion, we shall provide in Section 5.2.4 an answer the second question about the chances of persistence in terms of the fluctuations of the environment and of the diffusivity of the species. These results will be obtained by considering a fitness function $r(x/L,\theta)$ and by adding a diffusion coefficients d in front of Δ_x, then modulating the parameters L, d. In loose terms, we will show that persistence becomes harder when the heterogeneity of the environment increases, as well as when the diffusivity grows. Other optimisation problems, under some specific structural assumptions on the landscape, will be addressed in Chapter 6.

5.1.2 Related models

Let us explain where the model (5.1) comes from, and relate it to the existing literature.

The classical Fischer-KPP equation. The following equation has been independently introduced in 1937 by Fisher [94] and Kolmogorov, Petrovsky and Piskunov [143] :

$$\partial_t u(t,x) = \Delta_x u + ru - u^2, \qquad t > 0, \qquad x \in \mathbb{R}. \tag{5.4}$$

Since then, it has been widely studied, both from a mathematical point of view (e.g. [14]) and for applications in population dynamics (e.g. [210]). Let us imagine that u is the distribution of a population living on $\mathbb{R}$. The term $\Delta_x u$ then stands for the movements of the individuals, the term ru stands for the demography in the absence of competition, and the nonlinear term $-u^2$ encodes the competition pressure.

When the individuals of a population move and reproduce, it can be expected that they will eventually invade their environment. One of the most important aspects of the Fisher-KPP equation is that it shows an invasion taking place at the asymptotic linear speed $c_{KPP} := 2\sqrt{r}$, in the following sense. If the initial condition is bounded, nonnegative, not identically equal to zero and has a compact support, then:

$$\forall c \in (0, c_{KPP}), \quad \lim_{t\to+\infty} u(t,ct) = r,$$

and

$$\forall c > c_{KPP}, \quad \lim_{t\to+\infty} u(t,ct) = 0.$$

The standard Fisher-KPP equation has been extended in several ways, in order to make it more realistic and adapted to capture some relevant biological properties. Our model (5.1) tries to circumvent two of the limitations of the standard equation. First, the environment in which individuals live is rarely homogeneous [181, 208, 209]. This is why the environmental conditions should affect the growth rate r, according to the spatial position x. Second, the population itself is heterogeneous: for example, individuals with distinct phenotypes may react differently to the same environmental conditions. The interplay between the different phenotypes can have a true impact on the dynamics of the population [82, 169].

In model (5.1), the phenotype is taken into account through the new variable θ. Then, all individuals located at the same position compete with each other, regardless of their phenotypes. Thus, the nonlinear term $-u^2$ is replaced by the nonlocal term $-\rho u$. Finally, we add a term $\Delta_\theta u$, to account for mutations (which induce variations in phenotype); this modelling means that the mutations are small and frequent.

Models similar to (5.1) appeared for the first time in the work of Prévost [194]. Champagnat and Méléard [61] derived variants of (5.1) as large population limits of individual-based models (in their models, the mutations are rarer but larger than in ours). Their derivations allow one to understand better where the different terms of the equation come from.

We now go back to the standard Fisher-KPP equation, and we progressively add features to it until we get equations similar to (5.1), in order to understand the different mathematical properties that these features entail.

Heterogeneous landscape. If the demography is affected by the environment, and changes from place to place, then one is led to consider a growth rate that depends on the spatial

variable, i.e. $r = r(x)$. This results in the following N-dimensional spatially heterogeneous version of the Fisher-KPP equation (typically $N = 2$ in applications):

$$\partial_t u(t,x) = \Delta_x u + r(x)u - u^2, \qquad t > 0, \qquad x \in \mathbb{R}^N. \tag{5.5}$$

We have seen that in the homogeneous setting (5.4), provided $r > 0$ (i.e. the environment is favourable to the species) and the initial condition is nonzero and nonnegative, the population persists and actually invades the whole environment. This is called the *hair-trigger effect*.

The model (5.5) allows one to consider environments composed also of unfavourable regions, that is, $r(x)$ can be negative for some $x \in \mathbb{R}$. Then, the question of the *persistence* of the population is no longer trivial. A sharp criterion to determine whether the population persists or, on the contrary, eventually gets extinct, is provided by the sign of the principal eigenvalue of the operator linearised around the steady state $u \equiv 0$, i.e. the operator

$$\Delta_x + r(x).$$

(More details about principal eigenvalues are given in Section 5.2.3 below.) This criterion was first derived in [56] for problems set in bounded domains. When dealing with unbounded environments, a typical modelling assumption is that the landscape is *periodic*, see e.g. [209]. This can be viewed as a mathematical approximation of more complex situations. In such a framework, the characterisation in terms of the principal eigenvalue of an operator acting on the space of periodic functions has been derived in [27].

As in the homogeneous setting, for the heterogeneous equation (5.5) with periodic r, when there is persistence there is also complete invasion towards a positive steady state. The invasion occurs with some spreading speed c_{het}, which replaces the quantity c_{KPP}. When $N \geqslant 2$, the spreading speed c_{het} may depend on the direction of spreading. A formula for c_{het} has been derived by Gärtner and Freidlin [103] using probabilistic techniques, and later with PDEs techniques, along with some extensions, see e.g. [25, 203, 220]. A general survey of mathematical works and methods for reaction-diffusion equation in heterogeneous environments is given in [224].

Structured population. Consider now a heterogeneous population structured according to the phenotype. A first situation is when there is a finite number of phenotypes: this leads to a system of Fisher-KPP equations, each of them accounting for a given phenotype, competing with the other ones. In this direction, let us mention [109] for homogeneous environments and [110, 115] for heterogeneous environments.

In the present chapter, we shall use another formalism, and assume that the phenotype is a continuous parameter. Let us first stick to a homogeneous environment; we get a simplified version of (5.1):

$$\begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + u\,(r(\theta) - \rho(t,x)), & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \nu \cdot \nabla_\theta u = 0, & t > 0,\ (x,\theta) \in \mathbb{R}^N \times \partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R}^N \times \Theta, \end{cases} \tag{5.6}$$

with ρ defined by (5.2). Here, contrarily to (5.1), the coefficient r depends on θ only. This model is studied in [30] in the case $\Theta = \mathbb{R}^P$, under the assumption that $-r$ is coercive. The latter condition allows the authors to define in a standard way the principal eigenvalue λ of

the operator

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

acting on a Hilbert space. One then has a dichotomy analogous to that for the spatially heterogeneous Fisher-KPP equation (5.5): if $\lambda < 0$, then the population eventually gets extinct, while if $\lambda > 0$, then the population persists. Moreover, in the latter case, the homogeneity of the environment (i.e. the independence in x of r) and the coercivity of $-r$ entail that the equation admits a unique positive steady state $V(\theta)$, despite the lack of comparison principle, and any nontrivial solution converges towards V with a spreading speed equal to $c_{phen} := 2\sqrt{\lambda}$.

Recent models. Several spatially-heterogeneous versions of (5.6) have been studied in the literature. In [4, 187], the authors consider the case of a population evolving along an environmental gradient, that is,

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

where the function $R : \mathbb{R} \to \mathbb{R}$ is positive on the interval $(-1,1)$, negative outside $[-1,1]$, and $R(y)$ tends quadratically to $-\infty$ as $|y| \to \infty$. In this model, the fittest phenotype at position x lies on the interval $((x-1)/B, (x+1)/B)$, so the phenotype is driven by the spatial variable x. As a consequence, evolution is necessary for the spatial propagation of the population. This is relevant when one studies, for example, migrations along the north-south axis, or uphill-downhill for populations living in the mountains. In [4] again, using the coercivity of $-r$, the authors give a criterion based on a principal eigenvalue to determine whether the population persists or gets extinct.

Additionally to spatial heterogeneity, the authors of [3] add a heterogeneity in time corresponding to climate change. Their growth rate takes the form $r(x - ct, \theta)$. Different shapes of the favourable space/phenotype zone are studied (confined zone, environmental gradient, or a mixing of the two). In each case, the authors find a criterion for persistence and propagation of the species. The criteria, again, are based on the principal eigenvalue of linear operators.

There seems to be few works considering the phenotype together with a periodic heterogeneous environment. In [9], Alfaro and Peltier focus on homogeneous environments with a very small periodic perturbation. When the perturbation is small enough, they show the existence of stationary states and pulsating travelling waves. In [44], Bouin and Mirrahimi focus on a situation where evolutionary events (mutations) occur on a much faster timescale than ecological events (movements). In a similar vein, but in the stationary setting, Léculier and Mirrahimi [151] studied the weak mutation limit of the stationary version of a model related to ours. They also give biological properties of the solution; in some cases, they are able to determine if the population at equilibrium is polymorphic or monomorphic.

5.2 Main results

5.2.1 Assumptions on the landscape

The set Θ is either $\mathbb{R}^P$ or a C^2 bounded domain in $\mathbb{R}^P$. We shall make the following assumptions on r:

$$\begin{cases} r \in L^\infty_{loc}(\mathbb{R}^N \times \overline{\Theta}),\ r \text{ is bounded above;} \\ r(x+h,\theta) = r(x,\theta) \ \text{ for all } (x,\theta) \in \mathbb{R}^N \times \Theta \text{ and } h \in \mathbb{Z}^N. \end{cases} \tag{5.7}$$

Throughout this chapter, for a given function defined on $\mathbb{R}^N \times \Theta$, we shall refer to the second condition in (5.7) as "1-periodicity in x". We point out that in the case where Θ is bounded, the function r is globally bounded. In the case $\Theta = \mathbb{R}^P$, we will sometimes assume that

$$\limsup_{\|\theta\| \to \infty} r(x,\theta) \leqslant 0, \quad \text{uniformly with respect to } x \in \mathbb{R}^N, \tag{5.8}$$

which means

$$\lim_{R \to +\infty} \left(\sup_{x \in \mathbb{R}^N,\ \|\theta\| \geqslant R} r(x,\theta) \right) \leqslant 0.$$

We point out that, unlike in other mathematical studies in the literature, we do not assume $-r$ to be coercive. This will entail a loss of compactness that we will face using the notion of *generalised principal eigenvalue*.

5.2.2 Well-posedness of the problem

We now state the well-posedness result for (5.1)–(5.3). Solutions are understood in the weak sense, namely: $u \in L^\infty([0,T) \times \mathbb{R}^N \times \overline{\Theta}) \cap L^\infty([0,T) \times \mathbb{R}^N; L^1(\Theta))$ for all $T > 0$, and it holds

$$\begin{aligned} &\forall \phi \in C^\infty_c([0,+\infty) \times \mathbb{R}^N \times \overline{\Theta}), \\ &\quad -\int u(\partial_t \phi) - \int_{\mathbb{R}^N \times \Theta} u_0(\cdot,\cdot)\phi(0,\cdot,\cdot) = \int u\,(\Delta_x \phi + \Delta_\theta \phi) + \int u\phi \left(r - \int_\Theta u(t,x,\cdot) \right) \end{aligned} \tag{5.9}$$

(the non-specified integrals are taken on $[0,+\infty) \times \mathbb{R}^N \times \Theta$). In fact, solutions to the Cauchy problem (5.1)–(5.3) satisfy the first equation in (5.1) also in the strong sense, i.e., they belong to $W^{1,2}_{p,loc}((0,+\infty) \times \mathbb{R}^N \times \overline{\Theta})$ for all $p > 1$, where, here and in the sequel, $W^{1,2}_p$ (resp. $W^{1,2}_{p,loc}$) is the set of functions that belong to L^p (resp. L^p_{loc}) together with their first order derivative with respect to t and their partial derivatives up to order 2 with respect to (x,θ). In particular, solutions belong to $W^1_{p,loc}((0,+\infty) \times \mathbb{R}^N \times \overline{\Theta})$ with respect to all variables (t,x,θ). Hence, by Morrey's inequality, the solutions are continuous, so (5.2) holds for every $(t,x) \in [0,+\infty) \times \mathbb{R}^N$ (and not just almost everywhere). Moreover, since the initial datum will be assumed to be continuous, the initial condition is attained in the classical sense too. However, without further regularity assumptions on r, the solution u cannot be expected to be more than Lipschitz continuous in the (x,θ) variables, so the weak formulation of the Cauchy problem is needed to give meaning to the boundary condition in (5.1).

Theorem 5.2.1 (Well-posedness)**.** *Let $r \in L^\infty_{loc}(\mathbb{R}^N \times \overline{\Theta})$ be bounded from above (not necessarily periodic in x), and let $u_0 \in C^0(\mathbb{R}^N \times \overline{\Theta}) \cap L^\infty(\mathbb{R}^N; L^1(\Theta))$ be nonnegative and bounded.*

Then, there exists a unique solution u to the Cauchy problem (5.1)–(5.3)*. Moreover, u and ρ are bounded and nonnegative, and if $u_0 \not\equiv 0$, then they are strictly positive.*

5.2.3 Long-time behaviour of the solution

The long-time behaviour of solutions of the Fisher-KPP equation is characterised by the sign of the principal eigenvalue of the linearised operator around the null state. This is a well-known fact when the problem is set on a smooth bounded domain, see e.g. [56]. This is also known if the operator is periodic, thanks to [27]. In both cases, the principal eigenvalue is provided by the classical Krein-Rutman theory. The characterisation has been extended in [29] to the non-compact setting by using the notion of the *generalised principal eigenvalue* inspired by [21]. It has then been employed in several different frameworks, see e.g. [3, 4, 22, 110, 111, 118]. This notion is required to study our model when $\Theta = \mathbb{R}^P$.

More precisely, we call $\mathcal{L}[r]$ the linearised operator associated with (5.1), that is

$$\mathcal{L}[r]\phi := \Delta_x\phi + \Delta_\theta\phi + r(x,\theta)\phi.$$

We emphasise that $\mathcal{L}[r]$ is a local operator.

Definition 5.2.2. *The generalised principal eigenvalue of $\mathcal{L}[r]$ is*

$$\lambda[r] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ \mathcal{L}[r]\phi \leqslant \lambda\phi \text{ in } \mathbb{R}^N \times \Theta,\ \nu \cdot \nabla_\theta \phi \geqslant 0 \text{ on } \mathbb{R}^N \times \partial\Theta\right\}.$$

In the above definition, and throughout this chapter, the functions ϕ are understood to belong to $W^2_{p,loc}(\mathbb{R}^N \times \overline{\Theta})$ for some $p > 1 + N + P$, hence to be C^1 up to the boundary by Morrey's embedding, so the boundary condition holds in the classical sense.

Definition 5.2.2 applies to both cases Θ bounded and $\Theta = \mathbb{R}^P$ (in the latter, the boundary condition is ignored, as usual). We point out that, even in the case of bounded Θ, the domain of the functions ϕ on which the operator acts is not compact, since we do not assume ϕ to be periodic in x. However, despite the lack of compactness, it turns out that $\lambda[r]$ is indeed a *generalised principal eigenvalue* for the operator $\mathcal{L}[r]$ acting on spatially-periodic functions, in the sense that it admits a positive eigenfunction in that space.

Proposition 5.2.3. *Let r satisfy* (5.7) *and let $\lambda[r]$ be the generalised principal eigenvalue of $\mathcal{L}[r]$ given by Definition 5.2.2. There exists a solution φ of the problem*

$$\begin{cases} \mathcal{L}[r]\varphi(x,\theta) = \lambda[r]\varphi(x,\theta), & (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \nu \cdot \nabla_\theta \varphi(x,\theta) = 0, & (x,\theta) \in \mathbb{R}^N \times \partial\Theta, \\ \varphi(x,\theta) > 0, & (x,\theta) \in \mathbb{R}^N \times \Theta, \\ \varphi \text{ is 1-periodic in } x. \end{cases} \tag{5.10}$$

We call *any* solution φ of (5.10) a *principal eigenfunction* associated with $\lambda[r]$. When Θ is bounded, the Krein-Rutman theory [145] provides the existence, uniqueness and simplicity of the principal eigenvalue for problem (5.10), which furthermore can be expressed through the Rayleigh quotient; in such a case, Proposition 5.2.3 asserts that this principal eigenvalue is characterised by the formula in Definition 5.2.2. In the case where Θ is unbounded, the Krein-Rutman theory does not apply and indeed neither simplicity nor uniqueness hold for the eigenproblem (5.10), and there is actually a half-line of eigenvalues admitting positive

eigenfunctions, see [33]. This is why we call ϕ in (5.10) "a" – rather than "the" – principal eigenfunction.

Making use of some results concerning the generalised principal eigenvalue, we are able to establish the "standard" extinction/persistence dichotomy for the the long-time behaviour of the solution for our model.

Theorem 5.2.4. *Let r satisfy (5.7)–(5.8) and let $\lambda[r]$ be the generalised principal eigenvalue of $\mathcal{L}[r]$. Let u be the solution to (5.1)–(5.3) with $u_0 \in C^0(\mathbb{R}^N \times \overline{\Theta}) \cap L^\infty(\mathbb{R}^N; L^1(\Theta))$ bounded, nonnegative and not identically equal to 0.*

- *If $\lambda[r] < 0$, and in addition u_0 is compactly supported, then the population gets extinct, in the sense that*

$$\lim_{t \to +\infty} u(t,x,\theta) = 0 \qquad \text{uniformly in } (x,\theta) \in \mathbb{R}^N \times \Theta.$$

- *If $\lambda[r] > 0$ then the population persists, in the sense that*

$$\liminf_{t \to +\infty} \left[\sup_{x \in \mathbb{R}^N} \rho(t,x) \right] > 0.$$

We point out that the persistence property in the case $\lambda[r] > 0$ does not provide us with a complete description of the long-time behaviour of the solution, but it just ensures that it stays bounded from below away from zero. In particular, we do not know whether the solution converges towards a positive stationary state (as in the case without phenotype (5.5) or in the spatially homogeneous case with phenotype (5.6)); for instance, we cannot rule out the possibility that the solution approaches a time-periodic cycle, which is a behaviour observed in some nonlocal reaction-diffusion equations, see e.g. [171].

As a matter of fact, the hypothesis that u_0 is compactly supported in the persistence result is not needed in the case Θ bounded, cf. Remark 5.5.2 below.

Finally, the borderline case $\lambda[r] = 0$ is not treated in this chapter. In some related reaction-diffusion models, it is known that when the principal eigenvalue of the linearised operator is zero, the population gets extinct. This is the case when the phenotype is not taken into account [27], or when the phenotype is taken into account through a quadratically decreasing Fisher geometric model and the spatial structure is discrete, with the spatial variable limited to two possible values [118].

5.2.4 Influence of the heterogeneity of the environment and of the diffusivity

We introduce two positive parameters L, d in our model by replacing the first equation in (5.1) by either

$$\partial_t u = \Delta_x u + \Delta_\theta u + u\left(r(x/L,\theta) - \rho(t,x)\right), \qquad t > 0,\ (x,\theta) \in \mathbb{R}^N \times \Theta,$$

or

$$\partial_t u = d\Delta_x u + \Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), \qquad t > 0,\ (x,\theta) \in \mathbb{R}^N \times \Theta.$$

The quantity $1/L$ represents the frequency of oscillations of the landscape, while the diffusion coefficient d accounts for the mobility of individuals. Observe that one can pass from one

of the above equations to the other by a simple change of variable. It is clear that all our previously stated results hold true if one replaces the 1-periodicity in x with the L-periodicity, hence the same is true for the model with diffusivity d.

Let us write for short

$$r^L(x,\theta) := r\left(\frac{x}{L},\theta\right).$$

Thus, extinction or persistence for the model with L-periodicity are determined by the sign of the generalised principal eigenvalue $\lambda[r^L]$ given by Definition 5.2.2, while for the model with spatial diffusivity d they are determined by the sign of the generalised principal eigenvalue $\lambda_d[r]$ of the linearised operator

$$\mathcal{L}_d[r] := d\Delta_x + \Delta_\theta + r.$$

We derive the following.

Proposition 5.2.5. *Let r satisfy the assumptions (5.7)–(5.8) and let $\lambda[r^L]$ and $\lambda_d[r]$ denote the generalised principal eigenvalue of the linearised operator $\mathcal{L}[r^L]$ and $\mathcal{L}_d[r]$ respectively.*

(i) The function $L \mapsto \lambda[r^L]$ is continuous and nondecreasing on $(0,+\infty)$.

(ii) The function $d \mapsto \lambda_d[r]$ is continuous and nonincreasing on $(0,+\infty)$.

This result, combined with Theorem 5.2.4, shows that persistence becomes harder for the population if either the frequency of oscillations of the landscape or the mobility of individuals increase. This means that habitat fragmentation is armful for the species, and the same is true for the mobility. While the first fact is rather intuitive, the second one can be surprising, because one might expect that a faster diffusivity could provide higher chances of adaptation. Our result shows that in our context, the opposite is true. From a modelling perspective, this is in accordance with the conclusion of [118, Proposition 2.7.*i*)], where a spatially discrete system is considered and an analogous monotonicity property with respect to the migration rate is obtained.

5.2.5 A variant with heterogeneous diffusion

For simplicity, we have considered that only the fitness of an individual is affected by its position and its phenotype. We may also deem it relevant to assume that the mobility and the mutation rate are anisotropic and depend on the position and the phenotype of the individual. This leads to the following extension of (5.1):

$$\begin{cases} \partial_t u = \nabla_x \cdot (a(x,\theta)\nabla_x u) + \nabla_\theta \cdot (\mu(x,\theta)\nabla_\theta u) \\ \qquad\quad + u\left(r(x,\theta) - \displaystyle\int_\Theta u(t,x,\sigma)\,\mathrm{d}\sigma\right), & t>0,\ (x,\theta)\in\mathbb{R}^N\times\Theta, \\ \nu\cdot(\mu(x,\theta)\nabla_\theta u) = 0, & t>0,\ (x,\theta)\in\mathbb{R}^N\times\partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta)\in\mathbb{R}^N\times\Theta, \end{cases}$$

where the functions a,μ are ranged in two sets of uniformly positive definite, symmetric matrices of size $N\times N$ and $P\times P$ respectively, and are 1-periodic in the x variable. One may check that our arguments remain valid in this setting: the problem is well-posed, the long-time behaviour is described by the sign of the generalised principal eigenvalue (cf. Theorems 5.2.1 and 5.2.4), and the latter is continuous and nonincreasing with respect to the

frequency of oscillations of the habitat and to the amplitude of the spatial diffusivity (cf. Proposition 5.2.5).

5.3 Well-posedness of the model (Theorem 5.2.1)

Proof of Theorem 5.2.1. We derive the well-posedness of the Cauchy problem on the parabolic domain $[0,T]\times\mathbb{R}^N\times\Theta$, with arbitrary $T>0$. By uniqueness, this will provide us with a solution on the entire $[0,+\infty)\times\mathbb{R}^N\times\Theta$. The proof is based on a contraction argument. To make it work, we start by deriving a priori bounds on u and ρ.

In the sequel, the functions r and u_0 fulfil the hypotheses of the theorem.

Step 1. Global boundedness of u and ρ. Let $u:[0,+\infty)\times\mathbb{R}^N\times\Theta\to\mathbb{R}$ be a solution to (5.1)–(5.3) (in the weak sense, i.e., $u\in L^\infty((0,T)\times\mathbb{R}^N\times\Theta)\cap L^\infty((0,T)\times\mathbb{R}^N;L^1(\Theta))$ for all $T>0$ and (5.9) holds). Since u,ρ are bounded, locally in time, we can apply the parabolic maximum principle to (5.1), treating ρ as a datum, and infer that $u(t,x,\theta)\geqslant 0$ for all $t>0$, $(x,\theta)\in\mathbb{R}^N\times\Theta$. Moreover, the strict inequality holds as soon as $u_0\not\equiv 0$, owing to the strong maximum principle. Furthermore, it holds that

$$\partial_t u\leqslant\Delta_x u+\Delta_\theta u+(\bar r-\rho)\,u,\qquad t>0,\ (x,\theta)\in\mathbb{R}^N\times\Theta, \tag{5.11}$$

where $\bar r:=\sup_{\mathbb{R}^N\times\Theta}r$, which is finite by assumption. Again, this is understood in the weak sense, namely, the inequality "$\leqslant$" holds in (5.9) for nonnegative ϕ's. Restricting to ϕ independent of θ in this weak formulation, and taking first the integral on θ over Θ by Fubini's theorem, one finds that the function ρ satisfies in the weak sense

$$\partial_t\rho\leqslant\Delta_x\rho+(\bar r-\rho)\rho,\qquad t>0,\ x\in\mathbb{R}^N,$$

together with the initial condition $\rho(0,x)=\int_\Theta u_0(x,\sigma)\,\mathrm{d}\sigma$. From this, one gets, again by comparison,

$$\forall t>0,\quad \|\rho(t,\cdot)\|_\infty\leqslant A:=\max\{\|\rho(0,\cdot)\|_\infty,\bar r\}. \tag{5.12}$$

Last, we show that u is globally bounded. For this, we treat the term ρ as a given coefficient, that we know being bounded, of the equation in (5.1), which is then seen as a local linear parabolic equation.

We first deal with the case Θ bounded. We use the parabolic Harnack inequality. In order to rule out the boundary of Θ, we use the C^2-regularity of $\partial\Theta$ to extend the solution u in the θ variable by orthogonal reflection with respect to $\partial\Theta$ and get a function defined for all θ on an open set $\widetilde\Theta$ containing $\overline\Theta$. The extended function is a solution of a parabolic equation of the same type as the one in (5.1), with Δ_θ extended outside Θ by an elliptic operator with coefficients depending on Θ, hence regular (Lipschitz-continuous). See e.g. the proof of Theorem 3.1 in [33]. This allows us to apply the parabolic interior Harnack inequality, cf. [146, Theorem 1.1], which, for any $R>0$, gives a constant $C_R>0$ such that

$$\forall t\geqslant 1,\ \forall x\in\mathbb{R}^N,\qquad \sup_{B_{\mathbb{R}^N}(x,R)\times\Theta}u(t,\cdot,\cdot)\leqslant C_R\inf_{B_{\mathbb{R}^N}(x,R)\times\Theta}u(t+1,\cdot,\cdot), \tag{5.13}$$

where $B_{\mathbb{R}^N}(x,R)$ is the open ball in $\mathbb{R}^N$ with centre x and radius R. We emphasise that the constant C_R is independent of t and x, because the coefficients of the equation (including ρ) are uniformly bounded. Since $\rho(t+1,x)\geqslant|\Theta|\inf_\Theta u(t+1,x,\cdot)$, with $|\Theta|$ denoting the measure

of Θ, we deduce in particular

$$\forall t \geqslant 1,\ \forall x \in \mathbb{R}^N, \qquad \sup_{\Theta} u(t,x,\cdot) \leqslant C_1 \inf_{\Theta} u(t+1,x,\cdot) \leqslant \frac{C_1}{|\Theta|}\rho(t+1,x),$$

hence the global boundedness of u follows from the one of ρ.

Now, let us deal with the case $\Theta = \mathbb{R}^P$. We see u as a subsolution to the equation (5.11) and we apply the local maximum principle, see e.g. [153, Theorem 7.36]: there exists a constant $C > 0$ such that for any $t \geqslant 2$, $x_0 \in \mathbb{R}^N$ and $\theta_0 \in \mathbb{R}^P$, there holds:

$$\sup_{(t-1/2,t)\times B_{\mathbb{R}^N}(x_0,1/2)\times B_{\mathbb{R}^P}(\theta_0,1/2)} u \leqslant C \int_{t-1}^{t} \int_{B_{\mathbb{R}^N}(x_0,1)} \int_{B_{\mathbb{R}^P}(\theta_0,1)} u.$$

We emphasise that the constant C is independent of t and x_0, because the coefficients of the equation (5.11) (including ρ) are uniformly bounded. We obtain in particular:

$$u(t,x_0,\theta_0) \leqslant C \int_{t-1}^{t} \int_{B_{\mathbb{R}^N}(x_0,1)} \rho \leqslant C|B_{\mathbb{R}^N}(x_0,1)| \sup \rho,$$

where $|B_{\mathbb{R}^N}(x_0,1)|$ denotes the volume of $B_{\mathbb{R}^N}(x_0,1)$. Then, ρ being uniformly bounded, we conclude that u is uniformly bounded too.

Step 2. Contraction argument. Now, we fix an arbitrary $T > 0$ and we take $\tau \in (0,T)$ to be determined later. For a given function $w : [0,\tau] \times \mathbb{R}^N \to L^1(\Theta)$, we set

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

Then, we consider the set of functions K defined by

$$K := \left\{ w \in L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta)) \ / \ 0 \leqslant \rho[w](t,x) \leqslant 2Ae^{\bar{r}T} \ \text{ for } (t,x) \in [0,\tau]\times\mathbb{R}^N \right\}.$$

Next, for a given initial datum $\varpi \in L^\infty(\mathbb{R}^N\times\Theta) \cap L^\infty(\mathbb{R}^N; L^1(\Theta))$ satisfying

$$\varpi \geqslant 0 \quad \text{in } \mathbb{R}^N\times\Theta, \qquad \operatorname*{ess\,sup}_{x\in\mathbb{R}^N} \|\varpi(x,\cdot)\|_{L^1(\Theta)} \leqslant Ae^{\bar{r}T}, \tag{5.14}$$

and for given $w \in K$, we consider the following problem:

$$(E_w) \qquad \begin{cases} \partial_t u = \Delta_x u + \Delta_\theta u + (r(x,\theta) - \rho[w](t,x))u, & (t,x,\theta) \in (0,\tau)\times\mathbb{R}^N\times\Theta, \\ \nu\cdot\nabla_\theta u = 0, & (t,x,\theta) \in (0,\tau)\times\mathbb{R}^N\times\partial\Theta, \\ u(0,x,\theta) = \varpi(x,\theta), & (x,\theta) \in \mathbb{R}^N\times\Theta. \end{cases}$$

Since r is bounded from above and $\rho[w]$ is bounded, the comparison principle holds for the above problem, and it is standard that it admits a unique bounded weak solution (in the sense precised at the beginning of Section 5.2.2), which we call u^w. It also follows that $u^w \in W^{1,2}_{p,loc}((0,\tau]\times\mathbb{R}^N\times\overline{\Theta})$ and that it is nonnegative, and thus by the same argument as in the Step 1, the function $\rho[u^w](t,x)$ fulfils in the weak sense

$$\partial_t \rho[u^w] \leqslant \Delta_x \rho[u^w] + (\bar{r} - \rho[w])\rho[u^w], \qquad t \in (0,\tau),\ x \in \mathbb{R}^N.$$

Then, owing to (5.14), we derive

$$\forall t \in [0,\tau], \forall x \in \mathbb{R}^N, \qquad \rho[u^w](t,x) \leqslant A e^{\bar r\,(T+t)}\,.$$

It follows that u^w belongs to K provided $e^{\bar r\,\tau} \leqslant 2$.

Next, take $w_1, w_2 \in K$. Let us write for short $u_1 := u^{w_1}$, $u_2 := u^{w_2}$ and $\rho_1 := \rho[w_1]$, $\rho_2 := \rho[w_2]$. The function $v := u_1 - u_2$ vanishes identically at $t = 0$ and satisfies

$$\begin{aligned}\partial_t v - \Delta_x v - \Delta_\theta v &= r v - \rho_1 v - (\rho_1 - \rho_2) u_2 \\ &\leqslant (r - \rho_1) v + \|w_1 - w_2\|_{L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))} u_2\,. \end{aligned} \tag{5.15}$$

Let $\bar v$ be the solution of the equation

$$\partial_t \bar v - \Delta_x \bar v - \Delta_\theta \bar v = \bar r\,\bar v + \|w_1 - w_2\|_{L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))} u_2, \qquad (t,x,\theta) \in (0,\tau)\times\mathbb{R}^N\times\Theta,$$

with Neumann boundary conditions and initial datum identically equal to 0. On the one hand, $\bar v$ is nonnegative, so we have $\bar r \bar v \geqslant (r - \rho_1)\bar v$; thus $\bar v$ is a supersolution of the equation (5.15), for which v is a subsolution. We deduce by comparison that $v \leqslant \bar v$. On the other hand, in the case Θ bounded, as done before, we can integrate the equation for $\bar v$ on Θ. Hence, since $u_2 \in K$, we get

$$\begin{aligned}\partial_t \rho[\bar v] - \Delta_x \rho[\bar v] &= \bar r\,\rho[\bar v] + \|w_1 - w_2\|_{L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))} \rho[u_2] \\ &\leqslant \bar r\,\rho[\bar v] + \|w_1 - w_2\|_{L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))} \times 2A e^{\bar r T}\,.\end{aligned}$$

It follows that, for τ sufficiently small, only depending on $\bar r$, A and T, it holds

$$\forall t \in [0,\tau], \forall x \in \mathbb{R}^N, \qquad \rho[\bar v](t,x) \leqslant \frac{1}{2}\|w_1 - w_2\|_{L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))}\,.$$

Instead, in the case $\Theta = \mathbb{R}^P$, one can explicitly compute the solution $\bar v$ through the heat kernel and check that the above estimate holds true, again for τ depending on $\bar r$, A and T. This gives a one-side inequality for $\rho[v]$. The same argument for $-\rho[v] = \rho[-v]$ follows reverting the roles of u_1 and u_2. In conclusion, we have shown that the mapping $w \mapsto u^w$ is a contraction from the closed set K into itself, with respect to the $L^\infty([0,\tau]\times\mathbb{R}^N; L^1(\Theta))$ norm, for any $\tau \in (0,\tau_0]$, where $\tau_0 > 0$ is sufficiently small and depends only on $\bar r$, A and T. Therefore, $w \mapsto u^w$ has a unique fixed point, which implies that (5.1) has a unique solution on $(0,\tau)\times\mathbb{R}^N\times\Theta$ for any $\tau \in (0,\tau_0]$ and any initial condition ϖ satisfying (5.14).

Step 3. Conclusion. Step 2 provides us with a unique solution u to problem (5.1) $(0,\tau_0)\times\mathbb{R}^N\times\Theta$ with initial datum u_0. Take $\varepsilon \in (0,1/2)$ and consider the new initial datum $\varpi = u((1-\varepsilon)\tau_0,\cdot,\cdot)$. By (5.12), ϖ satisfies (5.14), hence by Step 2 the corresponding problem E_w admits a unique solution on $(0,\tau_0)\times\mathbb{R}^N\times\Theta$, which overlaps with $u(\cdot + (1-\varepsilon)\tau_0,\cdot,\cdot)$ on $[0,\varepsilon\tau_0)\times\mathbb{R}^N\times\Theta$. We may thus extend u to a solution of (5.1) for $t \in [0,(2-\varepsilon)\tau_0)$. Iterating this argument, we have that u solves (5.1) for all times $t \in (0,T]$, hence for all $t > 0$, by the arbitrariness of T. We further know by Step 1 that u is globally bounded, together with its associated function ρ. □

5.4 Properties of the principal eigenfunction and eigenvalue

Before studying the long-time behaviour of the solution, we derive some properties of the generalised principal eigenvalue $\lambda[r]$ of Definition 5.2.2.

We start with the case Θ bounded. We derive a result containing two statements: the first one follows from the arguments of [33] and provides us with an approximation of the principal eigenvalue $\lambda[r]$ by principal eigenvalues in the domains $B_{\mathbb{R}^N}(0,R)\times\Theta$ under mixed Dirichlet-Neumann boundary conditions. The second statement asserts that $\lambda[r]$ coincides with the standard periodic principal eigenvalue on $\mathbb{R}^N\times\Theta$. This implies in particular that Proposition 5.2.3 holds in the case Θ bounded.

Proposition 5.4.1. *Assume Θ is bounded and has C^2 boundary. Let r satisfy (5.7).*

(i) For all $R>0$, the mixed eigenproblem

$$\begin{cases} \mathcal{L}[r]\varphi_R^m = \lambda_R^m\varphi_R^m & \text{in } B_{\mathbb{R}^N}(0,R)\times\Theta,\\ \nu\cdot\nabla_\theta\varphi_R^m = 0 & \text{over } B_{\mathbb{R}^N}(0,R)\times\partial\Theta,\\ \varphi_R^m = 0 & \text{over } (\partial B_{\mathbb{R}^N}(0,R))\times\Theta,\\ \varphi_R^m > 0 & \text{in } B_{\mathbb{R}^N}(0,R)\times\Theta, \end{cases}$$

admits a unique solution $\lambda_R^m\in\mathbb{R}$ and a unique (up to a scalar multiple) generalised solution $\varphi_R^m\in W_2^1(B_{\mathbb{R}^N}(0,R)\times\Theta)\cap C^0(\overline{B_{\mathbb{R}^N}(0,R)\times\Theta})$. Moreover, the function $R\mapsto\lambda_R^m$ is increasing and satisfies $\lambda_R^m\to\lambda[r]$ as $R\to+\infty$. Finally, the following Rayleigh formula holds:

$$\lambda_R^m = \max_{\phi\in X_R}\left(\frac{-\int_{B_{\mathbb{R}^N}(0,R)\times\Theta}|\nabla\phi|^2+\int_{B_{\mathbb{R}^N}(0,R)\times\Theta}r\phi^2}{\int_{B_{\mathbb{R}^N}(0,R)\times\Theta}\phi^2}\right),$$

where

$$X_R := \left\{\phi\in W_2^1(B_{\mathbb{R}^N}(0,R)\times\Theta)\cap C^0(\overline{B_{\mathbb{R}^N}(0,R)\times\Theta})\ /\ \phi\equiv 0 \text{ over } \partial B_{\mathbb{R}^N}(0,R)\times\Theta\right\}.$$

(ii) The problem

$$\begin{cases} \mathcal{L}[r]\varphi(x,\theta) = \lambda\varphi(x,\theta) & \text{in } \mathbb{R}^N\times\Theta,\\ \nu\cdot\nabla_\theta\varphi(x,\theta) = 0 & \text{over } \mathbb{R}^N\times\partial\Theta,\\ \varphi(x,\theta) > 0 & \text{in } \mathbb{R}^N\times\Theta,\\ \varphi \text{ is 1-periodic in } x, \end{cases}$$

admits as a solution the unique eigenvalue $\lambda=\lambda[r]$ and a unique (up to a scalar multiple) eigenfunction $\varphi\in W^1_{2,loc}(\mathbb{R}^N\times\overline{\Theta})$. In particular, the generalised principal eigenvalue given by Definition 5.2.2 coincides with the classical x-periodic principal eigenvalue of the above problem.

Proof. **Statement** (i)**.** We point out that the eigenproblem stated in (i) is not completely standard due to the presence of the "corners" $\partial B_{\mathbb{R}^N}(0,R))\times\partial\Theta$. However, the existence

and uniqueness up to a scalar multiple of φ_R^m is derived in [33, Theorem 3.1] in dimension $N=1$. The arguments, which rely on the solvability, in the generalised sense, of the mixed boundary value problem (see e.g. the Notes to Chapter 8 in [106]) and on the construction of some barriers to get continuity up to the corners, holds true without modification in the higher dimensional case. The monotonicity and the convergence of λ_R^m to $\lambda[r]$ are due to [33, Proposition 1] (again in dimension $N=1$, but the argument works in arbitrary dimension).

We now show the Rayleigh formula for λ_R^m. Let $W^1_{2,0}(B_{\mathbb{R}^N}(0,R)\times\overline{\Theta})$ denote the closure in $W^1_2(B_{\mathbb{R}^N}(0,R)\times\Theta)$ of

$$\left\{\phi\in C^1(B_{\mathbb{R}^N}(0,R)\times\overline{\Theta})\ /\ \phi\equiv 0 \text{ over } \partial B_{\mathbb{R}^N}(0,R)\times\Theta\right\}.$$

By the classical elliptic theory (see e.g. the Notes to Chapter 8 in [106]), for all $f\in L^2(B_{\mathbb{R}^N}(0,R)\times\Theta)$, there exists a unique weak solution $\phi\in W^1_{2,0}(B_{\mathbb{R}^N}(0,R)\times\overline{\Theta})$ to the mixed boundary value problem

$$\begin{cases}(\Delta_x+\Delta_\theta)\phi+(r-\bar r)\phi=f & \text{in } B_{\mathbb{R}^N}(0,R)\times\Theta,\\ \nu\cdot\nabla\phi=0 & \text{over } B_{\mathbb{R}^N}(0,R)\times\partial\Theta,\\ \phi=0 & \text{over } \partial B_{\mathbb{R}^N}(0,R)\times\Theta,\end{cases}$$

where $\bar r=\sup r$. Let $T:\ L^2(B_{\mathbb{R}^N}(0,R)\times\Theta)\to L^2(B_{\mathbb{R}^N}(0,R)\times\Theta)$ be the operator which assigns to f the solution ϕ. Owing to the C^2 regularity of Θ and to the Neumann boundary condition, one may extend ϕ by reflection to a larger domain $B_{\mathbb{R}^N}(0,R)\times\widetilde{\Theta}$ with $\overline{\Theta}\subset\widetilde{\Theta}$, which satisfies there a uniformly elliptic equation. This allows one to apply standard elliptic estimates and a compact injection theorem to infer that the operator T is compact. See e.g. the argument of Step 2 of the proof of [33, Theorem 3.1]. Thus, the operator T being symmetric, there exists an orthonormal basis composed of eigenvectors of T. Those eigenvectors are also eigenvectors of the mixed eigenproblem

$$\begin{cases}\mathcal{L}[r]\phi=\lambda_k\phi & \text{in } B_{\mathbb{R}^N}(0,R)\times\Theta,\\ \nu\cdot\nabla_\theta\phi=0 & \text{over } B_{\mathbb{R}^N}(0,R)\times\partial\Theta,\\ \phi=0 & \text{over } (\partial B_{\mathbb{R}^N}(0,R))\times\Theta,\end{cases}$$

for some eigenvalues $\lambda_k\in\mathbb{R}$. Therefore, the Rayleigh formula holds for the mixed eigenproblem, see e.g. the proof of [88, Theorem 6.5.2]:

$$\lambda_R^m=\max_{\phi\in W^1_{2,0}(B_{\mathbb{R}^N}(0,R)\times\overline{\Theta})}\left(\frac{-\int_{\mathbb{R}^N\times\Theta}|\nabla\phi|^2+\int_{\mathbb{R}^N\times\Theta}r\phi^2}{\int_{\mathbb{R}^N\times\Theta}\phi^2}\right).$$

We point out that the max is reached by the principal eigenfunction φ_R^m, which belongs to the space X_R defined in the statement of the proposition. Therefore, we may replace $W^1_{2,0}(B_{\mathbb{R}^N}(0,R)\times\overline{\Theta})$ by the subspace X_R in the variational formula.

Statement (ii)**.** The classical Krein-Rutman theory [145] (see e.g. the proof of [33, Theorem 5.1]) yields the uniqueness and simplicity of the Neumann/periodic eigenproblem of statement (ii). Namely, the problem admits a unique eigenvalue λ and a unique (up to a scalar multiple) eigenfunction φ. What we need to show is that $\lambda=\lambda[r]$.

The inequality $\lambda[r]\leqslant\lambda$ directly follows from Definition 5.2.2. In order to show the reverse inequality, we make use of the Rayleigh formula for λ_R^m. Consider a family of cutoff functions

$(\zeta_R)_{R>1}$ in $C^\infty(\mathbb{R}^N)$ satisfying $\zeta_R \equiv 1$ in $B_{\mathbb{R}^N}(0,R-1)$, $\zeta_R \equiv 0$ on $\partial B_{\mathbb{R}^N}(0,R)$, $0 \leqslant \zeta_R \leqslant 1$ and $\|\nabla \zeta_R\|_\infty \leqslant 2$. We then apply the Rayleigh formula given in (i) to the test function $\phi = \varphi\zeta_R \in X_R$. Let us call for short $B_R := B_{\mathbb{R}^N}(0,R)$ and, for $R>1$,

$$U_R := \bigcup_{h\in\mathbb{Z}^N \text{ s.t. } \mathcal{C}+\{h\}\subset B_{R-1}} \mathcal{C}+\{h\},$$

where $\mathcal{C} := [0,1]^N$ is the periodic cell. We get:

$$\lambda_R^m \geqslant \frac{-\int_{U_R\times\Theta}|\nabla\varphi|^2 + \int_{U_R\times\Theta} r\varphi^2 - \int_{(B_R\setminus U_R)\times\Theta}\left(|\nabla(\varphi\zeta_R)|^2 + |r|\varphi^2\right)}{\int_{B_R\times\Theta}\varphi^2}.$$

Using the 1-periodicity of φ and r, and noticing that U_R contains exactly $|U_R|$ distinct cells $\mathcal{C}+\{h\}$, $h\in\mathbb{Z}^N$, we obtain

$$\lambda_R^m \geqslant \frac{|U_R|\left(-\int_{\mathcal{C}\times\Theta}|\nabla\varphi|^2 + \int_{\mathcal{C}\times\Theta} r\varphi^2\right) - |B_R\setminus U_R|\times|\Theta|\left[\sup(|\nabla\varphi|+2\varphi)^2 + |r|\varphi^2\right]}{|U_R|\int_{\mathcal{C}\times\Theta}\varphi^2 + |B_R\setminus U_R|\times|\Theta|\sup\varphi^2},$$

where $|\cdot|$ stands for the volume. Therefore, since $\frac{|B_R\setminus U_R|}{|U_R|}\to 0$ as $R\to+\infty$, letting $R\to+\infty$ in the above expression yields

$$\lambda[r] = \lim_{R\to+\infty}\lambda_R^m \geqslant \frac{-\int_{\mathcal{C}\times\Theta}|\nabla\varphi|^2 + \int_{\mathcal{C}\times\Theta} r\varphi^2}{\int_{\mathcal{C}\times\Theta}\varphi^2},$$

and the right-hand side is equal to λ, thanks to the standard Rayleigh formula for λ (or even by direct computation, integrating by parts). Thus, by (i) we conclude $\lambda[r]\geqslant\lambda$. □

Let us turn to the case $\Theta = \mathbb{R}^P$. Using again the results from [33], we now show that the principal eigenvalue $\lambda[r]$ of $\mathcal{L}[r]$ coincides with the limit as $R\to+\infty$ of both the Dirichlet principal eigenvalue in the domain $B_{\mathbb{R}^{N+P}}(0,R)$, and the x-periodic principal eigenvalue in the domain $\mathbb{R}^N\times B_{\mathbb{R}^P}(0,R)$. These last two notions of principal eigenvalue are provided by the classical Krein-Rutman theory [145]. Namely, the eigenproblems

$$\begin{cases} \mathcal{L}[r]\varphi_R^d = \lambda_R^d\varphi_R^d & \text{in } B_{\mathbb{R}^{N+P}}(0,R),\\ \varphi_R^d = 0 & \text{over } \partial B_{\mathbb{R}^{N+P}}(0,R),\\ \varphi_R^d > 0 & \text{in } B_{\mathbb{R}^{N+P}}(0,R), \end{cases} \tag{5.16}$$

and

$$\begin{cases} \mathcal{L}[r]\varphi_R = \lambda_R\varphi_R & \text{in } \mathbb{R}^N\times B_{\mathbb{R}^P}(0,R),\\ \varphi_R = 0 & \text{over } \mathbb{R}^N\times\partial B_{\mathbb{R}^P}(0,R),\\ \varphi_R > 0 & \text{in } \mathbb{R}^N\times B_{\mathbb{R}^P}(0,R),\\ \varphi_R \text{ is 1-periodic in } x, \end{cases} \tag{5.17}$$

admit a unique eigenpair $(\lambda_R^d,\varphi_R^d)$ and (λ_R,φ_R) respectively (uniqueness for φ_R^d and φ_R is

understood up to a scalar multiple).

Proposition 5.4.2. *Assume $\Theta = \mathbb{R}^P$ and let r satisfy (5.7). Let $(\lambda_R^d, \varphi_R^d)$ and (λ_R, φ_R) be the eigenpairs of the problems (5.16) and (5.17) respectively.*

(i) The functions $R \mapsto \lambda_R^d$ and $R \mapsto \lambda_R$ are nondecreasing and satisfy

$$\lambda_R^d \to \lambda[r], \qquad \lambda_R \to \lambda[r], \qquad \text{as } R \to +\infty.$$

(ii) The principal eigenfunctions φ_R, normalised by $\varphi_R(0,0) = 1$, converge locally uniformly, as $R \to +\infty$, to a function $\varphi \in W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ satisfying the periodic principal eigenproblem

$$\begin{cases} \mathcal{L}[r]\varphi = \lambda\varphi & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi > 0 & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi \text{ is 1-periodic in } x. \end{cases}$$

Proof. On the one hand, [33, Proposition 4] implies that $\lambda_R^d \to \lambda[r]$ as $R \to +\infty$ and that $R \mapsto \lambda_R^d$ is nondecreasing. On the other hand, [33, Proposition 5] and its proof imply that $R \mapsto \lambda_R$ is nondecreasing and that there exist $\lambda \in \mathbb{R}$ and $\varphi \in W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ such that $\lambda_R \to \lambda$, $\varphi_R \to \varphi$ locally uniformly, and

$$\begin{cases} \mathcal{L}[r]\varphi = \lambda\varphi & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi > 0 & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi \text{ is 1-periodic in } x. \end{cases}$$

By [33, Proposition 6], we also have $\lambda = \lambda[r]$ [1] (in the notation of [33], $\lambda = -\lambda_{1,l}$ and $\lambda[r] = -\lambda_1$). This concludes the proof. □

Statements *(ii)* of Propositions 5.4.1 and 5.4.2 yield Proposition 5.2.3 in both cases Θ bounded and unbounded.

5.5 Long-time behaviour of the solution (Theorem 5.2.4)

We start with a technical lemma which, together with hypothesis (5.8), will allow us to translate the $L^1_{loc}(\Theta)$ convergence of u to 0 into $L^1(\Theta)$ convergence. This will be used to prove the extinction result in the case $\Theta = \mathbb{R}^P$ and, curiously, also the persistence property. In contrast with Harnack-type inequalities, the proof exploits the nonlinear term of the equation.

Lemma 5.5.1. *Let $\Theta = \mathbb{R}^P$ and let r satisfy (5.7)–(5.8). Let u solve (5.1)–(5.3) with $u_0 \in C^0(\mathbb{R}^N \times \overline{\Theta}) \cap L^\infty(\mathbb{R}^N; L^1(\Theta))$ nonnegative and not identically equal to 0. For given $t_0 \geqslant 0$ and $\tau, M > 0$, call*

$$H := \bar{r} \sup_{s \in (t_0, t_0+\tau),\, x \in \mathbb{R}^N} \int_{\|\sigma\| \leqslant M} u(s,x,\sigma)\, \mathrm{d}\sigma + \|\rho\|_\infty \sup_{x \in \mathbb{R}^N,\, \|\theta\| > M} r^+(x,\theta),$$

[1] We point out that although these results are stated in [33] for bounded potential r, the proofs rely on [32], which only requires r to be locally bounded, which is the case in our setting.

where $\bar r := \sup_{\mathbb{R}^N\times\mathbb{R}^P} r$, *and* $r^+ := \max\{r,0\}$ *denotes the positive part of* r. *Then it holds that*

$$\sup_{x\in\mathbb{R}^N} \rho(t_0+\tau,x) \leqslant \sqrt{H}\coth\left(\sqrt{H}\,\tau + \operatorname{arcoth}\left(\frac{\|\rho\|_\infty+\sqrt{H}}{\sqrt{H}}\right)\right). \tag{5.18}$$

Moreover, the expression at the right-hand side in (5.18) *is increasing with respect to* H, *for all* $\tau \geqslant 0$.

Proof. We recall that Theorem 5.2.1 ensures that both u and ρ are bounded. Take $t_0 \geqslant 0$, $\tau, M > 0$, and define H as in the statement of the lemma. As in the proof of Theorem 5.2.1, restricting to θ-independent test functions in the weak formulation (5.9), and using Fubini's theorem, one finds that the function ρ satisfies in the weak sense

$$\partial_t\rho = \Delta_x\rho + \int_{\mathbb{R}^P} r(x,\sigma)u(t,x,\sigma)\,\mathrm{d}\sigma - \rho^2, \qquad t>0,\ x\in\mathbb{R}^N. \tag{5.19}$$

For $t\in(t_0,t_0+\tau)$ and $x\in\mathbb{R}^N$, we see that

$$\partial_t\rho - \Delta_x\rho \leqslant \bar r\int_{\|\sigma\|\leqslant M} u(t,x,\sigma)\,\mathrm{d}\sigma + \|\rho\|_\infty \sup_{x\in\mathbb{R}^N,\ \|\theta\|>M} r^+(x,\theta) - \rho^2 \leqslant H - \rho^2.$$

Let V be the solution of $V' = H - V^2$, with initial datum $V(t_0) = \|\rho\|_\infty + \sqrt{H}$. We point out that $\coth' = 1-\coth^2$; thus

$$\forall t\geqslant 0,\quad V(t_0+t) = \sqrt{H}\coth\left(\sqrt{H}t + \operatorname{arcoth}\left(\frac{\|\rho\|_\infty+\sqrt{H}}{\sqrt{H}}\right)\right).$$

Moreover, $\rho(t_0,x)\leqslant V(t_0)$, so by the parabolic comparison principle, $\rho(t_0+t,x)\leqslant V(t_0+t)$ for $t\in[0,\tau]$ and $x\in\mathbb{R}^N$. The inequality (5.18) is proved.

Finally, Grönwall's inequality implies that V is strictly increasing with respect to H. The proof is concluded. □

Proof of Theorem 5.2.4, item 1. Assume that $\lambda[r]<0$. Let $\varphi>0$ be a generalised principal eigenfunction corresponding to $\lambda[r]$, i.e. a solution of (5.10). The function $e^{\lambda[r]t}\varphi(x,\theta)$ is 1-periodic in x and it is a positive solution of the linear equation

$$\partial_t v = \Delta_x v + \Delta_\theta v + r(x,\theta)v,$$

and additionally fulfils the boundary condition $\nu\cdot\nabla_\theta v = 0$ if Θ is bounded. The function u is a subsolution of the above equation. Moreover, since u_0 has a compact support in $\mathbb{R}^N\times\overline{\Theta}$, and $\varphi>0$ on $\mathbb{R}^N\times\overline{\Theta}$ (owing to the Hopf lemma in the case Θ bounded), there exists a large $a>0$ such that $a\varphi\geqslant u_0$. It follows from the comparison principle that $u(t,x,\theta)\leqslant ae^{\lambda[r]t}\varphi(x,\theta)$ for all $t\geqslant 0$, $(x,\theta)\in\mathbb{R}^N\times\Theta$. This concludes the proof in the case Θ bounded. When $\Theta=\mathbb{R}^P$, we deduce that $u(t,x,\theta)\to 0$ as $t\to+\infty$, uniformly in $x\in\mathbb{R}^N$ and locally uniformly in $\theta\in\mathbb{R}^P$. It then follows from Lemma 5.5.1 and assumption (5.8) that $\rho(t,x)\to 0$ as $t\to+\infty$, uniformly in $x\in\mathbb{R}^N$, which implies in turn, owing to the Harnack inequality, that $u(t,x,\theta)\to 0$ as $t\to+\infty$, uniformly in $\theta\in\mathbb{R}^P$ as well. □

Remark 5.5.2. The hypothesis that u_0 is compactly supported is only used in the above proof in order to ensure the inequality $a\varphi\geqslant u_0$ for large enough a. However, when Θ is

bounded, this property automatically holds because $\inf\varphi > 0$ due to the periodicity in x and the Hopf lemma. Thus, when Θ is bounded, the assumption that u_0 has compact support can be dropped. When $\Theta = \mathbb{R}^P$, again due to the periodicity in x of φ, the assumption that u_0 has compact support can be weakened to the existence of some $A > 0$ such that the support of u_0 is included in $\mathbb{R}^N \times B_{\mathbb{R}^P}(0, A)$.

We now turn to the proof of the persistence property. In this case we cannot neglect the nonlocal nonlinear term $-\rho u$, as we have done in the proof of extinction, so we need to handle it in some way, despite it prevents the validity of the maximum principle. We treat separately the case where Θ is bounded and the case where Θ is unbounded.

Proof of Theorem 5.2.4, item 2, when Θ is bounded. We consider a subset of times where ρ fulfils a suitable lower bound, namely:

$$\mathcal{T} := \left\{ t \in [1, +\infty) \ \ / \ \sup_{x \in \mathbb{R}^N} \rho(t, x) \geqslant \frac{\lambda[r]}{2} \right\}.$$

Of course, it may happen that $\mathcal{T} = \emptyset$. We first derive a lower bound for u on the set of times

$$\mathcal{T} + \{1\} := \{t + 1 \ / \ t \in \mathcal{T}\},$$

using the parabolic Harnack inequality; next we prove a lower bound for u for times outside

$$\mathcal{T} + [0, 1] := \{t + s \ / \ t \in \mathcal{T}, \ s \in [0, 1]\},$$

exploiting the principal eigenfunction; we finally derive a lower bound for ρ on $\mathcal{T} + [0, 1]$.

Step 1. Lower bound for u for on $\mathcal{T} + \{1\}$. By the definition of $\mathcal{T}$ and the positivity of $\lambda[r]$, for any $t \in \mathcal{T}$ there exists $x_t \in \mathbb{R}^N$ such that $\rho(t, x_t) \geqslant \lambda[r]/4$. Letting $|\Theta|$ denote the measure of Θ, one then deduces

$$\forall t \in \mathcal{T}, \quad \sup_{\theta \in \Theta} u(t, x_t, \theta) \geqslant \frac{\rho(t, x_t)}{|\Theta|} \geqslant \frac{\lambda[r]}{4|\Theta|}.$$

Therefore, by the Harnack inequality (5.13) derived before in the case Θ bounded, one infers that, for any $R > 0$, there exists $C_R > 0$ such that

$$\forall t \in \mathcal{T}, \quad \inf_{B_{\mathbb{R}^N}(x_t, R) \times \Theta} u(t + 1, \cdot, \cdot) \geqslant \frac{1}{C_R} \sup_{\Theta} u(t, x_t, \cdot) \geqslant \frac{\lambda[r]}{4 C_R |\Theta|}. \tag{5.20}$$

Step 2. Lower bound for u on $[1, +\infty) \setminus (\mathcal{T} + [0, 1])$. First of all, we derive an estimate similar to (5.20) at time 1. Namely, it follows from the parabolic strong maximum principle that $u(t, x, \theta) > 0$ for $t > 0$, $x \in \mathbb{R}^N$, $\theta \in \Theta$. Moreover, owing to the Hopf lemma, the Neumann boundary condition prevents u from vanishing on $\partial\Theta$. One deduces in particular that $u(1, x, \theta) > 0$ for $x \in \mathbb{R}^N$, $\theta \in \overline{\Theta}$. This, together with (5.20), implies that, for any $R > 0$, there exists $C'_R > 0$ such that

$$\forall t \in \mathcal{T} \cup \{0\}, \quad \inf_{B_{\mathbb{R}^N}(x_t, R) \times \Theta} u(t + 1, \cdot, \cdot) \geqslant C'_R, \tag{5.21}$$

where we can choose, for instance, $x_0 = 0$. Next, by Proposition 5.4.1 (and with the same notations), there exists $\bar{R} > 0$, such that $\lambda^m_{\bar{R}} > \lambda[r]/2$. It follows that the associated $\varphi^m_{\bar{R}}$, extended to 0 for $x \notin B_{\mathbb{R}^N}(0, \bar{R})$, is a generalised subsolution of the equation

$$\partial_t v = \Delta_x v + \Delta_\theta v + v\,(r(x,\theta) - \lambda[r]/2)\,, \tag{5.22}$$

and fulfils the Neumann boundary condition for $\theta \in \partial\Theta$. By periodicity, the same is true for any translation $\varphi^m_{\bar{R}}(\cdot - h, \cdot)$ with $h \in \mathbb{Z}^N$. We normalise $\varphi^m_{\bar{R}}$ by $\|\varphi^m_{\bar{R}}\|_\infty = 1$.

Consider now a time $t \in [1, +\infty) \setminus (\mathcal{T} + [0,1])$, that is, $t \geqslant 1$ and $(t-1, t) \cap \mathcal{T} = \emptyset$. Call

$$t_0 := \max\{s \leqslant t-1 \ / \ s \in \mathcal{T} \cup \{0\}\}.$$

On the one hand, we know from (5.21) that

$$\inf_{B_{\mathbb{R}^N}(x_{t_0}, \bar{R}+\sqrt{N}) \times \Theta} u(t_0 + 1, \cdot, \cdot) \geqslant C'_{\bar{R}+\sqrt{N}}.$$

On the other hand, taking $h \in \mathbb{Z}^N$ (depending on t_0) such that $x_{t_0} - h \in \mathcal{C} = [0,1]^N$, we have that the function $\varphi^m_{\bar{R}}(\cdot - h, \cdot)$ vanishes outside $B_{\mathbb{R}^N}(h, \bar{R}) \subset B_{\mathbb{R}^N}(x_{t_0}, \bar{R} + \sqrt{N})$ and therefore $C'_{\bar{R}+\sqrt{N}} \varphi^m_{\bar{R}}(\cdot - h, \cdot)$ lies below u at time $t_0 + 1$. Finally, since $(t_0 + 1, t) \cap \mathcal{T} = \emptyset$, it follows from the definition of $\mathcal{T}$ that u is a subsolution to (5.22) on $(t_0 + 1, t) \times \mathbb{R}^N \times \Theta$. We can then apply the parabolic comparison principle and infer that $C'_{\bar{R}+\sqrt{N}} \varphi^m_{\bar{R}}(\cdot - h, \cdot)$ lies below u for all times in $[t_0 + 1, t]$, hence in particular

$$\sup_{x \in \mathbb{R}^N} \left(\min_{\theta \in \overline{\Theta}} u(t, x, \theta) \right) \geqslant C'_{\bar{R}+\sqrt{N}} \min_{\theta \in \overline{\Theta}} \varphi^m_{\bar{R}}(0, \theta) > 0.$$

This immediately gives a uniform lower bound for $\sup_{x \in \mathbb{R}^N} \rho(\cdot, x)$ on $[1, +\infty) \setminus (\mathcal{T} + [0,1])$. Thus, in order to conclude the proof, it remains to get an estimate on $\mathcal{T} + [0,1]$.

Step 3. Lower bound for ρ on $\mathcal{T} + [0,1]$. Integrating with respect to θ the weak formulation (5.9), one ends up with the equation (5.19) for ρ. We rewrite it as

$$\partial_t \rho = \Delta_x \rho + \tilde{r}(t,x)\rho - \rho^2, \qquad t > 0,\ x \in \mathbb{R}^N,$$

where

$$\tilde{r}(t,x) := \frac{1}{\rho(t,x)} \int_\Theta r(x,\theta) u(t,x,\theta)\, \mathrm{d}\theta$$

satisfies $\inf r \leqslant \tilde{r} \leqslant \sup r$ (recall that r is bounded in the case Θ bounded). Standard parabolic estimates and Morrey's inequality then yield $\rho \in C^{0,\alpha}([1, +\infty) \times \mathbb{R}^N)$ (for any $\alpha \in (0,1)$). Hence ρ is uniformly continuous on $[1, +\infty) \times \mathbb{R}^N$.

Consider $t \in \mathcal{T}$ and, as in the Step 1, let x_t be such that $\rho(t, x_t) > \lambda[r]/4$. By the uniform continuity of ρ, there exists $\delta > 0$ independent of t such that, for all $t \in \mathcal{T}$, we have $\rho(t, \cdot) > \lambda[r]/8$ on $B_{\mathbb{R}^N}(x_t, \delta)$. Therefore, calling w the solution to

$$\partial_t w = \Delta_x w + (\inf r) w - w^2, \qquad t > 0,\ x \in \mathbb{R}^N,$$

with initial datum equal to $\lambda[r]/8$ on $B_{\mathbb{R}^N}(0,\delta)$ and 0 outside, we have that

$$\min_{s\in[t,t+1]} \rho(s,x_t) \geqslant \min_{s\in[0,1]} w(s,0),$$

which is positive due to the strong maximum principle, and independent of t. This is the uniform lower bound on $\mathcal{T}+[0,1]$ which concludes the proof. □

Proof of Theorem 5.2.4, item 2, when $\Theta=\mathbb{R}^P$. Owing to Lemma 5.5.1, we are able to prove the result following essentially the same strategy as in the case Θ bounded. However, several modifications are needed.

First of all, by the positivity of $\lambda[r]$ and hypothesis (5.8), there exists $M>0$ such that

$$r(x,\theta) < \frac{\lambda[r]^2}{8\|\rho\|_\infty} \qquad \text{for all } \ x\in\mathbb{R}^N,\ \|\theta\|\geqslant M \tag{5.23}$$

(recall that ρ is bounded, as well as u). We call as usual $\bar r := \sup r$. We then define

$$\mathcal{T} := \left\{ t\in[1,+\infty) \ \ / \ \sup_{x\in\mathbb{R}^N} \int_{\|\sigma\|\leqslant M} u(t,x,\sigma)\,\mathrm{d}\sigma \geqslant \frac{\lambda[r]^2}{8\bar r} \right\}.$$

As before, but in a slightly more general setting, we will derive a uniform lower bound for u on the set of times $\mathcal{T}+\{T\}$, depending on $T>0$. In contrast with the case Θ bounded, using a principal eigenfunction of the linearised operator, we will be able to obtain a lower bound for u outside $\mathcal{T}+[0,T]$ only for T sufficiently large. We will then conclude by an estimate for u on $\mathcal{T}+[0,T]$.

Step 1. Lower bound for u on $\mathcal{T}+\{T\}$, for $T>0$. For $t\in\mathcal{T}$, we take $x_t\in\mathbb{R}^N$ such that

$$\int_{\|\sigma\|\leqslant M} u(t,x_t,\sigma)\,\mathrm{d}\sigma \geqslant \frac{\lambda[r]^2}{16\bar r}.$$

We use the standard interior Harnack inequality which gives, for any $T,R>0$, a constant $C_{T,R}>0$ such that

$$\forall t\in\mathcal{T},\qquad \sup_{B_{\mathbb{R}^P}(0,R)} u(t,x_t,\cdot) \leqslant C_{T,R} \inf_{B_{\mathbb{R}^{N+P}}((x_t,0),R)} u(t+T,\cdot,\cdot).$$

One then finds, for $R\geqslant M$,

$$\begin{aligned}
\forall t\in\mathcal{T},\qquad \inf_{B_{\mathbb{R}^{N+P}}((x_t,0),R)} u(t+T,\cdot) &\geqslant \frac{1}{C_{T,R}} \sup_{B_{\mathbb{R}^P}(0,R)} u(t,x_t,\cdot) \\
&\geqslant \frac{1}{C_{T,R}} \sup_{B_{\mathbb{R}^P}(0,M)} u(t,x_t,\cdot) \\
&\geqslant \frac{1}{C_{T,R}|B_{\mathbb{R}^P}(0,M)|} \int_{\|\sigma\|\leqslant M} u(t,x_t,\sigma)\,\mathrm{d}\sigma \\
&\geqslant \frac{\lambda[r]^2}{16\bar r C_{T,R}|B_{\mathbb{R}^P}(0,M)|}.
\end{aligned}$$

Step 2. Lower bound for u on $[T,+\infty)\setminus(\mathcal{T}+[0,T])$, for T sufficiently large. Consider an arbitrary quantity $T>0$, that we will fix later. We start by deriving a lower bound for u at time T. This is simply given by the parabolic strong maximum principle, which ensures that $u>0$ on $(0,+\infty)\times\mathbb{R}^N\times\mathbb{R}^P$. Thus, owing to Step 1, we deduce that for any $T>0$ and $R\geqslant M$, there exists $C'_{T,R}>0$ such that

$$\forall t\in\mathcal{T}\cup\{0\},\qquad \inf_{B_{\mathbb{R}^{N+P}}((x_t,0),R)} u(t+T,\cdot,\cdot)\geqslant C'_{T,R}, \tag{5.24}$$

where we have set, say, $x_0:=0$.

Next, by Proposition 5.4.2 there exists $\bar{R}\geqslant M$ such that $\lambda^d_{\bar{R}}>3\lambda[r]/4$. It follows that the associated $\varphi^d_{\bar{R}}$, extended to 0 outside $B_{\mathbb{R}^{N+P}}(0,\bar{R})$, is a generalised subsolution of the equation

$$\partial_t v=\Delta_x v+\Delta_\theta v+v\,(r(x,\theta)-3\lambda[r]/4)\,. \tag{5.25}$$

By periodicity, the same is true for each of its translations $\varphi^d_{\bar{R}}(\cdot-h,\cdot)$ by $h\in\mathbb{Z}^N$. We normalise $\varphi^d_{\bar{R}}$ by $\|\varphi^d_{\bar{R}}\|_\infty=1$.

Consider now a time $t\in[T,+\infty)\setminus(\mathcal{T}+[0,T])$, that is, $t\geqslant T$ and $(t-T,t]\cap\mathcal{T}=\emptyset$. Call

$$t_0:=\max\{s\leqslant t-T\ /\ s\in\mathcal{T}\cup\{0\}\}.$$

On the one hand, we know from (5.24) that

$$\inf_{B_{\mathbb{R}^{N+P}}((x_{t_0},0),\bar{R}+\sqrt{N})} u(t_0+T,\cdot,\cdot)\geqslant C'_{T,\bar{R}+\sqrt{N}}.$$

On the other hand, taking $h\in\mathbb{Z}^N$ (depending on t_0) such that $x_{t_0}-h\in\mathcal{C}=[0,1]^N$, we have that the function $\varphi^d_{\bar{R}}(\cdot-h,\cdot)$ vanishes outside $B_{\mathbb{R}^{N+P}}((h,0),\bar{R})\subset B_{\mathbb{R}^{N+P}}((x_{t_0},0),\bar{R}+\sqrt{N})$. It follows that $C'_{T,\bar{R}+\sqrt{N}}\varphi^d_{\bar{R}}(\cdot-h,\cdot)$ lies below u at time t_0+T.

Finally, in order to compare $C'_{T,\bar{R}+\sqrt{N}}\varphi^d_{\bar{R}}(\cdot-h,\cdot)$ with u at time t, we now show that if $T>0$ is chosen large enough, then u is a supersolution to (5.25) on $[t_0+T,t]\times\mathbb{R}^N\times\mathbb{R}^P$. Take any $\tau\in[T,t-t_0]$. We apply estimate (5.18) from Lemma 5.5.1. We recall that the expression at the right-hand side there is increasing with respect to H. In the present case, H is bounded from above by $\lambda[r]^2/4$, thanks to (5.23) and the definition of $\mathcal{T}$ (we have indeed $(t_0,t_0+\tau)\subset(t_0,t)$, which does not intersect $\mathcal{T}$). This shows that

$$\sup_{x\in\mathbb{R}^N}\rho(t_0+\tau,x)\leqslant\frac{\lambda[r]}{2}\coth\left(\frac{\lambda[r]}{2}\tau+\operatorname{arcoth}\left(\frac{2\|\rho\|_\infty+\lambda[r]}{\lambda[r]}\right)\right).$$

Choosing T large enough so that $\coth(\lambda[r]T/2)\leqslant 3/2$, the above estimate yields

$$\forall\tau\in[T,t-t_0],\qquad \rho(t_0+\tau,\cdot)\leqslant 3\lambda[r]/4,$$

which implies in turn that u is a supersolution to (5.25) on $[t_0+T,t]\times\mathbb{R}^N\times\mathbb{R}^P$.

We can then apply the parabolic comparison principle and infer that $C'_{T,\bar{R}+\sqrt{N}}\varphi^d_{\bar{R}}(\cdot-h,\cdot)$ lies below u on $[t_0+T,t]\times\mathbb{R}^N\times\mathbb{R}^P$, whence in particular

$$\sup_{x\in\mathbb{R}^N}\left(\inf_{\theta\in B_{\mathbb{R}^P}(0,R/2)}u(t,x,\theta)\right)\geqslant C'_{\bar{R}+\sqrt{N}}\inf_{\theta\in B_{\mathbb{R}^P}(0,R/2)}\varphi^d_{\bar{R}}(0,\theta)>0.$$

This is the uniform lower bound for $\sup_{x\in\mathbb{R}^N}\rho(\cdot,x)$ on $[T,+\infty)\setminus(\mathcal{T}+[0,T])$.

Step 3. Lower bound for u on $\mathcal{T}+[0,T]$. Consider $t\in\mathcal{T}$. Let x_t be as in the Step 1 and let $\theta_t\in\mathbb{R}^P$ be such that $\|\theta_t\|\leqslant M$ and

$$u(t,x_t,\theta_t)=\max_{\|\theta\|\leqslant M}u(t,x_t,\theta).$$

Then one has

$$u(t,x_t,\theta_t)\geqslant\frac{1}{|B_{\mathbb{R}^P}(0,M)|}\int_{\|\sigma\|\leqslant M}u(t,x_t,\sigma)\,\mathrm{d}\sigma\geqslant\frac{\lambda[r]^2}{8\bar{r}|B_{\mathbb{R}^P}(0,M)|}.$$

In the equation in (5.1), the term ρ is globally bounded and $r(x,\theta)$ is bounded uniformly in $x\in\mathbb{R}^N$ and locally uniformly in $\theta\in\mathbb{R}^P$, so, due to interior parabolic estimates, the function u is uniformly continuous on $[1,+\infty)\times\mathbb{R}^N\times B_{\mathbb{R}^P}(0,M)$. Therefore, there exists $\delta>0$ independent of t such that

$$\inf_{B_{\mathbb{R}^{N+P}}((x_t,\theta_t),\delta)}u(t,\cdot,\cdot)\geqslant\frac{\lambda[r]^2}{16\bar{r}|B_{\mathbb{R}^P}(0,M)|}.$$

(We point out that the centre of the ball (x_t,θ_t) does depend on t.) In order to translate this lower bound into an estimate which holds on the time interval $[t,t+T]$ and which is independent of t, we need to be careful due to the possible unboundedness of r. We circumvent this difficulty by considering the solution w to the Dirichlet problem

$$\begin{cases}\partial_t w=\Delta_x w+w\left(\inf\limits_{\mathbb{R}^N\times B_{\mathbb{R}^P}(0,M+\delta)}r-\|\rho\|_\infty\right) & \text{in } (0,+\infty)\times B_{\mathbb{R}^{N+P}}(0,\delta),\\ w=0 & \text{over } (0,+\infty)\times\partial B_{\mathbb{R}^{N+P}}(0,\delta),\end{cases}$$

with initial datum equal to $\frac{\lambda[r]^2}{16\bar{r}|B_{\mathbb{R}^P}(0,M)|}$. Observe that for $(x,\theta)\in B_{\mathbb{R}^{N+P}}(0,\delta)$ it holds that $(x+x_t,\theta+\theta_t)\in\mathbb{R}^N\times B_{\mathbb{R}^P}(0,M+\delta)$, hence the function $u(\cdot+t,\cdot+x_t,\cdot+\theta_t)$ is a supersolution of the above problem, and moreover it lies above w at time 0. It follows that

$$\min_{[t,t+T]\times B_{\mathbb{R}^{N+P}}(0,\delta/2)}u(\cdot,\cdot+x_t,\cdot+\theta_t)\geqslant\min_{[0,T]\times B_{\mathbb{R}^{N+P}}(0,\delta/2)}w,$$

for any $T>0$, and in particular for the value of T provided by the Step 2. By the strong maximum principle, the right-hand side is a positive number. This is the estimate on the set of times $\mathcal{T}+[0,T]$ concluding the proof. □

5.6 Dependence of the principal eigenvalue on the spatial period and on the mobility (Proposition 5.2.5)

We recall that r^L stands for the L-periodic version of r, i.e.,

$$r^L(x,\theta):=r\left(\frac{x}{L},\theta\right).$$

Proof of Proposition 5.2.5. Let us start with the statement (i) of the proposition. We first consider the case $\Theta = \mathbb{R}^P$. For $L > 0$, we let $\mathcal{C}^L := [0, L]^N$ denote the periodic cell of size L. For $R > 0$, we call for short $B_R := B_{\mathbb{R}^P}(0, R)$ the ball of $\mathbb{R}^P$ with radius R and centre 0. We let $(\varphi_R^L, \lambda_R^L)$ satisfy the periodic eigenproblem analogous to (5.17), but with L-periodicity instead of 1-periodicity, that is,

$$\begin{cases} \mathcal{L}[r^L]\varphi_R^L = \lambda_R^L \varphi_R^L & \text{in } \mathbb{R}^N \times B_R, \\ \varphi_R^L = 0 & \text{over } \mathbb{R}^N \times \partial B_R, \\ \varphi_R^L > 0 & \text{in } \mathbb{R}^N \times B_R, \\ \varphi_R^L & \text{is } L\text{-periodic in } x, \end{cases}$$

with the normalisation $\left\|\varphi_R^L\right\|_{L^2(\mathcal{C}^L \times B_R)} = 1$. Take $L, L' > 0$. We make now use of the Rayleigh formula for $\lambda_R^{L'}$ in order to estimate it in terms of λ_R^L. The Rayleigh formula, which is classical in the present case because the eigenfunctions act on a compact set (due to the x-periodicity), implies that

$$\lambda_R^{L'} \geqslant \left[-\int_{\mathcal{C}^{L'} \times B_R} |\nabla \phi|^2 + \int_{\mathcal{C}^{L'} \times B_R} \phi^2 r^{L'} \right] \left(\int_{\mathcal{C}^{L'} \times B_R} \phi^2 \right)^{-1},$$

for any function $\phi \in W_2^1(\mathcal{C}^{L'} \times B_R) \cap C^0(\mathbb{R}^N \times \overline{B_R})$ which is L'-periodic in x and vanishes on $\mathbb{R}^N \times \partial B_R$. We call $h(x, \theta) := (\frac{L}{L'} x, \theta)$ and we take $\phi = \varphi_R^L \circ h$ (which is L'-periodic) in the formula. This gives:

$$\begin{aligned} \lambda_R^{L'} \geqslant \left[-\int_{\mathcal{C}^{L'} \times B_R} \left(\left(\frac{L}{L'} \right)^2 \left| \nabla_x \varphi_R^L \right|^2 \circ h + \left| \nabla_\theta \varphi_R^L \right|^2 \circ h \right) + \int_{\mathcal{C}^{L'} \times B_R} (\varphi_R^L \circ h)^2 r^{L'} \right] \\ \times \left(\int_{\mathcal{C}^{L'} \times B_R} (\varphi_R^L \circ h)^2 \right)^{-1}. \end{aligned}$$

By the change of variables $(x', \theta') = h(x, \theta)$, we obtain, since $\left\|\varphi_R^L\right\|_{L^2(\mathcal{C}^L \times B_R)} = 1$:

$$\begin{aligned} \lambda_R^{L'} &\geqslant -\int_{\mathcal{C}^L \times B_R} \left(\left(\frac{L}{L'} \right)^2 \left| \nabla_x \varphi_R^L \right|^2 + \left| \nabla_\theta \varphi_R^L \right|^2 \right) + \int_{\mathcal{C}^L \times B_R} (\varphi_R^L)^2 r^L \\ &= \lambda_R^L + \left(1 - \left(\frac{L}{L'} \right)^2 \right) \int_{\mathcal{C}^L \times B_R} \left| \nabla_x \varphi_R^L \right|^2. \end{aligned}$$

Hence, for $L' > L$, we have $\lambda_R^{L'} > \lambda_R^L$, that is, $L \mapsto \lambda_R^L$ is increasing for all $R > 0$. Since by Proposition 5.4.2 (i) (which holds true with 1-periodicity replaced by L-periodicity) we have that $\lambda_R^L \to \lambda[r^L]$ as $R \to +\infty$, it follows that $L \mapsto \lambda[r^L]$ is nondecreasing.

Let us now prove that $L \mapsto \lambda[r^L]$ is continuous. We have shown before that

$$\lambda_R^L - \lambda_R^{L'} \leqslant \left(\left(\frac{L}{L'} \right)^2 - 1 \right) \int_{\mathcal{C}^L \times B_R} \left| \nabla_x \varphi_R^L \right|^2,$$

therefore it will suffice to derive a bound for $\|\nabla_x \varphi_R^L\|_{L^2(\mathcal{C}^L \times B_R)}$ which is locally uniform with respect to $L > 0$ and uniform with respect to $R \geqslant 1$. This follows by integrating on $\mathcal{C}^L \times B_R$ the equation satisfied by φ_R^L multiplied by φ_R^L itself. Namely, recalling that $\left\|\varphi_R^L\right\|_{L^2(\mathcal{C}^L \times B_R)} = 1$,

one gets

$$\int_{\mathcal{C}^L\times B_R}\left|\nabla_x\varphi_R^L\right|^2=\int_{\mathcal{C}^L\times B_R}(r^L-\lambda_R^L)(\varphi_R^L)^2\leqslant\left(\sup r-\lambda_R^L\right).$$

Then, since λ_R^L is increasing with respect to R by Proposition 5.4.2 (i), and it is nondecreasing with respect to L, as we showed before, we find, for any given $L_0>0$,

$$\forall R\geqslant 1,\ \forall L,L'\geqslant L_0,\qquad \lambda_R^L-\lambda_R^{L'}\leqslant\left|\left(\frac{L}{L'}\right)^2-1\right|\left(\sup r-\lambda_1^{L_0}\right).$$

Passing to the limit as $R\to+\infty$ we derive the same inequality for the difference $\lambda[r^L]-\lambda[r^{L'}]$, which yields the continuity of $L\mapsto\lambda[r^L]$.

Let us consider now the case where Θ is a smooth bounded subset of $\mathbb{R}^P$. The generalised principal eigenvalue $\lambda[r^L]$ coincides now with the principal eigenvalue of the Neumann problem on $\mathbb{R}^N\times\Theta$, under L-periodicity condition in x, which is then a standard compact setting. We let φ^L denote the (unique up to a scalar multiple) corresponding principal eigenfunction, provided by Proposition 5.4.1 (ii). Again, the Rayleigh formula is classical in such a framework. It implies

$$\lambda[r^{L'}]\geqslant\left[-\int_{\mathcal{C}^{L'}\times\Theta}|\nabla\phi|^2+\int_{\mathcal{C}^{L'}\times\Theta}\phi^2r^{L'}\right]\left(\int_{\mathcal{C}^{L'}\times\Theta}\phi^2\right)^{-1},$$

for any function $\phi\in W_2^1(\mathcal{C}^{L'}\times\Theta)$ which is L'-periodic in x. Taking $\phi=\varphi^L\circ h$, with the same function h as above, one infers in the same way that $L\mapsto\lambda[r^L]$ is continuous and nonincreasing.

Therefore, item (i) is proved in both cases Θ bounded or $\Theta=\mathbb{R}^P$.

Let us now prove item (ii). For a x-periodic function $\phi(x,\theta)$, we let $\phi^L(x,\theta):=\phi(x/L,\theta)$ be its L-periodic version. We have

$$\left(\mathcal{L}[r^L]\phi^L\right)(Lx,\theta)=\left(\mathcal{L}_{L^{-2}}[r]\right)\phi(x,\theta).$$

It then follows from Definition 5.2.2 that the eigenvalue $\lambda_d[r]$ associated with the operator $\mathcal{L}_d[r]$ satisfies

$$\lambda_d[r]=\lambda[r^{d^{-1/2}}].$$

Thus, item (ii) is a consequence of item (i).

□

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Chapter 6

Optimisation of the ability of persistence

This chapter is based on the work [50]:

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Abstract

In this chapter, we consider a nonlocal reaction-diffusion equation that models a population structured in space and in phenotype. We assume that the population lives in a heterogeneous environment, so that the same individual may be more or less fit according to its spatial position. In Chapter 5, which was motivated by the present chapter, we gave a criterion for the persistence of the population, based on the principal eigenvalue of an elliptic operator. We now give, in a particular case involving the Fisher Geometric Model, some optimisation results about the shape that the environment should take to make persistence as hard or as easy as possible.

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6.1 Introduction

We focus on a classical reaction-diffusion equation of the Fisher-KPP type, enriched by two features: spatial heterogeneity of the environment and phenotypical structure of the population. In Chapter 5, we proved the well-posedness of our model and gave a criterion for the persistence of the population. This work is a follow-up of Chapter 5, and our goal is to give optimisation results on the criterion for persistence.

Let us describe the model of Chapter 5 that we will study here. We consider a function $u(t,x,\theta)$ representing the density at time t of a population structured in space (x-variable) and in phenotype (θ-variable). The domain of the spatial variable is the whole space $\mathbb{R}^N$, $N \in \mathbb{N}$, and the domain of the phenotype is $\mathbb{R}^P$, $P \in \mathbb{N}$. (Contrarily to Chapter 5, we do not consider bounded Θ here.)

Our model is

$$\partial_t u = \Delta_x u + \Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), \quad t > 0, (x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P, \tag{6.1}$$

with

$$\rho(t,x) := \int_{\mathbb{R}^P} u(t,x,\sigma)\,\mathrm{d}\sigma. \tag{6.2}$$

We supplement the problem (6.1)–(6.2) with an initial condition

$$u(0,x,\theta) = u_0(x,\theta), \qquad (x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P. \tag{6.3}$$

The nonlocal term $\rho(t,x)$ represents the total population at a given time and location. The value $r(x,\theta)$ corresponds to the fitness of an individual of phenotype θ at location x, in the absence of competition. We refer to r as the *space/phenotype fitness landscape*. We will assume that r is periodic in the spatial variable x. Below, we shall make more specific assumptions on r, namely, we shall assume that r has the form of a *patchwork-like* space/phenotype fitness landscape.

Equation (6.1) is a variant of the Fisher-KPP equation, which was independently introduced in 1937 by Fisher [94] and Kolmogorov, Petrovsky and Piskunov [143]:

$$\partial_t u(t,x) = \Delta_x u + ru - u^2, \tag{6.4}$$

for a positive constant r. A motivation for (6.4) comes from biology: if u is the distribution of a population living on $\mathbb{R}$, then $\Delta_x u$ stands for the movements of individuals, the term ru stands for the demography in the absence of interactions, and the nonlinear term $-u^2$ encodes the competition pressure.

Compared with the classical Fisher-KPP equation, the equation in (6.1) displays the new variable $\theta \in \mathbb{R}^P$, describing the *phenotype* of the individuals. Then, all individuals located at the same position compete with each other, regardless of their phenotypes. Thus, the nonlinear term $-u^2$ is replaced with the nonlocal term $-\rho u$. Finally, we add a term $\Delta_\theta u$, to account for mutations (which induce variations in phenotype); this modelling means that mutations are small and frequent.

Models similar to (6.1) appeared for the first time in the work of Prévost [194], and as large population limits of individual-based models studied by Champagnat and Méléard [61]. Later, models similar to (6.1) have been studied in [3, 4, 9, 30, 44, 45, 151, 187]. Different equations, but with the same idea of space and population structure behind, have been studied in [109, 110, 115] (continuous space, discrete phenotype) and in [8, 118] (discrete space,

continuous phenotype). See the introduction of Chapter 5 for a more thorough bibliographical survey.

Let us now describe the particular form of the space/phenotype-fitness landscape $r(x,\theta)$ that we will study here.

A patchwork-like space/phenotype-fitness landscape. A widespread way to model the genetic adaptation of a population to environmental conditions is the Fisher Geometric Model (FGM), see [93, 162]. This model is characterised by a fitness function r_0 having a single maximum at $O \in \mathbb{R}^P$ and decaying as the phenotype θ moves away from the optimum O. Typically, one may take as in [214]:

$$r_0(\theta) = \chi(\|O-\theta\|),$$

with $\chi(R) = -a\,|R|^d$, for some $a, d > 0$ and fixed $O \in \mathbb{R}^P$. The function χ encodes how fitness is affected by the distance of the phenotype θ from the optimum O.

One may also consider situations where the optimum O depends on the environmental conditions. The present work is devoted to the study of a version of the FGM in which the environment is composed of a patchwork of regions, each one characterised by a fittest optimum O. More precisely, we consider a fitness landscape $r(x,\theta)$ which is 1-periodic in the x variable. We assume that the periodicity cell $\mathcal{C} := [0,1]^N$ is divided into a finite number of patches $\mathcal{C}_1, \dots, \mathcal{C}_K$, which are measurable sets, with positive measures, forming a partition of $\mathcal{C}$, and that to each patch $\mathcal{C}_i$ there corresponds an optimal phenotype $O_i \in \mathbb{R}^P$. The space/phenotype-fitness landscape function is then $r : \mathbb{R}^N \times \mathbb{R}^P \to \mathbb{R}$ satisfying

$$r(x,\theta) := \begin{cases} \chi(\|\theta - O_1\|) & \text{if } x \in \mathcal{C}_1, \\ \quad\vdots & \\ \chi(\|\theta - O_K\|) & \text{if } x \in \mathcal{C}_K, \end{cases} \tag{6.5}$$

and extended periodically to all $x \in \mathbb{R}^N$.

Jointly with (6.5), we will always assume that $\chi : [0,+\infty) \to \mathbb{R}$ satisfies

$$\begin{cases} \chi \in L^\infty_{loc}([0,+\infty)), & \chi \text{ is globally bounded from above,} \\ \text{There exists } \sigma > 0 \text{ such that } \chi(R)e^{-\sigma R} \to 0 \text{ as } R \to +\infty. \end{cases} \tag{6.6}$$

For our monotonicity results, we will also need:

$$\chi \text{ is decreasing on } [0,+\infty). \tag{6.7}$$

Here, χ represents the decay of the fitness when the phenotype moves away from the optimum. Further, for the persistence result, we assume that

$$\chi_\infty := \lim_{R\to+\infty} \chi(R) \leqslant 0. \tag{6.8}$$

We emphasise that we might have $\chi_\infty = -\infty$. With this construction, r satisfies the assumption used in Chapter 5. We point out that the assumption $\chi_\infty \leqslant 0$ comes from Chapter 5, where it is needed for the persistence result (Theorem 6.2.2), but no proof in the present chapter uses it.

We will sometimes denote the function r by $r[O_1, \dots, O_K]$ in order to stress its dependence

on the optimal phenotypes $O_1, \dots, O_K \in \mathbb{R}^P$ (the patches $\mathcal{C}_i$ being fixed).

With the patchwork landscape described by (6.5), our model is reminiscent of the models studied in [8, 118], which are discrete in space. In those models, the population is structured in phenotype and lives on two [118] or three [8] patches, with a possibility of jumping from one to another. The relation between the fitness and the phenotype of an individual is described by a particular Fisher geometric setting, encoded by the function χ: each patch has an optimal phenotype and the fitness decreases *quadratically* as the phenotype goes away from this optimum (we do not make such an assumption here). Hence, when an individual jumps from one patch to another, it may have to mutate in order to be adapted to its new environment. In particular, these papers study – as we will do – how the ability of persistence depends on the relative positions of the optima.

Biological interpretation. The biological situation that one can bear in mind is the following. Consider a crop pathogen living on a patchwork of fields. Each field $\mathcal{C}_i$ is planted with one crop variety i, on which the optimal phenotype for the pathogen is O_i. See Figure 6.1 for a schematic representation. With the above notations, K is the number of crop varieties, P is the dimension of the phenotypic space, and N is the dimension of the fields (from the point of view of modelling, it is only relevant to consider $N \in \{1, 2\}$). Our problem is then seen from an agroecological perspective: one of the goals of agroecology is indeed to use landscape heterogeneity as a tool to protect cultures from pathogens [40, 58]. In view of this application, the following questions arise:

1. Under which conditions does the pathogen persist?
2. How to arrange the fields $\mathcal{C}_i$ and the corresponding optima O_i so that the persistence is as difficult as possible?

We dealt with the first question in the companion chapter. Our current goal is to deal with the second question.

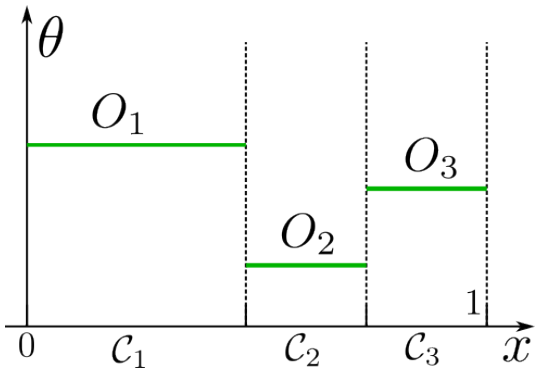

Figure 6.1: Representation of the patchwork landscape (6.5) with $N = P = 1$ and $K = 3$. Here, $\mathcal{C}_1$, $\mathcal{C}_2$, $\mathcal{C}_3$ represent three 1-dimensional fields, each one planted with a different variety, then repeated periodically. On each field $\mathcal{C}_i$, the pathogen has an optimal phenotype $O_i \in \mathbb{R}$.

Layout. First, in Section 6.2, we recall the results of the companion chapter. Next, in Section 6.3, we present our main results: in Subsection 6.3.2, we give asymptotic results as the period of the environment goes to 0 or to $+\infty$; in Subsection 6.3.3, we give monotonicity

properties of the ability of persistence as the optima O_i move in $\mathbb{R}^P$; and in Subsection 6.3.4, we give optimisation results that address the second question asked above. In Section 6.4, we derive some estimates on the principal eigenvalue $\lambda[r]$ and on an associated principal eigenfunction. Last, Sections 6.5 and 6.6 are devoted to the proofs of our results.

6.2 Summary of the results of Chapter 5

Well-posedness and regularity. Theorem 2.1 in Chapter 5 implies that for a bounded and nonnegative initial condition $u_0 \in C^0(\mathbb{R}^N \times \mathbb{R}^P) \cap L^\infty(\mathbb{R}^N; L^1(\mathbb{R}^P))$, the problem (6.1)–(6.3) has a unique strong solution $u \in W^{1,2}_{p,loc}((0,+\infty) \times \mathbb{R}^N \times \mathbb{R}^P)$ (for all $p > 1$) such that u and ρ are globally bounded. Here and in the sequel, $W^{1,2}_{p,loc}$ is the set of functions that belong to L^p_{loc} together with their first order derivative with respect to t and their partial derivatives up to order 2 with respect to (x, θ). In particular, Morrey's inequality implies that solutions are continuous.

Criterion for persistence. Following Chapter 5, we call $\mathcal{L}[r]$ the linearised operator associated with (6.1), that is

$$\mathcal{L}[r]\phi := \Delta_x \phi + \Delta_\theta \phi + r(x,\theta)\phi.$$

We then define the generalised principal eigenvalue of $\mathcal{L}[r]$.

Definition 6.2.1. *The (generalised) principal eigenvalue of* $\mathcal{L}[r]$ *is*

$$\lambda[r] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ \mathcal{L}[r]\phi \leqslant \lambda\phi \ \textit{in}\ \mathbb{R}^N \times \mathbb{R}^P\right\}.$$

Here, and throughout the chapter, the functions ϕ are understood to belong to $W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ for some $p > 1 + N + P$ (in particular they are of class C^1 by Morrey's embedding).

We point out that the domain of the functions on which the operator acts is not compact, since $\mathbb{R}^P$ is unbounded and the test functions ϕ are not assumed to be periodic in x. This results in a lack of compactness, which prevents one from using the classical Krein-Rutman theory. Still, it turns out that $\lambda[r]$ is a real number and that it is indeed a *generalised principal eigenvalue* for the operator $\mathcal{L}[r]$ acting on spatially-periodic functions, namely, there exists φ solution of

$$\begin{cases} \mathcal{L}[r]\varphi(x,\theta) = \lambda[r]\varphi(x,\theta), & (x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi(x,\theta) > 0, & (x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi \text{ is 1-periodic in } x. \end{cases} \tag{6.9}$$

Nevertheless, $\lambda[r]$ is not the unique value for which $\mathcal{L}[r]$ admits a positive periodic eigenfunction, but actually, any $\lambda \geqslant \lambda[r]$ does. Moreover, none of these eigenvalues is simple, in general. We call *any* solution φ of (6.9) a *principal eigenfunction* of $\mathcal{L}[r]$.

Making use of some results regarding the generalised principal eigenvalue, we were able in Chapter 5 to establish the "standard" extinction/persistence dichotomy for the the long-time behaviour of the solution for our model.

Theorem 6.2.2 (Theorem 2.4 in Chapter 5)**.** *Let* (6.5)–(6.8) *hold. Assume that* $u_0 \in C^0(\mathbb{R}^N \times \mathbb{R}^P) \cap L^\infty(\mathbb{R}^N; L^1(\mathbb{R}^P))$ *is nonnegative, not identically equal to* 0 *and has a compact support. Let* u *solve* (6.1)–(6.3)*.*

- *If $\lambda[r] < 0$ then the population gets extinct, in the sense that*

$$\lim_{t\to+\infty} u(t,x,\theta) = 0 \quad \textit{uniformly in } (x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P;$$

- *If $\lambda[r] > 0$, then the population persists, in the sense that*

$$\liminf_{t\to+\infty} \left[\sup_{x\in\mathbb{R}^N} \rho(t,x) \right] > 0.$$

We point out that the persistence property in the case $\lambda[r] > 0$ does not provide us with a precise description of the long-time behaviour of the solution, but it only means that it stays bounded from below away from zero. See the conclusion for more discussion on this point.

6.3 Main results

Thanks to the criterion given by Theorem 6.2.2, it is reasonable to dub the principal eigenvalue $\lambda[r]$ the "ability of persistence" of the species. Then, optimisation problems for the persistence of the species reduce to the optimisation of $\lambda[r]$ with respect to the spatial configuration of the fitness landscape. The point of view of modelling can help us to frame the results that follow. They are in fact an incarnation of the following ecological intuition:

The more homogeneous is the environment, the easier is the persistence of the species.
"More homogeneous" roughly means that the fluctuations of the landscape function are milder.

Problematic of this work. We devote particular attention to the dependence of the principal eigenvalue $\lambda[r]$ on the size of the periodicity cell, as well as on the location of the optima $O_1, \dots, O_K \in \mathbb{R}^P$. For the former, we derive both a homogenisation and a large scale limit, i.e. a rapidly and a slowly varying environment. For the latter, according to the ecological intuition illustrated above, it should hold that the closer the optima $O_1, \dots, O_K$ are to each other, the easier it is for the population to persist. Our Theorem 6.3.9 goes indeed in that direction, namely, the configuration maximising λ is the one with all points O_i coinciding. However, if one wants to compare two given configurations, then the notion of "being closer to each other" should be specified. At least, one can ask the following.

Question 4. *Given two configurations $O_1, O_2 \dots, O_K$ and $\widehat{O}_1, O_2 \dots, O_K$ satisfying*

$$\left\| \widehat{O}_1 - O_i \right\| \leqslant \|O_1 - O_i\| \quad \textit{for all } i = 2, \dots, K,$$

is it true that

$$\lambda[r[\widehat{O}_1, O_2 \dots, O_K]] \geqslant \lambda[r[O_1, O_2 \dots, O_K]] \ ?$$

We are able to answer this question in the affirmative when the number of patches is not too large, and precisely when $K \leqslant P$ (see Theorem 6.3.7 below).

Given the biological application that we have in mind, our goal would be to minimise $\lambda[r]$ with respect to $O_1, \dots, O_K$. We will show that there is no global minimiser (Proposition 6.3.10). Questions of minimisation under constraints, therefore, are natural.

Question 5. *How to minimise $\lambda[r[O_1, \dots, O_K]]$ among all configurations that satisfy $\|O_i - O_j\| \leqslant D$ for all $i, j = 1, \dots, K$?*

In Theorem 6.3.11, we will answer the above question if the number of optima is not too large (precisely, if $K \leqslant \min(5, P+1)$).

All in all, the results in the present chapter always give an affirmative answer to the following question, which is more ambitious than Question 4.

Question 6. *Given two configurations $O_1, O_2 \ldots, O_K$ and $\widehat{O}_1, \widehat{O}_2 \ldots, \widehat{O}_K$ satisfying*

$$\left\|\widehat{O}_i - \widehat{O}_j\right\| \leqslant \|O_i - O_j\| \quad \textit{for all } i,j = 2,\ldots,K,$$

is it true that

$$\lambda[r[\widehat{O}_1, \widehat{O}_2 \ldots, \widehat{O}_K]] \geqslant \lambda[r[O_1, O_2 \ldots, O_K]] \ ?$$

Before answering these questions, let us state and comment some additional hypotheses that we will need throughout our work.

6.3.1 Additional hypotheses

To prove our main monotonicity result, we will need the following technical assumption:

$$\chi \in C^2([0,+\infty)), \quad \chi'(0) = 0 \quad \text{and for every } \eta > 0,\ R \mapsto \chi''(R)e^{-\eta R} \text{ is bounded.} \quad (6.10)$$

We will also need the principal eigenfunction to decay as $\|\theta\| \to +\infty$. According to [32, Proposition 1.11], this is guaranteed by the condition $\lambda[r] > \chi_\infty$ (see Proposition 6.4.3 below for the result in the present setting). Such condition also implies that $\lambda[r]$ is a simple eigenvalue, and that the associated eigenfunction has *minimal growth at infinity* (see [32, Theorem 8.5]). Clearly, the inequality $\lambda[r] > \chi_\infty$ is automatically fulfilled when $\chi_\infty = -\infty$. In the case $\chi_\infty > -\infty$, it always holds that $\lambda[r] \geqslant \chi_\infty$ (since $r \geqslant \chi_\infty$), but we need to require a strict inequality as an hypothesis. Moreover, since we will consider situations where the function r varies by changing the position of the optima, we need a condition that is invariant under such changes. To state the condition, we introduce the following definition, which will also be useful in the case $\chi_\infty = -\infty$.

Definition 6.3.1. *For $i = 1,\ldots,K$, we define the* principal eigenvalue restricted to $\mathcal{C}_i$, *denoted by $\lambda[i]$, in the following way:*

1. *If $\chi_\infty > -\infty$ then*

$$\lambda[i] := \lambda[r_i] \quad \textit{with} \quad r_i(x,\theta) := \begin{cases} \chi(\|\theta\|) & x \in \mathcal{C}_i, \\ \chi_\infty & x \notin \mathcal{C}_i, \end{cases}$$

   and r_i is extended by periodicity to all $x \in \mathbb{R}^N$.

2. *If $\chi_\infty = -\infty$ then we set*

$$\lambda[i] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ \mathcal{L}[r]\phi \leqslant \lambda\phi \text{ in } (\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P\right\}.$$

Remark 6.3.2. The case $\chi_\infty = -\infty$ is formally obtained from the case $\chi_\infty > -\infty$ by letting χ_∞ go to $-\infty$ (see also Lemma 6.4.7). In such case, if the set $\mathcal{C}_i + \mathbb{Z}^N$ is smooth enough, then $\lambda[i]$ reduces to the principal eigenvalue of $\mathcal{L}[r]$ on the cylindrical periodic domain $(\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P$, under Dirichlet boundary condition on $\partial(\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P$, see [32].

For $\chi_\infty > -\infty$, we have $r_i \geqslant \chi_\infty$, so $\lambda[i] = \lambda[r_i] \geqslant \chi_\infty$. The condition we will require is the inequality being strict for at least one i, namely:

$$\exists i \in \{1,\dots,K\}, \qquad \lambda[i] > \chi_\infty. \tag{6.11}$$

We point out that $\lambda[r] \geqslant \lambda[i]$ for all $i = 1,\dots,K$ (for $\chi_\infty > -\infty$, this follows from $r(x,\theta) \geqslant r_i(x,\theta - O_i)$, and for $\chi_\infty = -\infty$, this follows from the definition). Therefore, assumption (6.11) implies that $\lambda[r] > \chi_\infty$, whatever the relative positions of the O_i are.

Assumption (6.11) is implicit; we derive two distinct sufficient conditions which ensure its validity, besides the trivial one $\chi_\infty = -\infty$.

Proposition 6.3.3. *Under assumption* (6.7)*, property* (6.11) *holds in each of the following cases:*

(*a*) *the dimension of the phenotypic space* $\mathbb{R}^P$ *is* $P \leqslant 2$ *;*

(*b*) *there exists* $j \in \{1,\dots,K\}$ *such that*

$$\exists \alpha > 0, \qquad \forall R \in \mathbb{R}, \qquad \chi(R) - \chi_\infty > -\lambda\left[\mathcal{C}_j\right] + 2\alpha P - 4\alpha^2 R^2,$$

where $\lambda[\mathcal{C}_j] := \inf\left\{\lambda > 0 \ / \ \exists \psi > 0,\ \Delta\psi \leqslant \lambda\psi \text{ on } \mathcal{C}_j + \mathbb{Z}^N\right\}$ *is the generalised principal eigenvalue of the Laplacian on* $\mathcal{C}_j + \mathbb{Z}^N$ *with Dirichlet boundary condition on* $\partial(\mathcal{C}_j + \mathbb{Z}^N)$.

The sufficient condition (*a*) is obtained using a Liouville-type result (this can be related to the fact that the Laplacian operator is critical in dimension 1 and 2, see [190, Section 4.3]). The sufficient condition (*b*) is derived by exploiting the Gaussian decay of the Dirichlet principal eigenfunction associated with a suitable problem. Condition (*b*) gives a lower bound on the gap between $\chi(R)$ and χ_∞, that is, a quantification of how much it is "worth" to be close to the optimal phenotype.

6.3.2 Asymptotics as $L \to 0$ and $L \to +\infty$

We begin by "forgetting" the spatial structure of the problem, by considering asymptotics of $\lambda[r_L]$ as $L \to 0$ and $L \to +\infty$, where $r_L(x,\theta) := r\left(\frac{x}{L},\theta\right)$ is the L-periodic version of r. We introduce the following notations.

First, we let $\lambda[\chi] \in \mathbb{R}$ be the generalised principal eigenvalue associated with the operator $\Delta_\theta + \chi(\|\theta\|)$ in $\mathbb{R}^P$, namely:

$$\lambda[\chi] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \psi > 0,\ (\Delta_\theta + \chi(||\cdot||))\psi \leqslant \lambda\psi \text{ in } \mathbb{R}^P\right\}, \tag{6.12}$$

where ψ is understood to belong to $W^2_{p,loc}(\mathbb{R}^P)$ for some $p > 1 + P$. We will show that this notation is coherent with Definition 6.2.1, namely, if $r(x,\theta) \equiv \chi(\|\theta\|)$ then $\lambda[r] = \lambda[\chi]$, see Corollary 6.4.2 below. Analogously to $\lambda[r]$, the generalised principal eigenvalue $\lambda[\chi]$ admits a (positive) principal eigenfunction on $\mathbb{R}^P$. Second, we call

$$\overline{r}(\theta) := \int_{\mathcal{C}} r(x,\theta)\,\mathrm{d}x.$$

Since r is a patchwork landscape of the form (6.5), we have:

$$\overline{r}(\theta) = \sum_{i=1}^{K} |\mathcal{C}_i|\, \chi(\|\theta - O_i\|).$$

Again, we can define the generalised principal eigenvalue associated with the operator $\Delta_\theta + \overline{r}$ in $\mathbb{R}^P$, namely:

$$\lambda[\overline{r}] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \psi > 0,\ (\Delta_\theta + \overline{r})\psi \leqslant \lambda\psi \text{ in } \mathbb{R}^P\right\},$$

and $\lambda[\overline{r}]$ admits a principal eigenfunction on $\mathbb{R}^P$.

Using these notations, we may now state the following result.

Proposition 6.3.4. *The following properties hold:*

(*i*) *if* (6.5)–(6.7) *and* (6.10)–(6.11) *hold, then*

$$\lim_{L \to +\infty} \lambda[r_L] = \lambda[\chi];$$

(*ii*) *if* (6.5)–(6.7) *hold and* $\lambda[\overline{r}] > \chi_\infty$, *then*

$$\lim_{L \to 0} \lambda[r_L] = \lambda[\overline{r}].$$

By Proposition 2.5 of Chapter 5, the function $L \mapsto \lambda[r_L]$ is nondecreasing, hence one infers from Proposition 6.3.4 that $\lambda[\overline{r}] \leqslant \lambda[\chi]$. This inequality can also be obtained from the convexity of the function $r \mapsto \lambda[r]$ (which in turn follows from the Rayleigh formula), namely,

$$\lambda[\overline{r}] \leqslant \sum_{i=1}^{K} |\mathcal{C}_i|\, \lambda[\chi(\|\theta - O_i\|)] = \lambda[\chi].$$

To conclude on the dependence of $\lambda[r]$ in the period, let us mention that there is a biological interpretation to the transformations $L \to 0$ and $L \to +\infty$: they correspond to changes in scales. In the original case $L > 0$, movements and mutations occur on the same timescale. In the limit $L \to 0$, movements occur much more frequently than mutations. This limit is encoded by the homogenised landscape $\overline{r}$, which is the worst case scenario for the survival of the population. In the limit $L \to +\infty$, movements are much smaller than mutations. The principal eigenvalue in the limit $L \to +\infty$ is independent of the relative positions of the points O_i, corresponding to a loss of heterogeneity of the landscape and thus to the most favourable environment for the species. We point out that the work of Bouin and Mirrahimi [44] focuses on yet another change of scales, where mutations occur on a much faster timescale than movements and than the timescale of the equation (Δ_θ is replaced with $\mu\Delta_\theta$ with $\mu \to +\infty$). Various changes of scales, and their effects on the spreading speed of the population in a similar model, have been considered in Chapter 7.

6.3.3 Varying the positions of the optima

In this section, we present some monotonicity results about the principal eigenvalue, always in the patchwork landscape setting (6.5), when the relative positions of the optima $O_1, \dots, O_K$ change, while the function χ and the cells $\mathcal{C}_i$ are fixed.

The building block of all our comparison and optimisation results is the following monotonicity property of the generalised principal eigenvalue. An illustration is given by Figure 6.2.

Theorem 6.3.5. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. If* $\gamma : [0,1] \to \mathbb{R}^P$ *is a* C^1 *regular curve (i.e. with* $\gamma' \neq 0$ *on* $[0,1]$*) such that* $s \mapsto \|\gamma(s) - O_i\|$ *is nonincreasing for all* $i = 2, \dots, K$*, then*

$$\lambda[r[\gamma(1), O_2, \dots, O_K] \geqslant \lambda[r[\gamma(0), O_2, \dots, O_K]. \tag{6.13}$$

If, in addition, there exists $j \in \{2, \dots, K\}$ *for which*

$$\|\gamma(1) - O_j\| < \|\gamma(0) - O_j\|,$$

then the inequality in (6.13) *is strict.*

Remark 6.3.6. If $s \mapsto \|\gamma(s) - O_i\|$ is constant for all $i = 2, \dots, K$, then applying Theorem 6.3.5 to $s \mapsto \gamma(s)$ and $s \mapsto \gamma(1-s)$ shows that $\lambda[r[\gamma(1), O_2, \dots, O_K] = \lambda[r[\gamma(0), O_2, \dots, O_K]$.

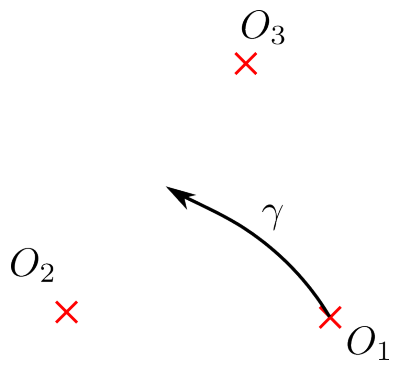

Figure 6.2: Illustration of Theorem 6.3.5. As O_1 follows the path γ, the environment becomes more favourable.

Theorem 6.3.5 asserts that a configuration is more favourable than another if it is possible to pass from the latter to the former by a continuous transformation along which the distance between optima never increases. Its proof relies on a reflection argument.

Thanks to Theorem 6.3.5, we are able to answer Question 4 when the number of patches is not too large.

Theorem 6.3.7. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Assume that* $2 \leqslant K \leqslant P$*. Given two configurations* $O_1, O_2 \dots, O_K$ *and* $\widehat{O}_1, O_2 \dots, O_K$ *satisfying*

$$\left\|\widehat{O}_1 - O_i\right\| \leqslant \|O_1 - O_i\| \quad \text{for all } i = 2, \dots, K,$$

we have:

$$\lambda[r[\widehat{O}_1, O_2 \dots, O_K]] \geqslant \lambda[r[O_1, O_2 \dots, O_K]]. \tag{6.14}$$

Moreover, if there is $i \in \{2, \dots, K\}$ *for which* $\left\|\widehat{O}_1 - O_i\right\| < \|O_1 - O_i\|$*, then the inequality* (6.14) *is strict, otherwise the inequality* (6.14) *is an equality.*

Owing to Theorem 6.3.5, the proof of Theorem 6.3.7 consists in constructing a path from one configuration to another along which the distances of optima decreases, but this is only possible in general if K is no larger than P, see Remark 6.6.6 below.

As a matter of fact, condition (6.11) can be weakened by

$$\lambda[r[\gamma(0), O_2, \dots, O_K] > \chi_\infty$$

in Theorem 6.3.5. In turn, this implies that (6.11) can be weakened by

$$\lambda[r[O_1, O_2 \dots, O_K]] > \chi_\infty$$

in Theorem 6.3.7. See Remark 6.6.2 below for details.

Next, we address Question 6 by studying the dependency of the quantity $\lambda[r[O_1, \dots, O_K]]$ with respect to simultaneous movements of all optima $O_1, \dots, O_K$. We point out that $\lambda[r[O_1, \dots, O_K]]$ is invariant by rigid movements of the set of optima. We then consider dilatations of the optima. For this, we will restrict to the configurations satisfying the following condition:

$$\exists \mathcal{O} \in \mathbb{R}^P, \qquad \forall i, j = 1, \dots, K, \qquad \langle O_i - \mathcal{O}, O_i - O_j \rangle \geqslant 0. \tag{6.15}$$

This condition means that all the triangles $O_i O_j \mathcal{O}$ have an acute angle at O_i. Note that (6.15) is always satisfied when the O_i belong to a common sphere (taking as $\mathcal{O}$ the centre of the sphere) or when $K \leqslant 3$. However, when $K = 4$ and the O_i are aligned and distinct, (6.15) is not satisfied.

Theorem 6.3.8 (Dilatation)**.** *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Let* $O_1, \dots, O_K \in \mathbb{R}^P$ *be distinct points satisfying* (6.15)*.*

(*i*) *The function*

$$a \mapsto \lambda[r[aO_1, \dots, aO_K]] \quad \text{is strictly decreasing for } a \geqslant 0.$$

(*ii*) *There holds*

$$\lim_{a \to 0} \lambda[r[aO_1, \dots, aO_K]] = \lambda[\chi].$$

(*iii*) *If furthermore we have* $\chi_\infty > -\infty$ *and* $\lambda[i] > \chi_\infty$ *for all* $i = 1, \dots, K$ *(where* $\lambda[i]$ *is given in Definition 6.3.1), then*

$$\lim_{a \to +\infty} \lambda[r[aO_1, \dots, aO_K]] = \max_{i=1,\dots,K} \lambda[i].$$

(*iv*) *The conclusion of* (*iii*) *holds true if we replace the additional assumption of* (*iii*) *by:* $\chi_\infty = -\infty$ *and for all* $i = 1, \dots, K$, $\overline{\mathcal{C}_i} = \overline{Int(\mathcal{C}_i)}$ *and* $Int(\mathcal{C}_i + \mathbb{Z}^N)$ *has* $C^{1,1}$ *boundary.*

This result is again a manifestation of the principle that reducing the distances between the optima increases the chances of persistence. In the case $\chi_\infty = -\infty$, letting these distances tend to infinity "splits" the problem into decoupled Dirichlet problems posed on the spatial domains $\mathcal{C}_i$; persistence then occurs if and only if it is possible on at least one of these domains, under Dirichlet boundary condition. If instead $\lambda[\chi] > 0 > \max_i \lambda[i]$, then there is a threshold value a_* for the dilatation of the optima, below which the species persists and above which the species gets extinct.

In the next subsection, we shall again address the question of the dependence of the quantity $\lambda[r[O_1, \dots, O_K]]$ with respect to simultaneous movements of all optima $O_1, \dots, O_K$,

from the point of view of optimisation. We will give an affirmative answer to Question 6 in some particular cases, as well as the solution to Question 5 when the number K of patches is not too large.

6.3.4 Optimisation results

We now focus on optimisation problems. As mentioned above, it is useful to keep the model in mind to better understand the results. Recall in particular that the principal eigenvalue encodes the ability of persistence of the pathogen.

We start with the *maximisation* problem. Using our previous results we derive the following.

Theorem 6.3.9. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Then:*

- (*i*) *The maximum of* $(O_1,\dots,O_K)\mapsto\lambda[r[O_1,\dots,O_K]]$ *is equal to* $\lambda[\chi]$ *and is attained by, and only by,* $O_1=\dots=O_K$*;*
- (*ii*) *For given* $H\in\{1,\dots,K-1\}$*, and fixed* $O_{H+1},\dots,O_K$*, the maximum of* $(O_1,\dots,O_H)\mapsto\lambda[r[O_1,\dots,O_K]]$ *is attained by some points* $O_1,\dots,O_H$ *that necessarily belong to the convex hull of* $\{O_{H+1},\dots,O_K\}$*;*
- (*iii*) *Assume that* $\chi(\|\theta\|)=A-\|\theta\|^2$ *for some constant* $A>0$*. For given* $H\in\{1,\dots,K-1\}$*, the maximum of*

$$(O_1,\dots,O_H)\mapsto\lim_{L\to 0}\lambda[r[O_1,\dots,O_K]]$$

is attained by

$$O_1=\ \dots\ =O_H=\frac{\sum_{i=H+1}^{K}|\mathcal{C}_i|\,O_i}{\sum_{i=H+1}^{K}|\mathcal{C}_i|},$$

that is, when all the free optima $O_1,\dots,O_H$ *are equal to the barycentre of the fixed optima* $O_{H+1},\dots,O_K$*, weighted by the sizes of their patches.*

We point out that the above results do not simply follow by the straightforward monotonicity property of $\lambda[r]$ with respect to r, because for instance, for statement (i), it is not true that $r(x,\theta)\leqslant\chi(\|\theta\|)$. They rather follow from the monotonicity with respect to the distance between the optima, provided by Theorem 6.3.5. Let us also emphasise that one can recover the first part of statement (i) from Proposition 6.3.4 (i) and the monotonicity of $L\mapsto\lambda[r_L]$. However, we proceed the other way around: we prove Theorem 6.3.9 (i) independently and actually use it as a crucial step to prove Proposition 6.3.4 (i).

Concerning the *minimisation* problem – which is the relevant one in agroecology – we show that it does not admit a solution, and that the infimum of the principal eigenvalue is reached when the distances between all optima tend to infinity.

Proposition 6.3.10. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Assume* $K\geqslant 2$*. Then the function* $(O_1,\dots,O_K)\mapsto\lambda[r[O_1,\dots,O_K]]$ *does not admit a minimum. Let* $\lambda[i]$ *be given by Definition 6.3.1. Assume that either* $\chi_\infty>-\infty$ *and* (6.11) *holds, or that* $\chi_\infty=-\infty$ *and for each* i*,* $\overline{\mathcal{C}_i}=\overline{Int(\mathcal{C}_i)}$ *and* $Int(\mathcal{C}_i+\mathbb{Z}^N)$ *has* $C^{1,1}$ *boundary. Then*

$$\inf_{O_1,\dots,O_K\in\mathbb{R}^P}\lambda[r[O_1,\dots,O_K]]=\max_{i=1,\dots,K}\lambda[i].$$

We then consider the minimisation problem under a constraint on the distances between the optima – see Question 5. We are able to solve the problem when the number K of patches is not too large.

Theorem 6.3.11. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Assume that* $K \leqslant 5$ *and* $K \leqslant P+1$. *Let the sets* $\mathcal{C}_1, \dots, \mathcal{C}_K$ *be fixed, while* $O_1, \dots, O_K$ *vary in* $\mathbb{R}^P$. *For a given* $D > 0$, *the solutions of the problem:*

$$\textit{Minimise } \lambda[r[O_1, \dots, O_K]] \textit{ under the constraint } \|O_i - O_j\| \leqslant D \textit{ for all } i, j = 1, \dots, K,$$

are the vertices $O_1, \dots, O_K$ *of a regular polyhedron of side of length* D. *Namely:*

$$\lambda[r[Q_1, \dots, Q_K]] = \min\Big\{\lambda[r[O_1, \dots, O_K]] \ / \ \|O_i - O_j\| \leqslant D \textit{ for all } i \neq j\Big\}$$

if and only if $\|Q_i - Q_j\| = D$ *for all* $i \neq j$.

6.3.5 Conclusion and open problems

We have been focusing on a reaction-diffusion equation modelling a population structured in space and in phenotype. The main ingredient of our model is a *space/phenotype-fitness landscape*, which is a function $r(x, \theta)$ representing the fitness of an individual of phenotype θ living at the spatial position x. The landscape is assumed to be periodic in the spatial position. Although the results stated in Chapter 5 are valid for very general space/phenotype-fitness landscapes, our main focus here is on an "agroecological model". We consider a population of crop pathogens living on a patchwork of fields, each of which is planted with one crop variety. For each crop variety, there is a phenotype (for the pathogen) which maximises the fitness, and the fitness of the pathogen decreases as its phenotype drifts away from this optimal phenotype.

In the companion chapter, for general space/phenotype-fitness landscapes, we have characterised the long-time behaviour of the population (extinction or persistence) in terms of the sign of the generalised principal eigenvalue of the linearised operator around 0. The use of a generalised principal eigenvalue is made necessary by the facts that the space of the phenotype may be unbounded and that the fitness function is not confining, which prevent us from using the classical eigenvalue theory.

In the present chapter, with this persistence/extinction result in hand, we have compared the ability of persistence of the population in different space/phenotype-fitness landscapes, according to the corresponding values of the generalised principal eigenvalue. We proved, in different ways, that the ability of persistence increases as the environment becomes "more homogeneous".

First, we proved in Chapter 5 that the ability of persistence increases as the period of the environment increases. Here, we have analysed the limits as the period goes to zero or to infinity, showing that this brings us back to the study of a space-homogeneous equation. Namely, as the period goes to zero, the ability of persistence is that of a homogeneous environment with an averaged fitness landscape, whereas, as the period goes to infinity, the ability of persistence is that of a homogeneous environment with only one variety.

Second, we have compared the ability of persistence in terms of the relative positions of the fitness optima of the patches. We have proved that the closer the optima are to one another, the easier persistence is. Here, "closer" is understood in some restrictive sense. Namely, if an optimum goes continuously closer to each of the other optima, then the ability

of persistence increases (see Theorem 6.3.5). As a first consequence of this, we show that under suitable assumptions, a dilatation of the position of the optima decreases the ability of persistence (see Theorem 6.3.8). Another consequence concerns the maximisation of the ability of persistence, which is achieved when all optima coincide (or equivalently when the environment is spatially homogeneous, see Theorem 6.3.9). We then address the minimisation problem. We first show that there is no global minimiser of the ability of persistence. Next, we prove that the minimisation problem under a constraint on the distances between the optima is solved by polyhedral configurations, at least when the number of patches is not too large (see Theorem 6.3.11).

Let us mention some open problems and perspectives of this work. First of all, we were able to answer Questions 4–6 only when the number of patches is not too large; the general case is open. Next, from an agroecological point of view, it is also interesting to study the effect of adding a new crop variety: does it decrease or increase the ability of persistence of a pathogen? In a discrete space setting, the authors of [8] study the effect on the ability of persistence if a third variety is added to a set of two varieties. See also the discussions in [8, 118] for more comments about the agroecological implications of our model. Another problem concerns the precise description of the long-time behaviour of the population in the case of persistence. We actually do not know whether the solution converges to a positive stationary state (as in the case without phenotype or the homogeneous case with phenotype [30]), or for instance if it approaches a time-periodic solution. With this respect, let us mention the work of Léculier and Mirrahimi [151], who showed that there exists a stationary solution in the weak mutation limit of a related model, and gave some qualitative properties. Finally, other questions are related to the spreading properties of the equation and the existence of *pulsating travelling waves* analogous to those that exist for the heterogeneous Fisher-KPP equation. The invasion property and the study of the spreading speed in various scaling limits are the object of Chapter 7.

6.4 General properties of the principal eigenvalue and eigenfunction

6.4.1 Estimates on the principal eigenfunction

As reclaimed in Section 6.2, the generalised principal eigenvalue $\lambda[r]$ given by Definition 6.2.1, associated with the linearised operator $\mathcal{L}[r]$, admits a positive, x-periodic eigenfunction, which is not necessarily unique up to multiplication. In this section, we derive a condition that guarantees the exponential decay of one of these principal eigenfunctions (and in fact, using the techniques of [32], one can deduce from the exponential decay that the principal eigenfunction is unique up to a scalar multiple). Such principal eigenfunction is the one obtained as the limit of the principal eigenfunctions in bounded domains. Let us reclaim its construction, given in Chapter 5, adapting the arguments of [33].

First of all, we shall need the results stated in the present section for functions more general than r in the form (6.5). Therefore, just for this section, we work with a function $\widehat{r} \in L^\infty_{loc}(\mathbb{R}^N \times \mathbb{R}^P)$ which is only assumed to be 1-periodic in x and globally bounded from above. Then we define, as in Section 6.2,

$$\mathcal{L}[\widehat{r}]\phi := \Delta_x \phi + \Delta_\theta \phi + \widehat{r}(x,\theta)\phi$$

and the associated generalised principal eigenvalue

$$\lambda[\widehat{r}] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0, \ \mathcal{L}[\widehat{r}]\phi \leqslant \lambda\phi \text{ in } \mathbb{R}^N \times \mathbb{R}^P\right\}.$$

The standard Krein-Rutman theory implies that, for all $R > 0$, there exists a unique $\lambda_R \in \mathbb{R}$ and a unique (up to scalar multiple) $\varphi_R \in W^2_{2,loc}(\mathbb{R}^N \times \overline{B}_{\mathbb{R}^P}(0,R))$ satisfying the periodic principal eigenvalue problem with Dirichlet boundary conditions in θ, namely

$$\begin{cases} \mathcal{L}[\widehat{r}]\varphi_R = \lambda_R \varphi_R & \text{in } \mathbb{R}^N \times B_{\mathbb{R}^P}(0,R), \\ \varphi_R = 0 & \text{over } \mathbb{R}^N \times \partial B_{\mathbb{R}^P}(0,R), \\ \varphi_R > 0 & \text{in } \mathbb{R}^N \times B_{\mathbb{R}^P}(0,R), \\ \varphi_R \text{ is 1-periodic in } x. \end{cases} \tag{6.16}$$

Here and throughout this work, $B_{\mathbb{R}^P}(0,R)$ denotes the ball of $\mathbb{R}^P$ with centre 0 and radius R, for the Euclidean distance. Then *a* generalised principal eigenfunction is given by the following.

Proposition 6.4.1 (Proposition 4.2 in Chapter 5)**.** *Let $\widehat{r} \in L^\infty_{loc}(\mathbb{R}^N \times \mathbb{R}^P)$ be 1-periodic in x and globally bounded from above, and let (λ_R, φ_R) be the principal eigenpair of* (6.16)*, with φ_R normalised by $\varphi_R(0,0) = 1$. Then the following hold.*

(*i*) *The function $R \mapsto \lambda_R$ is nondecreasing and:*

$$\lambda_R \to \lambda[\widehat{r}], \qquad \text{as } \ R \to +\infty.$$

(*ii*) *The principal eigenfunctions φ_R converge locally uniformly, as $R \to +\infty$, to a function $\varphi \in W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ satisfying the periodic principal eigenvalue problem*

$$\begin{cases} \mathcal{L}[\widehat{r}]\varphi(x,\theta) = \lambda[\widehat{r}]\varphi(x,\theta) & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi(x,\theta) > 0 & \text{in } \mathbb{R}^N \times \mathbb{R}^P, \\ \varphi \text{ is 1-periodic in } x. \end{cases}$$

Before deriving the exponential decay of the generalised principal eigenfunction φ, we establish a general principle, which roughly says that the generalised principal eigenvalue does not vary if one adds some variable to the operator.

Namely, in the case where the function $\widehat{r}$ is independent of x, by the uniqueness up to multiplicative constants and the boundedness of the principal eigenfunction for problem (6.16), one infers that φ_R is independent of x as well. This implies that (λ_R, φ_R) is also the principal eigenpair of the operator $\Delta_\theta + \widehat{r}(\theta)$ in $B_{\mathbb{R}^P}(0,R)$ under Dirichlet boundary condition. We then know by [32, Proposition 2.2 (*iv*)] that as $R \to +\infty$, λ_R converges to the generalised principal eigenvalue of the latter operator on $\mathbb{R}^P$. But, on the other hand, Proposition 6.4.1 implies that λ_R converges to $\lambda[\widehat{r}]$. Summing up, we have the following.

Corollary 6.4.2. *Let $\widehat{r}(x,\theta) = \widehat{r}(\theta)$ for all $(x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P$, with $\widehat{r} \in L^\infty_{loc}(\mathbb{R}^P)$ bounded from above. Then the quantity*

$$\lambda[\widehat{r}] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0, \ \mathcal{L}[\widehat{r}]\phi \leqslant \lambda\phi \ \textit{in } \mathbb{R}^N \times \mathbb{R}^P\right\},$$

can equivalently be defined as

$$\lambda[\widehat{r}] := \inf\left\{\lambda \in \mathbb{R} \ / \ \exists \psi > 0,\ (\Delta_\theta + \widehat{r}(\theta))\psi \leqslant \lambda\psi \ \text{ in } \mathbb{R}^P\right\},$$

where the functions ϕ are understood to belong to $W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ for some $p > 1+N+P$, and the functions ψ are understood to belong to $W^2_{p,loc}(\mathbb{R}^P)$ for some $p > 1+P$.

We now establish a uniform exponential bound for the principal eigenfunctions φ_R of problem (6.16). By Proposition 6.4.1, this provides us with the exponential decay for the generalised principal eigenfunction φ.

Proposition 6.4.3. *Let $\widehat{r}$, λ_R, φ_R, φ be as in Proposition 6.4.1. Assume that $\lambda[\widehat{r}] > \inf \widehat{r}$. Assume that there exist $\eta > 0$ and $R_0 > 0$ such that for all $R > R_0$, $x \in \mathbb{R}^N$ and $\|\theta\| \geqslant R_0$, we have*

$$\lambda_R - \widehat{r}(x,\theta) \geqslant \eta^2.$$

Then, there exists a constant $A > 0$, depending only on η, N, P, R_0, $\|\widehat{r}\|_{L^\infty(0,R_0+1)}$ and $\sup \widehat{r}$, such that for all $R > R_0$, there holds:

$$\forall x \in \mathbb{R}^N,\ \forall \theta \in B_{\mathbb{R}^P}(0,R), \qquad \varphi_R(x,\theta) \leqslant Ae^{-\eta\|\theta\|},$$

and

$$\forall x \in \mathbb{R}^N,\ \forall \theta \in \mathbb{R}^P, \qquad \varphi(x,\theta) \leqslant Ae^{-\eta\|\theta\|}.$$

Proof. The proof is similar to that of [32, Proposition 1.10]. Let $\eta > 0$ and $R_0 > 0$ be as in the statement.

The eigenfunctions φ_R satisfy

$$\Delta_{x,\theta}\varphi_R + (\widehat{r} - \lambda_R)\varphi_R = 0 \quad \text{ on } \mathbb{R}^N \times B_{\mathbb{R}^P}(0,R),$$

and the Dirichlet boundary condition. For $R > R_0$ and $\|\theta\| \geqslant R_0$, we have $\lambda_R - \widehat{r} \geqslant \eta^2$, so

$$\Delta_{x,\theta}\varphi_R \geqslant \eta^2\varphi_R \quad \text{ on } \mathbb{R}^N \times (B_{\mathbb{R}^P}(0,R) \setminus B_{\mathbb{R}^P}(0,R_0)).$$

A supersolution of the above operator is $\overline{\varphi}(x,\theta) := e^{-\eta\|\theta\|}$. Indeed, on $\mathbb{R}^N \times (\mathbb{R}^P \setminus \{0\})$,

$$\Delta_{x,\theta}\overline{\varphi} = \left(\eta^2 - \eta\frac{P-1}{\|\theta\|}\right)\overline{\varphi} \leqslant \eta^2\overline{\varphi}.$$

Thanks to the 1-periodicity in x of φ and the normalisation $\varphi_R(0,0) = 1$, the Harnack inequality implies that there exists a constant $A' > 0$ such that for all $R > R_0 + 1$,

$$\sup_{\mathbb{R}^N \times B_{\mathbb{R}^P}(0,R_0)} \varphi_R \leqslant A',$$

where $A' > 0$ depends only on N, P, R_0, $\|\widehat{r}\|_{L^\infty(0,R_0+1)}$ and λ_R. But, on the one hand, $\lambda_R \geqslant -\|\widehat{r}\|_{L^\infty(0,R_0)}$ by hypothesis, and, on the other hand, $\lambda_R \leqslant \sup \widehat{r}$ as it is seen by evaluating $\Delta_{x,\theta}\varphi_R + (\widehat{r} - \lambda_R)\varphi_R = 0$ at a maximum point of φ_R. Thus, A' only depends on N, P, R_0, $\|\widehat{r}\|_{L^\infty(0,R_0+1)}$ and $\sup \widehat{r}$.

Then, calling $A := A'e^{\eta R_0}$, one has that $A\overline{\varphi} \geqslant \varphi_R$ on $\mathbb{R}^N \times \partial B_{\mathbb{R}^P}(0,R_0)$, for $R > R_0 + 1$. Moreover, $A\overline{\varphi} > \varphi_R$ on $\mathbb{R}^N \times \partial B_{\mathbb{R}^P}(0,R)$, where φ_R vanishes. As a consequence, for $R >$

R_0+1, we can apply the standard maximum principle to the operator $\Delta_x+\Delta_\theta-\eta^2$ (whose zero order term is negative) and infer that $A\overline{\varphi}\geqslant\varphi_R$ on $\mathbb{R}^N\times(B_{\mathbb{R}^P}(0,R)\setminus B_{\mathbb{R}^P}(0,R_0))$, and thus on $\mathbb{R}^N\times B_{\mathbb{R}^P}(0,R)$. Eventually, Proposition 6.4.1 yields $A\overline{\varphi}\geqslant\varphi$ on $\mathbb{R}^N\times\mathbb{R}^P$, and A depends only on η, N, P, R_0, $\|\widehat{r}\|_{L^\infty(0,R_0+1)}$ and $\sup\widehat{r}$. □

Remark 6.4.4. By Proposition 6.4.1, the assumptions of Proposition 6.4.3 hold if $\lambda[\widehat{r}]>\inf\widehat{r}$ and

$$\limsup_{\|\theta\|\to+\infty}\left(\sup_{x\in\mathbb{R}^N}\widehat{r}(x,\theta)\right)=\inf_{x\in\mathbb{R}^N,\theta\in\mathbb{R}^P}\widehat{r}.$$

For example, if $\widehat{r}=r$ satisfies the general assumptions (6.5)–(6.7) and $\lambda[r]>\inf r$, then Proposition 6.4.3 can be applied.

Proof of Proposition 6.3.3 (*a*). Assume that (6.7) holds and that $\Theta=\mathbb{R}^P$ with $P=1$ or $P=2$. Let us show that (6.11) holds. Assume that $\chi_\infty>-\infty$ (otherwise (6.11) holds automatically). Since $\lambda[r-\chi_\infty]=\lambda[r]-\chi_\infty$, we may assume without loss of generality that $\chi_\infty=0$. Then $r\geqslant0$ and $r\not\equiv0$ (thanks to (6.7)) and we want to show that $\lambda[r_i]>0$ for some $i\in\{1,\dots,K\}$.

Take any i and define

$$\underline{r}(\theta):=\inf_{x\in\mathbb{R}^N}r_i(x,\theta).$$

Owing to Corollary 6.4.2, we can equivalently consider $\lambda[\underline{r}]$ as the generalised principal eigenvalue of the operator $\mathcal{L}[\underline{r}]$ defined on $\mathbb{R}^N\times\mathbb{R}^P$, with x-independent coefficients, or of the operator $\Delta_\theta+\underline{r}$ defined on $\mathbb{R}^P$. Using the former point of view, together with the inequality $r_i\geqslant\underline{r}$, one immediately gets $\lambda[r_i]\geqslant\lambda[\underline{r}]$.

For the remainder of the proof, we use the latter point of view:

$$\lambda[\underline{r}]=\inf\left\{\lambda\in\mathbb{R}\ /\ \exists\psi>0,\,(\Delta_\theta+\underline{r})\psi\leqslant\lambda\psi\text{ in }\mathbb{R}^P\right\},$$

where $\psi\in W^2_{p,loc}(\mathbb{R}^P)$ for some $p>1+P$. With this definition, we will show that $\lambda[\underline{r}]>0$.

Since $\underline{r}\geqslant0$, we have $\lambda[\underline{r}]\geqslant0$. Thus it is enough to show that $\lambda[\underline{r}]\neq0$. We argue by contradiction and assume that $\lambda[\underline{r}]=0$. By the results of [32], there exists a principal eigenfunction $\psi\in W^p_{2,loc}(\mathbb{R}^P)$ associated with the principal eigenvalue $\lambda[\underline{r}]=0$:

$$\begin{cases}\Delta_\theta\psi(\theta)+\underline{r}\psi(\theta)=0, & \theta\in\mathbb{R}^P,\\ \psi(\theta)>0, & \theta\in\mathbb{R}^P.\end{cases}$$

Since $\underline{r}\geqslant0$,

$$\begin{cases}\Delta_\theta\psi(\theta)\leqslant0, & \theta\in\mathbb{R}^P,\\ \psi(\theta)>0, & \theta\in\mathbb{R}^P.\end{cases}$$

If $P=1$, ψ is a concave function on $\mathbb{R}$ which is bounded from below, so ψ is constant. This is impossible since r_i is not constant (by virtue of assumption (6.7)).

We now focus on the case $P=2$. We take

$$A<\sup_{\theta\in\mathbb{R}^P}\psi(\theta)$$

and we show that $\psi\geqslant A$. Let $w:=\psi-A$. There exist $R>0$ and $\theta_0\in\mathbb{R}^P$ such that $w(\theta)>0$ for $\theta\in B_R$, with $B_R:=B_{\mathbb{R}^P}(\theta_0,R)$. Let $v(\theta):=-\ln(\|\theta-\theta_0\|)+\ln(R)$. Then $v=0$ on ∂B_R,

$\Delta v \equiv 0$ on $\mathbb{R}^P \setminus B_R$ and

$$\lim_{\|\theta\| \to +\infty} v(\theta) = -\infty.$$

Therefore, for all $\alpha > 0$,

$$\begin{cases} w(\theta) \geqslant \alpha v(\theta), & \theta \in \partial B_R, \\ \Delta_\theta w(\theta) \leqslant \alpha \Delta_\theta v(\theta), & \theta \in \mathbb{R}^P \setminus B_R, \\ \limsup_{\|\theta\| \to +\infty} w(\theta) > \limsup_{\|\theta\| \to +\infty} \alpha v(\theta). \end{cases}$$

Thus we can apply the maximum principle on $\mathbb{R}^P \setminus B_R$: for all $R > 0$ small enough and for all $\alpha > 0$, $w \geqslant \alpha v$ outside B_R. Taking $\alpha \to 0$ gives: $w \geqslant 0$ outside B_R. Taking $R \to 0$ gives: $w \geqslant 0$ on $\mathbb{R}^P$. Hence $\psi \geqslant A$. Since this holds for all $A < \sup \psi$, we conclude that $\psi \equiv \sup \psi$. This means that ψ is a constant, which is impossible since r_i is not constant (by virtue of assumption (6.7)). □

Proof of Proposition 6.3.3 (b). Assume that (6.7) holds and that there exist $j \in \{1, \dots, K\}$ and $\alpha > 0$ such that for all $R > 0$,

$$\chi(R) - \chi_\infty + \lambda[\mathcal{C}_j] > 2\alpha P - 4\alpha^2 R^2.$$

Fix j and α satisfying this property. Fix also $\varepsilon > 0$ so small that for all $R > 0$,

$$\chi(R) - \chi_\infty + \lambda[\mathcal{C}_j] > \varepsilon + 2\alpha P - 4\alpha^2 R^2.$$

Let us show that (6.11) holds. Assume that $\chi_\infty > -\infty$ (otherwise (6.11) holds automatically). We will show that $\lambda[r_j] > \chi_\infty$, which implies (6.11). For $A > 0$, we let

$$\underline{r}^A(x, \theta) := -\lambda[\mathcal{C}_j] + \chi_\infty + 2\alpha P - 4\alpha^2 \|\theta\|^2 - A \mathbb{1}_{\{x \notin \mathcal{C}_j\}}.$$

For $A \geqslant -\chi_\infty$, we have $r_j \geqslant \underline{r}^A + \varepsilon$, so $\lambda[r_j] \geqslant \lambda[\underline{r}^A] + \varepsilon$. Now, let us compute $\lambda[\underline{r}^A]$. Let $(\Gamma^A, \lambda^A) \in W^2_{p,loc}(\mathbb{R}^N) \times \mathbb{R}$ satisfy

$$\begin{cases} \Delta_x \Gamma^A - A \mathbb{1}_{\{x \notin \mathcal{C}_j\}} \Gamma^A = \lambda^A \Gamma^A & \text{in } \mathbb{R}^N, \\ \Gamma^A > 0 & \text{in } \mathbb{R}^N, \\ \Gamma^A \text{ is 1-periodic.} \end{cases}$$

Let $\phi^A(x, \theta) := \Gamma^A(x) e^{-\alpha \|\theta\|^2}$. We have:

$$\Delta_x \phi^A + \Delta_\theta \phi^A = \left(\lambda^A + A \mathbb{1}_{\{x \notin \mathcal{C}_j\}} \right) \phi^A - \left(2\alpha P - 4\alpha^2 \|\theta\|^2 \right) \phi^A.$$

Therefore

$$\Delta_x \phi^A + \Delta_\theta \phi^A + \underline{r}^A \phi^A = \left(\chi_\infty + \lambda^A - \lambda[\mathcal{C}_j] \right) \phi^A.$$

Thus $\chi_\infty + \lambda^A - \lambda[\mathcal{C}_j]$ is an eigenvalue for $\mathcal{L}[\underline{r}^A]$ associated with a positive eigenfunction. Since $\underline{r}^A$ is periodic in x and goes to $-\infty$ as $\|\theta\| \to -\infty$ (uniformly in x), the standard

compact theory applies and we obtain $\lambda[\underline{r}^A] = \chi_\infty + \lambda^A - \lambda[\mathcal{C}_j]$. To conclude, we note that

$$\lambda^A = \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0, \Delta_x \phi \leqslant \lambda\phi \text{ in } \mathcal{C}_j + \mathbb{Z}^N \text{ and } \Delta_x \phi \leqslant (\lambda + A)\phi \text{ in } (\mathcal{C} \setminus \mathcal{C}_j) + \mathbb{Z}^N\Big\},$$

and

$$\lambda[\mathcal{C}_j] = \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0, \Delta_x \phi \leqslant \lambda\phi \text{ in } \mathcal{C}_j + \mathbb{Z}^N\Big\},$$

where the functions ϕ belong to $W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ for some $p > 1 + N + P$ and the functions ψ belong to $W^2_{p,loc}(\mathbb{R}^N)$ for some $p > 1 + P$. Thus $\lambda^A \geqslant \lambda[\mathcal{C}_j]$. This yields: $\lambda[r_j] \geqslant \lambda[\underline{r}^A] + \varepsilon \geqslant \chi_\infty + \varepsilon > \chi_\infty$. □

6.4.2 Continuity properties of the principal eigenvalue

We still consider here a general function $\widehat{r}$. To start with, we show an approximation result that will allow us to reduce the case $\widehat{r}$ unbounded to $\widehat{r}$ bounded. Notably, this will be useful to prove the continuity of λ with respect to the points $O_1, \dots, O_K$.

Lemma 6.4.5. *Let $\widehat{r} \in L^\infty_{loc}(\mathbb{R}^N \times \mathbb{R}^P)$ be 1-periodic in x and globally bounded from above. Assume that either $\widehat{r}$ is globally bounded, or that*

$$\limsup_{\|\theta\| \to +\infty} \left[\sup_{x \in \mathbb{R}^N} \widehat{r}(x, \theta)\right] = -\infty, \tag{6.17}$$

and that there exists $\sigma > 0$ such that

$$\limsup_{\|\theta\| \to +\infty} \left[\sup_{x \in \mathbb{R}^N} \widehat{r}(x, \theta) e^{-\sigma\|\theta\|}\right] = 0. \tag{6.18}$$

Then, as $M \searrow \inf \widehat{r}$, we have $\lambda[\max(\widehat{r}, M)] \searrow \lambda[\widehat{r}]$.

Proof. If $\inf \widehat{r} > -\infty$, then $\max(\widehat{r}, M) \to \widehat{r}$ uniformly as $M \searrow \inf \widehat{r}$, so the result comes from [32, Proposition 9.2]. Now, assume that (6.17)–(6.18) hold.

We first point out that $\lambda[\max(\widehat{r}, M)] \geqslant \lambda[\widehat{r}]$ for all $M < 0$, as a consequence of the definition. Next, for $M < 0$ and $R > 0$, we let $(\varphi^M_R, \lambda^M_R)$ satisfy

$$\begin{cases} \Delta_{x,\theta} \varphi^M_R + \max(\widehat{r}(x,\theta), M)\varphi^M_R = \lambda^M_R \varphi^M_R & \text{in } \mathbb{R}^N \times B_{\mathbb{R}^P}(0,R), \\ \varphi^M_R = 0 & \text{over } \mathbb{R}^N \times \partial B_{\mathbb{R}^P}(0,R), \\ \varphi^M_R > 0 & \text{in } \mathbb{R}^N \times B_{\mathbb{R}^P}(0,R), \\ \varphi^M_R \text{ is 1-periodic in } x, \end{cases}$$

with the normalisation $\varphi^M_R(0,0) = 1$. We now invoke the Rayleigh formula for $\lambda_R[\widehat{r}]$ (defined by (6.16)), which is standard because $\lambda_R[\widehat{r}]$ is a classical principal eigenvalue. Taking the

function φ_R^M in the Rayleigh quotient gives

$$\begin{aligned}\lambda_R[\widehat{r}] &\geqslant \frac{-\int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} |\nabla_{x,\theta}\varphi_R^M|^2 + \int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \widehat{r}(\varphi_R^M)^2}{\|\varphi_R^M\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))}} \\ &= \lambda_R^M + \frac{\int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} (\widehat{r} - \max(\widehat{r}, M))(\varphi_R^M)^2}{\|\varphi_R^M\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))}}.\end{aligned}$$

Notice that $\widehat{r} - \max(\widehat{r}, M) = 0$ at points where $\widehat{r} \geqslant M$, and, when $M < 0$, $\widehat{r} - \max(\widehat{r}, M) > \widehat{r}$ at points where $\widehat{r} < M$. The above formula becomes, for $M < 0$,

$$\lambda_R[\widehat{r}] \geqslant \lambda_R^M + \frac{\int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \widehat{r}\,\mathbb{1}_{\{\widehat{r}<M\}}(\varphi_R^M)^2}{\|\varphi_R^M\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))}}. \tag{6.19}$$

We claim that the fraction on the right-hand side goes to 0 as $M \to -\infty$, uniformly in $R > 1$. First, $\varphi_R^M(0,0) = 1$, and, the functions $\max(\widehat{r}, M)$ being locally bounded and globally bounded from above, uniformly in $M < 0$, λ_R^M is bounded uniformly in $R > 1$ and $M < 0$. Therefore, applying the interior Harnack inequality on $\mathcal{C} \times B_{\mathbb{R}^P}(0, 1/2)$ implies that

$$\inf_{R>1,\, M<0} \left\|\varphi_R^M\right\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))} > 0.$$

Second, let $\sigma > 0$ be given by assumption (6.18). Recall that λ_R^M is bounded uniformly in $R > 1$ and $M < 0$. Thus, Assumption (6.17) implies that there exist $R_0 > 0$ and $M_0 < 0$ such that for all $R > R_0$, $M < M_0$, $x \in \mathbb{R}^N$ and $\|\theta\| \geqslant R_0$, we have

$$\lambda_R^M \geqslant \max(\widehat{r}(x,\theta), M) + \sigma^2.$$

Proposition 6.4.3 implies that there exists $A > 0$ such that for all $M < M_0$ and all $R > R_0$, there holds

$$\forall x \in \mathbb{R}^N,\ \forall \theta \in B_{\mathbb{R}^P}(0,R), \qquad \varphi_R^M(x,\theta) \leqslant A e^{-\sigma\|\theta\|}.$$

Hence, assumption (6.18) and estimate (6.19) give, for some $A' \geqslant A$ (independent of R and M),

$$\lambda_R[\widehat{r}] \geqslant \lambda_R^M - A' \int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \mathbb{1}_{\{\widehat{r}<M\}} e^{-\sigma\|\theta\|}\,\mathrm{d}x\,\mathrm{d}\theta.$$

Taking $R \to +\infty$ gives

$$\lambda[\widehat{r}] \geqslant \lambda[(\max(r, M)] - A' \int_{\mathcal{C}\times\mathbb{R}^P} \mathbb{1}_{\{\widehat{r}<M\}} e^{-\sigma\|\theta\|}\,\mathrm{d}x\,\mathrm{d}\theta.$$

Since $\widehat{r}$ is locally bounded, the integral on the right-hand side converges to 0 as $M \to -\infty$. Therefore,

$$\lambda[\widehat{r}] \geqslant \limsup_{M\to-\infty} \lambda[(\max(r, M)].$$

Conversely, recall that $\lambda[\max(\widehat{r}, M)] \geqslant \lambda[\widehat{r}]$. This proves that $\lambda[\max(\widehat{r}, M)] \to \lambda[\widehat{r}]$ as $M \to -\infty$. □

Using Lemma 6.4.5, we prove a continuity result.

Lemma 6.4.6. *Let* (6.5) *and* (6.6) *hold. The function*

$$(O_1, \dots, O_K) \mapsto \lambda[r[O_1, \dots, O_K]]$$

is continuous.

Proof. Let $r^{(n)} := r[O_1^n, \dots, O_K^n]$ and $r := r[O_1, \dots, O_K]$, with $O_i^n \to O_i$ as $n \to +\infty$, for all $i = 1, \dots, K$. If χ is bounded, then $r^{(n)} \to r$ uniformly, so, by the general continuity results [32, Proposition 9.2], we have

$$\lambda[r^{(n)}] \to \lambda[r].$$

On the other hand, if χ is unbounded, $r^{(n)}$ converges to r as $n \to +\infty$ only locally uniformly, but not globally uniformly. This prevents us from invoking the previous argument. We will use Lemma 6.4.5 to get back to the bounded case.

First, for all $R > 0$, $r^n \to r$ uniformly on $B_{\mathbb{R}^P}(0, R)$, so [32, Proposition 9.2] implies that $\lambda_R[r^{(n)}] \to \lambda_R[r]$ as $n \to +\infty$. Hence, by Proposition 6.4.1, we have for all $R_0 > 0$:

$$\liminf_{n \to +\infty} \lambda[r^{(n)}] = \liminf_{n \to +\infty} \sup_{R > 0} \lambda_R[r^{(n)}] \geqslant \liminf_{n \to +\infty} \lambda_{R_0}[r^{(n)}] = \lambda_{R_0}[r].$$

Taking $R_0 \to +\infty$, we get

$$\liminf_{n \to +\infty} \lambda[r^{(n)}] \geqslant \lambda[r].$$

To prove the reverse inequality, we use Lemma 6.4.5. For all $M \in \mathbb{R}$, $\max(r, M)$ and $\max(r^{(n)}, M)$ are uniformly bounded, so $\max(r^{(n)}, M) \to \max(r, M)$ globally uniformly. As a consequence of [32, Proposition 9.2], we get, for all $M \in \mathbb{R}$,

$$\lambda[\max(r^{(n)}, M)] \underset{n \to +\infty}{\to} \lambda[\max(r, M)].$$

Thus, taking $M \to -\infty$ on the left-hand side and using Lemma 6.4.5 gives, for all $M_0 \in \mathbb{R}$,

$$\limsup_{n \to +\infty} \lambda[r^{(n)}] \leqslant \lambda[\max(r, M_0)].$$

Taking $M_0 \to -\infty$ and using Lemma 6.4.5 again gives

$$\limsup_{n \to +\infty} \lambda[r^{(n)}] \leqslant \lambda[r].$$

This concludes the proof. □

The following lemma will be helpful to prove Theorem 6.3.8 about dilatations.

Lemma 6.4.7. *Let* (6.5) *and* (6.6) *hold and let* $i \in \{1, \dots, K\}$. *Suppose in addition that if* $\chi_\infty = -\infty$, *then* $\overline{\mathcal{C}_i} = \overline{Int(\mathcal{C}_i)}$ *and* $Int(\mathcal{C}_i + \mathbb{Z}^N)$ *has* $C^{1,1}$ *boundary. For* $M > \chi_\infty$, *define* $\lambda^M[i] := \lambda[r_i^M]$, *where* r_i^M *is defined in item* 1 *of Definition 6.3.1 with* χ *replaced by* $\max(\chi, M)$. *Then*

$$\lambda^M[i] \searrow \lambda[i] \qquad \text{as } M \searrow \chi_\infty.$$

Proof. If $\chi_\infty > -\infty$, then $r_i^M \to r_i$ uniformly as $M \searrow \chi_\infty$, so the result follows from [32, Proposition 9.2].

Now, assume that $\chi_\infty = -\infty$ and that $\overline{\mathcal{C}_i} = \overline{Int(\mathcal{C}_i)}$ and $Int(\mathcal{C}_i + \mathbb{Z}^N)$ has $C^{1,1}$ boundary. By definition, we have

$$\lambda[i] = \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ (\Delta_{x,\theta} + \chi(\|\cdot\|))\phi \leqslant \lambda\phi \text{ in } (\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P\Big\},$$

and, for $M \in \mathbb{R}$,

$$\lambda^M[i] = \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ (\Delta_{x,\theta} + \max(\chi(\|\cdot\|), M))\phi \leqslant \lambda\phi \text{ in } (\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P \\ \text{and } \Delta_{x,\theta}\phi + M\phi \leqslant \lambda\phi \text{ in } (\mathcal{C} \setminus \mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P\Big\}.$$

Therefore, $\lambda[i] \leqslant \lambda^M[i]$.

Let us now prove that the converse equality holds in the limit $M \to -\infty$. To this aim, we introduce the following variants of the quantity $\lambda^M[i]$. For $M < 0$, we set

$$\underline{\lambda}^M[i] := \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ (\Delta_{x,\theta} + \max(\chi(\|\cdot\|), M))\phi \leqslant \lambda\phi \text{ in } (\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P\Big\},$$

and for $M, M' < 0$, we set

$$\lambda^{M,M'}[i] := \inf\Big\{\lambda \in \mathbb{R} \ / \ \exists \phi > 0,\ (\Delta_{x,\theta} + \max(\chi(\|\cdot\|), M))\phi \leqslant \lambda\phi \text{ in } (\mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P \\ \text{and } \Delta_{x,\theta}\phi + M'\phi \leqslant \lambda\phi \text{ in } (\mathcal{C} \setminus \mathcal{C}_i + \mathbb{Z}^N) \times \mathbb{R}^P\Big\}.$$

Then, $\underline{\lambda}^M[i]$ is the principal eigenvalue of $\Delta_{x,\theta} + \max(\chi, M)$ with Dirichlet conditions on $\partial\mathcal{C}_i$, and $\lambda^{M,M'}[i]$ is analogous to $\lambda^M[i]$ but a distinction is made between the "thresholding on χ" (denoted by M) and the "thresholding outside of $\mathcal{C}_i$" (denoted by M'). We have for all M: $\underline{\lambda}^M[i] \leqslant \lambda^M[i] = \lambda^{M,M}[i]$.

In Steps 1 and 2, we first prove the following convergence, using exterior perturbations of $\mathcal{C}_i$:

$$\lambda^{M,M'} \to \underline{\lambda}^M[i] \qquad \text{as } M' \to -\infty. \tag{6.20}$$

Next, in Step 3, we will conclude by taking $M \to -\infty$ and applying Lemma 6.4.5.

Step 1. Eigenvalues of the Laplacian on $\mathcal{C}_i$. First, we prove that $\lambda[i] = \lambda[\chi] + \lambda[\mathcal{C}_i]$, where $\lambda[\mathcal{C}_i]$ is the principal eigenvalue of the Laplacian in $\mathcal{C}_i + \mathbb{Z}^N$ with periodicity in $\mathcal{C}_i + \mathbb{Z}^N$ and Dirichlet conditions on $\partial(\mathcal{C}_i + \mathbb{Z}^N)$. Let $\psi(x) > 0$ be a periodic principal eigenfunction associated with $\lambda[\mathcal{C}_i]$.

Next, let $R > 0$ and let $\varphi_R(\theta)$ be a principal eigenfunction of the operator $\Delta_\theta + \chi(\|\cdot\|)$ on $B_{\mathbb{R}^P}(0, R)$ with Dirichlet conditions on $\partial B_{\mathbb{R}^P}(0, R)$. Let $\lambda_R[\chi]$ be the associated principal eigenvalue. Let $\phi_R(x, \theta) := \psi(x)\varphi_R(\theta)$. Then $\phi_R > 0$, $\phi_R \in W^2_{p,loc}(\mathcal{C}_i \times B_{\mathbb{R}^P}(0, R))$ for all $p > 0$, and

$$\Delta_{x,\theta}\phi_R + \chi(\|\cdot\|)\phi_R = (\lambda_R[\chi] + \lambda[\mathcal{C}_i])\phi_R.$$

By the standard Krein-Rutman theorey, therefore, the periodic principal eigenvalue $\lambda_R[i]$ of $\Delta_{x,\theta} + \chi(\|\cdot\|)$ with Dirichlet conditions on $\partial((\mathcal{C}_i + \mathbb{Z}^N) \times B_{\mathbb{R}^P}(0, R))$ satisfies $\lambda_R[i] = \lambda_R[\chi] + \lambda[\mathcal{C}_i]$. Taking $R \to +\infty$ gives (by the results of [32]):

$$\lambda[i] = \lambda[\chi] + \lambda[\mathcal{C}_i].$$

If χ is replaced with $\max(\chi, M)$, we obtain:

$$\underline{\lambda}^M[i] = \lambda[\max(\chi, M)] + \lambda[\mathcal{C}_i],$$

where $\lambda[\max(\chi, M)]$ is defined analogously to $\lambda[\chi]$.

Step 2. Proof of (6.20)**.** Throughout Step 2, we fix $M < 0$. We consider smooth exterior perturbations $\mathcal{C}_i^{(n)} \subset \mathbb{R}^N$ of $\mathcal{C}_i + \mathbb{Z}^N$, i.e. $\mathcal{C}_i^{(n)}$ is bounded, $\overline{\mathcal{C}_i^{(n)}} = \overline{Int(\mathcal{C}_i^{(n)})}$, $Int(\mathcal{C}_i^{(n)} + \mathbb{Z}^N)$ has $C^{1,1}$ boundary, and:

$$\mathcal{C}_i + \mathbb{Z}^N \subset \mathcal{C}_i^{(n+1)} + \mathbb{Z}^N \subset \mathcal{C}_i^{(n)} + \mathbb{Z}^N, \qquad \bigcap_{n \geqslant 0} \overline{\mathcal{C}_i^{(n)} + \mathbb{Z}^N} = \overline{\mathcal{C}_i + \mathbb{Z}^N}.$$

We also require that for all n,

$$d(\partial(\mathcal{C}_i + \mathbb{Z}^N), \partial(\mathcal{C}_i^{(n)} + \mathbb{Z}^N)) > 0, \qquad d(\partial(\mathcal{C}_i^{(n)} + \mathbb{Z}^N), \partial(\mathcal{C}_i^{(n+1)} + \mathbb{Z}^N)) > 0,$$

where $d(A, B)$ denotes the distance between two closed sets A and B. For each n, we let $\psi^{(n)} > 0$ be a periodic principal eigenfunction associated with the periodic/Dirichlet principal eigenvalue $\lambda[\mathcal{C}_i^{(n)}]$ of the Laplacian in $\mathcal{C}_i^{(n)} + \mathbb{Z}^N$. By interior elliptic estimates, $\psi^{(n)}$ is locally of class C^∞ in $Int(\mathcal{C}_i^{(n)} + \mathbb{Z}^N)$; in particular, $\psi^{(n)}$ is C^∞ on $\mathcal{C}_i^{(n+1)} + \mathbb{Z}^N$. We let $w^{(n)} \in C^\infty(\mathbb{R}^N)$ be 1-periodic and satisfy $\inf w^{(n)} > 0$ and $w^{(n)} \equiv \psi^{(n)}$ on $\mathcal{C}_i^{(n+1)} + \mathbb{Z}^N$. Last, let φ be a positive principal eigenfunction of $\Delta_\theta + \max(\chi(\|\cdot\|), M)$ associated with $\lambda[\max(\chi, M)]$.

Now, define

$$\phi^{(n)}(x, \theta) := w^{(n)}(x)\varphi(\theta).$$

For $x \in \mathcal{C}_i$, $w^{(n)}$ and $\psi^{(n)}$ coincide in a neighbourhood of x, so

$$(\Delta_{x,\theta} + \chi(\|\cdot\|))\phi^{(n)} = (\lambda[\max(\chi, M)] + \lambda[\mathcal{C}_i^{(n)}])\phi^{(n)}.$$

For $x \in \mathcal{C} \setminus \mathcal{C}_i$ and $M' < 0$, we have:

$$(\Delta_{x,\theta} + M')\phi^{(n)} = \left(\frac{\Delta_x w^{(n)}}{w^{(n)}} + \lambda[\max(\chi, M))] - \max(\chi(\|\cdot\|), M) \right) \phi^{(n)} + M'\phi^{(n)}.$$

Note that $\Delta w^{(n)}$ is globally bounded and recall that $\inf w^{(n)} > 0$. Thus the term in parentheses on the right-hand side is bounded on $\mathcal{C}_i^{(n)}$. Hence, for $M' < 0$ sufficiently small, we have: $(\Delta_{x,\theta} + M')\phi^{(n)} \leqslant 0$ on $(\mathcal{C} \setminus \mathcal{C}_i) \times \mathbb{R}^P$.

Since $\phi^{(n)}$ is positive and belongs to $W^2_{p,loc}$ for all $p > 0$, we may use $\phi^{(n)}$ as a test function in the definition of $\lambda^{M,M'}[i]$ above. We obtain, for all n, for all $M < 0$,

$$\limsup_{M' \to -\infty} \lambda^{M,M'}[i] \leqslant \lambda[\max(\chi, M)] + \lambda[\mathcal{C}_i^{(n)}].$$

Now, since $\mathcal{C}_i^{(n)} + \mathbb{Z}^N$ and $\mathcal{C}_i + \mathbb{Z}^N$ have $C^{1,1}$ boundaries and are periodic, they are $C^{1,1}$ uniformly in x. Further, the principal eigenfunctions for the Laplacian in $\mathcal{C}_i^{(n)} + \mathbb{Z}^N$ and $\mathcal{C}_i + \mathbb{Z}^N$ are periodic. Therefore, the arguments at the beginning of [32, Section 7.2] apply,

so we have:

$$\lambda[\mathcal{C}_i^{(n)}] \to \lambda[\mathcal{C}_i] \qquad \text{as } n \to +\infty,$$

which gives, owing to Step 1,

$$\limsup_{M' \to -\infty} \lambda^{M,M'}[i] \leqslant \lambda[\max(\chi, M)] + \lambda[\mathcal{C}_i] = \underline{\lambda}^M[i].$$

To conclude Step 2, we note that by definition, $\underline{\lambda}^M[i] \geqslant \lambda^{M,M'}[i]$ as long as $M' < M$. Equation (6.20) follows.

Step 3. Conclusion. Owing to (6.20), we have, for all fixed $M < 0$,

$$\limsup_{M' \to -\infty} \lambda^{M'}[i] \leqslant \limsup_{M' \to -\infty} \lambda^{M,M'}[i] = \underline{\lambda}^M[i].$$

Recall that $\underline{\lambda}^M[i] = \lambda[\max(\chi, M)] + \lambda[\mathcal{C}_i]$. By Lemma 6.4.5 (recalling the correspondence of Corollary 6.4.2), we have $\lambda[\max(\chi, M)] \to \lambda[\chi]$ as $M \to -\infty$. Taking $M \to -\infty$ in the above equation, therefore, we obtain

$$\limsup_{M' \to -\infty} \lambda^{M'}[i] \leqslant \lambda[\chi] + \lambda[\mathcal{C}_i].$$

By Step 1, we have $\lambda[\chi] + \lambda[\mathcal{C}_i] = \lambda[i]$. This concludes. □

6.5 Dependence on the period

In this section, we prove Proposition 6.3.4. The points $O_1, \dots, O_K$ are fixed, and we look at the effect of the period on the principal eigenvalue associated with $r_L(x, \theta) := r(\frac{x}{L}, \theta)$, which is the L-periodic version of r.

Throughout Section 6.5, for $L, R > 0$, we let φ_R^L be defined as φ_R in (6.16) with $\widehat{r} = r_L$ and L-periodicity instead of 1-periodicity, and normalised by $\varphi_R^L(0,0) = 1$. We let $\lambda_R[r_L]$ be the associated principal eigenvalue. We let φ^L be the principal eigenfunction associated with $\lambda[r_L]$ and normalised by $\varphi^L(0,0)$, as defined by Proposition 6.4.1 (with $\widehat{r} = r_L$ and L-periodicity instead of 1-periodicity). Then, as $R \to +\infty$, $\lambda_R[r_L]$ converges to $\lambda[r_L]$ and φ_R^L converges locally uniformly to φ^L.

6.5.1 When the period is large (Proposition 6.3.4 (i))

A crucial point of Proposition 6.3.4 (i) is the inequality $\lambda[r_L] \leqslant \lambda[\chi]$. This follows from the maximisation result, Theorem 6.3.9 (i), which we prove later on in this chapter. We recall that, owing to Corollary 6.4.2, the quantity $\lambda[\chi]$ is equivalently defined by (6.12) or as $\lambda[r]$ in Definition 6.2.1 with $O_1 = \cdots = O_K = 0$ (in which case r is independent of x).

Proof of Proposition 6.3.4 (i). First of all, we know from Proposition 2.5 of Chapter 5 that $L \mapsto \lambda[r_L]$ is nondecreasing, hence the limit of $\lambda[r_L]$ as $L \to +\infty$ exists. Then, Theorem 6.3.9 (i) (which can be applied owing to assumptions (6.5)–(6.7) and (6.10)–(6.11)) implies that such limit is no larger than $\lambda[\chi]$. Therefore, it remains to show that

$$\lim_{L \to +\infty} \lambda[r_L] \geqslant \lambda[\chi]. \tag{6.21}$$

We focus on a patch $\mathcal{C}_i$ with positive measure, which exists because $\sum_{i=1}^K |\mathcal{C}_i| = |\mathcal{C}| = 1$. Then, applying Lebesgue's theorem to the indicator function of $\mathcal{C}_i$, we deduce that the following limit holds for a.e. $x_0 \in \mathcal{C}_i$:

$$\frac{|B_{\mathbb{R}^N}(x_0,\varepsilon)\cap\mathcal{C}_i|}{|B_{\mathbb{R}^N}(0,\varepsilon)|} \to 1 \quad \text{as } \varepsilon \to 0. \tag{6.22}$$

As a consequence, we also have at the same points x_0,

$$\forall j \neq i, \quad \frac{|B_{\mathbb{R}^N}(x_0,\varepsilon)\cap\mathcal{C}_j|}{|B_{\mathbb{R}^N}(0,\varepsilon)|} \to 0 \quad \text{as } \varepsilon \to 0. \tag{6.23}$$

We then fix a point $x_0 \in \mathcal{C}_i \cap (0,1)^N$ for which (6.22)–(6.23) hold. Moreover, up to translation of r_L in the θ variable, we can assume that the optimum on $\mathcal{C}_i$ is $O_i = 0$. Next, let $(w_L)_{L>1}$ be a family of smooth cut-off functions on $\mathbb{R}^N$ satisfying, for any $L > 1$: $0 \leqslant w_L \leqslant 1$ and

$$w_L(x) = 1 \quad \text{if } \|x - Lx_0\| \leqslant \sqrt{L} - 1, \qquad w_L(x) = 0 \quad \text{if } \|x - Lx_0\| \geqslant \sqrt{L},$$

and $\|\nabla w_L\|_{L^\infty(\mathbb{R}^N)} \leqslant 2$. Then, for given $R > 0$, we consider an eigenpair $(\lambda_R[\chi], \psi_R)$ (unique up to multiplication of ψ_R) solution to

$$\begin{cases} (\Delta_\theta + \chi(\|\cdot\|))\psi_R = \lambda_R[\chi]\psi_R & \text{in } B_{\mathbb{R}^P}(0,R), \\ \psi_R = 0 & \text{over } \partial B_{\mathbb{R}^P}(0,R), \\ \psi_R > 0 & \text{in } B_{\mathbb{R}^P}(0,R). \end{cases}$$

The principal eigenvalue $\lambda_R[r_L]$ satisfies the standard Rayleigh formula with L-periodicity in the x-variable. We apply it with, as a test function, $\phi(x,\theta) := \psi_R(\theta) w_L(x)$ for $x \in \mathcal{C}^L$, $\theta \in B_{\mathbb{R}^P}(0,R)$, and extended by L-periodicity in x (here, $\mathcal{C}^L := [0,L]^N$ denotes the L-periodic cell). This can be done for L larger than some quantity L_1 which guarantees that w_L is supported in the interior of $\mathcal{C}^L$, and thus ϕ is regular. We obtain

$$\begin{aligned} \lambda_R[r_L] &\geqslant \frac{\displaystyle\int_{\mathcal{C}^L \times B_{\mathbb{R}^P}(0,R)} \Big(-\left|\nabla_{x,\theta}\phi\right|^2 + r_L\phi^2 \Big)\,\mathrm{d}x\,\mathrm{d}\theta}{\displaystyle\int_{\mathcal{C}^L \times B_{\mathbb{R}^P}(0,R)} \phi^2\,\mathrm{d}x\,\mathrm{d}\theta} \\ &= \frac{\displaystyle\int_{\mathcal{C}^L \times B_{\mathbb{R}^P}(0,R)} \Big(-|\nabla_x w_L(x)|^2 \psi_R^2(\theta) - w_L^2(x)\,|\nabla_\theta \psi_R(\theta)|^2 + r_L(x,\theta) w_L^2(x)\psi_R^2(\theta) \Big)\,\mathrm{d}x\,\mathrm{d}\theta}{\displaystyle\int_{\mathcal{C}^L} w_L^2(x)\,\mathrm{d}x \int_{B_{\mathbb{R}^P}(0,R)} \psi_R^2(\theta)\,\mathrm{d}\theta}. \end{aligned}$$

We now estimate the various terms as $L \to +\infty$. Since the measure of the annulus $B_{\mathbb{R}^N}(0,\sqrt{L}) \setminus B_{\mathbb{R}^N}(0,\sqrt{L}-1)$ grows as $\sqrt{L}^{N-1}$, we have

$$\lim_{L\to+\infty} \frac{\displaystyle\int_{\mathcal{C}^L} w_L^2(x)\,\mathrm{d}x}{|B_{\mathbb{R}^N}(0,\sqrt{L}-1)|} = 1,$$

and therefore

$$\lim_{L\to+\infty} \frac{\displaystyle\int_{\mathcal{C}^L} |\nabla_x w_L(x)|^2 \,\mathrm{d}x}{\displaystyle\int_{\mathcal{C}^L} w_L^2(x)\,\mathrm{d}x} \leqslant 4 \lim_{L\to+\infty} \frac{|B_{\mathbb{R}^N}(0,\sqrt{L}) \setminus B_{\mathbb{R}^N}(0,\sqrt{L}-1)|}{|B_{\mathbb{R}^N}(0,\sqrt{L}-1)|} = 0.$$

Furthermore, since r_L is bounded, locally in θ but uniformly in L, we also deduce that, uniformly on $\theta \in B_{\mathbb{R}^P}(0,R)$,

$$\begin{aligned}\lim_{L\to+\infty} \frac{\displaystyle\int_{\mathcal{C}^L} r_L(x,\theta) w_L^2(x)\,\mathrm{d}x}{\displaystyle\int_{\mathcal{C}^L} w_L^2(x)\,\mathrm{d}x} &= \lim_{L\to+\infty} \frac{\displaystyle\int_{B_{\mathbb{R}^N}(Lx_0,\sqrt{L})} r_L(x,\theta)\,\mathrm{d}x}{|B_{\mathbb{R}^N}(0,\sqrt{L})|} \\ &= \lim_{L\to+\infty} \frac{\displaystyle\int_{B_{\mathbb{R}^N}(x_0,1/\sqrt{L})} r(y,\theta)\,\mathrm{d}y}{|B_{\mathbb{R}^N}(0,1/\sqrt{L})|}.\end{aligned}$$

Recalling the definition of r and using (6.22)–(6.23), we get

$$\lim_{L\to+\infty} \frac{\displaystyle\int_{\mathcal{C}^L} r_L(x,\theta) w_L^2(x)\,\mathrm{d}x}{\displaystyle\int_{\mathcal{C}^L} w_L^2(x)\,\mathrm{d}x} = \sum_{j=1}^{K} \lim_{\varepsilon\to 0} \frac{|B_{\mathbb{R}^N}(x_0,\varepsilon)\cap \mathcal{C}_j|}{|B_{\mathbb{R}^N}(0,\varepsilon)|}\, \chi(\|\theta - O_j\|) = \chi(\|\theta\|).$$

Plugging these estimates in the inequality obtained from the Rayleigh formula yields

$$\liminf_{L\to+\infty} \lambda_R[r_L] \geqslant \frac{\displaystyle\int_{B_{\mathbb{R}^P}(0,R)} \Big(-|\nabla_\theta \psi_R(\theta)|^2 + \chi(\|\theta\|)\psi_R^2(\theta)\Big)\,\mathrm{d}\theta}{\displaystyle\int_{B_{\mathbb{R}^P}(0,R)} \psi_R^2(\theta)\,\mathrm{d}\theta},$$

and the right-hand side is equal to $\lambda_R[\chi]$ by integration by parts. We then conclude, owing to Proposition 6.4.1, that

$$\lim_{L\to+\infty} \lambda[r_L] \geqslant \liminf_{L\to+\infty} \lambda_R[r_L] \geqslant \lambda_R[\chi],$$

which tends to $\lambda[\chi]$ as $R \to +\infty$. □

Remark 6.5.1. The above proof makes use of the Rayleigh formula for the classical principal eigenvalue, which holds because the operator is self-adjoint. We mention that another, simpler proof could be given without exploiting self-adjointness, but which would require to assume that one of the $\mathcal{C}_i$ has non-empty interior (this alternative proof is based on the fact that the principal eigenvalue of the Laplacian on $B_{\mathbb{R}^N}(0,R)$ with Dirichlet conditions goes to 0 as R goes to infinity).

6.5.2 When the period is small (Proposition 6.3.4 (ii))

Proof of Proposition 6.3.4 (ii). We first assume that $r \in L^\infty(\mathbb{R}^N \times \mathbb{R}^P)$. Since $L \mapsto \lambda[r_L]$ is monotonic, it converges as $L \to 0$.

Step 1. $\lambda[r_L] \geqslant \lambda[\overline{r}]$**, bounded** r**.** Let $\overline{r}$ be defined by

$$\overline{r}(\theta) := \int_{\mathcal{C}} r(x,\theta)\,\mathrm{d}x.$$

We recall that, according to Corollary 6.4.2, $\lambda[\overline{r}]$ can be equivalently defined using either the operator acting on functions defined on $(x,\theta) \in \mathbb{R}^N \times \mathbb{R}^P$, or the operator acting on functions defined on $\theta \in \mathbb{R}^P$ only. We use here the former point of view. Let $(\overline{\lambda}_R, \overline{\varphi}_R)$ be the principal eigenpair of the problem (6.16) with $\widehat{r} = \overline{r}$. The operator $\mathcal{L}[\overline{r}]$ is invariant by translation in x, so, by uniqueness of the principal eigenfunction, $\overline{\varphi}_R$ is independent of x for all $R > 0$. The function $\overline{\varphi}_R$ is thus L-periodic in x and satisfies the Dirichlet boundary condition. Therefore, owing to the Rayleigh formula applied to $\lambda_R[r_L]$ with the test function $\overline{\varphi}_R$,

$$\begin{aligned}
\lambda_R[r_L] &\geqslant \frac{-\int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \left|\nabla_{x,\theta}\overline{\varphi}_R\right|^2 + \int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} r_L \overline{\varphi}_R^2}{\|\overline{\varphi}_R\|^2_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))}} \\
&= \frac{-\int_{B_{\mathbb{R}^P}(0,R)} |\nabla_\theta \overline{\varphi}_R|^2 + \int_{B_{\mathbb{R}^P}(0,R)} \overline{r}\,\overline{\varphi}_R^2}{\|\overline{\varphi}_R\|^2_{L^2(B_{\mathbb{R}^P}(0,R))}} \\
&= \overline{\lambda}_R.
\end{aligned}$$

The last line follows from an integration by parts. By Proposition 6.4.1, as $R \to +\infty$, we have $\overline{\lambda}_R \to \lambda[\overline{r}]$ and $\lambda_R[r_L] \to \lambda[r_L]$. Therefore, we have shown that $\lambda[r_L] \geqslant \lambda[\overline{r}]$ for all $L > 0$.

Step 2. $\lim_{L\to 0} \lambda[r_L] \leqslant \lambda[\overline{r}]$**, bounded** r**.** As $R \to +\infty$, $\lambda_R[r_L]$ converges to $\lambda[r_L]$ and φ_R^L converges locally uniformly to a principal eigenfunction φ^L associated with $\lambda[r_L]$.

By assumption, we have $\lambda[\overline{r}] > \inf r$. Let $\eta \in (0, \frac{1}{2}\sqrt{\lambda[\overline{r}] - \inf r})$, and let $R_1 > 0$ such that

$$\lambda_{R_1}[\overline{r}] \geqslant \inf r + 2\eta^2.$$

By the monotonicity of $R \mapsto \lambda_R[\overline{r}]$ and by Step 1, we conclude that for all $L > 0$ and $R > R_1$,

$$\begin{aligned}
\lambda_R[r_L] &\geqslant \lambda_R[\overline{r}] \geqslant \lambda_{R_1}[\overline{r}] \\
&\geqslant \inf r + 2\eta^2.
\end{aligned}$$

By assumption (6.7), χ is decreasing, so there exists $R_0 > R_1$ such that for all $x \in \mathbb{R}^N$ and $\|\theta\| > R_0$, for all $L > 0$,

$$\lambda_R[r_L] > r(x,\theta) + \eta^2.$$

By Proposition 6.4.3, therefore, there exists $A > 0$ (independent of R and L) such that

$$\forall R > R_0, \forall L > 0, \forall x \in \mathbb{R}^N, \forall \theta \in \mathbb{R}^P, \qquad \varphi_R^L(x,\theta) \leqslant A e^{-\eta\|\theta\|} \text{ and } \varphi^L(x,\theta) \leqslant A e^{-\eta\|\theta\|}. \quad (6.24)$$

Owing to (6.24), the local uniform convergence $\varphi_R^L \to \varphi^L$ is in fact globally uniform. Moreover, the boundedness of r implies the boundedness of $\overline{r}$ and r_L. Therefore, injecting φ_R^L into the

Rayleigh formula for $\lambda_R[\overline{r}]$, and then taking $R \to +\infty$ gives,

$$\lambda[\overline{r}] \geqslant \lambda[r_L] + \frac{\displaystyle\int_{\mathcal{C}\times\mathbb{R}^P} (\varphi^L)^2(\overline{r} - r_L)}{\|\varphi^L\|_{L^2(\mathcal{C}\times\mathbb{R}^P)}}.$$

By the assumption that $r \in L^\infty(\mathbb{R}^N \times \mathbb{R}^P)$, by the boundedness of $(\lambda[r_L])_{L>0}$, and by (6.24), elliptic estimates imply that the family $(\varphi^L)_{0<L<1}$ is bounded in $W^1_2(\mathcal{C}\times\mathbb{R}^P)$. A diagonal extraction argument tells us that up to an extraction $L_k \to 0$ from the subsequence $\left(\frac{1}{2^k}\right)_{k\geqslant 0}$, φ^{L_k} converges in $L^2_{loc}(\mathcal{C}\times\mathbb{R}^P)$, as $k \to +\infty$, to a function Φ. The function Φ must be independent of x, owing to Φ being $\frac{1}{2^k}$-periodic for all integer k. Next, using the fact that the exponential decay of φ^L is uniform in L, the convergence $\varphi^{L_k} \to \Phi$ actually holds in $L^2(\mathcal{C}\times\mathbb{R}^P)$. Last, $(\overline{r} - r_L)_{L>0}$ is bounded in $L^\infty(\mathcal{C}\times\mathbb{R}^P)$. Therefore, we have,

$$\int_{\mathcal{C}\times\mathbb{R}^P} \left[(\varphi^{L_k})^2 - \Phi^2\right](\overline{r} - r_{L_k}) \underset{k\to+\infty}{\to} 0.$$

Last, $\varphi^L(0,0) = 1$ and $(\lambda[r_L])_{L>0}$ is bounded, so the Harnack inequality implies that $\inf_{L>0} \left\|\varphi^L\right\|_{L^2(\mathcal{C}\times\mathbb{R}^P)} > 0$. Thus, taking $L_k \to 0$ in the equation above gives

$$\lambda[\overline{r}] \geqslant \limsup_{k\to+\infty} \left(\lambda[r_{L_k}] + \frac{\displaystyle\int_{\mathcal{C}\times\mathbb{R}^P} \Phi^2(\overline{r} - r_{L_k})}{\|\varphi^{L_k}\|_{L^2(\mathcal{C}\times\mathbb{R}^P)}} \right) = \limsup_{k\to+\infty} \lambda[r_{L_k}].$$

The last equality follows from Φ being independent of x. Since $L \mapsto \lambda[r_L]$ is monotonic, it converges as $L \to 0$, so the whole family $\lambda[r_L]$ converges to $\lambda[\overline{r}]$ (and not just a subsequence). This concludes for bounded r.

Step 3. Unbounded r. Now, let us drop the assumption that r is bounded. For $M \in \mathbb{R}$, let $r_{L,M}$ and $\overline{r}_M$ be defined as r_L and $\overline{r}$ but with $\chi_M := \max(\chi, M)$ instead of χ (in general, $\overline{r}_M \not\equiv \max(\overline{r}, M)$). We have, using the monotonicity of $L \mapsto \lambda[r_L]$ (which comes from Proposition 2.5 (i) of Chapter 5):

$$\lim_{L\to 0} \lambda[r_L] = \inf_{L>0} \lambda[r_L].$$

Using Steps 1 and 2, we have $\lambda[r_{L,M}] \to \lambda[\overline{r}_M]$ as $L \to 0$. Thus, using Lemma 6.4.5 and the monotonicity of $L \mapsto \lambda[r_{L,M}]$ and $M \mapsto \lambda[r_{L,M}]$, we get

$$\lim_{L\to 0} \lambda[r_L] = \inf_{L>0,\, M\in\mathbb{R}} \lambda[r_{L,M}] = \inf_{M\in\mathbb{R}} \lambda[\overline{r}_M].$$

Using Lemma 6.4.5 and the monotonicity of $M \mapsto \lambda[r_{L,M}]$ again, we then derive $\lim_{L\to 0} \lambda[r_L] = \lambda[\overline{r}]$. □

6.6 Comparison of configurations

In this section, we study the dependence of $\lambda[r[O_1, \ldots, O_K]]$ in terms of $O_1, \ldots, O_K$. The key result of this question is Theorem 6.3.5, which we prove first.

6.6.1 A transformation that increases the ability of persistence (Theorem 6.3.5)

Let r be a patchwork landscape of the form (6.5). We assume throughout that the additional assumptions (6.7), (6.10) and (6.11) hold. The following lemma is the infinitesimal version of Theorem 6.3.5 and is illustrated by Figure 6.3, left. The proof is inspired by that of [118, Proposition 2.7 (*ii*)], which had a discrete space composed of two patches, while our space is continuous. The main ingredient of the proof is that the principal eigenfunction is asymmetric with respect to some subspace of the phenotypic space $\mathbb{R}^P$. Our proof deals with only one elliptic equation, and in this regard it is simpler than that of [118], which deals with a system of elliptic equations.

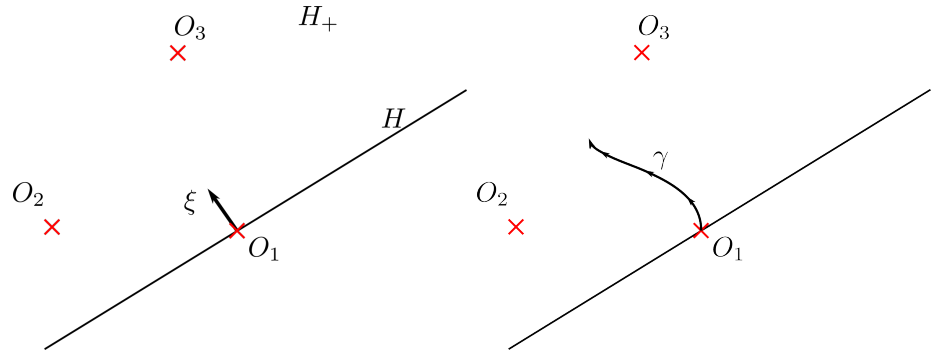

Figure 6.3: Illustration of Lemma 6.6.1 (left) and comparison with Theorem 6.3.5 (right). The left figure is an "infinitesimal version" of the right figure: here, $\xi = \gamma'(0)$. If O_1 follows the arrows, then the principal eigenvalue $\lambda[r[O_1,\dots,O_K]]$ increases.

Lemma 6.6.1. *Let* (6.5)–(6.7) *and* (6.10)–(6.11) *hold. Assume that there exists a unit vector* $\xi \in \mathbb{R}^P$ *such that*

$$\forall i = 2,\dots,K, \qquad \langle \xi, O_i - O_1\rangle \geqslant 0,$$

with a strict inequality for at least one $i \in \{2,\dots,K\}$. *Then for* $\delta \in [0,1]$, *it holds*

$$\lambda[r[O_1+\delta\xi, O_2,\dots,O_K]] \geqslant \lambda[r[O_1,\dots,O_K]] + C_1\delta - C_2\delta^2, \tag{6.25}$$

for some constants $C_1, C_2 > 0$ *depending only on* $r[O_1,\dots,O_K]$ *and* $\max_{i\in\{2,\dots,K\}} \langle \xi, O_i - O_1\rangle$.

Proof. We will use a reflection argument. Let

$$H := \Big\{\theta \in \mathbb{R}^P \ / \ \langle \theta, \xi\rangle = \langle O_1, \xi\rangle\Big\},$$
$$H_+ := \Big\{\theta \in \mathbb{R}^P \ / \ \langle \theta, \xi\rangle \geqslant \langle O_1, \xi\rangle\Big\}.$$

We let $\iota : \mathbb{R}^P \to \mathbb{R}^P$ be the orthogonal reflection with respect to H, i.e.

$$\iota(\theta) := \theta + 2\,\langle (O_1 - \theta), \xi\rangle\,\xi.$$

For the sake of convenience, and with a slight abuse of notation, we also call ι the isometry on $\mathbb{R}^N \times \mathbb{R}^P$ defined by

$$\iota(x,\theta) := (x, \iota(\theta)).$$

We let $\varphi \in W^2_{p,loc}(\mathbb{R}^N \times \mathbb{R}^P)$ be the 1-periodic principal eigenfunction defined by the second statement of Proposition 6.4.1, associated with the function $\widehat{r} = r[O_1, \dots, O_K]$. By assumption (6.11) and pointing out that $\lambda[r] \geqslant \lambda[i]$ for all $i = 1, \dots, K$, we have $\lambda[r] > \chi_\infty$. By Proposition 6.4.3 (see Remark 6.4.4), therefore, φ decays exponentially as $\|\theta\| \to +\infty$, uniformly in $x \in \mathbb{R}^N$. Thus we may renormalise it so that $\|\varphi\|_{L^2(\mathcal{C}\times\mathbb{R}^P)} = 1$ (instead of $\varphi(0,0) = 1$).

Step 1. Prove that $\varphi > \varphi \circ \iota$ on $\mathbb{R}^N \times (H_+ \setminus H)$. Consider $\overline{\varphi}(x,\theta) := \varphi(\iota(x,\theta))$ and

$$\phi(x,\theta) := \varphi(x,\theta) - \overline{\varphi}(x,\theta).$$

Let us show that $\phi \geqslant 0$ over $\mathbb{R}^N \times H_+$. In order to apply the maximum principle, we reduce to a bounded domain in the θ variable. Namely, for $R > 0$, we call $B_R := B_{\mathbb{R}^P}(0,R)$. We only work with R so large that $H_+ \cap B_R$ is nonempty. We let (λ_R, φ_R) be defined as in (6.16), with $\widehat{r} = r$, and we renormalise φ_R by $\|\varphi_R\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))} = 1$. With this renormalisation, $\varphi_R \to \varphi$ locally uniformly as $R \to +\infty$. Accordingly with previous notations, we set $\overline{\varphi}_R(x,\theta) := \varphi_R(\iota(x,\theta))$ and

$$\phi_R(x,\theta) := \varphi_R(x,\theta) - \overline{\varphi}_R(x,\theta).$$

First, $\phi_R = 0$ on $\mathbb{R}^N \times \partial B_R$ and $\phi_R = 0$ on $\mathbb{R}^N \times H$. Therefore, $\phi_R = 0$ over $\mathbb{R}^N \times \partial(H_+ \cap B_R)$. Second, observing that $\Delta_{x,\theta}\overline{\varphi}_R + (r \circ \iota)\overline{\varphi}_R = \lambda_R \overline{\varphi}_R$, one derives

$$\Delta_{x,\theta}\phi_R + (r - \lambda_R)\phi_R = (r \circ \iota - r)\,\overline{\varphi}_R \quad \text{on } \mathbb{R}^N \times (H_+ \cap B_R).$$

By the assumptions of the lemma, we have $O_2, \dots, O_K \in H_+$, so $\|\theta - O_i\| \leqslant \|\iota(\theta) - O_i\|$ for all $\theta \in H_+$ and $i \in \{2, \dots, K\}$. Therefore, since χ is decreasing on $[0, +\infty)$, we have $r \geqslant r \circ \iota$ on $\mathbb{R}^N \times H_+$. It follows that

$$\Delta_{x,\theta}\phi_R + (r - \lambda_R)\phi_R \leqslant 0 \quad \text{on } \mathbb{R}^N \times (H_+ \cap B_R). \tag{6.26}$$

Now, we want to apply the maximum principle to show that $\phi_R \geqslant 0$ over $\mathbb{R}^N \times (H_+ \cap B_R)$. The periodic principal eigenvalue of the operator

$$\mathcal{L}_R := \Delta_x + \Delta_\theta + (r - \lambda_R)$$

over $\mathbb{R}^N \times B_R$ is 0. Since $\mathbb{R}^N \times (H_+ \cap B_R)$ is a strict subset of $\mathbb{R}^N \times B_R$ and $(H_+ \cap B_R)$ is bounded, the periodic principal eigenvalue of $\mathcal{L}_R$ over $\mathbb{R}^N \times (H_+ \cap B_R)$ with Dirichlet boundary condition on $\mathbb{R}^N \times \partial(H_+ \cap B_R)$ is negative [32, Proposition 2.2 (*iii*)]. Hence, one can apply the maximum principle to the operator $\mathcal{L}_R$ over $\mathbb{R}^N \times (H_+ \cap B_R)$. Therefore, using $\phi_R = 0$ on $\mathbb{R}^N \times \partial(H_+ \cap B_R)$ and (6.26), we have $\phi_R \geqslant 0$ over $\mathbb{R}^N \times (H_+ \cap B_R)$. This allows us to conclude that $\varphi_R \geqslant \overline{\varphi}_R$ over $\mathbb{R}^N \times (H_+ \cap B_R)$, for all $R > 0$.

Recall that φ_R converges locally uniformly to φ as R grows to infinity. Therefore, taking $R \to +\infty$ gives $\varphi \geqslant \overline{\varphi}$ on $\mathbb{R}^N \times H_+$. Moreover, there holds $r \geqslant r \circ \iota$ on $\mathbb{R}^N \times H_+$, and since by the assumptions of the lemma there exists $i \in \{2, \dots, K\}$ such that $O_i \in H_+ \setminus H$, one actually has $r > r \circ \iota$ on $\mathcal{C}_i \times H_+$. As a consequence, one deduces that

$$\Delta_{x,\theta}(\varphi - \overline{\varphi}) + (r - \lambda[r])(\varphi - \overline{\varphi}) = (r \circ \iota - r)\overline{\varphi}$$

is nonpositive on $\mathbb{R}^N \times H_+$ and strictly negative on $\mathcal{C}_i \times H_+$. The elliptic strong maximum

principle then yields that $\varphi > \overline{\varphi}$ on $\mathbb{R}^N \times H_+$, i.e., $\varphi > \varphi \circ \iota$ on $\mathbb{R}^N \times H_+$.

Step 2. Lower bound on λ. For $\delta > 0$, we use the shortcut

$$r_\delta(x,\theta) := r[O_1 + \delta\xi, O_2, \dots, O_K](x,\theta).$$

As in Step 1, but changing notation in order to stress the dependence of λ_R on r, we consider the solution $(\lambda_R[r], \varphi_R)$ of the periodic principal eigenvalue problem (6.16), with $\widehat{r} = r$, and with the normalisation $\|\varphi_R\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))} = 1$. Likewise, we consider the solution $(\lambda_R[r_\delta], \varphi_{R,\delta})$ of the periodic principal eigenvalue problem (6.16), with $\widehat{r} = r_\delta$, and with the normalisation $\|\varphi_{R,\delta}\|_{L^2(\mathcal{C}\times B_{\mathbb{R}^P}(0,R))} = 1$. We have, injecting φ_R into the standard periodic Rayleigh formula applied to $\lambda_R[r_\delta]$,

$$\begin{aligned}\lambda_R[r_\delta] &\geqslant -\int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} |\nabla\varphi_R|^2 + \int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \varphi_R^2 r_\delta \\ &= \lambda_R[r] + \int_{\mathcal{C}\times B_{\mathbb{R}^P}(0,R)} \varphi_R^2 (r_\delta - r).\end{aligned}$$

(Recall that $\mathcal{C}$ is the periodicity cell $[0,1]^N$.)

By the first point of Proposition 6.4.1, as $R \to +\infty$, $\lambda_R[r]$ converges to $\lambda[r]$ and $\lambda_R[r_\delta]$ converges to $\lambda[r_\delta]$. Recall also that φ_R converges locally uniformly to φ. Finally, owing to Proposition 6.4.3 (see also Remark 6.4.4), there exist $\eta > 0$ and $A > 0$ such that for all R large enough, for all $x \in \mathbb{R}^N$ and $\theta \in B_{\mathbb{R}^P}(0,R)$,

$$0 \leqslant \varphi_R(x,\theta) \leqslant A e^{-2\eta\|\theta\|}.$$

We conclude that $(x,\theta) \mapsto \varphi_R^2(x,\theta) e^{\eta\|\theta\|}$ (extended to 0 outside $\mathbb{R}^N \times B_{\mathbb{R}^P}(0,R)$) converges in $L^2(\mathcal{C}\times\mathbb{R}^P)$ to $(x,\theta) \mapsto \varphi^2(x,\theta) e^{\eta\|\theta\|}$. Moreover, by assumption (6.10), we have $(x,\theta) \mapsto (r_\delta - r) e^{-\eta\|\theta\|} \in L^2(\mathcal{C}\times\mathbb{R}^P)$. Therefore, taking the limit $R \to +\infty$ in the above expression, we obtain:

$$\lambda[r_\delta] \geqslant \lambda[r] + \int_{\mathcal{C}\times\mathbb{R}^P} \varphi^2 (r_\delta - r).$$

We now use the fact that r and r_δ coincide when $x \in \mathcal{C}_2, \dots, \mathcal{C}_K$. We have

$$\begin{aligned}\lambda[r_\delta] &\geqslant \lambda[r] + \int_{\mathcal{C}_1}\int_{\mathbb{R}^P} \varphi^2 (r_\delta - r) \\ &= \lambda[r] + \int_{\mathcal{C}_1} \mathrm{d}x \int_{\mathbb{R}^P} \varphi^2(x,\theta) \left[\chi\left(\|\theta - O_1 - \delta\xi\|\right) - \chi\left(\|\theta - O_1\|\right)\right] \mathrm{d}\theta.\end{aligned}$$

Step 3. Conclusion. We estimate the function

$$I_\xi(\delta) := \int_{\mathcal{C}_1} \mathrm{d}x \int_{\mathbb{R}^P} \varphi^2(x,\theta) \left[\chi\left(\|\theta - O_1 - \delta\xi\|\right) - \chi\left(\|\theta - O_1\|\right)\right] \mathrm{d}\theta.$$

It satisfies $I_\xi(0) = 0$. Moreover, a computation shows

$$\frac{\mathrm{d}}{\mathrm{d}\delta}\chi(\|\theta - O_1 - \delta\xi\|) = -\chi'(\|\theta - O_1 - \delta\xi\|) \frac{\langle \theta - O_1 - \delta\xi, \xi\rangle}{\|\theta - O_1 - \delta\xi\|}.$$

Owing to assumption (6.10), χ' decays more slowly than any exponential. It follows from the exponential estimate on φ that $I'_\xi(0)$ exists and

$$I'_\xi(0) = \int_{\mathcal{C}_1} \mathrm{d}x \int_{\mathbb{R}^P} \varphi^2(x,\theta)\chi'(\|\theta - O_1\|)\frac{\langle O_1 - \theta, \xi\rangle}{\|\theta - O_1\|}\,\mathrm{d}\theta.$$

We claim that this quantity is positive. Indeed, for given $x \in \mathbb{R}^N$ we have

$$\int_{\mathbb{R}^P} \varphi^2(x,\theta)\chi'(\|\theta - O_1\|)\frac{\langle O_1 - \theta, \xi\rangle}{\|\theta - O_1\|}\,\mathrm{d}\theta \\ = \int_{H_+} \Big(\varphi^2(x,\theta) - \varphi^2(\iota(x,\theta))\Big)\chi'(\|\theta - O_1\|)\frac{\langle O_1 - \theta, \xi\rangle}{\|\theta - O_1\|}\,\mathrm{d}\theta,$$

whence, recalling that χ is decreasing, that $\varphi > \varphi\circ\iota$ on $\mathbb{R}^N \times (H_+ \setminus H)$ (by Step 1) and that $\langle O_1 - \theta, \xi\rangle > 0$ for $\theta \in H_+ \setminus H$, one infers that $I'_\xi(0) > 0$. Finally, consider, for given $m > 0$ as in the statement, the compact set

$$\mathcal{S}_m := \Big\{\xi' \in \mathbb{R}^P \,/\, \big\|\xi'\big\| = 1, \big\langle \xi', O_i - O_1\big\rangle \geqslant 0 \text{ for all } i \in \{2,\dots,K\}, \max_{i\in\{2,\dots,K\}} \big\langle \xi', O_i - O_1\big\rangle \geqslant m\Big\}.$$

Noticing that the mapping $\xi' \mapsto I'_{\xi'}(0)$ is continuous, we find that

$$C_1 := \inf_{\xi'\in\mathcal{S}_m} I'_{\xi'}(0) = \min_{\xi'\in\mathcal{S}_m} I'_{\xi'}(0) \\ = \min_{\xi'\in\mathcal{S}_m} \int_{\mathcal{C}_1} \mathrm{d}x \int_{\mathbb{R}^P} \varphi^2(x,\theta)\chi'(\|\theta - O_1\|)\frac{\langle O_1 - \theta, \xi'\rangle}{\|\theta - O_1\|}\,\mathrm{d}\theta$$

is positive. The quantity C_1 only depends on m, P, χ, and φ, so C_1 only depends on m and $r[O_1,\dots,O_K]$.

On the other hand,

$$\frac{\mathrm{d}^2}{\mathrm{d}\delta^2}\chi(\|\theta - O_1 - \delta\xi\|) = \chi''(\|\theta - O_1 - \delta\xi\|)\frac{\langle \theta - O_1 - \delta\xi, \xi\rangle^2}{\|\theta - O_1 - \delta\xi\|^2} \\ + \frac{\chi'(\|\theta - O_1 - \delta\xi\|)}{\|\theta - O_1 - \delta\xi\|}\left(1 - \frac{\langle \delta\xi + O_1 - \theta, \xi\rangle^2}{\|\theta - O_1 - \delta\xi\|^2}\right).$$

Using the Cauchy-Schwarz inequality and $\|\xi\| = 1$, we have $\langle \theta - O_1 - \delta\xi, \xi\rangle^2 \leqslant \|\theta - O_1 - \delta\xi\|^2$. Recalling that $\chi' \leqslant 0$ gives

$$\left|\frac{\mathrm{d}^2}{\mathrm{d}\delta^2}\chi(\|\theta - O_1 - \delta\xi\|)\right| \leqslant |\chi''(\|\theta - O_1 - \delta\xi\|)| - \frac{\chi'(\|\theta - O_1 - \delta\xi\|)}{\|\theta - O_1 - \delta\xi\|}.$$

Therefore, owing to assumption (6.10) and the exponential estimate on φ, I''_ξ exists and

$$|I''_\xi(\delta)| \leqslant \int_{\mathcal{C}_1} \mathrm{d}x \int_{\mathbb{R}^P} \varphi^2(x,\theta)\Big(|\chi''(\|\theta - O_1 - \delta\xi\|)| - \frac{\chi'(\|\theta - O_1 - \delta\xi\|)}{\|\theta - O_1 - \delta\xi\|}\Big)\,\mathrm{d}\theta.$$

By Proposition 6.4.3 and hypothesis (6.10) (which implies in particular that $\frac{\chi'(R)}{R}$ is bounded for R near 0), the right hand side is bounded for $\delta \in [0,1]$, by a constant C_2 only depending

on φ, χ and P, and thus depending only on $r[O_1,\dots,O_K]$.

Summing up, we have shown that

$$\forall \delta \in [0,1], \quad I_\xi(\delta) \geqslant C_1\delta - \frac{1}{2}C_2\delta^2 \geqslant C_1\delta - C_2\delta^2,$$

which concludes the proof. □

We are now ready to prove Theorem 6.3.5, which is central to the whole Section 6.6.

Proof of Theorem 6.3.5. Throughout the proof, we use the shortcut

$$r^\theta := r[\theta, O_2, \dots, O_K], \qquad \theta \in \mathbb{R}^P.$$

The hypothesis that $s \mapsto \|\gamma(s) - O_i\|$ is nonincreasing rewrites as follows:

$$\forall i \in \{2,\dots,K\}, \qquad \Big\langle \gamma'(s), O_i - \gamma(s) \Big\rangle \geqslant 0 \quad \text{for all} \quad s \in [0,1]. \tag{6.27}$$

We first work with the additional assumption that

$$\exists j \in \{2,\dots,K\}, \qquad \Big\langle \gamma'(s), O_j - \gamma(s) \Big\rangle > 0 \quad \text{for all} \quad s \in [0,1]. \tag{6.28}$$

Step 1. Under conditions (6.27)–(6.28)**, the function** $s \mapsto \lambda[r^{\gamma(s)}]$ **is strictly increasing.** Fix $s_0 \in [0,1)$. To start with, we observe that the nonincreasing monotonicity of $s \mapsto \|\gamma(s) - O_i\|$, $i = 2,\dots,K$, yields, for $s \in (s_0, 1]$,

$$\begin{aligned} \|\gamma(s_0) - O_i\|^2 &\geqslant \|\gamma(s) - O_i\|^2 \\ &= \|\gamma(s_0) - O_i\|^2 + \|\gamma(s) - \gamma(s_0)\|^2 + 2\left\langle \gamma(s) - \gamma(s_0), \gamma(s_0) - O_i \right\rangle, \end{aligned}$$

whence

$$\langle \gamma(s) - \gamma(s_0), O_i - \gamma(s_0) \rangle \geqslant 0.$$

We call

$$\xi_s := \frac{\gamma(s) - \gamma(s_0)}{s - s_0}.$$

Thus, we have $\langle \xi_s, O_i - \gamma(s_0) \rangle \geqslant 0$ for all $i = 2,\dots,K$ and $s \in (s_0, 1]$. Moreover, since $\xi_s \to \gamma'(s_0)$ as $s \to s_0$ and we are assuming in the present case that $\langle \gamma'(s_0), O_j - \gamma(s_0) \rangle > 0$, there exists $s_1 \in (s_0, 1]$ such that

$$\inf_{s \in (s_0, s_1]} \langle \xi_s, O_j - \gamma(s_0) \rangle > 0.$$

We can then apply Lemma 6.6.1 to $O_1 = \gamma(s_0)$ and $\xi = \xi_s / \|\xi_s\|$ and find two positive constants C_1, C_2 such that, for $s \in (s_0, s_1]$, it holds

$$\lambda[r^{\gamma(s)}] = \lambda[r^{\gamma(s_0) + (s - s_0)\xi_s}] \geqslant \lambda[r^{\gamma(s_0)}] + C_1(s - s_0)\|\xi_s\| - C_2(s - s_0)^2\|\xi_s\|^2.$$

As a consequence, up to reducing s_1 if need be, we have

$$\forall s \in (s_0, s_1], \quad \lambda[r^{\gamma(s)}] > \lambda[r^{\gamma(s_0)}]. \tag{6.29}$$

The continuity of $s \mapsto \lambda[r^{\gamma(s)}]$, guaranteed by Lemma 6.4.6, allows us to define

$$\bar{\lambda} := \max_{s\in[0,1]} \lambda[r^{\gamma(s)}].$$

Then, property (6.29) implies that such a maximum cannot be attained at any point $\bar{s} \in [0,1)$. This shows that $\lambda[r^{\gamma(1)}] = \bar{\lambda} > \lambda[r^{\gamma(0)}]$. Up to rescaling, this inequality holds true in any subinterval of $[0,1]$, showing the strict monotonicity of $s \mapsto \lambda[r^{\gamma(s)}]$.

Step 2. Without condition (6.28)**, the function** $s \mapsto \lambda[r^{\gamma(s)}]$ **is nondecreasing.** The idea here is to slightly move the points $O_2, \dots, O_K$ in order to fulfill condition (6.28), apply the result in such a case, and then come back to the original $O_2, \dots, O_K$ and use the continuity of $\lambda[r[O_1, \dots, O_K]]$ with respect to $O_2, \dots, O_K$.

Specifically, fix $s_0 \in [0,1)$. For $\ell > 0$ and $i = 2, \dots, K$, we call

$$O_i^\ell := O_i + \ell\gamma'(s_0).$$

By (6.27), we have for all $s \in [s_0, 1]$,

$$\forall i = 2, \dots, K, \qquad \Big\langle \gamma'(s), O_i^\ell - \gamma(s) \Big\rangle = \Big\langle \gamma'(s), O_i - \gamma(s) \Big\rangle + \ell \Big\langle \gamma'(s), \gamma'(s_0) \Big\rangle \geqslant \ell \Big\langle \gamma'(s), \gamma'(s_0) \Big\rangle.$$

Therefore, by the continuity of γ', there exists $s_1 > s_0$ such that the above terms are strictly positive for all $s \in [s_0, s_1]$ and all $\ell > 0$. Then, Step 1 yields

$$\forall s \in (s_0, s_1], \qquad \lambda[r[\gamma(s), O_2^\ell, \dots, O_K^\ell] > \lambda[r[\gamma(s_0), O_2^\ell, \dots, O_K^\ell]].$$

This being true for all $\ell > 0$, letting $\ell \to 0$ and using the continuity of $\lambda[r[O_1, \dots, O_K]]$, provided by Lemma 6.4.6, one gets

$$\forall s \in [s_0, s_1], \qquad \lambda[r[\gamma(s), O_2, \dots, O_K] \geqslant \lambda[r[\gamma(s_0), O_2, \dots, O_K]].$$

Then, take $S \in [0,1)$. The above property, which holds for any $s_0 \in [0,1)$, implies that the quantity

$$S' := \max\{S_1 \in [S,1] \ / \ \lambda[r[\gamma(s), O_2, \dots, O_K]] \geqslant \lambda[r[\gamma(S), O_2, \dots, O_K]] \text{ for all } s \in [S, S_1]\},$$

whose existence is guaranteed by the continuity of $\lambda[r[O_1, \dots, O_K]]$, is given by $S' = 1$. This shows the monotonicity.

Step 3. Conclusion under the condition $\|\gamma(1) - O_j\| < \|\gamma(0) - O_j\|$ **for some** $j \in \{2, \dots, K\}$**.** The condition $\|\gamma(1) - O_j\| < \|\gamma(0) - O_j\|$ implies the existence of some $\bar{s} \in [0,1)$ at which $\langle \gamma'(\bar{s}), O_j - \gamma(\bar{s}) \rangle > 0$. By continuity, this inequality holds true in some nontrivial interval $[\bar{s}, s'] \subset [0,1]$. Applying Step 1 we infer $\lambda[r^{\gamma(s')}] > \lambda[r^{\gamma(\bar{s})}]$. This, together with the weak monotonicity given by Step 2, yields $\lambda[r^{\gamma(1)}] > \lambda[r^{\gamma(0)}]$ and concludes the proof. □

Remark 6.6.2. Let us now show how the condition (6.11) in Theorem 6.3.5 can be weakened by

$$\lambda[r[\gamma(0), O_2, \dots, O_K] > \chi_\infty. \tag{6.30}$$

Condition (6.11) is only used in the proof of Theorem 6.3.5 to ensure that

$$\lambda[r[\gamma(s), O_2, \dots, O_K] > \chi_\infty \quad \text{for all } s \in (0,1),$$

allowing us to apply Lemma 6.6.1 at $(\gamma(s), O_2, \dots, O_K)$ for any $s \in (0,1)$. In fact, the above property holds as soon as (6.30) is satisfied. Indeed, assume that (6.30) holds and, by contradiction, that

$$s_0 := \sup \{ s \in (0,1) \ / \ \lambda[r[\gamma[s], O_2, \dots, O_K]] > \chi_\infty \} < 1.$$

Then, by continuity, cf. Lemma 6.4.6, we have $s_0 > 0$ and $\lambda[r[\gamma[s_0], O_2, \dots, O_K]] = \chi_\infty$. However, applying Theorem 6.3.5 to $\gamma : [0, s_0] \to \mathbb{R}^P$, we have $\lambda[r[\gamma[s_0], O_2, \dots, O_K]] \geqslant \lambda[r[\gamma[0], O_2, \dots, O_K]] > \chi_\infty$. This is a contradiction. Thus $s_0 = 1$ and the proof of Theorem 6.3.5 holds.

6.6.2 Dilatation (Theorem 6.3.8)

We now prove Theorem 6.3.8, which deals with dilatations of the phenotypic space. First, we prove a monotonicity result (item (i) of Theorem 6.3.8). Next, we will make the ratio of the dilatation tend to 0 or $+\infty$ (items (ii)–(iv) of Theorem 6.3.8).

Proof of Theorem 6.3.8 (i). If $O_1, \dots, O_K$ satisfy property (6.15), then for all $a > 0$, $aO_1, \dots, aO_K$ satisfy property (6.15) (with $\mathcal{O}$ replaced with $a\mathcal{O}$). Hence, to prove the result, it is sufficient to prove

$$\lambda[r[O_1, \dots, O_K]] < \lambda[r[aO_1, \dots, aO_K]]$$

for all $a \in (0,1)$ and any distinct points $O_1, \dots, O_K$ satisfying (6.15). We let $\mathcal{H}$ be the smallest affine subspace containing all the O_i. Up to orthogonal projection on $\mathcal{H}$, we may assume that $\mathcal{O} \in \mathcal{H}$. For convenience, we assume that $\mathcal{O} = 0$ (we can get this case by translation). We let, for $a \in (0,1)$,

$$\mathcal{Q} := \left\{ (R_1, \dots, R_K) \in \left(\mathbb{R}^P\right)^K \ / \ \forall i \in \{1, \dots, K\}, R_i \in [O_i, aO_i] \right\},$$

where $[O_i, aO_i]$ denotes the segment between O_i and aO_i. We point out that $\mathcal{Q} \subset \mathcal{H}^K$. The set $\mathcal{Q}$ is compact and the function $(O_1, \dots, O_K) \mapsto \lambda[r[O_1, \dots, O_K]]$ is continuous (see Lemma 6.4.6). Thus there exists $(Q_1, \dots, Q_K) \in \mathcal{Q}$ such that

$$\lambda[r[Q_1, \dots, Q_K]] = \max \{ \lambda[r[R_1, \dots, R_K]] \ / \ (R_1, \dots, R_K) \in \mathcal{Q} \}. \tag{6.31}$$

We assume that there exist $1 \leqslant i \leqslant K$ such that $Q_i \neq aO_i$. We shall reach a contradiction.

We define $r_j := 0$ if $O_j = 0$ and

$$r_j := \frac{\|Q_j\|}{\|O_j\|}$$

otherwise. Up to relabelling the points, we can assume that

$$r_1 = \max_{j=1,\dots,K} r_j.$$

Since the O_i are distinct points, we cannot have $r_j = 0$ for all j. So $r_1 > 0$ and $O_1 \neq 0$. Moreover, we must have $r_1 > a$ (otherwise we would have $(Q_1, \dots, Q_K) = (aO_1, \dots, aO_K)$).

For $j = 1, \dots, K$, we have

$$\begin{aligned}\langle Q_1 - Q_j, Q_1 \rangle &= \langle r_1 O_1 - r_j O_j, r_1 O_1 \rangle \\ &= r_j \langle O_1 - O_j, r_1 O_1 \rangle + (r_1 - r_j) \langle O_1, r_1 O_1 \rangle .\end{aligned}$$

Thus, by assumption (6.15), for all $j = 1, \dots, K$,

$$\langle Q_1 - Q_j, Q_1 \rangle \geqslant 0.$$

If we had $\langle Q_1 - Q_j, Q_1 \rangle = 0$ for all j, then, owing to $Q_1 \neq 0$, the points Q_j would belong to an affine subspace $\mathcal{H}'$ of $\mathcal{H}$, with $0 \notin \mathcal{H}'$. Recalling that $0 = \mathcal{O} \in \mathcal{H}$, we have $\mathcal{H}' \neq \mathcal{H}$, $\mathcal{H}' \subset \mathcal{H}$. This contradicts the assumption of minimality of $\mathcal{H}$.

Thus there exists $j_0 \in \{2, \dots, K\}$ such that $\langle Q_1 - Q_{j_0}, Q_1 \rangle > 0$. We can now apply Lemma 6.6.1 with $O_i = Q_i$ (for all $i = 1, \dots, K$) and $\xi = -Q_1$. Thus, for small $t > 0$, we have

$$\lambda[r[Q_1 + \delta\xi, Q_2, \dots, Q_K]] > \lambda[r[Q_1, \dots, Q_K]].$$

Moreover, since $r_1 > a$, we also have for small $t > 0$: $Q_1 + t\xi \in [O_1, aO_1]$. With (6.31), we get a contradiction. Hence $(Q_1, \dots, Q_K) = (aO_1, \dots, aO_K)$. This concludes the proof. □

Proof of Theorem 6.3.8 (ii). The function $(O_1, \dots, O_K) \mapsto \lambda[r[O_1, \dots, O_K]]$ is continuous (Lemma 6.4.6) so, by Corollary 6.4.2,

$$\lim_{a \to 0} \lambda[r[aO_1, \dots, aO_K]] = \lambda[r[0, \dots 0]] = \lambda[\chi].$$

□

To derive the limit of $\lambda[r[aO_1, \dots, aO_K]]$ as $a \to +\infty$, we crucially use Lemma 6.4.7.

Proof of Theorem 6.3.8 (iii)–(iv). Let us prove that

$$\lim_{a \to +\infty} \lambda[r^a] = \max_{i=1,\dots,K} \lambda[i].$$

We first assume that $\chi_\infty > -\infty$. Recall that r_i is defined in Definition 6.3.1 and that $\lambda[i] := \lambda[r_i]$. For all $a > 0$ and $i = 1, \dots, K$, we have $r[aO_1, \dots, aO_K](x, \theta) \geqslant r_i(x, \theta - aO_i)$. Thus

$$\lambda[r[aO_1, \dots, aO_K]] \geqslant \max_{i=1,\dots,K} \lambda[r_i(x, \cdot - aO_i)] = \max_{i=1,\dots,K} \lambda[i].$$

Let us now prove that the reverse inequality (and thus equality) holds in the limit $a \to +\infty$. We first assume that $\chi(R) = \chi_\infty$ for R large enough, and we then prove the general result (in both cases $\chi > -\infty$ and $\chi = -\infty$) using Lemma 6.4.7.

Step 1. If $\chi(R) = \chi_\infty$ for R large enough. We first assume that there exists $R_0 > 0$ such that $\chi(R) = \chi_\infty$ for all $R \geqslant R_0$ (hence we relax the assumption that χ is strictly decreasing, but we keep χ nonincreasing). We let $\varphi_i > 0$ be defined by Proposition 6.4.1 (*ii*) with $\widehat{r} = r_i$; in particular

$$\Delta_{x,\theta} \varphi_i + r_i \varphi_i = \lambda[i] \varphi_i.$$

Now, for $a > 0$, we let

$$\varphi^a(x, \theta) := \sum_{i=1}^{K} \varphi_i(x, \theta - aO_i).$$

Take $\delta > 0$. Let us show that for a large enough, we have

$$\Delta_{x,\theta}\varphi^a + r^a\varphi^a \leqslant \left(\max_{i=1,\dots,K} \lambda[i] + \delta\right)\varphi^a, \tag{6.32}$$

where we used the shortcut $r^a := r[aO_1,\dots,aO_K]$. Take $i \in \{1,\dots,K\}$ and $x \in \mathcal{C}_i$. For $j \neq i$, we have $(\Delta_{x,\theta} + r^a(x,\cdot))\varphi_j^a(x,\cdot) = (\lambda[j] + r^a(x,\cdot) - \chi_\infty)\varphi_j^a(x,\cdot)$. For $j = i$, we have $(\Delta_{x,\theta} + r^a(x,\cdot))\varphi_j^a(x,\cdot) = \lambda[j]\varphi_j^a(x,\cdot)$. We get, for $x \in \mathbb{R}^N$ and $\theta \in \mathbb{R}^P$, for $i \in \{1,\dots,K\}$ such that $x \in \mathcal{C}_i + \mathbb{Z}^N$,

$$(\Delta_{x,\theta} + r^a(x,\theta))\varphi^a(x,\theta) \leqslant \left(\max_{i=1,\dots,K} \lambda[i]\right)\varphi^a(x,\theta) + \sum_{j\neq i}(r^a(x,\theta) - \chi_\infty)\varphi_j^a(x,\theta - aO_i).$$

First, the assumption of Step 1 means that for $\|\theta - aO_i\| \geqslant R_0$ and $x \in \mathcal{C}_i$, we have $r^a(x,\theta) = \chi_\infty$. Thus (6.32) holds for all $a > 0$, $i = 1,\dots,K$, $x \in \mathcal{C}_i$ and $\theta \in \mathbb{R}^P$ such that $\|\theta - aO_i\| \geqslant R_0$.

Second, we use the assumption that for all $i = 1,\dots,K$, we have $\lambda[i] > \chi_\infty$. By Proposition 6.4.3 (see Remark 6.4.4) there exists $\eta > 0$ such that for all i,

$$\varphi_i(x,\theta) = O(e^{-\eta\|\theta\|}) \qquad \text{as } \|\theta\| \to +\infty.$$

Now, let

$$\varepsilon := \min_{i=1,\dots,K}\left(\inf_{x\in\mathcal{C}_i,\ \|\theta\|\leqslant R_0} \varphi_i(x,\theta)\right),$$

which is positive since the φ_i are positive and continuous on $\mathbb{R}^N \times \mathbb{R}^P$. By the above estimate, there exists $R_1 > R_0$ such that for all $i = 1,\dots,K$,

$$\forall x \in \mathcal{C}_i,\ \forall \theta \in \mathbb{R}^P \setminus B_{\mathbb{R}^P}(0,R_1), \qquad \varphi_i(x,\theta) < \frac{\delta\varepsilon}{K(\sup r - \chi_\infty)}. \tag{6.33}$$

Take $a_0 > 0$ such that for all $a > a_0$ and for all $i \neq j$, we have $\|aO_i - aO_j\| > 2R_1$. For $a > a_0$, $i = 1,\dots,K$, $x \in \mathcal{C}_i$ and $\|\theta - aO_i\| \leqslant R_1$, we have, thanks to estimate (6.33),

$$\sum_{j\neq i}(r^a - \chi_\infty)\varphi_j^a(x,\theta - aO_i) \leqslant (\sup r - \chi_\infty)\frac{\delta\varepsilon}{\sup r - \chi_\infty} = \delta\varepsilon.$$

Hence, for $x \in \mathcal{C}_i$ and $\|\theta - aO_i\| \leqslant R_0 < R_1$,

$$(\Delta_{x,\theta} + r)\varphi^a \leqslant \lambda[i]\varphi^a + \delta\varepsilon \leqslant (\lambda[i] + \delta)\varphi^a.$$

Thus (6.32) holds also for $\|\theta - aO_i\| \leqslant R_0$, provided $a \geqslant a_0$. Thus (6.32) holds for all $\delta > 0$ as long as a is large enough (depending on δ). We conclude

$$\lim_{a\to+\infty} \lambda[r[aO_1,\dots,aO_K]] = \max_{i=1,\dots,K} \lambda[i].$$

Step 2. Conclusion for general χ. Consider $M > \chi_\infty$ and define r^M, $r^{M,a}$ and $\lambda^M[i]$ in the same way as r, r^a and $\lambda[i]$ but with $\chi^M := \max\{\chi, M\}$ instead of χ. By Step 1, we have, for all $M > \chi_\infty$,

$$\lim_{a\to+\infty} \lambda[r^{M,a}] = \max_{i=1,\dots,K} \lambda^M[i].$$

As $M \searrow \chi_\infty$, we have $\lambda^M[i] \searrow \lambda[i]$ (using Lemma 6.4.7, (i) or (ii) depending on χ_∞). Finally, using the decreasing monotonicity in a (Theorem 6.3.8 (i)) and the nondecreasing monotonicity of $M \mapsto \lambda[r^{M,a}]$, we have

$$\begin{aligned}\lim_{a\to+\infty} \lambda[r^a] = \inf_{a>0} \lambda[r^a] &= \inf_{M>\chi_\infty, a>0} \lambda[r^{M,a}] \\ &= \inf_{M>\chi_\infty} \left(\lim_{a\to+\infty} \lambda[r^{M,a}] \right).\end{aligned}$$

Therefore, using Step 1 and then the nondecreasing monotonicity of $M \mapsto \lambda[r^{M,a}]$, we obtain

$$\begin{aligned}\lim_{a\to+\infty} \lambda[r^a] &= \inf_{M>\chi_\infty} \left(\max_{i=1,\dots,K} \lambda^M[i] \right) \\ &= \lim_{M\searrow\chi_\infty} \left(\max_{i=1,\dots,K} \lambda^M[i] \right).\end{aligned}$$

Lemma 6.4.7 gives the conclusion:

$$\lim_{a\to+\infty} \lambda[r^a] = \max_{i=1,\dots,K} \lambda[i].$$

□

6.6.3 Global and partial optimisation results (Theorem 6.3.9 and Proposition 6.3.10)

The goal of this section is to prove Theorem 6.3.9 and Proposition 6.3.10. In the sequel, we denote by $\mathrm{Conv}(A)$ the convex hull of a given set $A \subset \mathbb{R}^P$, i.e. the smallest convex set containing A.

The following geometric lemma is useful for the proof of Theorem 6.3.9.

Lemma 6.6.3. *Let $K \geqslant 3$ and let $Q_1, \dots, Q_K \in \mathbb{R}^P$ be such that $Q_1 \neq Q_2$ and*

$$Q_1 \in \mathrm{Conv}(\{Q_2, \dots, Q_K\}), \qquad Q_2 \in \mathrm{Conv}(\{Q_1, Q_3, \dots, Q_K\}).$$

Then Q_1 and Q_2 belong to $\mathrm{Conv}(\{Q_3, \dots, Q_K\})$.

Proof. By the assumptions of the lemma, there exist $a_i, b_i \in \mathbb{R}$, $i = 1, \dots, K$, such that

$$Q_1 = \sum_{i=2}^K a_i Q_i, \qquad Q_2 = b_1 Q_1 + \sum_{i=3}^K b_i Q_i$$

with

$$a_i, b_i \geqslant 0, \qquad \sum_{i=2}^K a_i = b_1 + \sum_{i=3}^K b_i = 1.$$

We then have:

$$Q_2 = a_2 b_1 Q_2 + \sum_{i=3}^K (a_i b_1 + b_i) Q_i.$$

Since $Q_1 \neq Q_2$, we have $a_2 b_1 \neq 1$, whence

$$Q_2 = \sum_{i=3}^{K} \frac{b_1 a_i + b_i}{1 - a_2 b_1} Q_i.$$

We have $\frac{b_1 a_i + b_i}{1 - a_2 b_1} \geqslant 0$ and

$$\sum_{i=3}^{K} \frac{b_1 a_i + b_i}{1 - a_2 b_1} = \frac{1}{1 - a_2 b_1} \left(b_1 (1 - a_2) + 1 - b_1 \right) = 1,$$

so $Q_2 \in \mathrm{Conv}(\{Q_3, \ldots, Q_K\})$. Switching the roles of Q_1 and Q_2, one shows that $Q_2 \in \mathrm{Conv}(\{Q_3, \ldots, Q_K\})$. □

We prove the statements of Theorem 6.3.9 in a different order.

Proof of Theorem 6.3.9 (ii). We start by proving the statement (*ii*). Let $O_{H+1}, \ldots, O_K \in \mathbb{R}^P$ be given. Fix $M > \|O_K\|$ and consider the compact set

$$\mathcal{Q}_{H,M} := \left\{ (R_1, \ldots, R_H) \in (\mathbb{R}^P)^H \,/\, \|R_i\| \leqslant M \text{ for all } 1 \leqslant i \leqslant H \right\}.$$

By the continuity of $(R_1, \ldots, R_H) \mapsto \lambda[r[R_1, \ldots, R_H, O_{H+1}, \ldots, O_K]]$, there exists $(Q_1, \ldots, Q_H) \in \mathcal{Q}_{H,M}$ such that

$$\lambda[r[Q_1, \ldots, Q_H, O_{H+1}, \ldots, O_K]] = \max_{(R_1, \ldots, R_H) \in \mathcal{Q}_{H,M}} \lambda[r[R_1, \ldots, R_H, O_{H+1}, \ldots, O_K]].$$

We want to avoid repetitions among the points $Q_1, \ldots, Q_H$, so we extract from them the points $Q'_1, \ldots, Q'_{H'}$ (for some $1 \leqslant H' \leqslant H$), in such a way that $\{Q_1, \ldots, Q_H\} = \{Q'_1, \ldots, Q'_{H'}\}$ and $Q'_i \neq Q'_j$ if $i \neq j$. We then merge together the patches $\mathcal{C}_i$ with the same optimum Q'_j. Namely we call

$$\mathcal{C}'_j := \bigcup_{1 \leqslant i \leqslant H \,:\, Q_i = Q'_j} \mathcal{C}_i.$$

We claim that necessarily

$$\forall j \in \left\{1, \ldots, H'\right\}, \qquad Q'_j \in \mathrm{Conv}\left(\left\{ Q'_1, \ldots, Q'_{j-1}, Q'_{j+1}, \ldots, Q'_{H'}, O_{H+1}, \ldots, O_K \right\} \right). \tag{6.34}$$

Assume by contradiction that the above property fails. Up to relabelling the points $Q'_1, \ldots, Q'_{H'}$, we can assume without loss of generality that it fails for $j = 1$, that is, $Q'_1 \notin \mathrm{Conv}(A)$ with

$$A := \left\{ Q'_2, \ldots, Q'_{H'}, O_{H+1}, \ldots, O_K \right\}.$$

There exists then an open half-space $\mathcal{V}^+ \subset \mathbb{R}^P$ such that $Q'_1 \in \partial \mathcal{V}^+$ and $\mathrm{Conv}(A) \subset \mathcal{V}^+$. Let ξ be the unit vector orthogonal to $\partial \mathcal{V}^+$ and pointing towards $\mathrm{Conv}(A)$. Set $\gamma(t) := Q_1 + \varepsilon t \xi$, for some $\varepsilon > 0$. For $\varepsilon > 0$ small enough, γ satisfies the assumptions of Theorem 6.3.5, with strict inequality, which implies

$$\lambda[r[\gamma(1), Q_2, \ldots, Q_H, O_{H+1}, \ldots, O_K]] > \lambda[r[Q_1, Q_2, \ldots, Q_H, O_{H+1}, \ldots, O_K]].$$

Moreover, it may happen that $\|Q_1\| = M$, but in such a case $\mathcal{V}^+$ necessarily contains the origin, because it contains O_K and $\|O_K\| < M$. Therefore, up to reducing ε if need be, one

has that $\|\gamma(1)\| < M$, hence $(\gamma(1), Q_2, \dots, Q_H) \in \mathcal{Q}_{H,M}$. We have found a contradiction with the optimality of $(Q_1, \dots, Q_H)$ in $\mathcal{Q}_{H,M}$. This proves the necessity of condition (6.34).

Now, we show iteratively that the following property holds for any $n \in \{1, \dots, H'+1\}$:

$$\forall j \in \Big\{1, \dots, H'\Big\}, \qquad Q'_j \in \mathrm{Conv}\Big(\{Q'_i \ / \ n \leqslant i \leqslant H', \ i \neq j\} \cup \{O_{H+1}, \dots, O_K\}\Big). \tag{6.35}$$

The case $n = 1$ is precisely condition (6.34). We then assume that (6.35) holds for some $n \in \{1, \dots, H'\}$, and we want to show that

$$\forall j \in \Big\{1, \dots, H'\Big\}, \qquad Q'_j \in \mathrm{Conv}\Big(\{Q'_i \ / \ n+1 \leqslant i \leqslant H', \ i \neq j\} \cup \{O_{H+1}, \dots, O_K\}\Big). \tag{6.36}$$

Thanks to the iterative assumption (6.35), property (6.36) automatically holds for $j = n$. Thus

$$\mathrm{Conv}\Big(\{Q'_i \ / \ n \leqslant i \leqslant H'\} \cup \{O_{H+1}, \dots, O_K\}\Big) \\ = \mathrm{Conv}\Big(\{Q'_i \ / \ n+1 \leqslant i \leqslant H'\} \cup \{O_{H+1}, \dots, O_K\}\Big),$$

so, by the iterative assumption (6.35), property (6.36) also holds for $1 \leqslant j < n$. For $n < j \leqslant H'$, one can apply Lemma 6.6.3, with $Q_1 = Q'_j$, $Q_2 = Q'_n$ and $\{Q'_n, \dots, Q'_H, O_{H+1}, \dots, O_K\}$ instead of $\{Q_1, \dots, Q_K\}$. Again, we obtain that property (6.36) holds for $n < j \leqslant H'$.

We have then shown that (6.35) holds for all $n \in \{1, \dots, H'+1\}$. In the case $n = H'+1$ means that $Q'_j \in \mathrm{Conv}(\{O_{H+1}, \dots, O_K\})$ for all $j \in \{1, \dots, H\}$. Recalling that any Q_i coincides with one of the Q'_j, we have eventually shown that all the points of the maximiser $(Q_1, \dots, Q_H)$ on $\mathcal{Q}_{H,M}$ necessarily belong to $\mathrm{Conv}(\{O_{H+1}, \dots, O_K\})$.

Finally, notice that any configuration $R_1, \dots, R_H \in \mathbb{R}^P$ belongs to $\mathcal{Q}_{H,M}$ for M large enough. Therefore, what we have shown above yields that, for any $R_1, \dots, R_H \in \mathbb{R}^P$, it holds

$$\lambda[r[R_1, \dots, R_H, O_{H+1}, \dots, O_K]] \leqslant \max_{R_1, \dots, R_H \in \mathrm{Conv}(\{O_{H+1}, \dots, O_K\})} \lambda[r[R_1, \dots, R_H, O_{H+1}, \dots, O_K]],$$

(the latter maximum exists because $\mathrm{Conv}(\{O_{H+1}, \dots, O_K\})$ is compact) with a strict inequality if $\{R_1, \dots, R_H\} \not\subset \mathrm{Conv}(\{O_{H+1}, \dots, O_K\})$. This concludes the proof of (ii). □

Proof of Theorem 6.3.9 (i). Statement (i) immediately follows from statement (ii). Indeed, for any $O_1, \dots, O_K \in \mathbb{R}^P$, applying the latter with $H = K - 1$ yields

$$\lambda[r[O_1, \dots, O_K]] \leqslant \lambda[r[O_K, \dots, O_K]],$$

with a strict inequality unless $O_1 = O_2 = \ldots = O_K$. Observe that $r[O_K, \dots, O_K](x, \theta) \equiv \chi(\|\theta - O_K\|)$. Hence, owing to the invariance by translations of the generalised principal eigenvalue, we conclude from Corollary 6.4.2 that $\lambda[r[O_K, \dots, O_K]] = \lambda[\chi]$. □

Proof of Theorem 6.3.9 (iii). Assume that $\chi(\|\theta\|) = A - \|\theta\|^2$ for some constant $A > 0$. We have

$$\overline{r}(\theta) := \int_{\mathcal{C}} r(x, \theta) \, \mathrm{d}x = A - \sum_{i=1}^{K} |\mathcal{C}_i| \, \|\theta - O_i\|^2 .$$

We first compute explicitly $\lambda[\overline{r}]$. We have:

$$\overline{r}(\theta) = A - \langle \theta, \theta \rangle + 2\sum_{i=1}^{K} |\mathcal{C}_i| \langle \theta, O_i \rangle - \sum_{i=1}^{K} |\mathcal{C}_i| \langle O_i, O_i \rangle ,$$

where $\langle \cdot, \cdot \rangle$ is the Euclidean scalar product. On the one hand,

$$\left\| \theta - \sum_{i=1}^{K} |\mathcal{C}_i| O_i \right\|^2 = \langle \theta, \theta \rangle - 2\sum_{i=1}^{K} |\mathcal{C}_i| \langle \theta, O_i \rangle + \sum_{i=1}^{K} |\mathcal{C}_i|^2 \langle O_i, O_i \rangle + \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \langle O_i, O_j \rangle .$$

On the other hand,

$$\begin{aligned} \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \|O_i - O_j\|^2 &= \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \left(\langle O_i, O_i \rangle + \langle O_j, O_j \rangle - 2 \langle O_i, O_j \rangle \right) \\ &= 2\sum_{i=1}^{K} |\mathcal{C}_i| \left(\sum_{j=1, j\neq i}^{K} |\mathcal{C}_j| \right) \langle O_i, O_i \rangle - 2 \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \langle O_i, O_j \rangle , \end{aligned}$$

so

$$\begin{aligned} \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \|O_i - O_j\|^2 &= 2\sum_{i=1}^{K} |\mathcal{C}_i| (1 - |\mathcal{C}_i|) \langle O_i, O_i \rangle - 2 \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \langle O_i, O_j \rangle \\ &= 2\sum_{i=1}^{K} |\mathcal{C}_i| \langle O_i, O_i \rangle - 2\sum_{i=1}^{K} |\mathcal{C}_i|^2 \langle O_i, O_i \rangle - 2 \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \langle O_i, O_j \rangle . \end{aligned}$$

Therefore

$$\overline{r}(\theta) = A - \left\| \theta - \sum_{i=1}^{K} |\mathcal{C}_i| O_i \right\|^2 - \frac{1}{2} \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \|O_i - O_j\|^2 .$$

Let us denote

$$\mathcal{O} = \sum_{i=1}^{K} |\mathcal{C}_i| O_i .$$

Setting $\overline{\varphi}(x, \theta) = e^{-(\|\theta\| - \mathcal{O})^2/2} > 0$ gives

$$\Delta_{x,\theta} \overline{\varphi} + \overline{r}\, \overline{\varphi} = \lambda \overline{\varphi},$$

with (recalling that P is the dimension of the phenotypic space)

$$\lambda := A - P - \frac{1}{2} \sum_{i,j=1, i\neq j}^{K} |\mathcal{C}_i| |\mathcal{C}_j| \|O_i - O_j\|^2 .$$

Thus λ is an eigenvalue for $\mathcal{L}[\overline{r}]$ associated with a positive eigenfunction. Since $\overline{r}$ is periodic in x and goes to $-\infty$ as $\|\theta\| \to -\infty$ (uniformly in x), the standard compact theory applies and we obtain $\lambda[\overline{r}] = \lambda$.

Therefore, to minimise $\lambda[\overline{r}]$, we want to find $O_1,\dots,O_H$ that minimise the sum

$$\sum_{i,j=1,i\neq j}^{K} |\mathcal{C}_i|\,|\mathcal{C}_j|\,\|O_i-O_j\|^2.$$

This is equivalent to minimising

$$\sum_{i=1}^{H}\sum_{j=H+1}^{K} |\mathcal{C}_i|\,|\mathcal{C}_j|\,\|O_i-O_j\|^2 + \sum_{i,j=1}^{H} |\mathcal{C}_i|\,|\mathcal{C}_j|\,\|O_i-O_j\|^2.$$

The sum on the left is minimised when the O_i, $1\leqslant i\leqslant H$, are equal to $\mathcal{O}$. The sum on the right is minimised when all the O_i, $1\leqslant i\leqslant H$ are equal. Therefore the minimum is reached when all the free O_i are equal to $\mathcal{O}$. □

Proof of Proposition 6.3.10. First, we show that the function

$$(O_1,\dots,O_K)\mapsto \lambda[r[O_1,\dots,O_K]].$$

does not admit a minimiser. By contradiction, assume that there exists $(Q_1,\dots,Q_K)\in(\mathbb{R}^P)^K$ such that

$$\lambda[r[Q_1,\dots,Q_K]] = \inf_{O_1,\dots,O_K\in\mathbb{R}^P} \lambda[r[O_1,\dots,O_K]].$$

Let $\mathcal{Q}$ be the convex hull of $\{Q_1,\dots,Q_K\}$. Up to relabelling the points, we may assume that $Q_1\in\partial\mathcal{Q}$. Since $\mathcal{Q}$ is convex, there exists a $(P-1)$-dimensional open affine half-space $\mathcal{V}^+$ such that $Q_1\in\partial\mathcal{V}^+$ and $\mathcal{Q}\setminus\{Q_1\}\subset\mathcal{V}^+$. We let ξ be the unit orthogonal vector to $\partial\mathcal{V}^+$ pointing towards $\mathcal{V}^+$. For $\varepsilon>0$ and $t\in[0,1]$, we let $\gamma_\varepsilon(t):=Q_1-(1-\varepsilon t)\xi$. Then, for $\varepsilon>0$ sufficiently small, γ_ε satisfies the assumptions of Theorem 6.3.5 (with strict inequality) so

$$\lambda[r[Q_1,Q_2,\dots,Q_K]] = \lambda[r[\gamma(1),Q_2,\dots,Q_K]] > \lambda[r[\gamma(0),Q_2,\dots,Q_K]].$$

This contradicts the fact that $Q_1,\dots,Q_K$ is a minimiser.

Now, we compute the infimum. First assume that $\chi_\infty>-\infty$. For all $i=1,\dots,K$ and $O_1,\dots,O_K\in\mathbb{R}^P$, we have $r[O_1,\dots,O_K](x,\theta)\geqslant r_i(x,\theta-O_i)$, where r_i is defined by Definition 6.3.1. Thus

$$\lambda[r[O_1,\dots,O_K]]\geqslant \max_{i=1,\dots,K}\lambda[i].$$

We conclude by Theorem 6.3.8 (*iii*) that

$$\inf_{O_1,\dots,O_K\in\mathbb{R}^P} \lambda[r[O_1,\dots,O_K]] = \max_{i=1,\dots,K}\lambda[i].$$

For the case $\chi_\infty=-\infty$, we note that the Definition 6.2.1 of $\lambda[r]$ and the Definition 6.3.1 of $\lambda[i]$ yield $\lambda[r]\geqslant\lambda[i]$ for all $i=1,\dots,K$. The conclusion then follows from Theorem 6.3.8 (*iv*). □

6.6.4 Comparison of nontrivial configurations (Theorems 6.3.7 and 6.3.11)

In this section, we prove Theorems 6.3.7 and 6.3.11. The goal of the proofs is to construct paths γ which satisfy the assumptions of Theorem 6.3.5. Such paths must be supported on intersections of spheres. The following lemma is helpful to show that the intersections of spheres that we will consider are nontrivial.

Lemma 6.6.4. *Let $P, H \in \mathbb{N}$ with $2 \leqslant H \leqslant P$. Let $O_1, \dots, O_H \in \mathbb{R}^P$. Let $S(O_i, \|O_1 - O_i\|) \subset \mathbb{R}^P$ be the $(P-1)$-dimensional sphere with centre O_i and radius $\|O_1 - O_i\|$. Let*

$$\mathcal{S} := \bigcap_{i=2}^{H} S(O_i, \|O_1 - O_i\|).$$

If $\mathcal{S}$ contains at least two different points, then $\mathcal{S}$ is a sphere of dimension greater than or equal to $P - H + 1$.

Proof. If $H = 2$, then $\mathcal{S} = S(O_2, \|O_1 - O_i\|)$ is a sphere of dimension $P-1$. We now assume $H \geqslant 3$. We show that $\mathcal{S}$ is the intersection of the sphere $S(O_2, \|O_1 - O_2\|)$ with an affine subspace of dimension at least $P - H + 2$. The affine subspace is

$$\mathcal{G} := \bigcap_{i=2}^{H-1} \left\{ \theta \in \mathbb{R}^P \ / \ \langle \theta - O_1, O_{i+1} - O_i \rangle = 0 \right\},$$

which is the intersection of $H-2$ affine hyperplanes and contains O_1, so is nonempty. Thus the dimension of $\mathcal{G}$ is at least $P - H + 2$. Furthermore, for $\theta \in S(O_2, \|O_1 - O_2\|) \cap \mathcal{G}$, we find

$$\begin{aligned} \|\theta - O_3\|^2 &= \|\theta - O_2\|^2 + \|O_2 - O_3\|^2 + 2\langle \theta - O_2, O_2 - O_3 \rangle \\ &= \|O_1 - O_2\|^2 + \|O_2 - O_3\|^2 + 2\langle O_1 - O_2, O_2 - O_3 \rangle \\ &= \|O_1 - O_3\|^2, \end{aligned}$$

i.e., $\theta \in S(O_3, \|O_1 - O_3\|)$. The same computation shows that if $\theta \in S(O_2, \|O_1 - O_2\|) \cap S(O_3, \|O_1 - O_3\|)$, then $\theta \in \mathcal{G}$. By iteration, we eventually derive

$$\mathcal{S} = S(O_2, \|O_1 - O_2\|) \cap \mathcal{G}.$$

Now, if $\mathcal{S}$ has at least two points, then $\mathcal{G}$ and $S(O_2, \|O_1 - O_2\|)$ have a nontrivial intersection. This implies that $\mathcal{S}$ is a sphere of dimension greater than or equal to $P - H + 1$. This concludes. □

Lemma 6.6.5. *Let $H, K, P \in \mathbb{N}$ satisfy $P \geqslant 2$, $1 \leqslant H \leqslant K$, $H \leqslant P$ and $K - H \leqslant P$. Let $\widehat{Q}_1, Q_1, \dots, Q_K \in \mathbb{R}^P$ be such that $\widehat{Q}_1 \neq Q_1$ and*

$$\begin{aligned} &\|\widehat{Q}_1 - Q_i\| = \|Q_1 - Q_i\| > 0 \qquad \text{if } 2 \leqslant i \leqslant H, \\ &\|\widehat{Q}_1 - Q_i\| < \|Q_1 - Q_i\| \qquad \text{for } H+1 \leqslant i \leqslant K. \end{aligned}$$

Then there exists a C^1-regular curve $\gamma : [0,1] \to \mathbb{R}^P$ (i.e. with $\gamma' \neq 0$ on $[0,1]$) such that $\gamma(0) = \widehat{Q}_1$, $\gamma(1) = Q_1$ and

$$t \mapsto \|\gamma(t) - Q_i\| \quad \begin{cases} \text{is constant if } 2 \leqslant i \leqslant H, \\ \text{is strictly increasing if } H+1 \leqslant i \leqslant K. \end{cases}$$

In both displays of the statement, the first line must be omitted if $H = 1$ and the second line must be omitted if $H = K$.

Proof. We can assume without loss of generality that the points $Q_2, \dots, Q_H$ are all distinct, up to merging the patches with the same optimum. Further, by hypothesis, the points $\widehat{Q}_1$ and Q_1 are distinct.

First, if $H=1$, then we add a new point $Q_2' \in \mathbb{R}^P$ such that $\|Q_2' - Q_1\| = \|Q_2' - \widehat{Q}_1\|$, and we shift the indices: Q_2 becomes Q_3, and similarly until: Q_K becomes Q_{K+1}. Then $H=1$ is replaced with $H'=2$ and K is replaced with $K'=K+1$. Thus the assumptions $1 \leqslant H' \leqslant K'$ and $K'-H' \leqslant P$ are still satisfied. Last, $P \geqslant 2$ so the assumption $H' \leqslant P$ is still satisfied.

Therefore, we shall assume throughout the proof that $H \geqslant 2$. We consider separately the different types of points $Q_2, \ldots, Q_H$ and $Q_{H+1}, \ldots, Q_K$.

Step 1. The points $Q_2, \ldots, Q_H$. Let

$$\mathcal{S} := \bigcap_{i=2}^{H} S(Q_i, \|\widehat{Q}_1 - Q_i\|).$$

We have $Q_1 \in \mathcal{S}$ and $\widehat{Q}_1 \in \mathcal{S}$ with $Q_1 \neq \widehat{Q}_1$, so, by Lemma 6.6.4, $\mathcal{S}$ is a sphere of dimension greater than or equal to $P-H+1 \geqslant 1$.

We will construct the curve γ with the following properties:

$$\gamma : [0, 2\pi] \to \mathcal{S}, \quad \gamma(0) = \widehat{Q}_1, \quad \exists \bar{t} \in (0, 2\pi), \ \ \gamma(\bar{t}) = Q_1. \tag{6.37}$$

In particular, being supported on $\mathcal{S}$, the path γ will fulfil the desired properties with respect to the points $Q_2, \ldots, Q_H$.

In the case $H=K$, the path γ can be any C^1 regular curve on $\mathcal{S}$ (recall that the dimension of $\mathcal{S}$ is at least $P-H+1 \geqslant 1$) and the proof is over. If $H=K-1$, Step 2 must be omitted.

Step 2. The points $Q_{H+1}, \ldots, Q_{K-1}$. By virtue of $K-H \leqslant P$, there exists an affine hyperspace $\mathcal{H} \subset \mathbb{R}^P$ (i.e. with dimension $P-1$) containing the points $\widehat{Q}_1, Q_{H+1}, \ldots, Q_{K-1}$. We then write $Q_1 = R_1 + zv$, for $R_1 \in \mathcal{H}$, a vector v orthogonal to $\mathcal{H}$ and with unit norm, and $z \in \mathbb{R}$. Since $Q_1, \widehat{Q}_1 \in \mathcal{S}$ and 0 is the centre of $\mathcal{S}$, we have the relation $\|R_1\|^2 + z^2 = \|Q_1\|^2 = \|\widehat{Q}_1\|^2$. We seek a circular support for γ, with centre

$$\mathcal{O} := \widehat{Q}_1 + r(R_1 - \widehat{Q}_1) \in \mathcal{H},$$

with $r \geqslant 0$ chosen in such a way that $\|Q_1 - \mathcal{O}\| = \|\widehat{Q}_1 - \mathcal{O}\|$, that is,

$$\|Q_1 - \widehat{Q}_1 - r(R_1 - \widehat{Q}_1)\|^2 = r^2 \|R_1 - \widehat{Q}_1\|^2.$$

See Figure 6.4. The above relation rewrites as

$$\|Q_1 - \widehat{Q}_1\|^2 - 2r \left\langle Q_1 - \widehat{Q}_1, R_1 - \widehat{Q}_1 \right\rangle = 0,$$

from which, using that $R_1 = Q_1 - zv$ with v orthogonal to $\mathcal{H}$ (and thus $\left\langle R_1 - \widehat{Q}_1, v \right\rangle = 0$), one finds

$$r = \frac{\|Q_1 - \widehat{Q}_1\|^2}{2\left\langle Q_1 - \widehat{Q}_1, R_1 - \widehat{Q}_1 \right\rangle} = \frac{\|Q_1 - \widehat{Q}_1\|^2}{2\|R_1 - \widehat{Q}_1\|^2}.$$

Note that $R_1 \neq \widehat{Q}_1$ because otherwise $Q_1 = \widehat{Q}_1$. Finally, we define the curve γ as follows:

$$\gamma(t) := \mathcal{O} + \cos(t)(\widehat{Q}_1 - \mathcal{O}) + \sin(t)\|\widehat{Q}_1 - \mathcal{O}\| v.$$

We have $\|\gamma(t) - \mathcal{O}\| = \|\widehat{Q}_1 - \mathcal{O}\| = \|Q_1 - \mathcal{O}\|$, for all $t \in [0, 2\pi]$. Hence γ describes a circle

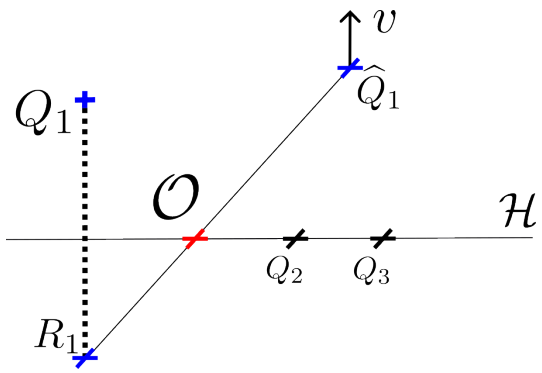

Figure 6.4: Illustration of the different notions introduced in the proof: $\mathcal{H}$, R_1, $\mathcal{O}$, v. Here, $\mathcal{H}$ is the plane containing $\mathcal{O}$, R_1, $\widehat{Q}_1$, Q_2 and Q_3.

in the affine plane going through $\widehat{Q}_1$ and generated by v and $\widehat{Q_1}-\mathcal{O}=-r(R_1-\widehat{Q}_1)$. Writing $Q_1=\widehat{Q}_1+(R_1-\widehat{Q}_1)+zv$ implies that Q_1 also belongs to this plane. One deduces that the support of γ contains both points $\widehat{Q}_1$ (at $t=0$) and Q_1 (at some $t=\bar{t}\in(0,2\pi)$).

Let us now consider a point Q_i with $i\in\{2,\dots,H\}$. Recalling that $Q_i\in\mathcal{H}$, we find that the vectors $Q_i-\mathcal{O}$ and v are orthogonal, so

$$\begin{aligned}\|\gamma(t)-Q_i\|^2 &= \left\|\mathcal{O}-Q_i+\cos(t)(\widehat{Q}_1-\mathcal{O})+\sin(t)\|\widehat{Q}_1-\mathcal{O}\|v\right\|^2\\ &= \|\mathcal{O}-Q_i\|^2+\|\widehat{Q}_1-\mathcal{O}\|^2+2\cos(t)\left\langle\mathcal{O}-Q_i,\widehat{Q}_1-\mathcal{O}\right\rangle. \qquad (6.38)\end{aligned}$$

We know that the above term is equal to $\|\widehat{Q}_1-Q_i\|^2=\|Q_1-Q_i\|^2$ for $t=0$ and for $t=\bar{t}\in(0,2\pi)$. It follows that

$$\left\langle\mathcal{O}-Q_i,\widehat{Q}_1-\mathcal{O}\right\rangle=0.$$

Hence, $\|\gamma(t)-Q_i\|^2=\|\widehat{Q}_1-Q_i\|^2$ for all t so γ is supported on $\mathcal{S}$. Summing up, we have that (6.37) holds.

Finally, let us consider a point Q_i with $i\in\{H+1,\dots,K-1\}$. We know from (6.37) that $\|\gamma(t)-Q_i\|$ is equal to $\|\widehat{Q}_1-Q_i\|$ for $t=0$, while it is equal to $\|Q_1-Q_i\|>\|\widehat{Q}_1-Q_i\|$ for $t=\bar{t}\in(0,2\pi)$. It then follows from (6.38) that

$$\left\langle\mathcal{O}-Q_i,\widehat{Q}_1-\mathcal{O}\right\rangle<0.$$

Therefore, using again (6.38), we obtain that up to reducing the domain of definition of the curve γ to $[0,\pi]$ (where $t\mapsto\cos(t)$ is decreasing), the curve γ fulfils the desired properties with respect to the points $Q_{H+1},\dots,Q_{K-1}$.

Importantly, we point out that the curve $t\mapsto\gamma(2\pi-t)=\gamma(-t)$ restricted to $[0,\pi]$ also fulfils the desired properties with respect to the points $Q_{H+1},\dots,Q_{K-1}$.

Step 3. The point Q_K. We can now deal with the last point Q_K. In the case $H=K-1$, the points $Q_{H+1},\dots,Q_{K-1}$ do not exist and we just take as γ any circle satisfying the conditions (6.37) (recall that the dimension of $\mathcal{S}$ is at least $P-H+1\geqslant 1$). Instead, if $K-H\geqslant 2$ then the curve γ has been constructed before. We recall that, in any case, both $\gamma(t)$ and $\gamma(-t)$ fulfil the desired properties with respect to $Q_2,\dots,Q_{K-1}$.

Now, if $\widehat{Q}_1-Q_K$ is orthogonal to $\gamma'(0)$ then the exact same arguments as above show

that $\|\gamma(t)-Q_K\|$ is increasing for $t\in[0,\pi]$, which concludes the proof. On the contrary, if $\widehat{Q}_1-Q_K$ is not orthogonal to $\gamma'(0)$, then we compute

$$\frac{\mathrm{d}}{\mathrm{d}t}\|\gamma(t)-Q_K\|^2\Big|_{t=0}=2\left\langle\widehat{Q}_1-Q_K,\gamma'(0)\right\rangle,$$

which is either positive or negative; then the desired monotonicity property with respect to Q_K is fulfilled by the function $\gamma(t)$ if $\left\langle\widehat{Q}_1-Q_K,\gamma'(0)\right\rangle>0$, or by $\gamma(-t)$ if $\left\langle\widehat{Q}_1-Q_K,\gamma'(0)\right\rangle<0$, for $t\geqslant 0$ sufficiently small. Therefore, in both cases we have obtained the desired curve, up to rescaling the variable t. □

Proof of Theorem 6.3.7. Let $\widehat{Q}_1:=\widehat{O}_1$, $Q_1:=O_1$. If $\widehat{Q}_1=Q_1$, then equality holds; so we assume that $\widehat{Q}_1\neq Q_1$. There exist $H\in\{1,\dots,K\}$ and a permutation $(Q_2,\dots,Q_K)$ of $(O_2,\dots,O_K)$ such that

$$\begin{aligned}&\|\widehat{Q}_1-Q_i\|=\|Q_1-Q_i\|>0 &&\text{for } i=2,\dots,H,\\&\|\widehat{Q}_1-Q_i\|<\|Q_1-Q_i\| &&\text{for } i=H+1,\dots,K.\end{aligned}$$

Since $K\geqslant 2$ and $1\leqslant H\leqslant K\leqslant P$, we have $P\geqslant 2$, $H\leqslant P$ and $K-H\leqslant P$. Thus we are in the setting of Lemma 6.6.5: there exists a regular curve $\gamma:[0,1]\to\mathbb{R}^P$ such that $\gamma(0)=\widehat{Q}_1$, $\gamma(1)=Q_1$ and $t\mapsto\|\gamma(t)-O_i\|$ is constant for all $i=2,\dots,H$ and strictly increasing for $i=H+1,\dots,K$. Therefore, by Theorem 6.3.5, we have:

$$\lambda[r[\widehat{O}_1,O_2\dots,O_K]]\geqslant\lambda[r[O_1,O_2\dots,O_K]]. \tag{6.39}$$

Further, if at least one strict inequality holds in the statement of the theorem, then $H\leqslant K-1$ so the strict inequality in Theorem 6.3.5 holds; therefore the inequality in (6.39) is strict. Otherwise, applying Theorem 6.3.5 to the path $t\mapsto\gamma(1-t)$ implies that the inequality in (6.39) is an equality. □

Remark 6.6.6. The assumption $K\leqslant P$ is needed in Theorem 6.3.7. Indeed, if $K>P$, it is in general not possible to construct a path from O_1 to $\widehat{O}_1$ with the properties of Theorem 6.3.5. A simple counter-example is: $P=1$, $K=2$ and $O_1=1$, $\widehat{O}_1=-1$ and $O_2=0$.

Proof of Theorem 6.3.11. In the case $K=2$, the theorem follows from the dilatation result of Theorem 6.3.8. Indeed, for given $O_1,O_2\in\mathbb{R}^P$ such that $0<\|O_1-O_2\|\leqslant D$, calling $a:=D/\|O_1-O_2\|\geqslant 1$ we have $\|aO_1-aO_2\|=D$ and

$$\lambda[r[aO_1,aO_2]]\leqslant\lambda[r[O_1,O_2]],$$

with strict inequality if $\|O_1-O_2\|<D$. Hence the case $K=2$ is proved, thanks to the invariance of $\lambda[r]$ by translation and rotation of the phenotypic space $\mathbb{R}^P$.

Let us turn to the case $K\geqslant 3$. We let

$$\mathcal{Q}:=\left\{(O_1,\dots,O_K)\in\left(\mathbb{R}^P\right)^K\ /\ \forall i,j\in\{1,\dots,K\},\|O_i-O_j\|\leqslant D\right\}$$

be the set of configurations satisfying the constraint of the optimisation problem. The set $\mathcal{Q}\cap\{O_1=0\}$ is compact and the function $(O_1,\dots,O_K)\mapsto\lambda[r[O_1,\dots,O_K]]$ is continuous (see Lemma 6.4.6) and invariant by translation. Thus there exists an optimal configuration

$(Q_1,\dots,Q_K)\in\mathcal{Q}$, that is:

$$\lambda[r[Q_1,\dots,Q_K]]=\min\{\lambda[r[O_1,\dots,O_K]]\ /\ (O_1,\dots,O_K)\in\mathcal{Q}\}.$$

We assume that there exist $1\leqslant i<j\leqslant K$ such that

$$\|Q_i-Q_j\|<D':=\max_{i,j}\|Q_i-Q_j\|.$$

There exist $H\in\{2,\dots,K-1\}$ and a relabelling of the Q_i such that

$$\begin{array}{ll}\|Q_1-Q_i\|=D' & \text{for } i=2,\dots,H,\\ \|Q_1-Q_i\|<D' & \text{for } i=H+1,\dots,K.\end{array}$$

We choose the relabelling in such a way that for all $i=1,\dots,K$, there are at least $H-1$ different indices $j\in\{1,\dots,K\}$ such that $\|O_i-O_j\|=D'$ (i.e. H is chosen as small as possible).

Our goal is to construct a path γ satisfying the assumptions of Theorem 6.3.5, and with $\gamma(0)=Q_1$. We shall then reach a contradiction using the strict inequality in Theorem 6.3.5. To start with, set

$$\mathcal{S}:=\bigcap_{i=2}^{H}S(Q_i,\|Q_1-Q_i\|)=\bigcap_{i=2}^{H}S(Q_i,D').$$

Step 1. Show that $\mathcal{S}$ is a sphere with dimension at least $P-H+1$. By Lemma 6.6.4, if $\mathcal{S}$ contains at least two distinct points, then $\mathcal{S}$ is a sphere with dimension at least $P-H+1$. We will show that $\mathcal{S}$ contains at least two distinct points. If $H=2$, then $\mathcal{S}=S(Q_2,D')$ and the conclusion follows. If $H=3$, then $\|Q_2-Q_3\|\leqslant D'$ implies that $\mathcal{S}$ contains at least two distinct points.

Since $K\leqslant 5$ and $2\leqslant H\leqslant K-1$, there only remains to deal with the case $K=5$ with $H=4$. Let $\mathcal{F}$ be the smallest affine subspace such that $Q_2,Q_3,Q_4\in\mathcal{F}$. First, let us assume that $Q_1\in\mathcal{F}$. Then $\mathcal{F}$ has dimension at most 2. Thus at least two of the following hold: (i) $\|Q_2-Q_3\|<D'$; (ii) $\|Q_2-Q_4\|<D'$ and/or (iii) $\|Q_3-Q_4\|<D'$. Assume, for example, that the two first ones hold, see Figure 6.5. Then, there are at most 2 indices ($j=1$ and perhaps $j=5$) such that $\|Q_2-Q_j\|=D'$. This contradicts the minimality assumption on $H=3$.

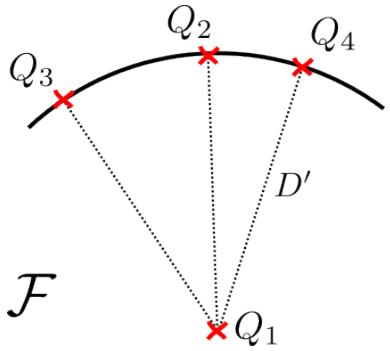

Figure 6.5: If $K=5$ and $H=4$, then $Q_1\in\mathcal{F}$ contradicts the minimality of H.

Therefore, $Q_1\notin\mathcal{F}$. Let $\overline{Q}_1$ be the orthogonal symmetric of Q_1 with respect to $\mathcal{F}$. Then $\overline{Q}_1\neq Q_1$, $Q_1\in\mathcal{S}$ and $\overline{Q}_1\in\mathcal{S}$. Thus $\mathcal{S}$ contains at least two distinct points. Therefore, Lemma 6.6.4 implies that $\mathcal{S}$ is a sphere with dimension at least $P-H+1$. Step 1 is over.

Now, we let $\mathcal{T}$ be the space tangent to $\mathcal{S}$ at the point Q_1; the space $\mathcal{T}$ has dimension at least $P-H+1$. Our goal now is to construct a vector $v\in\mathcal{T}$ and a path $\widehat{\gamma}:[0,1]\to\mathcal{S}$ such that

$$\begin{cases}\forall t\in[0,1],\quad \widehat{\gamma}'(t)\neq 0,\ \widehat{\gamma}(t)\in\mathcal{S},\\ \widehat{\gamma}(0)=Q_1,\ \widehat{\gamma}'(0)=v,\end{cases} \tag{6.40}$$

and such that $t\mapsto\|\widehat{\gamma}(t)-Q_i\|$ increases for all $i=H+1,\dots,K$. We point out that $v\in\mathcal{T}$ being given, a C^∞-path $\widehat{\gamma}$ satisfying (6.40) may be constructed as the converse image of a straight path on $\mathbb{R}^{\dim(\mathcal{S})}$ by a C^∞-diffeomorphism that straightens $\mathcal{S}$ near Q_1.

Step 2. Assume that $Q_1,\dots,Q_K$ are contained in a $(K-2)$-dimensional affine subspace. We let $\mathcal{H}$ be a $(K-2)$-dimensional affine subspace containing $Q_1,\dots,Q_K$. We let $v\in\mathbb{R}^P$ be a nonzero vector orthogonal to $\mathcal{H}$. In the proof of Lemma 6.6.4, we defined an affine subspace $\mathcal{G}\subset\mathbb{R}^P$ such that $\mathcal{S}=S(O_2,D')\cap\mathcal{G}$. We point out that v is tangent to $S(O_2,D')$ and to $\mathcal{G}$. Therefore, $\mathcal{G}$ being an affine subspace, we have: $v\in\mathcal{T}$. Hence, we may construct a C^∞-path $\widehat{\gamma}$ satisfying (6.40).

On the one hand, since $\widehat{\gamma}(t)\in\mathcal{S}$, the function $t\mapsto\|\widehat{\gamma}(t)-Q_j\|$ is constant on $[0,1]$ for all $j\in\{2,\dots,H\}$.

On the other hand, let $j\in\{H+1,\dots,K\}$. Since $\widehat{\gamma}'(0)=v$ is orthogonal to Q_1-Q_j, a Taylor expansion gives

$$\begin{aligned}\|\widehat{\gamma}(t)-Q_j\|^2&=\|Q_1-Q_j\|^2+\|\widehat{\gamma}(t)-Q_1\|^2+2\langle\widehat{\gamma}(t)-Q_1,Q_1-Q_j\rangle\\&=\|Q_1-Q_j\|^2+t^2\|v\|^2+t^2\left\langle\widehat{\gamma}''(0),Q_1-Q_j\right\rangle+O(t^3).\end{aligned}$$

Owing to $\widehat{\gamma}(t)\in\mathcal{S}$, we have: $\widehat{\gamma}(t)\in S(O_2,D')$. Therefore, $\|\widehat{\gamma}''(0)\|=\frac{\|v\|^2}{D'}$ and

$$\|\widehat{\gamma}(t)-Q_j\|^2\geqslant\|Q_1-Q_j\|^2+t^2\|v\|^2\left(1-\frac{\|Q_1-Q_j\|}{D'}\right)+O(t^3).$$

Recall that $\|Q_1-Q_j\|<D'$. Thus there is $\bar{t}>0$ sufficiently small so that $t\mapsto\|\widehat{\gamma}(t)-Q_j\|$ is strictly increasing on $[0,\bar{t}]$, for all $j=H+1,\dots,K$.

Before concluding the proof, let us consider the case where the assumption of Step 2 is not satisfied.

Step 3. Assume on the contrary that $Q_1,\dots,Q_K$ are *not* contained in a $(K-2)$-dimensional subspace. For $j=H+1,\dots,K$, we define $p_j\in\mathcal{T}$ as the orthogonal projection of the vector Q_1-Q_j on $\mathcal{T}$. Let us show that the vectors $p_{H+1},\dots,p_K$ are linearly independent in $\mathcal{T}$. Let $\mu_{H+1},\dots,\mu_K\in\mathbb{R}$ satisfy

$$\sum_{j=H+1}^{K}\mu_j p_j=0.$$

This means that

$$w:=\sum_{j=H+1}^{K}\mu_j(Q_1-Q_j)$$

is orthogonal to $\mathcal{T}$. The assumption that the points $Q_1,\dots,Q_K$ cannot be all included in a $(K-2)$-dimensional subspace implies in particular that the family of vectors $(Q_1-$

Q_i, $i = 2, \dots, K$), is linearly independent. Since $\mathcal{T}$ has dimension at least $P - H + 1$, the orthogonal $\mathcal{T}^\perp$ of $\mathcal{T}$ has dimension at most $P - (P - H + 1) = H - 1$, where

$$\mathcal{T}^\perp := \left\{ z \in \mathbb{R}^P \,/\, \forall z' \in \mathcal{T}, \left\langle z, z' \right\rangle = 0 \right\}.$$

Therefore, the vector $w \in \mathcal{T}^\perp$ can be expressed as a linear combination of $Q_1 - Q_2, \dots, Q_1 - Q_H$. Using again the fact that $Q_1 - Q_2, \dots, Q_1 - Q_K$ are linearly independent, we conclude that $\mu_j = 0$ for all $j = H+1, \dots, K$. Thus the vectors $p_{H+1}, \dots, p_K$ are linearly independent in $\mathcal{T}$.

Thereby, there exists a vector $v \in \mathcal{T}$ which solves the following system of inequations:

$$\begin{aligned} \langle p_{H+1}, v \rangle &> 0, \\ &\vdots \\ \langle p_K, v \rangle &> 0. \end{aligned} \tag{6.41}$$

We now construct a C^∞-path $\widehat{\gamma} : [0,1] \to \mathcal{S}$ satisfying (6.40). We have, for $j \in \{H+1, \dots, K\}$:

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} \left(\|\widehat{\gamma}(t) - Q_j\|^2 \right) \Big|_{t=0} &= 2 \left\langle \gamma'(0), \gamma(0) - Q_j \right\rangle \\ &= 2 \langle v, Q_1 - Q_j \rangle \\ &= 2 \langle v, p_j \rangle > 0, \end{aligned}$$

owing to (6.41). Thus, since $\widehat{\gamma}$ is of class C^∞, we have:

$$\frac{\mathrm{d}}{\mathrm{d}t} \left(\|\gamma(t) - Q_j\|^2 \right) > 0$$

for all $t \in [0, \bar{t}]$, for $\bar{t} > 0$ small enough.

Step 4. Conclusion. In Steps 2 and 3, we constructed a regular curve $\widehat{\gamma} : [0,1] \to \mathbb{R}^P$ such that $\gamma(0) = Q_1$ and $t \mapsto \|\gamma(t) - O_i\|$ is constant for all $i = 2, \dots, H$ and strictly increasing for all $i = H+1, \dots, K$. For t small enough, we have, on the one hand: $(\gamma(t), Q_2, \dots, Q_K) \in \mathcal{Q}$, and on the other hand, by Theorem 6.3.5 applied to $s \mapsto \widehat{\gamma}(1-s)$,

$$\lambda[r[\gamma(t), Q_2, \dots, Q_K]] < \lambda[r[Q_1, \dots, Q_K]].$$

This contradicts the optimality assumption on $(Q_1, \dots, Q_K)$. Therefore, we must have

$$\|Q_i - Q_j\| = D' \qquad \text{for all } 1 \leqslant i < j \leqslant K.$$

Such a configuration is unique up to rotation, symmetry, translation and permutation, and arises when $Q_1, \dots, Q_K$ are the vertices of a regular polyhedron of side of length D. In this situation, the assumption (6.15) is satisfied with $\mathcal{O} = Q_1$. By dilatation (Theorem 6.3.8 (i)), therefore, we must have $D' = D$. This concludes the proof. □

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Chapter 7

Spreading of a structured population

This chapter is based on the preprint [46]:

N. Boutillon, *Qualitative properties of the spreading speed of a population structured in space and in phenotype*, preprint arXiv:2410.01342.

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.

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7.1 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:

$$\begin{cases} \partial_t u = a\Delta_x u + m\Delta_\theta u + u\left(r(x,\theta) - \rho(t,x)\right), & t>0,\,(x,\theta)\in\mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta u = 0, & t>0,\,(x,\theta)\in\mathbb{R}\times\partial\Theta, \\ u(0,x,\theta) = u_0(x,\theta), & (x,\theta)\in\mathbb{R}\times\Theta, \end{cases} \tag{7.1}$$

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. [116, 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 (7.1) 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 (7.1) comes from. The Fisher-KPP equation was introduced in 1937 by Fisher [94] and Kolmogorov, Petrovsky and Piskunov [143]. It reads:

$$\partial_t u(t,x) = a\Delta_x u + ru - u^2, \tag{7.2}$$

where $a>0$ and $r>0$ are constant. A motivation for Equation (7.2) 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 (7.2). 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. [208, 210, 215]). However, because of its simplicity, the Fisher-KPP equation misses phenomena which may play an important role in invasions. Equation (7.1) 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:

$$\partial_t u(t,x) = a\Delta_x u + r(x)u - u^2, \tag{7.3}$$

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 [103] 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

$$c_{het} := \inf_{\lambda>0} \frac{k^\lambda}{\lambda}. \tag{7.4}$$

Since Gärtner and Freidlin, numerous work have proved different versions of Equation (7.4) for various settings, e.g. [25, 26, 109, 115, 220]. 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 (7.3) 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 [23, 28]. In [224], Xin gives a survey of results and methods for reaction-diffusion equations in heterogeneous environments.

Heterogeneous population. A second phenomenon which is missed by the basic Fisher-KPP equation (7.2) 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 (7.3), we get

$$\partial_t u(t,x,\theta) = a\Delta_x u + m\Delta_\theta u + r(x,\theta)u - u^2, \qquad x \in \mathbb{R}, \theta \in \Theta, \tag{7.5}$$

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 [220], and pulsating travelling waves also exist [25, 26].

The only difference between Equation (7.1) and Equation (7.5) 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 (7.1) (with rarer but larger mutations) appeared for the first time in the work of Prévost [194] and was then derived by Champagnat and Méléard [61] as a large population limit of an individual-based model.

The discussion above implies that (7.5) 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 (7.1) if we want the variable θ to represent a phenotype. Although we shall concentrate on Equation (7.1), our results only depend on the linear problem, so they are valid for the local equation (7.5) as well (in the latter setting, however, our results may be harder to interpret from a biological viewpoint).

For the sake of exposition, let us assume temporarily that the fitness r only depends on the phenotype θ in (7.1), 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 (7.1) 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 $c'' \in \big(0, c_{phenotype}\big)$,

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

Moreover, for all $c \geqslant c_{phenotype}$, there exists a profile U_c such that $u(t,x,\theta) := U(x - ct, \theta)$ solves (7.1). See [30]. 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 [4, 187], 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 [187], Peltier showed that if the tail of the initial condition is heavy enough, then an accelerating invasion arises, as in the 1-dimensional case [122]. In [4], 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 [3] 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 [41]. Then the interplay with the phenotype has a striking behaviour with respect to the spreading properties and real world biological consequences. In this chapter, however, most results do not apply to the cane-toad equation.

There are also works about periodic environments, as modelled by our equation (7.1). In [9], 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 [44], Bouin and Mirrahimi study the effect of large periods and get the precise position of the invasion, using Hamilton-Jacobi equation techniques. In [151], Léculier and Mirrahimi study the weak mutation limit of the equilibria of an equation which is related to ours, but displays nonlocal mutations. In Chapter 5, we focused on the same equation (7.1) but possibly set in an unbounded phenotype space. We proved the well-posedness of (7.1) and gave a criterion, based on a generalised principal eigenvalue, for 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 [109] for homogeneous environments, and [110, 115] or Chapter 8 for heterogeneous environments. In the latter, Freidlin-Gärtner formulas similar to ours (but in discrete-phenotype settings) are proved and their properties are studied.

Problematic and layout. Our main goal is to study the spreading speed of a population modelled by equations of the form (7.1). 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 7.2.1, 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 7.2.2 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 (7.1) 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 7.2.3, we shall give several results which are invisible when we forget the phenotypic dimension.

7.2 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

$$\mathcal{T}_{m,L}\phi := \partial_x\left(a_L(x,\theta)\partial_x\phi\right) + m\nabla_\theta \cdot \left(\mu_L(x,\theta)\nabla_\theta\phi\right) + r_L(x,\theta)\phi, \tag{7.6}$$

and we write a general version of main model (7.1) as:

$$\begin{cases} \partial_t u_{m,L} = \mathcal{T}_{m,L}u_{m,L} - u_{m,L} \times \rho_{m,L}(t,x), & t > 0, (x,\theta) \in \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta u_{m,L} = 0, & t > 0, (x,\theta) \in \mathbb{R} \times \partial\Theta, \\ u_{m,L}(0,x,\theta) = u_0(x,\theta), & (x,\theta) \in \mathbb{R} \times \Theta, \end{cases} \tag{7.7}$$

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 (7.1), a and μ are now allowed to depend on x and θ. These dependencies will be restricted in several of our results below.

Theorem 5.2.1 of Chapter 5 ensures that the problem (7.7) 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 continuous, globally bounded and nonnegative. If u_0 is nonzero, then u and ρ are strictly positive at all positive times.

7.2.1 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 $k^{\lambda}_{m,L} \in \mathbb{R}$ be the principal eigenvalue associated with the eigenproblem:

$$\begin{cases} \mathcal{L}^{\lambda}_{m,L}\,\varphi = k^{\lambda}_{m,L}\,\varphi & \text{in } \mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta\varphi = 0 & \text{over } \mathbb{R}\times\partial\Theta, \\ \varphi > 0 & \text{in } \mathbb{R}\times\Theta, \\ \varphi & \text{is } L\text{-periodic in } x. \end{cases} \tag{7.8}$$

Due to the periodicity of x of the model and to the smoothness of $\partial\Theta$, we are in a compact setting. Therefore, it follows from the standard Krein-Rutman theory [145] that $k^{\lambda}_{m,L}$ is well-defined and is associated with a unique (up to multiplication) principal eigenfunction.

Our first result means that the solutions of the equations of the type (7.7) have a spreading speed, and that the spreading speed is given by a formula analogous to the Freidlin-Gärtner formula (see Equation (7.4)). First, we extend the definition of the spreading speed to our framework.

Definition 7.2.1. *Let $c > 0$. We say that a solution u of (7.7) spreads at speed c if for all $c' > c$,*

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

and for all $c'' \in (0, c)$,

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

We call c the spreading speed of u.

Remark 7.2.2. Using a parabolic Harnack equality (see below), we may infer that u spreads at speed c if and only if: for all $c' > c$,

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

and for all $c'' \in (0, c)$,

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

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 5.2.4 in Chapter 5 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. For example, this condition is satisfied for all $m > 0$ and $L > 0$ if $r \geqslant 0$ and $r \not\equiv 0$.

We now have all the tools at hand to state the Freidlin-Gärtner formula in our context.

Theorem 7.2.3 (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 (7.7) gets extinct: $\|\rho(t,\cdot)\|_\infty \to 0$ as $t \to +\infty$;

(ii) If $k^0_{m,L} > 0$, then the solution of (7.7) has a positive spreading speed $c_{m,L}$ (in the sense of Definition 7.2.1). The spreading speed $c_{m,L}$ is given by

$$c_{m,L} := \inf_{\lambda > 0} \frac{k^\lambda_{m,L}}{\lambda}. \tag{7.9}$$

Remark 7.2.4. As mentioned in Chapter 5, the behaviour of the solution (extinction or persistence) in the borderline case $k^0_{m,L} = 0$ is not known.

7.2.2 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 (7.4), 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 let $H_m(x)$ be the principal eigenvalue

associated with the *local eigenproblem*:

$$\begin{cases} m\nabla_\theta \cdot (\mu \nabla_\theta \psi) + r(x,\cdot)\psi = H_m(x)\psi & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \psi = 0 & \text{over } \partial\Theta, \\ \psi > 0 & \text{in } \Theta. \end{cases} \tag{7.10}$$

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.

The following theorem is a consequence of Theorem 7.2.3 and of the results of Chapter 2.

Theorem 7.2.5. *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 7.2.5 allows one to find a more or less explicit formula for the limit, given in Proposition 7.4.3 below (see also [119]). 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:

$$c_H < \lim_{L\to+\infty} c_{m,L}. \tag{7.11}$$

This is proved after the proof of Theorem 7.2.5. The same phenomenon also occurs for the equation without the phenotypic dimension (see [119]). For bistable equations, the above heuristic does work, see [77].

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 [98, 130]. 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 [117]. 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 the limit $L \to +\infty$, and only then consider the infinite population limit; with this respect, see [161].

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 let $\widetilde{k}_m^\lambda$ be the principal eigenvalue associated with the *homogenised eigenproblem*:

$$\begin{cases} m\nabla_\theta \cdot \left(\widetilde{\mu}^A \nabla_\theta \psi\right) + \left(\widetilde{r}^A + \lambda^2 \widetilde{a}^H\right)\psi = \widetilde{k}_m^\lambda \psi & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \psi = 0 & \text{over } \partial\Theta, \\ \psi > 0 & \text{in } \Theta. \end{cases} \tag{7.12}$$

We call $\widetilde{k}_m^\lambda$ the *homogenised principal eigenvalue*. The following theorem is a consequence of homogenisation techniques.

Theorem 7.2.6. *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 are the principal eigenfunctions associated with the homogenised eigenproblem; thus

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

and we obtain, by the first equality in Theorem 7.2.6,

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

This is the result proved in [81] 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 7.2.7. *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 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. Item (i) of the theorem is a consequence of homogenisation techniques, and item (ii) is a consequence of the results in Chapter 2.

7.2.3 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 7.2.3 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:

$$\forall \theta \in \overline{\Theta}, \quad \exists (x, \sigma) \in \mathbb{R} \times \overline{\Theta}, \qquad r(x, \sigma) > r(x, \theta). \tag{7.13}$$

The following theorem shows that that under assumption (7.13), γ is well-defined, is positive and can be interpreted as the maximal potential effect of mutations on the spreading speed.

Theorem 7.2.8. *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* (7.13) *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 7.2.9. *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 [82, 169] and Chapter 8.

Third, we state a slightly counter-intuitive result.

Proposition 7.2.10. *Fix $L > 0$. The function $m \mapsto k^0_{m,L}$ is nonincreasing.*

Theorem 7.2.8 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 7.2.10 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 [173].

Proposition 7.2.11. *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 7.3, we will show that solutions of equations of the type (7.7) have a spreading speed which is given by a formula analogous to the Freidlin-Gärtner formula (Theorem 7.2.3). Using this formula, we will then look at the behaviour of the spreading speed of the solution of (7.7) as $L \to 0$, $L \to +\infty$ (Section 7.4), $m \to 0$ and $m \to +\infty$ (Section 7.5). The qualitative properties about the effect of the mutations are proved in Subsections 7.4.1, 7.5.3 and 7.5.4.

7.3 The Freidlin-Gärtner formula (Theorem 7.2.3)

In this part, we prove Theorem 7.2.3. For notational convenience, we shall assume throughout that $L = 1$ and $m = 1$. The notations thus simplify:

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

7.3.1 A Harnack inequality

We first state a nonstandard version of the parabolic Harnack inequality, which was found by Alfaro, Berestycki and Raoul in [3] 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.

Theorem 7.3.1 ([3]). *Let $f \in L^\infty([0,+\infty)\times\mathbb{R}\times\Theta)$. Let $\delta > 0$ and let $u(t,x,\theta)$ be a bounded nonnegative weak solution of*

$$\begin{cases} \partial_t u(t,x,\theta) = \partial_x(a\partial_x u) + \nabla_\theta\cdot(\mu\nabla_\theta u) + f(t,x,\theta)u, & t>0,\,(x,\theta)\in\mathbb{R}\times\Theta, \\ \nu\cdot\nabla_\theta u(t,x,\theta) = 0, & (x,\theta)\in\mathbb{R}\times\partial\Theta. \end{cases} \tag{7.14}$$

Then there exists a constant $C > 0$ depending only on δ, $\|u\|_\infty$, $\|f\|_\infty$, a, μ and Θ such that:

$$\forall t_0 \geqslant 1, \forall x_0 \in \mathbb{R}, \qquad \sup_{\theta\in\Theta} u(t_0,x_0,\theta) \leqslant C \inf_{\theta\in\Theta} u(t_0,x_0,\theta) + \delta.$$

Proof. The proof is almost the same as that of [3, Theorem 2.6], which holds only in the full space. The only difference is that we need to deal with the boundary $\partial\Theta$.

Without loss of generality, we prove the result for $t_0 = 2$ and $x_0 = 0$. We consider $R > diam(\Theta)$. For convenience, we note

$$U := \|u\|_\infty, \qquad K := \max\left(\|f\|_\infty, \|a\|_\infty, \|\partial_x a\|_\infty\right).$$

As in [3], 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:

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

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, for $\beta > 0$ large enough (depending only on R, U, K and δ),

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

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 [33, Theorem 3.1]. Applying the classical interior 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 $C>0$, depending only on K, βR, a, μ and Θ, 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

$$\sup_{\theta\in\Theta} u(2,0,\theta) \leqslant C \inf_{\theta\in\Theta} u(2,0,\theta) + \delta.$$

This is what we wanted to prove

□

7.3.2 An estimate on the principal eigenvalue

Lemma 7.3.2. *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 with the operator defined by

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

with periodicity in x and 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. □

7.3.3 Proof of Theorem 7.2.3

The extinction case for $k^0 < 0$ is proved in Chapter 5. From now on, we assume that $k^0 > 0$. We define

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

First, $\mathcal{L}^\lambda$ is the adjoint of $\mathcal{L}^{-\lambda}$, so the function $\lambda \in \mathbb{R} \mapsto k^\lambda$ is symmetric. Further, the argument of the proof of [28, Lemma 3.1] implies that $\lambda \in \mathbb{R} \mapsto k^\lambda$ is also convex. Hence $k^\lambda > 0$ for all $\lambda \in \mathbb{R}$. Therefore, the lower bound in Lemma 7.3.2 implies that $c_{FG} > 0$.

Now, let us show that a solution u of (7.7) starting from a bounded nonnegative initial condition with support bounded from above, has a spreading speed c_{FG}. The proof is cut into two parts: Proposition 7.3.3 below means that the first requirement of Definition 7.2.1 is satisfied; Proposition 7.3.4 below means that the second requirement of Definition 7.2.1 is satisfied.

Proposition 7.3.3. *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 (7.7). For each $c' > c_{FG}$,*

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

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

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

for some constant $C > 0$ 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 from 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 $t \geqslant 0$,

$$u(t, \cdot, \cdot) \leqslant \bar{u}(t, \cdot, \cdot). \tag{7.15}$$

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 (x, θ) as $t \to +\infty$. With (7.15), this proves the proposition. □

Proposition 7.3.4. *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 (7.7). For each $c'' \in (0, c_{FG})$,*

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

In order to prove the proposition, we first consider the auxiliary intrinsic growth rates defined for $\varepsilon > 0$ by

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

and the following auxiliary *local* problems:

$$\begin{cases} \partial_t u^\varepsilon(t,x,\theta) = \partial_x(a\partial_x u^\varepsilon) + \nabla_\theta \cdot (\mu \nabla_\theta u^\varepsilon) + u^\varepsilon \left(r^\varepsilon(x,\theta) - G u^\varepsilon\right), & t > 1, (x,\theta) \in \mathbb{R} \times \Theta, \\ u^\varepsilon(1,x,\theta) = \dfrac{1}{2} u(1,x,\theta), & (x,\theta) \in \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta u^\varepsilon(t,x,\theta) = 0, & t \geqslant 1, (x,\theta) \in \mathbb{R} \times \partial\Theta, \end{cases} \tag{7.16}$$

where the constant $G > 0$ is to be chosen in the proof of Lemma 7.3.5. We note that $u^\varepsilon(1, \cdot, \cdot) > 0$ 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, let us point out that u^ε spreads at a speed *independent* of G (the speed, indeed, only depends on the linear problem).

Lemma 7.3.5. *Let u be the solution of the nonlocal problem (7.7). Let $\varepsilon > 0$. There exists $G > 0$ such that the solution u^ε of (7.16) 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 (7.7) 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 Chapter 5, u and ρ are globally bounded. Further, r is bounded, so f is also globally bounded. Therefore, we can apply Theorem 7.3.1: for each $\delta > 0$, there exists $C_\delta > 0$ such that for all $t \geqslant 1$, $x \in \mathbb{R}$, $\theta \in \Theta$,

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

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

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

where $|\Theta|$ denotes the volume of Θ. We choose δ small enough that $|\Theta|\,\delta < \varepsilon/2$:

$$\rho(t,x) \leqslant |\Theta|\, C_\delta u(t,x,\theta) + \varepsilon/2. \tag{7.17}$$

Now, we set $G := |\Theta|\, C_\delta$ and we show that for this value of G, the lemma holds. Let

$$\mathcal{T} := \{t \geqslant 1 \,/\, \exists (x_0, \theta_0) \in \mathbb{R} \times \Theta,\, u(t,x_0,\theta_0) = u^\varepsilon(t,x_0,\theta_0)\}$$

If $\mathcal{T} = \emptyset$, then we are done. Now, we assume that we have $\mathcal{T} \neq \emptyset$ and we let $t_0 := \inf \mathcal{T}$. By continuity of u and u^ε, we have $t_0 \in \mathcal{T}$. Therefore, there exists $(x_0, \theta_0) \in \mathbb{R} \times \Theta$ such that

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

We recall that $u^\varepsilon(1, \cdot, \cdot) < u(1, \cdot, \cdot)$. Then we must have $t_0 > 1$ and

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

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:

$$Gu(t_0, x_0, \theta_0) \leqslant \rho(t_0, x_0) - \varepsilon. \tag{7.18}$$

This contact condition is impossible by virtue of (7.17) and of the definition of G. Therefore, we must have $\mathcal{T} = \emptyset$.

□

Proof of Proposition 7.3.4. 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

$$\begin{cases} \mathcal{L}^{\varepsilon,\lambda}\varphi^{\varepsilon,\lambda} = k^{\varepsilon,\lambda}\varphi^{\varepsilon,\lambda} & \text{in } \mathbb{R} \times \Theta, \\ \nu \cdot \nabla_\theta \varphi^{\varepsilon,\lambda} = 0 & \text{over } \mathbb{R} \times \partial\Theta, \\ \varphi^{\varepsilon,\lambda} > 0 & \text{in } \mathbb{R} \times \Theta, \\ \varphi^{\varepsilon,\lambda} & 1\text{-periodic in } x. \end{cases} \tag{7.19}$$

Let us denote by

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

the Freidlin-Gärtner speed corresponding to u^ε. By Section 8 of [220], the solution u^ε of the local problem (7.16) spreads (in the definition of [220]) at speed c^ε_{FG}. This implies in particular that for all $c'' \in (0, c^\varepsilon_{FG})$,

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

Since $r^\varepsilon = r - \varepsilon$, we have $k^{\varepsilon,\lambda} = k^\lambda - \varepsilon$. Since $c_{FG} > 0$, we have $\inf_{\lambda \geqslant 0} k^\lambda > 0$. Thus:

$$c_{FG}^\varepsilon = \inf_{\lambda > 0} \frac{k^\lambda - \varepsilon}{\lambda} = c_{FG} + o_{\varepsilon \to 0}(1).$$

Let $c'' \in (0, c_{FG})$. There exists $\varepsilon > 0$ so small that $c'' < c_{FG}^\varepsilon$. We then have:

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

This proves the proposition.

□

7.4 Behaviour of the spreading speed with respect to the period

This part is devoted to the proof of Proposition 7.2.11 and Theorems 7.2.5 and 7.2.6. For notational convenience, we shall assume throughout that $m = 1$. The notations thus simplify:

$$c_L = c_{m,L}, \qquad k_L^\lambda = k_{m,L}^\lambda.$$

In Subsection 7.4.1, we prove that the function $L \mapsto c_L$ is continuous and nondecreasing (Proposition 7.2.11). In Subsection 7.4.2, we compute the limit of c_L as $L \to +\infty$ (Theorem 7.2.5). In Subsection 7.4.3, we compute the limit of c_L as $L \to 0$ (Theorem 7.2.6).

7.4.1 Continuity and monotony (Proposition 7.2.11)

Proof of Proposition 7.2.11, part 1. Take $L_0 > 0$ such that $k_{L_0}^0 > \delta$. Take $L_1 > L_0$. Using Proposition 7.4.1 below, we have $k_L^0 > \delta$ for all $L \in [L_0, L_1]$, so c_L is well defined and positive for all $L \in [L_0, L_1]$. We prove that the function $L \mapsto c_L$ is continuous on $[L_0, L_1]$. The function $(\lambda, L) \mapsto k_L^\lambda$ is continuous. Hence, as $\lambda \to 0$, we have $k_L^\lambda / \lambda \to +\infty$ uniformly in $L \in [L_0, L_1]$. Moreover, by Lemma 7.3.2, as $\lambda \to +\infty$, we have $k_L^\lambda / \lambda \to +\infty$ uniformly in $L \in [L_0, L_1]$. Thus, there exist $\lambda_1 > 0$ and $\lambda_2 > \lambda_1$ such that for all $L \in [L_0, L_1]$,

$$c_L = \min_{\lambda \in [\lambda_1, \lambda_2]} \frac{k_L^\lambda}{\lambda}.$$

This implies that the function $L \mapsto c_L$ is continuous on (L_0, L_1), thus on $(L_0, +\infty)$. □

The second part of Proposition 7.2.11, i.e. the fact that $L \mapsto c_L$ is nondecreasing, is a consequence of the following proposition and of Theorem 7.2.3.

Proposition 7.4.1. *For all $\lambda \in \mathbb{R}$, the function $L \mapsto k_L^\lambda$ is nondecreasing on $(0, +\infty)$.*

The proof of the proposition is almost the same as that of [173, Proposition 4.1]. We give an idea of the proof to focus on the assumptions that are needed. For a 1-periodic function $f : \mathbb{R} \times \Theta \to \mathbb{R}$, 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 with 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 7.4.1 is the following theorem, which allows one to turn the study of a nonsymmetric operator into the study of a symmetric operator.

Theorem 7.4.2 (Theorem 2.2 in [173]). *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 7.4.2 is almost the same as that of [173, 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 7.4.2, we may conclude in exactly the same way as in the proof of [173, Proposition 4.1] that $L \mapsto k_L^\lambda$ is nondecreasing.

Thus Proposition 7.4.1, and with Theorem 7.2.3, we conclude that $L \mapsto c_L$ is nondecreasing.

7.4.2 When the period goes to infinity (Theorem 7.2.5)

We let $H(x) = H_m(x)$ be the local principal eigenvalue, defined by the local eigenproblem

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

The index m being fixed to 1, we drop it in this section for clarity. 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 7.4.3. *Assume that $k^0_{L_0} > 0$ 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 7.2.5 is a consequence of Proposition 7.4.3 and of [119, Theorem 2.3], which says that

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

To prove Proposition 7.4.3, we first prove the following lemma.

Lemma 7.4.4. *Let $\lambda > 0$. Let the assumptions of Proposition 7.4.3 hold. Then k^λ_L converges as $L \to +\infty$ and*

(i) If $\lambda \geqslant j(M)$, then

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

(ii) If $\lambda < j(M)$, then

$$\lim_{L\to+\infty} k^\lambda_L = M.$$

Proof. Let φ^λ_L be a positive principal eigenfunction associated with the Freidlin-Gärtner operator $\mathcal{L}^\lambda_L$. By considering the L-periodic version of φ^λ_L, which is $\varphi : (x,\theta) \mapsto \varphi^\lambda_L\left(\frac{x}{L},\theta\right)$, we see that k^λ_L is also a principal eigenvalue associated with the eigenproblem

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

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

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

We now apply Theorem 2.1.3 of Chapter 2. 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, Theorem 2.1.3 of Chapter 2 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 7.4.3.

Proof of Proposition 7.4.3. By the persistence assumption that $k_{L_0}^0 > 0$, and by Proposition 7.4.1, there exists $\delta > 0$ such that for each $L \geqslant L_0$: $k_L^0 > \delta$. This and the lower bound in Lemma 7.3.2 imply that for each $L \geqslant L_0$, there exists $\lambda_L > 0$ such that

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

and that there exist $\lambda_- > 0$ and $\lambda_+ > \lambda_-$ 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 $\lambda \mapsto k_{L_n}^\lambda$ converges increasingly, as $n \to +\infty$, to its limit, 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,

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

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

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

With the above, we obtain that c_{L_n} converges for all sequence $L_n \to +\infty$. Hence c_L also converges and:

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

To conclude, by Lemma 7.4.4, for $\lambda \geqslant j(M)$, we have

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

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

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

Thus

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

This concludes the proof. □

Proof of Equation (7.11). Now, let us prove that (7.11) holds when a is a constant. We assume without loss of generality that $a = 1$. On the one hand, we have by Proposition 7.4.3,

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

By Jensen's 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's 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 (7.11) is proved.

□

7.4.3 When the period goes to zero (Theorem 7.2.6)

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 an associated homogenised principal eigenfunction $\psi^\lambda \in \mathcal{C}^2(\overline{\Theta})$ by

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

Lemma 7.4.5. *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

$$\begin{cases} \partial_x\left(a_L \partial_x \varphi_L\right) + \nabla_\theta \cdot \left(\mu_L \nabla_\theta \varphi_L\right) - 2\lambda a_L \partial_x \varphi_L \\ \qquad + \left(r_L + \lambda^2 a_L - \lambda \partial_x a_L\right)\varphi_L = k_L \varphi_L & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \varphi_L = 0 & \text{over } \partial\Theta, \\ \varphi_L & \text{is } L\text{-periodic in } x, \end{cases} \tag{7.20}$$

with normalisation

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

(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

$$\begin{cases} \partial_x\left(a_L \partial_x \Phi_L\right) + \nabla_\theta \cdot \left(\mu_L \nabla_\theta \Phi_L\right) + r_L \Phi_L = k_L^\lambda \Phi_L & \text{in } \Theta, \\ \nu \cdot \nabla_\theta \Phi_L = 0 & \text{over } \partial\Theta. \end{cases} \tag{7.21}$$

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 (7.20) 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:

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

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

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

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 7.3.2) 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 7.3.2), 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 $\psi\Phi_{(0)}$, $\psi\Phi_L$, $\psi\partial_x\Phi_{(0)}$ and $\psi\partial_x\Phi_L$ are 1-periodic in x), and we show that

$$-\int_{[0,1]\times\Theta} \widetilde{a}^H(\partial_x\Phi_{(0)})(\partial_x\psi) - \int_{[0,1]\times\Theta} \widetilde{\mu}^A \nabla_\theta\Phi_{(0)}\cdot\nabla_\theta\psi + \int_{[0,1]\times\Theta} \left(\widetilde{r}^A - k_{(0)}\right)\Phi_{(0)}\psi = 0. \quad (7.22)$$

To this aim, we apply the oscillating test function method, which is classical in homogenisation theory [10]. 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 satisfies

$$a(x,\theta)(1+\partial_x w(x,\theta)) = \widetilde{a}^H(\theta).$$

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 (7.21) by ψ_n and integrating by parts on $[0,1]\times\Theta$ gives:

$$-\int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x\Phi_n)(\partial_x\psi_n) - \int_{[0,1]\times\Theta} \mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta\Phi_n\cdot\nabla_\theta\psi \\ + \int_{[0,1]\times\Theta}\left(r\left(\frac{x}{L_n},\theta\right) - k_n\right)\Phi_n\psi_n = o_{L\to 0}(1). \quad (7.23)$$

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 (7.23). First,

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

On the one hand,

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

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,

$$\lim_{n\to+\infty}\int_{[0,1]\times\Theta} a\left(\frac{x}{L_n},\theta\right)(\partial_x\Phi_n)(\partial_x\psi_n) = \int_{[0,1]\times\Theta}\widetilde{a}^H\partial_x\Phi_{(0)}\partial_x\psi. \quad (7.24)$$

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:

$$\lim_{n\to+\infty}\int_{[0,1]\times\Theta}\mu\left(\frac{x}{L_n},\theta\right)\nabla_\theta\Phi_n\cdot\nabla_\theta\psi=\int_{[0,1]\times\Theta}\widetilde{\mu}^A(\theta)\,(\nabla_\theta\Phi_{(0)})\cdot(\nabla_\theta\psi). \tag{7.25}$$

Finally,

$$\lim_{n\to+\infty}\int_{[0,1]\times\Theta}\left(r\left(\frac{x}{L_n},\theta\right)-k_{(0)}\right)\Phi_n\psi_n=\int_{[0,1]\times\Theta}\left(\widetilde{r}^A(\theta)-k_{(0)}\right)\Phi_{(0)}\psi. \tag{7.26}$$

Using Equations (7.23), (7.24), (7.25) and (7.26), we conclude that the weak formulation (7.22) holds for all test functions $\psi\in W_2^1(\mathbb{R}\times\Theta)$ such that $e^{-\lambda x}\psi$ is 1-periodic in x. Hence, by the notes at the end of [107, Chapter 8], the function $\Phi_{(0)}$ is the unique weak solution of

$$\begin{cases}\widetilde{a}^H\partial_{xx}\Phi_{(0)}+\nabla_\theta\cdot\left(\widetilde{\mu}^A\nabla_\theta\Phi_{(0)}\right)+\widetilde{r}^A\Phi_{(0)}=k_{(0)}\Phi_{(0)} & \text{in } \mathbb{R}\times\Theta,\\ \nu\cdot\nabla_\theta\Phi_{(0)}=0 & \text{over } \mathbb{R}\times\partial\Theta.\end{cases} \tag{7.27}$$

Step 3. Conclusion. By the regularity of the coefficients of (7.27) and the uniqueness of the classical solution, we conclude that $\Phi_{(0)}\in\mathcal{C}^2(\mathbb{R}\times\overline{\Theta})$, so (7.27) 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 $\varphi_{(0)}\geqslant 0$ and $\varphi_{(0)}\not\equiv 0$. Using the strong comparison principle, we obtain: $\varphi_{(0)}>0$.

Therefore, by the uniqueness of a principal eigenvalue, we have $k_{(0)}=\widetilde{k}$. To conclude, the family $(k_L)_{L>0}$ is bounded (see Lemma 7.3.2) and $\widetilde{k}$ is the only limit of a subsequence as $L\to 0$; hence the whole family converges to $\widetilde{k}$ as $L\to 0$.

□

From Lemma 7.4.5, we show the first equality in Theorem 7.2.6.

Proof of Theorem 7.2.6, part 1. By Lemma 7.4.5 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 7.2.11). 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 7.4.1), 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 7.2.6 by using the Rayleigh formula.

Proof of Theorem 7.2.6, part 2. For $\psi \in H^1(\Theta)$, we let

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

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 (7.20)). Recall the assumption that for all $L \in (0, L_0)$, $k^0_{m,L} > \delta$. By Lemma 7.4.5, therefore, we must have $\widetilde{k}^0 > 0$; due to the Rayleigh formula for $\widetilde{k}^0$, there exists ψ such that $R_\psi > 0$. 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

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

Hence

$$c_0 = \inf_{\lambda>0} \left[\max_{\psi\in H^1(\Theta),\, \|\psi\|_{L^2(\Theta)}=1} \left(\frac{1}{\lambda} R_\psi + \lambda A_\psi\right)\right]. \tag{7.28}$$

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

$$c_{var} = \sup_{\psi\in H^1(\Theta),\, \|\psi\|_{L^2(\Theta)}=1,\, R_\psi>0} \left[\min_{\lambda>0} \left(\frac{1}{\lambda} R_\psi + \lambda A_\psi\right)\right]. \tag{7.29}$$

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 (7.28) and (7.29), 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. □

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

This part is devoted to the proofs of Theorem 7.2.7 (limits of $c_{m,L}$ as $m \to 0$ and $m \to +\infty$), of Theorem 7.2.8 (optimal mutation coefficient), and of Propositions 7.2.9 and 7.2.10, which give various properties of the dependence in the parameter m of the spreading speed.

We shall use specific notations for principal eigenvalues for operators without phenotypic variable. If $A \in \mathcal{C}^{1,\alpha}(\mathbb{R})$ 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 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 7.5.1, we compute the limit of c_m as $m \to +\infty$. In Subsection 7.5.2, we compute the limit of c_m as $m \to 0$ and conclude the proof of Theorem 7.2.7. In Subsection 7.5.4, we prove Propositions 7.2.9 and 7.2.10. Finally, in Subsection 7.5.3, we prove Theorem 7.2.8.

7.5.1 When the mutation coefficient goes to infinity (Theorem 7.2.7, part (i))

For notational convenience, we shall assume throughout Subsections 7.5.1 and 7.5.2 that $L = 1$. The notations thus simplify:

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

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 7.5.1. *Let $\lambda \in \mathbb{R}$. Under the assumptions of Theorem 7.2.7 (part (i)), as $m \to +\infty$,*

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

Proof. We assume that $a = a(x)$ and $\mu = \mu(x)$ are independent of θ.

For all $m > 0$, we let $\varphi_m > 0$ be the principal eigenfunction associated with 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

$$\begin{cases} \partial_x(a\partial_x\varphi_m) + m\nabla_\theta \cdot (\mu\nabla_\theta\varphi_m) - 2\lambda a\partial_x\varphi + (r + \lambda^2 a - \lambda\partial_x a)\varphi_m = k_m^\lambda\varphi_m & \text{in } \mathbb{R}\times\Theta, \\ \nu \cdot \nabla_\theta\varphi_m = 0 & \text{over } \mathbb{R}\times\partial\Theta. \end{cases} \tag{7.30}$$

First, we show that $(\varphi_m)_{m>1}$ is bounded in $W_2^1([0,1]\times\Theta)$. Multiplying the first line of (7.30) 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

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

Since $(k_m)_{m>1}$ is bounded (see Lemma 7.3.2) 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, the upper bound above implies that as $m \to +\infty$,

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

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

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

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 (7.30), we have:

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

Note 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 limit of a subsequence of k_m^λ as $m \to +\infty$. Since $(k_m^\lambda)_{m>0}$ is bounded (Lemma 7.3.2), 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 7.2.7. Since $\kappa^1(0; a, \overline{r}) > 0$, Lemma 7.5.1 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 7.3.2, for all $m > \underline{m}$ and $\lambda > 0$,

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

Therefore,

$$\lim_{\lambda\to 0} \frac{k_m^\lambda}{\lambda} = +\infty, \qquad \lim_{\lambda\to+\infty} \frac{k_m^\lambda}{\lambda} = +\infty, \qquad \text{uniformly in } m > \underline{m}. \tag{7.31}$$

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 (7.31), 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 [28, 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 the lower bound in Lemma 7.3.2, 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 limit of a subsequence (c_{m_n}) such that $m_n \to +\infty$, we conclude that the whole family converges to $c^1(a, \overline{r})$.

□

7.5.2 When the mutation coefficient goes to zero (Theorem 7.2.7, parts *(ii)* and *(iii)*)

Here, we compute the limit of c_m as $m \to 0$ (part *(ii)* of Theorem 7.2.7) and we show part *(iii)* of Theorem 7.2.7.

Lemma 7.5.2. *Let $\lambda \in \mathbb{R}$. Under the assumptions of Theorem 7.2.7 (part (ii)), as $m \to 0$,*

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

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 7.5.1 by Lemma 7.5.2, the limit "$m \to +\infty$" by the limit "$m \to 0$", and $\kappa^1(\lambda; a, \overline{r})$ by $\max_{\theta \in \overline{\Theta}} \kappa^1(\lambda; a, r(\cdot, \theta))$. There only remains

to prove Lemma 7.5.2.

Proof of Lemma 7.5.2. The principal eigenfunction φ_m^λ solves

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

Setting $\varepsilon = m$ and letting $\varphi_\varepsilon = \varphi_m^\lambda$ brings us to the setting of Theorem 2.1.2 of Chapter 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 Theorem 2.1.2 of Chapter 2. □

There remains to prove the last statement of Theorem 7.2.7 about the comparison of the two limits $m\to+\infty$ and $m\to 0$.

Proof of Theorem 7.2.7, 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 [173, Proposition 2.4], the function $g\in L^\infty([0,1])\mapsto\kappa^1(\lambda;a,g)$ is convex. Hence, by Jensen's inequality, we conclude:

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

□

7.5.3 The optimal mutation coefficient (Theorem 7.2.8)

Proof of Theorem 7.2.8. 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 $L>0$, $\kappa^1(0; a, r_L(\cdot,\theta))>0$; thus by Lemma 7.5.2 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 7.2.5 and 7.2.7 (part (ii)). Finally, we assume that (7.13) 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 7.2.7:

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

Thus, using the monotony in L (Proposition 7.2.11),

$$\lim_{L\to+\infty}\lim_{m\to 0} c_{m,L} = \max_{\theta\in\overline{\Theta}}\left(\lim_{L\to+\infty} c^1(a_L(\cdot), r_L(\cdot,\theta))\right). \tag{7.32}$$

On the other hand, by Proposition 7.4.3,

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

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 7.2.5). By the Rayleigh formula,

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

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

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

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

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

Finally, we also have, for all y,

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

This proves that as $m\to 0$,

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

Therefore, as $m\to 0$, by the dominated convergence theorem,

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

Using the fact that $\frac{j_m^{-1}(\lambda)}{\lambda} \to +\infty$ uniformly in $m\in(0,1)$ as $\lambda\to 0$ and $\lambda\to+\infty$, we get

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

see e.g. the argument of the proof of Proposition 7.4.3. We obtain (using [119, 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 (7.13), 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 [119, 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 (7.32), 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. Now, we take $\overline{m}$ as large as possible, namely:

$$\overline{m} := \sup\left\{m'\in\mathbb{R}\ /\ \exists \underline{L}>0, \delta>0,\ \forall m\in(0,m'),\ k^0_{m,\underline{L}}>\delta\right\}\in(0,+\infty].$$

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 7.2.11), 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 $L_1>L_0$,

$$\sup_{m\in[m_0,m_1]}\left|c_{m,L_1} - \lim_{L\to+\infty} c_{m,L}\right| < \varepsilon. \tag{7.33}$$

We set:

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

(Recall that $\overline{m}$ may be infinite.) By the last point in Proposition 7.2.9 and by assumption (7.13) (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 is positive. Therefore, for $m_0>0$ small enough and $m_1\in(m_0,\overline{m})$ large enough, Equation (7.33) implies: for all $m\in(m_1,\overline{m})$, 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 7.2.11 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 (7.33) 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 7.2.11). 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 7.2.9, 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 (7.33) 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.

□

7.5.4 Other properties (Propositions 7.2.9 and 7.2.10)

Proof of Proposition 7.2.9. We first prove that

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

is nonincreasing (the limit exists thanks to the assumptions and Theorem 7.2.5). By Proposition 7.4.3, it is enough to show that for all $k \geqslant M$, $m \mapsto j_m(k)$ 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:

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

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 with the principal eigenvalue $H_{m_2}(x)$. Then:

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

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 7.2.6). This comes from the variational formulation in Theorem 7.2.6, 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

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

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

□

Proof of Proposition 7.2.10. By the Rayleigh formula,

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

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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Chapter 8

A population with two morphs

This chapter is based on the article [201]:

L. Roques, N. Boutillon, P. Zamberletti, J. Papaïx, *Polymorphic population expansion velocity in a heterogeneous environment*, Journal of Theoretical Biology (2024), p. 111932.

Abstract

How does the spatial heterogeneity of landscapes interact with the adaptive evolution of populations to influence their spreading speed? This question arises in agricultural contexts where a pathogen population spreads in a landscape composed of several types of crops, as well as in epidemiological settings where a virus spreads among individuals with distinct immune profiles. To address it, we introduce an analytical method based on reaction-diffusion models. We focus on spatially periodic environments with two distinct patches, where the dispersing population consists of two specialised morphs, each potentially mutating to the other. We present new formulas for the speed together with criteria for persistence, accounting for both rapidly and slowly varying environments, as well as small and large mutation rates. Altogether, our analytical and numerical results yield a comprehensive understanding of persistence and spreading dynamics. In particular, compared to a situation without mutations or to a single morph spreading in a heterogeneous landscape, the introduction of mutations to a second morph with reverse specialisation, while consistently impeding persistence, can significantly increase speed, even if the mutation rate between the two morphs is very small. Additionally, we find that the amplitude of the spatial fragmentation effect is significantly increased in this case. This has implications for agroecology, emphasising the higher importance of landscape structure in influencing adaptation-driven population dynamics.

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8.1 Introduction

One of the major aspects that has contributed to the success of reaction-diffusion approaches in spatial ecology is that their results can sometimes be expressed in the form of simple mathematical expressions. The most famous example is the Fisher-KPP model in a homogeneous one-dimensional environment. In the context of this model, a population that is initially confined to a limited area will spread with a speed $c = 2\sqrt{r\,D}$. This very simple formula provides valuable insight into the effects of the intrinsic growth rate (r) and the spatial diffusion parameter (D) on the speed at which the population spreads. This formula has had a considerable impact on theoretical ecology, see e.g. [168, 181, 210], whether in describing biological invasions or epidemiological phenomena. One can wonder if obtaining so simple formulas remains feasible as the model becomes more realistic.

The study of local adaptation and its role in driving population dynamics in heterogeneous environments has received considerable attention, both from an experimental and a theoretical perspective, see [133] and references therein. Local adaptation is a process whereby subpopulations evolve, through Darwinian selection, to become better adapted to their local environment [223]. In the absence of forces beyond Darwinian selection, genotype-environment interactions should cause each local population to adapt to its specific environmental conditions, regardless of the conditions present in other regions of space. We consider here the case of an asexual population expanding its spatial range in a heterogeneous environment. Then, several factors can prevent the population from reaching the local adaptive optimum, and can influence the spreading speed of the population. These factors include the mutation load (i.e. the reduction in the average fitness of a population due to the accumulation of deleterious mutations, [138, 163]), and migration of individuals from other regions of space [73]; see also [142, 186] for similar effects in sexually-reproducing populations. In addition to these evolutionary effects, the amplitude and spatial distribution of heterogeneity also contribute to the overall picture, as they are known to impact the spreading speed in non-adaptive contexts [28, 208]; see also [70] in the case of two competing species. In this chapter, we propose a method to characterise analytically, in some limiting cases, the spreading speed in models involving both spatial heterogeneity of the environment and adaptive evolution of the population.

The motivation for this chapter stems from the shift from an intensive cropping system supported by uniform agricultural landscapes to the agroecology paradigm, where crop diversification plays a central role to ensure the stability of yields [17, 58, 95, 104]. In particular, host diversity is known to influence disease spread through various mechanisms [134], one of which results from the interplay between the dispersal and competition among pathogen genotypes that adapt differentially to the various hosts present in the environment [40]. In this context, most studies emphasise the role of host diversity in shaping pathogen evolution [72], pathogen diversity [182], and the risk of disease persistence [154]. However, it is interesting to note that little effort has been dedicated to understanding how host diversity affects the speed of disease spread.

In heterogeneous spatially-periodic environments, and with a unique morph (i.e., without adaptation), Fisher-KPP type models have also seen some success, yielding numerous results on the connections between the spatial structure of the environment, persistence, and spreading [27, 28, 208, 220]. However, these connections have generally only been described in a qualitative manner, through results such as monotonic dependence between parameters characterising the environment and quantities characterising persistence and spreading. In particular, "Freidlin-Gärtner" formulas for the spreading speed are not as explicit as the for-

mula $c = 2\sqrt{r\,D}$ when $r(x)$ and $D(x)$ depend on the space variable x. One way to overcome this issue is to look at the limiting cases of small and large periods L, which respectively correspond to highly-fragmented and low-fragmented environments. The case of small periods naturally leads to a homogenisation limit and a simple formula $c(L \to 0) = 2\sqrt{\langle r \rangle_a \langle D \rangle_h}$, where $\langle r \rangle_a$ is the arithmetic mean of $r(x)$ and $\langle D \rangle_h$ is the harmonic mean of $D(x)$ over a period cell. This formula was originally derived by [209] for coefficients that vary sinusoidally and extended to general diffusion and growth rate profiles in [81]. It can be complemented by studying the other limit, where the period length becomes very large, to better capture the effect of heterogeneity [117, 119].

When adaptation occurs, the expanding population may consist of multiple morphs, each specialising in a limited number of hosts. In this scenario, polymorphism in life history traits among individuals, as discussed by [82] and [169], has the potential to influence the invasion speed. Both studies primarily focus on dispersal polymorphism and the complementarity between strategies that invest in growth and those that invest in dispersal. However, they considered only homogeneous environments. Our goal in this study is to examine the influence of adaptation on the spreading speed of a species within a heterogeneous environment. We specifically analyse scenarios in which the environment is periodic, consisting of two distinct patches. The spreading population is made up of two unique morphs, each specialised for one of the patch types. Crucially, part of the offspring of one morph can mutate at birth to become the other morph. We anticipate that the interaction between the two morphs will have a significant impact on the spreading speed. Some parameters can exhibit dual effects. For instance, a higher mutation rate is known to increase the mutation load and decrease the time needed for local environment adaptation [13, 149]. Predicting the effect of the mutation rate on the spreading speed, therefore, becomes a complex endeavor. Explicit analytic formulas will offer valuable insight into the intertwined roles of adaptive, demographic, and spatial factors.

Recent formulas have been derived [115], but they tend to be abstract and provide limited ecological insight. In this study, we present new formulas for the speed, accounting for both rapidly and slowly varying environments, as well as for small and large mutation rates. The rapidly varying environment limit is a direct consequence of the results in [115]. In contrast, determining the speed for slowly varying environments is notably more intricate and unveils some unexpected results, which stand as the cornerstone of our research. Altogether, our formulas, complemented by insight from numerical simulations, enhance our understanding of the specific impacts, on the expansion of the population, of the mutation rate and of the environmental fragmentation. In particular, our research reveals that allowing mutations between the two morphs results in a sudden increase of the speed, with respect to the scenario without mutations; this emerges as one of the primary and significant results of this chapter.

8.2 Material and methods

Model development. The model describes the spread of two distinct morphs of a single species within a heterogeneous 1-dimensional environment composed of two types of patches. This scenario mimics the spreading of pathogens in an environment with alternating hosts, see Figure 8.1 for a schematic description of the model. The two morphs are differentiated by their varying fitness levels (i.e. their growth rates), and interact through local competition. Additionally, a portion of the offspring of one morph may switch to the other morph through the process of mutation at birth (we assume here that the growth terms depend on the morph

and on x only through the death rate; the birth rate is independent of x). The spread of these morphs is further influenced by spatial diffusion. We represent the overall dynamics of this system with the following reaction-diffusion model:

$$\begin{cases} \partial_t u(t,x) = & D\,\partial_{xx} u + r_L^u(x)\,u - \gamma_L(x)\,u\,(u+v) + \mu\,(v-u), \\ \partial_t v(t,x) = & D\,\partial_{xx} v + r_L^v(x)\,v - \gamma_L(x)\,v\,(u+v) + \mu\,(u-v), \end{cases} \quad t>0,\ x\in\mathbb{R}. \tag{8.1}$$

In this context, x represents the spatial variable, while $u(t,x)$ and $v(t,x)$ are the population densities of the two morphs. The periodic functions $r_L^u(x)$ and $r_L^v(x)$ are the growth rates of the two morphs (which depend on the spatial position x). Additionally, D is the spatial diffusion coefficient, which is constant in space and shared by both morphs, and μ is a coefficient proportional to the mutation rate. Finally, $\gamma_L(x)$ is a competition coefficient. The environment, described by the functions r_L^u and r_L^v, is assumed to be periodic with a period L, where one half $[0, L/2)$ of the period cell corresponds to the first host, and the other half $[L/2, L)$ corresponds to the second host. Namely,

$$r_L^u(x) = r^u(x/L),\ r_L^v(x) = r^v(x/L) \text{ and } \gamma_L(x) = \gamma(x/L), \tag{8.2}$$

where r^u, r^v and γ are 1-periodic functions. We assume that the two morphs have distinct specialisations. One morph has a higher growth rate ($R^+ > 0$) on one of the patches and a lower growth rate ($R^- \leqslant R^+$) on the other patch, while the other morph has the opposite specialisation. In other words

$$\begin{cases} r_L^u(x) = R^+ \text{ and } r_L^v(x) = R^- \text{ for } x\in[0,L/2), \\ r_L^u(x) = R^- \text{ and } r_L^v(x) = R^+ \text{ for } x\in[L/2,L). \end{cases} \tag{8.3}$$

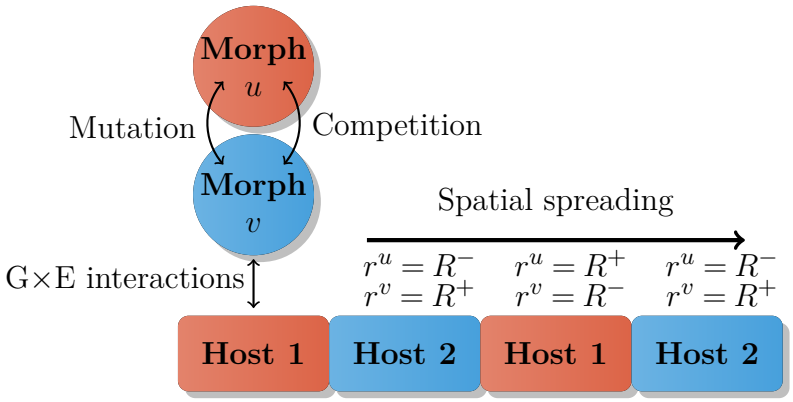

Figure 8.1: Schematic representation of the model in a spatially periodic environment. Morphs u and v have specialised interactions with their hosts: morph u has fitness R^+ on host 1 and R^- on host 2, and conversely morph v has fitness R^- on host 1 and R^+ on host 2 ($R^+ > R^-$). The horizontal arrow signifies spatial spreading of the morphs through the environment.

Persistence of the population. As shown in Theorem 2.9 of [115], the persistence or extinction of the population $u+v$ depends on the sign of k_0^{2m}, the principal eigenvalue of an elliptic operator $\mathcal{L}_0^{2m}$, that indicates whether the state $(u,v)=(0,0)$ is stable or not (see Section 8.5). Here, "$2m$" stands for 2 morphs; in contrast, k_0^{1m} corresponds to the 1 morph case.

When we study the spreading properties, we always assume that $k_0^{2m} > 0$, which ensures the persistence of the population. In our framework, a simple sufficient condition for this is $R^+ + R^- > 0$ (see Section 8.5). We obtain exact persistence conditions through explicit relations between R^+, R^-, μ and k_0^{2m} in the four limiting cases $L \to 0$, $L \to \infty$, $\mu \to 0$ and $\mu \to \infty$. We will describe them in Section 8.3.

Spreading properties. In the case of a spatially homogeneous environment, i.e. when the coefficients do not depend on x, [109] established the spreading properties of the system (8.1). The recent results of [115] extend these properties to systems with spatially periodic coefficients. Before going further on, we need to introduce precisely the notion of spreading speed. The spreading speed to the right (the spreading speed to the left could be considered as well) is the asymptotic rate at which a species, initially concentrated in a bounded spatial region, expands its spatial range to the right-hand side of the 1-dimensional environment [14]. See also [220] for a definition in a spatially-periodic setting. In our setting, with two morphs and with a spatially-periodic heterogeneity, the spreading speed can be defined in the following way. If an observer travels to the right (i.e., towards increasing x values) above that speed, the observer will see the total population density $u(t,x)+v(t,x)$ vanish. If the observer travels to the right below that speed, the observer will not see the total population density vanish. In mathematical terms, we consider initial conditions (u_0, v_0) which are non-negative, not identically equal to $(0,0)$ and such that $(u_0(x), v_0(x)) = 0$ for all x large enough. Then, c^{2m} is the spreading speed associated with the system (8.1) if

$$\begin{array}{ll} \lim\limits_{t\to\infty} \sup\limits_{x \geqslant w' t} u(t,x)+v(t,x) = 0 & \text{for all } w' > c^{2m}, \\ \liminf\limits_{t\to\infty} \inf\limits_{x \leqslant w'' t} u(t,x)+v(t,x) \neq 0 & \text{for all } w'' < c^{2m}. \end{array} \tag{8.4}$$

Let us first focus on the particular case $\mu = 0$: There are no mutations between the two morphs. Since the speed depends on the linearisation of the system at $(0,0)$ [115], the competition between the two morphs has no influence on the spreading speed. With this assumption, the spreading speed is the same as with a single morph ($c^{2m} = c^{1m}$), say u, in a heterogeneous environment: $\partial_t u(t,x) = d\,\partial_{xx} u + r_L^u(x)\,u - \gamma_L(x)\,u^2$. In this case, the existence of a spreading speed is well-known, as well as its dependence with respect to the period L, as we mentioned in the Introduction. In particular, the limit of rapidly oscillating environments (small values of L) has been studied extensively [81, 139, 209]: the spreading speed converges to the speed in a spatially averaged medium, where the growth rate is replaced by its mean value $(R^+ + R^-)/2$. Namely, $c^{1m}(L \to 0) = \sqrt{2\,D\,(R^+ + R^-)}$. The other limit, of slowly oscillating environments, was studied in [117]. Their results imply that

$$c^{1m}(L \to \infty) = 4\sqrt{D} \times \frac{(R^+)^2 + (R^-)^2 + (R^+ + R^-)\sqrt{\triangle}}{(R^+ + R^- + 2\sqrt{\triangle})^{\frac{3}{2}}}, \tag{8.5}$$

with $\triangle = (R^+)^2 + (R^-)^2 - R^+ R^-$. In cases where $R^- = 0$, the expression simplifies to

$$c^{1m}(L \to \infty) = (8/9)\sqrt{3\,D\,R^+} \approx 1.54\sqrt{DR^+}.$$

The authors of [119] also considered more general forms for the reaction and diffusion coefficients. The dependence of the spreading speed on the parameter L has also been recently analysed: the velocity has been found to be an increasing function of the period L, first

numerically for some specific examples in [140, 208], then analytically for the general case in [173]. This set of results provided a better understanding of the effect of resource fragmentation on the rate of spread of a single-morph population, in the absence of adaptation. In particular, because of the monotonicity of the spreading speed with respect to L, the difference $c^{1\,m}(L\to\infty)-c^{1\,m}(L\to 0)$ provides a quantitative measure of the potential effect of fragmentation.

Our objective in this study is to explore the scenario where $\mu>0$. The existence of a spreading speed follows from [115] (under the condition for persistence $k_0^{2\,m}>0$). The results in [115] imply that this spreading speed is characterised by the following formula:

$$c^{2\,m}=\min_{\lambda>0}\frac{k_\lambda}{\lambda}, \tag{8.6}$$

where k_λ is the unique real number (principal eigenvalue) such that there exists a pair of positive L-periodic functions (ϕ_1,ϕ_2) satisfying:

$$\begin{cases} D\,\phi_1''+2\,\lambda\,D\,\phi_1'+\lambda^2\,D\,\phi_1+r_L^u(x)\,\phi_1+\mu(\phi_2-\phi_1) &= k_\lambda\,\phi_1,\\ D\,\phi_2''+2\,\lambda\,D\,\phi_2'+\lambda^2\,D\,\phi_2+r_L^v(x)\,\phi_2+\mu(\phi_1-\phi_2) &= k_\lambda\,\phi_2, \end{cases}\quad\text{in }\mathbb{R}. \tag{8.7}$$

This type of "Freidlin-Gärtner" formula is classical in the scalar case (i.e., with one morph [25, 103, 220]). For systems such as (8.1), such a formula was first proved by [109] when the coefficients do not depend on x, and then extended by [115] to the general case. This theoretical formula, however, provides limited ecological insight. In this chapter, we derive explicit formulas for $c^{2\,m}$, in the limit of rapidly varying ($L\to 0$) and slowly varying environments ($L\to\infty$) and in the limit of small mutations ($\mu\to 0$) and large mutations ($\mu\to\infty$).

Numerical computations. We present a novel algorithm designed to numerically compute the speed $c^{2\,m}$. Our approach involves a finite difference approximation of the operator in (8.7), accounting for periodic conditions. Subsequently, we employ standard matrix methods (SciPy and ARPACK libraries using the eigs function) to determine the principal eigenvalue k_λ for discrete λ values. This information is then used in conjunction with the formula (8.6) to yield an approximate computation $c_{sim}^{2\,m}$ of $c^{2\,m}$. A Jupyter notebook is available at `https://doi.org/10.17605/OSF.IO/7RTFK`. It can be easily launched on Google Colab, requiring no technical skills. We also developed a basic finite difference algorithm to visualise the solutions of the system (8.1). It is used here for illustrative purposes and is notably less accurate when compared to the other code used for speed computation. This code is also available as Jupyter notebook (same url).

8.3 Main results

Persistence. We are equipped to provide a quantitative criterion for persistence in the limit of small or large periods and mutation rates. The outcomes are succinctly summarised in Table 8.1 and substantiated in Section 8.5. Most of these results are intuitive and are direct consequences of the Rayleigh formula, see (8.13)–(8.14) in Section 8.5.

In the scenario of rapidly varying environments ($L\to 0$), the application of homogenisation techniques allows the replacement of r_L^u and r_L^v by their spatial mean value $(R^+ + R^-)/2$, resulting in the convergence of $k_0^{2\,m}$ to $(R^+ + R^-)/2$. As the period L increases, $k_0^{2\,m}$ also

μ \ L	$L \to 0$	Arbitrary L	$L \to \infty$
$\mu = 0$	$R^+ + R^- > 0$	$k_0^{1m} > 0$	$R^+ > 0$
$\mu \to 0$	$R^+ + R^- > 0$	$k_0^{1m} > 0$	$R^+ > 0$
Arbitrary μ	$R^+ + R^- > 0$	$k_0^{2m} > 0$	$R^+ > \frac{\mu}{1+(\mu/(-R^-))}$ or $R^+ + R^- > 0$
$\mu \to \infty$	$R^+ + R^- > 0$	$R^+ + R^- > 0$	$R^+ + R^- > 0$

Table 8.1: Criterion for persistence. The result remains unchanged whether the limit is taken first in μ or L. Respectively, k_0^{1m} and k_0^{2m} correspond to the principal eigenvalues that determine the persistence condition for a one-morph problem and a two-morph problem, see formulas in Section 8.5. The condition $R^+ > \mu/[1+(\mu/(-R^-))]$ is valid when $R^- < 0$; otherwise persistence always holds for $R^+ > R^- > 0$.

increases and converges as $L \to +\infty$ towards

$$\frac{1}{2}\sqrt{(R^+ - R^-)^2 + 4\mu^2} - \mu + (R^+ + R^-)/2,$$

which leads to the condition $R^+ > \mu/[1+(\mu/(-R^-))]$ for persistence. The limit value of k_0^{2m} as $L \to +\infty$ is the principal eigenvalue for a homogeneous environment where $r_L^u = R^+$ and $r_L^v = R^-$: in the case of very large periods, the influence of spatial variations on persistence becomes negligible. We can observe from formulas (8.13)–(8.14) in Section 8.5, that k_0^{2m} increases with L and decreases with D. Additionally, k_0^{2m} decreases as μ increases. This implies that the impact of the mutation load outweighs other plausible beneficial effects of mutation. Consequently, as far as the population persistence is concerned, the potential to mutate into an alternative morph with a distinct adaptive profile consistently proves unfavourable (i.e., $k_0^{2m} < k_0^{1m}$ when $\mu > 0$). It is worth noting that the instances of $\mu = 0$ and $\mu \to 0$ are the same; the criterion characterising the persistence behaviour is continuous at $\mu = 0$, even when $L \to \infty$.

We notice that under our assumptions, where the growth rates r^u and r^v of the two morphs are symmetric (i.e. they mirror each other), the order of the limits taken with respect to μ and L can be interchanged in Table 8.1 without altering the outcomes. Moreover, the limits as $L \to 0$ and as $\mu \to \infty$ lead to the same homogenisation result. This actually conceals differences in the effects of these two limit transitions, which are elucidated in the proofs presented in Section 8.5. The case of $L \to 0$ corresponds to spatial homogenisation (where r^u and r^v are replaced by their respective spatial averages), whereas the case of $\mu \to \infty$ corresponds to homogenisation between the two morphs, but in a local spatial context (where $r^u(x)$ and $r^v(x)$ are replaced at each spatial point x by their average value $(r^u(x)+r^v(x))/2$). Without the symmetry assumption on r^u and r^v, there is no reason to expect that the limit $L \to 0$ should give the same behaviour as the limit $\mu \to \infty$.

Spreading speed. We obtain an analytical characterisation of the spreading speed in rapidly ($L \to 0$) and slowly ($L \to \infty$) varying environments, see Table 8.2 and Section 8.6 for technical details. In particular, we prove that, for arbitrary μ,

$$c^{2m}(L \to 0) = \sqrt{2D(R^+ + R^-)}, \tag{8.8}$$

μ \ L	$L \to 0$	Arbitrary L	$L \to \infty$
$\mu = 0$	$\sqrt{2D(R^+ + R^-)}$	$c^{1\,m}$	$c^{1\,m}(L \to \infty)$, see (8.5)
$\mu \to 0$	$\sqrt{2D(R^+ + R^-)}$	$c^{1\,m}$	$\mu \to 0$ then $L \to \infty$: $c^{1\,m}(L \to \infty)$, see (8.5) $L \to \infty$ then $\mu \to 0$: $2\sqrt{D\,R^+}$
Arbitrary μ	$\sqrt{2D(R^+ + R^-)}$	Fig. 8.3	$\sqrt{2D\left(R^+ + R^- + \sqrt{(R^+ - R^-)^2 + 4\mu^2} - 2\mu\right)}$
$\mu \to \infty$	$\sqrt{2D(R^+ + R^-)}$	$\sqrt{2D(R^+ + R^-)}$	$\sqrt{2D(R^+ + R^-)}$

Table 8.2: Spreading speed $c^{2\,m}$. Except for the limit $(L, \mu) \to (+\infty, 0)$, the results remain unchanged whether the limit is taken first in μ or L. The notation $c^{1\,m}$ stands for the spreading speed when there is only one morph.

and that

$$c^{2\,m}(L \to \infty) = \sqrt{2D\left(R^+ + R^- + \sqrt{(R^+ - R^-)^2 + 4\mu^2} - 2\mu\right)}. \tag{8.9}$$

Interestingly, although the model with two morphs is more intricate, the limiting spreading speed as $L \to +\infty$ is given by a formula (8.9) which seems simpler than the corresponding formula for the one morph model, see (8.5). In the limit $L \to \infty$, we observe that $c^{2\,m}$ is a decreasing function of the mutation coefficient: the highest speeds are achieved when $\mu \to 0$. In the limit $\mu \to 0$, $c^{2\,m} \to 2\sqrt{D\,R^+}$, which corresponds to the spreading speed of a single morph in a homogeneous and favourable environment (i.e., with constant growth rate R^+). Interestingly, this speed is much larger than in the case $\mu = 0$, see (8.5). This is more obvious in the case $R^- = 0$: when $\mu = 0$ we have $c^{2\,m}(L \to \infty) = c^{1\,m}(L \to \infty) = (8/9)\sqrt{3\,D\,R^+} \approx 1.54\sqrt{D\,R^+}$, to be compared to the limit $2\sqrt{D\,R^+}$ of $c^{2\,m}(L \to \infty)$ as $\mu \to 0$, which is 30% larger. Thus, the function $\mu \mapsto c^{2\,m}(L \to \infty)(\mu)$ admits a discontinuity at $\mu = 0$. Figure 8.2a illustrates solutions of the system (8.1), both with $\mu > 0$ and with $\mu = 0$, starting from the same compactly supported initial condition. The figure shows that the spreading is indeed faster when $\mu > 0$. This is corroborated in Figure 8.2b, which tracks the position of a level of $u + v$ over time. In particular, in the case of $\mu > 0$, the instantaneous speed is much less variable than in the case of $\mu = 0$.

Figure 8.3 gives a numerical description of the relationship between the speed c^{2m} and the parameters μ and L. It shows that, even if this discontinuity does not appear for finite values of L, there is a significant jump in speed for small values of μ. This sudden jump is particularly pronounced as L increases, demonstrating that the presence of a second morph may hold a more significant influence under such circumstances for large periods. The speed culminates at an optimum mutation rate, and after the optimal μ value, the speed becomes a decreasing function of μ, highlighting the dominance of the emergence of ill-adapted mutants (mutation load). According to Figure 8.3, the optimal value for the mutation rate μ decreases as L is increased, indicating that this mutation load effect arises sooner in low-fragmented environments. Consistently with our knowledge in the case of a single morph [140, 173, 208], we also observe in Figure 8.3 that the spreading speed increases with the period L, beginning at $c^{2\,m}(L \to 0)$ and reaching its maximum at $c^{2\,m}(L \to \infty)$. However, we observe that the range of variation, as indicated by the difference between the dashed and solid lines in Figure 8.3, is much more important in this context compared to the case of a single

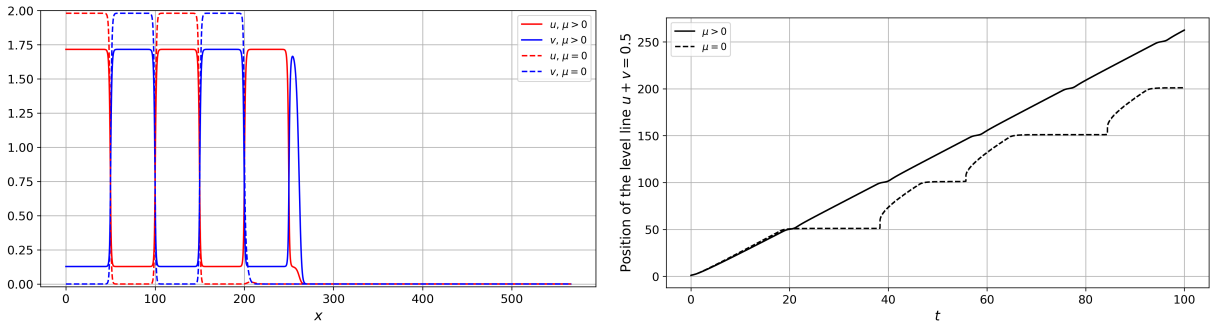

Figure 8.2: Solutions of the main system (8.1)**,** $\mu > 0$ **vs** $\mu = 0$**.** (a) The solutions are plotted at time $t = 100$; (b) Dynamics of the position of 0.5 level line of $u+v$, defined as the rightmost point $x_{0.5}(t)$ where $(u+v)(t, x_{0.5}(t)) = 0.5$. The parameter values are $R^+ = 2$, $R^- = 0$, $D = 1$, $\mu = 0.15$, $L = 100$ and the initial condition $u(0,x) = v(0,x) = 1$ for $x \leqslant 1$ and $u(0,x) = v(0,x) = 0$ for $x > 1$.

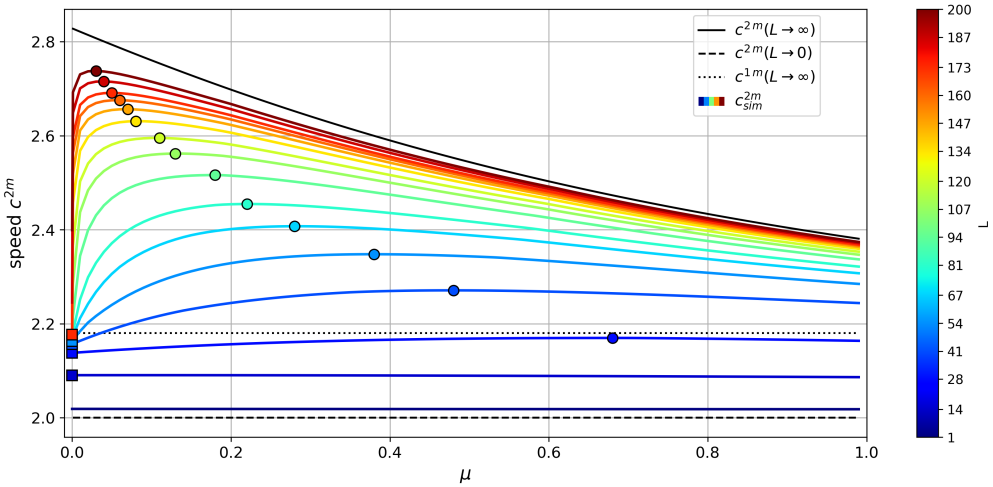

Figure 8.3: Theoretical and simulated speeds in terms of the mutation parameter μ **and spatial period** L**.** The circles indicate the maximum values of c^{2m}_{sim}, for each L. The leftmost points ($\mu = 0$, squares) indicate the numerical value of the speed c^{1m}_{sim}. The parameter values are $R^+ = 2$, $R^- = 0$, $D = 1$, leading to $c^{1m}(L \to 0) = 2$, $c^{2m}(L \to 0) = 2$, $c^{1m}(L \to \infty) \approx 2.18$, $c^{2m}(L \to \infty) = 2\sqrt{2} \approx 2.83$ as $\mu \to 0$, see Table 8.2.

morph, where the difference is between the dashed and dotted lines in Figure 8.3. This also follows from the results in Table 8.2. For instance, in the particular case $R^- = 0$ (as in Figure 8.3), the table shows that the maximum amplitude of variation as L is increased is $c^{1\,m}(L \to \infty) - c^{1\,m}(L \to 0) = ((8/9)\sqrt{3} - \sqrt{2})\sqrt{D\,R^+} \approx 0.13\sqrt{D\,R^+}$ in the case of one morph, vs $c^{2\,m}(L \to \infty) - c^{2\,m}(L \to 0) = (2 - \sqrt{2})\sqrt{D\,R^+} \approx 0.59\sqrt{D\,R^+}$ in the case of two morphs, for small μ.

When μ tends towards infinity, the spreading speed $c^{2\,m}(\mu \to \infty)$ converges to $\sqrt{2\,D\,(R^+ + R^-)}$, signifying yet another homogenisation limit. The system operates as though there were a single morph with a uniform growth rate of $(R^+ + R^-)/2$. Similar to our earlier observations on persistence, this homogenisation remains spatially local in the sense that large mutation rate induces the replacement of the growth rates r^u and r^v at each spatial point x by their averaged value $(r^u(x) + r^v(x))/2$.

Let us now state a conjecture for a general formula describing the limit spreading speed as L approaches infinity, considering arbitrary 1-periodic functions r^u and r^v. This means that we no longer assume these functions to be piecewise constant or to mirror each other. The idea is to adapt the results presented in [119], which addressed the limit as L tends to infinity for the critical invasion speed $c^{1\,m}$ in scenarios involving only one morph. This concept is elaborated upon in Section 8.7, where we aim at establishing a formula applicable when both r^u and r^v are spatially constant and then extend it to accommodate scenarios where these functions are not necessarily constant. Our argument is based on the observation that as the period becomes large, an individual should die before it manages to reach locations where the values of r^u and r^v deviate significantly from their values at the place of birth of the individual. Consequently, throughout its lifespan, an individual encounters nearly constant values of r^u and r^v. This leads us to propose the following conjecture, which is similar to Theorem 7.2.5 of Chapter 7 but in the setting of the present chapter:

Assume that r^u and r^v are arbitrary 1-periodic functions, and that persistence occurs (e.g., $\int_0^1 r^u + r^v > 0$). Define

$$j(k) := \int_0^1 \sqrt{k - \frac{1}{2}\left[r^u(x) + r^v(x) - 2\mu + \sqrt{(r^u(x) - r^v(x))^2 + 4\mu^2}\right]}\,\mathrm{d}x.$$

Then j is defined on a maximal interval of definition $[M, +\infty)$ (for some $M > 0$) and

$$c^{2\,m}(L \to \infty) = \sqrt{D} \inf_{\lambda \geqslant j(M)} \frac{j^{-1}(\lambda)}{\lambda}. \tag{8.10}$$

For instance, consider the scenario where r^u and r^v alternately take two values, denoted again as R^+ and R^-, such that $r^u(x) = R^+$ if and only if $r^v(x) = R^-$. In this case, we obtain formula (8.9). It is important to note that this result does not depend on the positions and sizes of the patches where $r^u = R^+$ in relation to those where $r^u = R^-$. This suggests that formula (8.9) should remain valid under more general assumptions than our initial ones.

Although the formula in (8.10) seems quite complex, it allows us to establish that $c^{2\,m}(L \to \infty)$ should be a decreasing (or nonincreasing) function of μ in the general case. Furthermore, it enables us to explore other biological scenarios, such as variations in diffusion terms, as discussed in [82, 169] in the spatially homogeneous case, or the comparison between generalist and specialist strategies, as detailed in Section 8.7.

8.4 Discussion

In this study, by using the period length as a proxy for the fragmentation of the environment, and by considering a simplified scenario involving a population made up of two morphs, we examined the intertwined influences of habitat heterogeneity, fragmentation, and adaptation. Our analytical and numerical results clarify how these various factors affect the persistence and spreading of the population. In particular, the introduction of mutations always leads to a decreased ability of persistence with respect to the setting without mutations. In some sense, mutation acts as a dispersal term along a phenotypic dimension. Similar to spatial diffusion in classical periodic Fisher-KPP models [27, 208], mutations reduce persistence by displacing individuals away from the optimal phenotype. Conversely, the introduction of mutations may lead to an increased spreading speed. This means that invasion dynamics can be "anomalous", i.e., faster than any of the morphs in isolation [221]. Since [221], several studies have focused on this type of phenomenon in spatially homogeneous landscapes, see [128] in a system of two Fisher-KPP equations with unidirectional coupling, and [191] in integrodifference models. Such anomalous spreading was also observed in the results of [82] and [169]. These two studies focused on the impact of varying growth rate R and diffusion rate D on the spreading speed of a system made up of two morphs, typically an R-specialist (with a high growth rate R^+ and low diffusion rate D^-) and a D-specialist (with a low growth rate $R^- < R^+$ and high diffusion rate $D^+ > D^-$) in a spatially homogeneous environment. They observed that, for some combinations of values of R and D, and with a low mutation rate between the two morphs, the system could spread faster when both morphs were present than when only one morph was present. This unexpected outcome appears to arise from the synergistic effect of the growth rate of the R-specialist and the diffusion rate of the D-specialist during expansion. We also observed an anomalous spreading speed, induced by mutations, and which can be interpreted by the fact that the population exploits the best morph at each spatial point: viewing mutations as a form of dispersal along a phenotypic dimension, mutations can increase the spreading speed by enabling individuals to spread while they follow a trajectory that winds through, predominantly remaining in the most favourable habitats.

When we observe habitats with minimal fragmentation ($L \to \infty$), there is a discontinuity in speed with respect to the parameter μ at $\mu = 0$. This means that introducing a second morph with reverse specialisation leads to a significantly higher speed, even if the mutation rate between the two morphs is very small. An explanation for this result comes from the idea that large host patches favour the selection of specialists that thrive on their preferred hosts [183]. Therefore, the mutation rate should be greater than 0 to allow the emergence of each morph in each newly colonised patch but as small as possible to minimise the mutation load from the appearance of ill-adapted morphs. From a mechanistic perspective, when a morph that is well-adapted to its current patch arrives in a new patch, it takes some time to switch to the other morph. This switching time should depend on the local conditions at the beginning of the new patch and go to infinity as $\mu \to 0$. Thus, for finite L, when μ is too small, mutating to the other morph with the right specialisation becomes useless in terms of speed, and the mutation load also becomes negligible. The system therefore behaves as in the one-morph case, leading to the continuity of the speed at $\mu = 0$. However, for each fixed small μ, when L is large enough, the switching time becomes negligible compared to the overall time it takes to cross the new patch with the highest growth rate. In particular, as $L \to \infty$, the impact of the switching time on the spreading speed vanishes, which explains the discontinuity of $c^{2m}(L \to \infty)$ at $\mu = 0$.

Given that c^{2m} is an increasing function of the period L, as observed in our numerical simulations, our results encompass the entire spectrum of spreading speed variation, contingent on environmental fragmentation. This range can be quantified analytically by the difference between $c^{2m}(L \to \infty)$ and $c^{2m}(L \to 0)$, thereby offering a quantitative measure of the potential impact of the fragmentation: it decreases as μ increases and is maximal as $\mu \to 0$. In this limiting scenario, the potential impact of the fragmentation amounts to $2\sqrt{D\,R^+} - \sqrt{2\,D\,(R^+ + R^-)}$. Therefore, it is much more important than in the one-morph setting (or $\mu = 0$). The cultivation of mixtures of susceptible ($R^+ > 0$) and resistant ($R^- = 0$) cultivars has been extensively studied in the literature [40, 170, 196]. While several studies have highlighted the role of spatial structure among host genotypes in influencing disease spread [184, 211], our results suggest that in scenarios where pathogens can adapt to different hosts, landscape configuration significantly influences the outcome. Therefore, landscape design can play a pivotal role in efforts to slow down pathogen spread.

Our results on the optimal value of the mutation parameter μ illustrate the dual nature of the impact of mutations on the spreading speed with respect to the fragmentation of the environment: (i) mutations allow the population to adapt to new environments, proving beneficial in highly fragmented settings (small L), while (ii) mutations can also give rise to a large mutation load, resulting in recurrent introduction of ill-adapted phenotypes, leading to decreased speeds in less fragmented environments (large L). This can also be interpreted through the trade-off between generalist and specialist morphs. It has been established that high migration rates between two patches [72] or highly fragmented environments [183] tend to favour generalist strategies. These strategies correspond to populations that are moderately adapted to both patches. Here, in highly fragmented environments, a higher optimal value of the mutation parameter μ appears to suggest the same principle, as the limit $\mu \to \infty$ yields the same results as a one-morph model with averaged parameters (refer to the following paragraph for details). As fragmentation decreases, specialists are favoured, and the value of μ that optimises the spreading speed decreases towards 0 as $L \to \infty$.

For clarity and to achieve simpler formulas, we only considered a scenario where the growth rates of the two morphs mirror each other ($r^u = R^+$ when $r^v = R^-$ and vice versa). However, the methodology introduced in this study paves the way for more complex situations, such as when R^+ and R^- have different values depending on the morph. First, when $L \to 0$, the system behaves as if r^u and r^v were replaced by their respective spatial averages. When $\mu \to \infty$, the ability of persistence and the spreading speed behave as if the growth rates r^u and r^v at each spatial point x were replaced by their averaged value $(r^u(x) + r^v(x))/2$. Thus in the case where $r^u = R^+$ when $r^v = R^-$ and vice versa, the two limits coincide; but this has no reason to be true in general. Second, we also proposed a conjecture for the limiting spreading speed in cases of minimal fragmentation ($L \to \infty$) with general growth rates and potentially different diffusion terms between morphs. This formula suggests that our result (8.9) for the spreading speed in low-fragmented environments is valid under slightly more general assumptions. Additionally, it could allow future works to consider other scenarios than the interaction between two specialist morphs, for example, the case of a specialist morph associated with a generalist, or the case of a D-specialist paired with an R-specialist, as seen in [82] and [169], but in the presence of spatial heterogeneity (see some calculations in Section 8.7).

Several other assumptions of this chapter could be revisited, and numerous extensions are conceivable. Among these, we discuss below what happens if one takes into account an Allee effect, discontinuities at the patch interfaces, or if one considers a continuous set of morphs.

First, we worked in the absence of an Allee effect (a positive relationship between individual fitness and population density at low densities [11]). Although the Allee effect is identified in numerous organisms and can result from various co-occurring processes [20], the combination of an Allee effect and evolutionary mechanisms is relatively rare in the literature (but see [158]). We expect that the dependency profile between c^{2m} and μ will be fundamentally different, especially with a strong Allee effect (negative growth rate at low densities), due to the stability of the steady state 0 (no hair-trigger effect). Compared to $\mu = 0$, a small mutation rate would only slow down the spreading by creating a load without creating a critical mass that allows the other morph to propagate. For larger values of μ, the ability to mutate to a more adapted morph could avoid blocking phenomena (zero speed) that arise in a heterogeneous environment and with a single morph (or with $\mu = 0$) in the presence of an Allee effect [117, 135, 219]. The methods developed in this chapter, which are mainly based on the analysis of principal eigenvalues of linear operators, however, will not be applicable. Although there is no general formula for the spreading speed in the presence of an Allee effect, homogenisation techniques can be used to obtain approximate expressions [159]. Recently, [77] obtained a limit speed as $L \to \infty$ in the one-morph case with a strong Allee effect. With a two-patch environment, and under conditions that guarantee the spreading in each homogeneous environment, it is simply given as the harmonic mean of the speeds associated with each homogeneous environment. Their methods, in the limit $L \to \infty$, could potentially be extended to study the spreading speed for a two-morph model with an Allee effect.

Second, given that each morph is specialised for a specific host, it would be natural to reevaluate our findings by considering a preference for certain types of patches in individual movements – specifically, minimal migration from favourable to unfavourable patches and vice versa, accompanied by variable diffusion rates that depend on both the patch and the morph. These factors challenge the usual assumption that population densities are continuous across patch interfaces. To reexamine this hypothesis, one could build upon the research conducted in single-species models by [160] and [226], where a formula for the spreading speed in scenarios with small periodic variations has been established, and homogenisation techniques have been developed.

Last, although the two-morph system has allowed us to identify certain key aspects related to the interactions between spatial heterogeneities and adaptation, in many real situations, mutations can lead to a multitude of morphs. An extension of our work is to consider, as in the approaches of [3, 4, 9, 187] and Chapters 5–7, a population structured in continuous space, via the variable x, and in continuous phenotypic traits, via another variable θ.

8.5 Population persistence, proofs of the results of Table 8.1

Theorem 2.9 of [115] shows that a necessary and sufficient condition for persistence is $k_0^{2m} > 0$, where k_0^{2m} is the principal eigenvalue of the operator $\mathcal{L}_0^{2m}$:

$$\mathcal{L}_0^{2m} : \ (\phi_1, \phi_2) \mapsto (D\phi_1'' + r_L^u(x/L)\phi_1 + \mu(\phi_2 - \phi_1), D\phi_2'' + r_L^v(x/L)\phi_2 + \mu(\phi_1 - \phi_2))$$

with periodicity conditions. In other words, there is a pair of positive principal eigenfunctions (ϕ_1, ϕ_2) satisfying $\mathcal{L}_0^{2m}(\phi_1, \phi_2) = (k_0^{2m}\phi_1, k_0^{2m}\phi_2)$ with periodicity conditions. Setting

$(\psi_1,\psi_2)(x)=(\phi_1,\phi_2)(L\,x)$ one may also write:

$$\left\{\begin{array}{ll}\frac{D}{L^2}\psi_1''+R^+\psi_1+\mu(\psi_2-\psi_1)= & k_0^{2\,m}\psi_1,\\ \frac{D}{L^2}\psi_2''+R^-\psi_2+\mu(\psi_1-\psi_2)= & k_0^{2\,m}\psi_2,\end{array}\right.\quad\text{in } [0,1/2)\tag{8.11}$$

and

$$\left\{\begin{array}{ll}\frac{D}{L^2}\psi_1''+R^-\psi_1+\mu(\psi_2-\psi_1)= & k_0^{2\,m}\psi_1,\\ \frac{D}{L^2}\psi_2''+R^+\psi_2+\mu(\psi_1-\psi_2)= & k_0^{2\,m}\psi_2,\end{array}\right.\quad\text{in } [1/2,1),\tag{8.12}$$

where ψ_1, ψ_2 are 1-periodic.

The following Rayleigh formula is also available:

$$k_0^{2\,m}=\max_{(\psi_1,\psi_2)\in E}Q(\psi_1,\psi_2),\tag{8.13}$$

where

$$Q(\psi_1,\psi_2):=-\frac{D}{L^2}\int_0^1[(\psi_1')^2+(\psi_2')^2]+\int_0^1(r^u\,\psi_1^2+r^v\,\psi_2^2)+\mu\left(2\int_0^1\psi_1\,\psi_2-1\right),\tag{8.14}$$

and

$$E:=\left\{(\psi_1,\psi_2)\in H^1_{per}(\mathbb{R})^2,\int_0^1\psi_1^2+\psi_2^2=1\right\}$$

and $H^1_{per}(\mathbb{R})$ is the subspace of the Sobolev space $H^1_{loc}(\mathbb{R})$, made of 1-periodic functions.

For completeness, we also recall the criterion for persistence in the case of a unique morph governed by the equation $\partial_t u(t,x)=d\,\partial_{xx}u+r_L^u(x)\,u-\gamma_L(x)\,u^2$ (see [27]). In this case, the criterion is $k_0^{1\,m}>0$, where $k_0^{1\,m}$ is the principal eigenvalue of the operator $\mathcal{L}_0^{1\,m}$: $(\psi,\psi_2)\mapsto\frac{D}{L^2}\psi_1''+r_L^u(x)\psi$ with periodicity conditions. This principal eigenvalue can be characterised by the Rayleigh formula:

$$k_0^{1\,m}=\max_{\psi\in G}\left(-\frac{D}{L^2}\int_0^1(\psi')^2+\int_0^1 r^u\,\psi^2\right),$$

with $G:=\left\{\psi\in H^1_{per}(\mathbb{R}),\int_0^1\psi^2=1\right\}$.

Arbitrary μ, with $L\to 0$. Taking two constant functions $\psi_1=\psi_2=1/\sqrt{2}$, we note that $Q(\psi_1,\psi_2)=\int_0^1 r^u+r^v=(R^++R^-)/2$. Thus (8.13) implies that $k_0^{2\,m}\geqslant(R^++R^-)/2$. Conversely, as $L\to 0$, due to the first term in (8.14), the functions ψ_1, ψ_2 that realise the maximum in (8.13) necessarily converge to constants. Maximising Q over the pairs of constant functions in E, we conclude that $\lim_{L\to 0}k_0^{2\,m}=(R^++R^-)/2$. This expression is independent of μ, and therefore remains unchanged if we pass to the limit $\mu\to 0$ or $\mu\to\infty$.

Arbitrary μ, with $L\to\infty$. Passing to the limit $L\to\infty$ in (8.11)–(8.12) means solving the system

$$\left\{\begin{array}{ll}a\,R^++\mu(b-a)= & \left(\lim\limits_{L\to+\infty}k_0^{2\,m}\right)a,\\ b\,R^-+\mu(a-b)= & \left(\lim\limits_{L\to+\infty}k_0^{2\,m}\right)b,\end{array}\right.\tag{8.15}$$

with $a, b > 0$. This leads to:

$$\lim_{L\to\infty} k_0^{2m} = \frac{1}{2}\sqrt{(R^+ - R^-)^2 + 4\mu^2} - \mu + (R^+ + R^-)/2.$$

To determine when persistence holds, we solve $\lim_{L\to\infty} k_0^{2m} > 0$, which is equivalent to

$$\sqrt{(R^+ - R^-)^2 + 4\mu^2} > 2\mu - (R^+ + R^-).$$

This always holds if $R^+ + R^- > 0$. If $R^+ + R^- < 0$ (so $R^+ > 0 > R^-$), this becomes:

$$R^+ > \frac{\mu}{1 + (\mu/(-R^-))}.$$

If we pass to the limit $\mu \to 0$, this condition becomes $R^+ > 0$, and if we pass to the limit $\mu \to \infty$, this condition becomes $R^+ + R^- > 0$.

Arbitrary L, with $\mu \to 0$. We denote by (ψ_1^μ, ψ_2^μ) the principal eigenfunctions in (8.11)–(8.12) and $k_0^\mu := k_0^{2m}$ the associated principal eigenvalue. We have:

$$\frac{D}{L^2}(\psi_1^\mu)'' + r^u(x)\psi_1^\mu + \mu(\psi_2^\mu - \psi_1^\mu) = k_0^\mu \psi_1^\mu.$$

The functions ψ_1^μ and ψ_2^μ are bounded. Using the so-called Schauder estimates, we obtain that as $\mu \to 0$, the functions ψ_1^μ and ψ_2^μ converge to functions ψ_1^0 and ψ_2^0 in a strong sense. Thus, taking $\mu \to 0$, the mutation term disappears and we obtain:

$$\frac{D}{L^2}(\psi_1^0)'' + r^u(x)\psi_1^0 + = k_0^0 \psi_1^0,$$

which is precisely the eigenvalue problem defining k_0^{1m}. Thus

$$\lim_{\mu\to 0} k_0^\mu = k_0^{1m}.$$

If we pass to the limit $L \to 0$, this leads to the condition for persistence $R^+ + R^- > 0$, and with $\mu \to 0$, this leads to the condition for persistence $R^+ > 0$.

Arbitrary L, with $\mu \to \infty$. With the same notations as in the previous paragraph, multiplying by ψ_1^μ the equation satisfied by ψ_1^μ and integrating by parts, we get:

$$-\frac{D}{L^2}\int_0^1 ((\psi_1^\mu)')^2 + \mu\int_0^1 (\psi_2^\mu - \psi_1^\mu)\psi_1^\mu = \int_0^1 k_0^\mu (\psi_1^\mu)^2 - \int_0^1 r^u(x)(\psi_1^\mu)^2. \tag{8.16}$$

Without loss of generality, we can assume that $\int_0^1 (\psi_1^\mu)^2 = 1$, and using the upper bound for k_0^μ obtained above (in the limit $L \to \infty$), we get that the right-hand side in (8.16) is bounded independently of μ. Moreover, by uniqueness and symmetry of the eigenvalue problem, we have $\psi_2^\mu(x) = \psi_1^\mu(1-x)$ for all x. Thus, the Cauchy-Schwarz inequality implies that the integral $\int_0^1 (\psi_2^\mu - \psi_1^\mu)\psi_1^\mu$ is negative. As the other term in the left-hand side of (8.16) is

negative, and the right-hand side is bounded, this implies that, as $\mu \to \infty$,

$$\int_0^1 (\psi_2^\infty - \psi_1^\infty)\psi_1^\infty(x)\,\mathrm{d}x = 0.$$

Since both functions ψ_1^∞ and $\psi_2^\infty(\cdot) = \psi_1^\infty(1-\cdot)$ are positive and share the same L^2 norm, the Cauchy-Schwarz inequality implies that $\psi_1^\infty(\cdot) \equiv \psi_2^\infty(\cdot)$. In other words, $\psi_1^\mu - \psi_2^\mu \to 0$. Adding the two lines (8.11)–(8.12), we obtain:

$$\frac{D}{L^2}(\psi_1^\mu + \psi_2^\mu)'' + r^u(x)\psi_1^\mu + r^v(x)\psi_2^\mu = k_0^\mu(\psi_1^\mu + \psi_2^\mu).$$

Thus, taking $\mu \to \infty$ in the last equation gives:

$$\frac{D}{L^2}(2\psi_1^\infty)'' + (R^+ + R^-)\psi_1^\infty = 2\,k_0^\infty\,\psi_1^\infty.$$

Therefore, the principal eigenfunction ψ_1^∞ is constant and the corresponding principal eigenvalue is

$$\lim_{\mu\to\infty} k_0^\mu = \frac{R^+ + R^-}{2}.$$

This formula is independent of L, and therefore remains unchanged if we pass to the limit $L \to 0$ or $L \to \infty$.

8.6 Spreading speed, proofs of the results of Table 8.2

Arbitrary L, with $\mu \to 0$. We denote by (ψ_1^μ, ψ_2^μ) the solution of the principal eigenvalue problem (8.7) and we let k_λ^μ be the associated principal eigenvalue. We focus on the first line:

$$(D\psi_1^\mu)'' + 2\lambda\,D\,(\psi_1^\mu)' + (\lambda^2\,D + r_L^u(x))\psi_1^\mu + \mu(\psi_2^\mu - \psi_1^\mu) = k_\lambda^\mu\psi_1^\mu. \tag{8.17}$$

The functions ψ_1^μ and ψ_2^μ are bounded. Using the so-called Schauder estimates, we obtain that as $\mu \to 0$, the functions ψ_1^μ and ψ_2^μ converge to functions ψ_1^0 and ψ_2^0 in a strong sense. Thus, taking $\mu \to 0$ in (8.17), the mutation term disappears and we obtain:

$$(D\psi_1^0)'' + 2\lambda\,D\,(\psi_1^0)' + (\lambda^2\,D + r_L^u(x))\psi_1^0 = k_\lambda^0\psi_1^0.$$

This is precisely the eigenvalue problem defining $k_\lambda^{1\,m}$, such that the spreading speed with a unique morph with growth rate r_L^u is given by the Freidlin-Gärtner formula (e.g. [26]):

$$c^{1\,m} = \min_{\lambda>0} \frac{k_\lambda^{1\,m}}{\lambda}.$$

Thus

$$\lim_{\mu\to 0} c^{2\,m} = c^{1\,m}.$$

The limits $L \to 0$ and $L \to \infty$ therefore correspond to the known limits in the one-morph setting, see [81] and [117].

Arbitrary L, with $\mu \to \infty$. We use the same notations as the previous paragraph. Multiplying by ψ_1^μ the equation satisfied by ψ_1^μ and integrating by parts, we get:

$$-D\int_0^L ((\psi_1^\mu)')^2 + \mu \int_0^L (\psi_2^\mu - \psi_1^\mu)\psi_1^\mu = \int_0^L k_\lambda^\mu (\psi_1^\mu)^2 - \int_0^L (\lambda^2 D + r^u(x))(\psi_1^\mu)^2. \tag{8.18}$$

Without loss of generality, we can assume that $\int_0^L (\psi_1^\mu))^2 = 1$, and Lemma 8.8.1 implies that the right-hand side in (8.18) is bounded independently of μ. Moreover, by uniqueness and symmetry of the eigenvalue problem, we have $\psi_2^\mu(x) = \psi_1^\mu(L-x)$ for all x. Thus, the Cauchy-Schwarz inequality implies that the integral $\int_0^L (\psi_2^\mu - \psi_1^\mu)\psi_1^\mu$ is negative. As the other term in the left-hand side of (8.18) is negative, and the right-hand side is bounded, this implies that, as $\mu \to \infty$,

$$\int_0^L (\psi_2^\infty - \psi_1^\infty)\psi_1^\infty(x)\,\mathrm{d}x = 0.$$

Since both functions ψ_1^∞ and $\psi_2^\infty(\cdot) = \psi_1^\infty(L-\cdot)$ are positive and share the same L^2 norm, Cauchy-Schwarz inequality implies that $\psi_1^\infty(\cdot) \equiv \psi_2^\infty$. In other words, $\psi_1^\mu - \psi_2^\mu \to 0$.

Adding the two lines of (8.7), we obtain:

$$D(\psi_1^\mu + \psi_2^\mu)'' + 2\lambda D(\psi_1^\mu + \psi_2^\mu)' + \lambda^2 D(\psi_1^\mu + \psi_2^\mu) + r^u(x)\psi_1^\mu + r^v(x)\psi_2^\mu = k_\lambda^\mu(\psi_1^\mu + \psi_2^\mu).$$

Therefore, as $\mu \to +\infty$,

$$(2D\psi_1^\infty)'' + 2\lambda D(2\psi_1^\infty)' + \lambda^2 D(2\psi_1^\infty) + (r^u(x) + r^v(x))\psi_1^\infty = k_\lambda^\infty(2\psi_1^\infty).$$

Now note that $r^u(x) + r^v(x) = R^+ + R^-$ is constant. Therefore, the principal eigenfunction ψ_1^∞ is also constant and the corresponding principal eigenvalue is

$$k_\lambda^\infty = \lim_{\mu\to\infty} k_\lambda^\mu = \lambda^2 D + \frac{R^+ + R^-}{2}.$$

Using the Freidlin-Gärtner formula (8.6), we get:

$$\lim_{\mu\to\infty} c^{2m} = \inf_{\lambda>0}\left(\lambda D + \frac{R^+ + R^-}{2\lambda}\right) = \sqrt{2D(R^+ + R^-)}.$$

This formula is independent of L, and therefore remains unchanged if we pass to the limit $L \to 0$ or $L \to \infty$.

Arbitrary μ, with $L \to 0$. The homogenisation results in [115] (Theorem 2.20) show that the spreading speed c^{2m} converges to the speed that would be obtained in a homogeneous environment where r_L^u and r_L^v would be replaced by their spatial average $(R^+ + R^-)/2$. In this last case, the solution of the eigenvalue problem (8.7) is a constant eigenfunction and the eigenvalue is $k_\lambda^0 = \lambda^2 D + (R^+ + R^-)/2$. Using the Freidlin-Gärtner formula (8.6), we get:

$$\lim_{L\to 0} c^{2m} = \inf_{\lambda>0}\left(\lambda D + \frac{R^+ + R^-}{2\lambda}\right) = \sqrt{2D(R^+ + R^-)}.$$

This formula is independent of μ, and therefore remains unchanged if we pass to the limit $\mu \to 0$ or $\mu \to \infty$.

Arbitrary μ, with $L \to \infty$. This is the most involved case. We set

$$I_L := \left(\frac{\sqrt{(R^+ - R^-)/2}}{\sqrt{D}}, \frac{\sqrt{R^+} + \sqrt{(R^+ - R^-)/2}}{\sqrt{D}} \right). \tag{8.19}$$

We begin by considering values of λ in I_L.

Let us set $(\varphi_1(x), \varphi_2(x)) = (e^{\lambda x}\,\phi_1(x), e^{\lambda x}\,\phi_2(x))$. The system (8.7) becomes

$$\begin{cases} D\varphi_1'' + r_L^u(x)\varphi_1 + \mu(\varphi_2 - \varphi_1) = & k_\lambda \varphi_1, \\ D\varphi_2'' + r_L^u(x)\varphi_2 + \mu(\varphi_1 - \varphi_2) = & k_\lambda \varphi_2, \end{cases} \quad \text{in } [0, L]. \tag{8.20}$$

Writing this system on each interval where the coefficients are constants, we get:

$$\begin{cases} D\varphi_1'' + R^+\varphi_1 + \mu(\varphi_2 - \varphi_1) = & k_\lambda \varphi_1, \\ D\varphi_2'' + R^-\varphi_2 + \mu(\varphi_1 - \varphi_2) = & k_\lambda \varphi_2, \end{cases} \quad \text{in } [0, L/2), \tag{8.21}$$

$$\begin{cases} D\varphi_1'' + R^-\varphi_1 + \mu(\varphi_2 - \varphi_1) = & k_\lambda \varphi_1, \\ D\varphi_2'' + R^+\varphi_2 + \mu(\varphi_1 - \varphi_2) = & k_\lambda \varphi_2, \end{cases} \quad \text{in } [L/2, L). \tag{8.22}$$

The functions φ_1, φ_2 are of class C^1 on the whole space $\mathbb{R}$, and are of class C^2 on the intervals $(k, k+L/2)$ and $(k+L/2, k+L)$, $k \in \mathbb{Z}$, i.e., on the intervals where the coefficients are constant. Without loss of generality, as the pair $(\varphi_1(x), \varphi_2(x))$ is defined up to a multiplicative constant, we may set $\varphi_1(0) = 1$. Altogether, with the periodicity and regularity conditions, we obtain the following constraints:

$$\begin{cases} \varphi_2(L) &= e^{\lambda L}\varphi_2(0), \\ \varphi_1'(L) &= e^{\lambda L}\varphi_1'(0), \\ \varphi_2'(L) &= e^{\lambda L}\varphi_2'(0), \\ \lim\limits_{s \to (L/2)^-} \varphi_1(s) &= \lim\limits_{s \to (L/2)^+} \varphi_1(s), \\ \lim\limits_{s \to (L/2)^-} \varphi_2(s) &= \lim\limits_{s \to (L/2)^+} \varphi_2(s), \\ \lim\limits_{s \to (L/2)^-} \varphi_1'(s) &= \lim\limits_{s \to (L/2)^+} \varphi_1'(s), \\ \lim\limits_{s \to (L/2)^-} \varphi_2'(s) &= \lim\limits_{s \to (L/2)^+} \varphi_2'(s), \end{cases} \tag{8.23}$$

and another constraint that we will treat separately:

$$\varphi_1(L) = e^{\lambda L}\varphi_1(0) = e^{\lambda L}. \tag{8.24}$$

We directly solve the two systems (8.21) and (8.22) of two constant coefficient second order linear homogeneous differential equations. Their general solution can be found, e.g., in [132]. The characteristic equation has the form:

$$X^4 - [(2k_\lambda + 2\mu - R^+ - R^-)/D]X^2 + (k_\lambda + \mu - R^+)(k_\lambda + \mu - R^-)/D^2 - \mu^2/D^2 = 0.$$

Under the conditions $(k_\lambda + \mu - R^+)(k_\lambda + \mu - R^-) - \mu^2 \neq 0$ (which follows from $\lambda \in I_L$, see Lemma 8.8.3) and $(R^+ - R^-)^2 + 4\,\mu^2 \neq 0$ (which is always satisfied), the characteristic equa-

tion has four distinct roots $\pm Z_1$ and $\pm Z_2$, with:

$$\left\{\begin{array}{rcl} \delta & := & \sqrt{(R^+-R^-)^2+4\,\mu^2}, \\ Z_1 & := & \sqrt{\dfrac{2\mu+2k_\lambda-\delta-R^+-R^-}{2D}}, \\ Z_2 & := & \sqrt{\dfrac{2\mu+2k_\lambda+\delta-R^+-R^-}{2D}}. \end{array}\right. \tag{8.25}$$

The solutions of (8.21) with the constraint $\varphi_1(0)=1$ are, for $x\in(0,L/2)$,

$$\left\{\begin{array}{rcl} \varphi_1(x) & = & (1-A_1-A_2-A_3)e^{-Z_1 x}+A_1e^{Z_1 x}+A_2e^{-Z_2 x}+A_3e^{Z_2 x}, \\ \varphi_2(x) & = & \dfrac{R^--R^++\delta}{2\,\mu}\left[(1-A_1-A_2-A_3)e^{-Z_1 x}+A_1\,e^{Z_1 x}\right] \\ & & +\dfrac{R^--R^+-\delta}{2\,\mu}\left[A_2e^{-Z_2 x}+A_3e^{Z_2 x}\right], \end{array}\right. \tag{8.26}$$

with $A_1,A_2,A_3\in\mathbb{R}$. Lemma 8.8.2 shows that $2\mu+2k_\lambda-\delta-R^+-R^->0$, which implies that Z_1, Z_2 are real.

Similarly, the solutions of (8.22) are, for $x\in(L/2,L)$,

$$\left\{\begin{array}{rcl} \varphi_1(x) & = & A_4\,e^{-Z_1 x}+A_5e^{Z_1 x}+A_6e^{-Z_2 x}+A_7e^{Z_2 x}, \\ \varphi_2(x) & = & \dfrac{R^+-R^-+\delta}{2\,\mu}\left[A_4e^{-Z_1 x}+A_5\,e^{Z_1 x}\right]+\dfrac{R^+-R^--\delta}{2\,\mu}\left[A_6e^{-Z_2 x}+A_7e^{Z_2 x}\right], \end{array}\right. \tag{8.27}$$

with $A_4,A_5,A_6,A_7\in\mathbb{R}$.

Plugging the constraints (8.23) in (8.26) and (8.27), we observe that the coefficients $A_1,\dots,A_7$ solve a linear system with 7 equations, for which we obtain an explicit solution which leads to explicit (but very lengthy) expressions for φ_1 and φ_2. Using $Z_1<Z_2$, one may then write the last constraint (8.24) in the form

$$\begin{aligned} &B_1e^{L(2Z_1+2Z_2+3\lambda)}-B_2e^{L(2Z_1+Z_2+4\lambda)}-B_3e^{L(3Z_1+2Z_2+2\lambda)} \\ &\quad+o(B_1e^{L(2Z_1+2Z_2+3\lambda)}+B_2e^{L(2Z_1+Z_2+4\lambda)}+B_3e^{L(3Z_1+2Z_2+2\lambda)})=0,\ \text{as } L\to\infty, \end{aligned} \tag{8.28}$$

where $B_1,B_2,B_3>0$ are bounded independently of L. See Supplementary Maple notebook (pdf file available as Supplementary Material and code available at `https://doi.org/10.17605/OSF.IO/7RTFK`).

Let us show that the term $\exp[L(3Z_1+2Z_2+2\lambda)]$ dominates $\exp[L(2Z_1+Z_2+4\lambda)]$ as $L\to\infty$. Assume by contradiction that there exists $C>0$ such that for all $L>0$, we have $\exp[L(2Z_1+Z_2+4\lambda)]\geqslant C\exp[L(3Z_1+2Z_2+2\lambda)]$. Then, using (8.28), we get that $2Z_1+2Z_2+3\lambda\sim 2Z_1+Z_2+4\lambda$ which implies that:

$$\lim_{L\to\infty} Z_2=\lambda. \tag{8.29}$$

Coming back to the expression of Z_2 in (8.25), and setting $k_\lambda^\infty:=\lim_{L\to\infty}k_\lambda$, this shows that $k_\lambda^\infty=\lambda^2\,D+(R^++R^--\delta)/2-\mu$. Thus, $k_\lambda^\infty<\lambda^2\,D+(R^++R^-)/2$, which is in contradiction with the lower bound in Lemma 8.8.1. Thus, $\exp[L(3Z_1+2Z_2+2\lambda)]$ dominates $\exp[L(2Z_1+Z_2+4\lambda)]$ as $L\to\infty$ and, with (8.28), we necessarily get $2Z_1+2Z_2+3\lambda\sim 3Z_1+2Z_2+2\lambda$.

This implies that:

$$\lim_{L\to\infty} Z_1 = \lambda. \tag{8.30}$$

Using the expression of Z_1 in (8.25), this shows that

$$k_\lambda^\infty = \lambda^2 D + \frac{1}{2}(R^+ + R^- + \delta) - \mu. \tag{8.31}$$

We note that this expression is consistent with the result of Lemma 8.8.1. We observe that $\lambda \mapsto k_\lambda^\infty$ is convex in I_L and that $\lambda \mapsto k_\lambda^\infty/\lambda$ reaches a (strict) minimum in I_L at $\lambda_m = \sqrt{(R^+ + R^- + \delta - 2\mu)/(2D)}$. From Proposition 2.2 in [115], we also know that $\lambda \mapsto k_\lambda$ is strictly convex in $\mathbb{R}^+$. Thus $\lambda \mapsto k_\lambda^\infty$ is convex in $\mathbb{R}^+$. This implies that k_λ^∞/λ reaches its (unique) strict minimum in I_L at $\lambda = \lambda_m$ (this is easily seen graphically, as k_λ^∞/λ reaches its minimum in $\mathbb{R}^+$ at values of λ such that $k_\lambda^\infty = \lambda \partial_\lambda(k_\lambda^\infty)$). Finally, this shows that

$$\lim_{L\to\infty} c^{2\,m} = \min_{\lambda>0} \frac{k_\lambda^\infty}{\lambda} = \min_{\lambda\in I_L} \frac{k_\lambda^\infty}{\lambda} = \sqrt{2D\left(R^+ + R^- + \sqrt{(R^+ - R^-)^2 + 4\mu^2} - 2\mu\right)}. \tag{8.32}$$

Using this formula, we readily obtain the limits:

$$\lim_{\mu\to 0}\lim_{L\to\infty} c^{2\,m} = 2\sqrt{D\,R^+} \text{ and } \lim_{\mu\to\infty}\lim_{L\to\infty} c^{2\,m} = \sqrt{2\,D\,(R^+ + R^-)}.$$

8.7 A conjecture for a general formula for the speed

We would like to adapt to our context the results of [119] (which deals with the limit as $L \to \infty$ of the spreading speed when there is only one morph) and of Chapter 7 (where we dealt with a continuum of phenotypes). For simplicity we assume that the diffusion coefficient is $D = 1$.

In the one-morph setting, [119] showed that the limit of the spreading speed as $L \to +\infty$ is

$$c^{1\,m}(L \to +\infty) = \inf_{\lambda>0} \frac{\bar{j}^{-1}(\lambda)}{\lambda},$$

where

$$\bar{j}(k) = \int_0^1 \sqrt{k - r(x)}\,\mathrm{d}x,$$

Here, r plays the role of r^u and r^v. If we adapt their calculations to our case, we find the same expression for the limiting speed $c^{2\,m}$, but $\bar{j}(k)$ is replaced by

$$j(k) = \int_0^1 \sqrt{k - \left(r^u(x) - \mu + \mu\frac{\psi_{2,\infty}(x)}{\psi_{1,\infty}(x)}\right)}\,\mathrm{d}x. \tag{8.33}$$

Here, the functions $\psi_{1,\infty}$ and $\psi_{2,\infty}$ are defined as the limits as $L \to \infty$ of the principal eigenfunctions $\psi_{1,L}(x) = \phi_{1,L}(Lx)$ and $\psi_{2,L} = \phi_{2,L}(Lx)$:

$$\psi_{1,\infty}(x) := \lim_{L\to\infty} \psi_{1,L}(x), \qquad \psi_{2,\infty}(x) := \lim_{L\to\infty} \psi_{2,L}(x).$$

The extra term $-\mu + \mu\frac{\psi_{2,\infty}}{\psi_{1,\infty}}$ arises because of the mutations between morphs. The hard part

is to compute the value of $\frac{\psi_{2,\infty}}{\psi_{1,\infty}}$. Let us first assume that r^u and r^v are constant (i.e., the environment is homogeneous): $r^u(x) \equiv r^u$ and $r^v(x) \equiv r^v$. Then the eigenfunctions ψ_1 and ψ_2 are independent of x, so the system (8.7) becomes:

$$\begin{cases} -(r^u - \mu + \lambda^2)\psi_1 - \mu\psi_2 = k_\lambda \psi_1 \\ -(r^v - \mu + \lambda^2)\psi_2 - \mu\psi_1 = k_\lambda \psi_2, \end{cases}$$

where ψ_1 and ψ_2 are real numbers (instead of functions). Solving this system, with the constraints that $\psi_1 > 0$ and $\psi_2 > 0$, yields:

$$\frac{\psi_{2,\infty}}{\psi_{1,\infty}} = \frac{1}{2\mu}\left(r^v - r^u + \sqrt{(r^u - r^v)^2 + 4\mu^2}\right).$$

Then, when r^u and r^v are constant, the expression of j (8.33) becomes:

$$j(k) := \int_0^1 \sqrt{k - \frac{1}{2}\left[r^u + r^v - 2\mu + \sqrt{(r^u - r^v)^2 + 4\mu^2}\right]}\,\mathrm{d}x. \tag{8.34}$$

Now we would like to extend this result to the case when r^u and r^v are not necessarily constant. In fact, as the period grows, the environment becomes more and more homogeneous. This suggests that the expression (8.34) of j, which holds when r^u and r^v are constant, should also hold for nonconstant r^u and r^v (this is the main idea exploited in Chapter 2, which deals with a continuum of phenotypes instead of two morphs). This is the following conjecture. Let us write

$$j(k) := \int_0^1 \sqrt{k - \frac{1}{2}\left[r^u(x) + r^v(x) - 2\mu + \sqrt{(r^u(x) - r^v(x))^2 + 4\mu^2}\right]}\,\mathrm{d}x.$$

Then

$$c^{2m}(L \to \infty) = \inf_{\lambda > 0} \frac{j^{-1}(\lambda)}{\lambda}.$$

This expression generalises the one we proved above for the particular form of r^u and r^v that was the main focus of this study. This new general expression is quite complicated, because we need to consider the inverse of the function j. Still, is is possible to find some qualitative properties.

Dependence of the speed on the mutation rate. We are interested in the variations of the speed $c^{2m}(L \to \infty)$ in terms of the mutation rate, so we will use the notations $j(k, \mu)$ and $c^{2m}(L \to \infty)(\mu)$ for clarity. We have:

$$\frac{\partial}{\partial \mu} j(k, \mu) = \int_0^1 \frac{1 - \frac{2\mu}{2\sqrt{(r^u(x) - r^v(x))^2 + 4\mu^2}}}{2\sqrt{k - \frac{1}{2}\left[r^u(x) + r^v(x) - 2\mu + \sqrt{(r^u(x) - r^v(x))^2 + 4\mu^2}\right]}}\,\mathrm{d}x.$$

Since $\sqrt{(r^u(x) - r^v(x))^2 + 4\mu^2} \geqslant \sqrt{4\mu^2} = 2\mu$, we conclude that

$$\frac{\partial}{\partial \mu} j(k, \mu) \geqslant 0.$$

Now, (8.6) implies that

$$c^{2m}(L\to\infty)(\mu) = \inf_k \frac{k}{j(k,\mu)}.$$

We conclude that $\mu \mapsto c^{2m}(L\to\infty)(\mu)$ is a *nonincreasing* function.

When the diffusion terms are different. If the diffusion terms are different for u and v, say D^u and D^v, then our conjecture implies that the formula for j becomes:

$$j(k) := \frac{1}{\sqrt{D^u}} \int_0^1 \sqrt{k - \frac{1}{2}\left[r^u(x) + r^v(x) + \lambda^2 D' - 2\mu + \sqrt{(r^u(x) - r^v(x) + \lambda^2 D')^2 + 4\mu^2}\right]}\,\mathrm{d}x,$$

with $D' = D^v - D^u$. We have not been able to turn this expression into an explicit formula for the spreading speed.

With one specialist and one generalist. Assume that u represents a specialist morph that is well-adapted on $(0,1/2)$ and ill-adapted on $(1/2,1)$, and that v represents a generalist morph that is everywhere equally adapted. This can be modeled by replacing the function $r^v(x)$ by a constant $r^v(x) \equiv r^v$, and by letting r^u takes two values R^+ and R^- over $(0,1/2)$ and $(1/2,1)$ respectively such that $R^- < r^v < R^+$. Then our conjecture implies that the expression for the speed is:

$$c^{2m}(L\to\infty) = \frac{2k_m}{\sqrt{k_m - A} + \sqrt{k_m - B}},$$

where

$$A = \frac{1}{2}\left(R^+ + r^v - 2\mu\sqrt{(R^+ - r^v)^2 + 4\mu^2}\right),$$
$$B = \frac{1}{2}\left(R^- + r^v - 2\mu\sqrt{(R^- - r^v)^2 + 4\mu^2}\right),$$

and

$$k_m = \frac{2}{3}\left(A + B + \sqrt{(A+B)^2 + 3\frac{AB^2 - A^2B}{A-B}}\right).$$

8.8 Technical lemmas

Lemma 8.8.1. *For all $\lambda > 0$ and $L > 0$, the principal eigenvalue k_λ in (8.7) satisfies*

$$\frac{R^+ + R^-}{2} + \lambda^2 D < k_\lambda < R^+ + \lambda^2 D.$$

Proof. First, adding the two equations in (8.7) and integrating over $(0,L)$, we get:

$$k_\lambda < R^+ + \lambda^2 D. \tag{8.35}$$

Second, dividing the two equations in (8.7) by ϕ_1 and ϕ_2 respectively, integrating by parts

over $(0,L)$, and using the periodicity of ϕ_1, ϕ_2 we get:

$$\begin{cases} D\int_0^L \frac{|\phi_1'|^2}{\phi_1^2} + \lambda^2 D\, L + \int_0^L r_L^u(x)\,\mathrm{d}x + \mu\left(\int_0^L \frac{\phi_2}{\phi_1} - L\right) &= k_\lambda L, \\ D\int_0^L \frac{|\phi_2'|^2}{\phi_2^2} + \lambda^2 D\, L + \int_0^L r_L^v(x)\,\mathrm{d}x + \mu\left(\int_0^L \frac{\phi_1}{\phi_2} - L\right) &= k_\lambda L, \end{cases} \quad \text{in } \mathbb{R}. \tag{8.36}$$

Adding the two equations, we obtain:

$$2D\int_0^L \left(\frac{|\phi_1'|^2}{\phi_1^2} + \frac{|\phi_2'|^2}{\phi_2^2}\right) + 2\lambda^2 D\, L + L(R^+ + R^-) + \mu\left(\int_0^L \left(\frac{\phi_2}{\phi_1} + \frac{\phi_2}{\phi_1}\right) - 2L\right) = 2k_\lambda L. \tag{8.37}$$

Note that $\phi_2/\phi_1 + \phi_2/\phi_1 \geqslant 2$ as $\phi_1, \phi_2 > 0$. Thus

$$k_\lambda > \frac{R^+ + R^-}{2} + \lambda^2 D. \tag{8.38}$$

□

Lemma 8.8.2. *Let $\lambda \in I_L$ (see (8.19)). We have*

$$2\mu + 2k_\lambda - \delta - R^+ - R^- > 0.$$

Proof. Using (8.38), we obtain

$$2\mu + 2k_\lambda - \delta - R^+ - R^- > 2\mu + 2\lambda^2 D - \sqrt{(R^+ - R^-)^2 + 4\mu^2},$$

and for $\lambda \in I_L$, $2\lambda^2 D > R^+ - R^-$ so

$$2\mu + 2k_\lambda - \delta - R^+ - R^- > R^+ - R^- + 2\mu - \sqrt{(R^+ - R^-)^2 + 4\mu^2} > 0.$$

□

Lemma 8.8.3. *Let $\lambda \in I_L$. We have $(k_\lambda - R^+ + \mu)(k_\lambda - R^- + \mu) - \mu^2 \neq 0$.*

Proof. The equation $(k - R^+ + \mu)(k - R^- + \mu) - \mu^2 = 0$ admits two roots $k_\pm = \frac{R^+ + R^-}{2} - \mu \pm \frac{\delta}{2}$. Lemma 8.8.2 implies that $k_\lambda > k_+ > k_-$, so k_λ cannot be a root of the equation. □

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Code availability. All of the codes used in this chapter are available at `https://doi.org/10.17605/OSF.IO/7RTFK`.

Declarations of interest: none

Part III

Loss of genetic diversity during an invasion

Chapter 9

The logarithmic correction in a nonlocal equation

This chapter is based on the article [45]:

N. Boutillon, *Large deviations and the emergence of a logarithmic delay in a nonlocal linearised Fisher–KPP equation*, Nonlinear Analysis, 240 (2024), p. 113465.

Abstract

We study a variant of the Fisher-KPP equation with nonlocal dispersal. Using the theory of large deviations, we show the emergence of a "Bramson-like" logarithmic delay for the linearised equation with step-like initial data. We conclude that the logarithmic delay emerges also for the solutions of the nonlinear equation. Previous papers found very precise results for the nonlinear equation with strong assumptions on the decay of the kernel. Our results are less precise, but they are valid for all thin-tailed kernels.

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9.1 Introduction

We are concerned with the spreading properties of the solution of the Fisher-KPP equation with nonlocal dispersal

$$\begin{cases} \partial_t v(t,x) = [J * v(t,x) - v(t,x)] + f(v(t,x)) & t > 0, x \in \mathbb{R}, \\ v(0,x) = \mathbb{1}_{(-\infty,0]}(x) & x \in \mathbb{R}, \end{cases} \tag{9.1}$$

where

$$J * v(t,x) = \int_{\mathbb{R}} v(t,x-y) J(\mathrm{d}y).$$

We shall look for the emergence of a "Bramson-like" logarithmic delay. Here, the reaction term f is monostable and satisfies the KPP condition, and the dispersal kernel J is thin-tailed. These assumptions are precised and explained below.

The Cauchy problem (9.1) is akin to the classical (local) Fisher-KPP equation [94, 143]

$$\begin{cases} \partial_t w(t,x) = \partial_{xx} w(t,x) + f(w(t,x)) & t > 0, x \in \mathbb{R}, \\ w(0,x) = \mathbb{1}_{(-\infty,0]}(x) & x \in \mathbb{R}, \end{cases} \tag{9.2}$$

but the diffusion term $\partial_{xx} w$ is replaced by the nonlocal dispersal term $J * v - v$.

In both Cauchy problems (9.1) and (9.2), under suitable assumptions on the reaction term f, the maximum principle holds and implies that $0 \leqslant v \leqslant 1$ and $0 \leqslant w \leqslant 1$ (see [143] for the local equation and [225] for the nonlocal equation). Therefore, in biological models, one can see $v(t,x)$ and $w(t,x)$ as the environment occupancy by an invading species at time t and at location x. For example, the Cauchy problem (9.1) arises in [97] as the infinite particle limit of a stochastic process modelling the range expansion of a plant. In this model, which stems from [37, 150], the reaction term $f(v)$ corresponds to the demography (birth and death) of individuals subject to competition, while the dispersal term $J * v - v$ (which is the generator of a jump process) describes the dispersal of the seeds. As $\frac{1}{2}\Delta$ is the generator of Brownian motion, the local equation (9.2) usually models small and frequent movements, as in the model of Fisher [94]. See also [210, 215] for related models.

Although our primary interest lies in the Cauchy problem (9.1), we shall focus on the *linearised* equation

$$\begin{cases} \partial_t u(t,x) = [J * u(t,x) - u(t,x)] + r u(t,x) & t > 0, x \in \mathbb{R}, \\ u(0,x) = \mathbb{1}_{(-\infty,0]}(x) & x \in \mathbb{R}, \end{cases} \tag{9.3}$$

where $r := f'(0) > 0$. The behaviour of the linear equation seems simpler to understand. From the study of the solutions of (9.3), we shall deduce a similar (weaker) result on the solutions of (9.1).

Now, let us focus on known results about the local equation, which has already been widely studied. We say that the reaction term f is *monostable* when it satisfies

$$f \in C^1([0,1]), \qquad f'(0) > 0, \qquad f(0) = f(1) = 0, \qquad \forall u \in (0,1)\,,\, f(u) > 0. \tag{9.4}$$

We assume throughout that the reaction term f is monostable. The solution w of the local Cauchy problem (9.2) is then known to propagate with a finite speed $c^* > 0$ ([14],

Theorems 4.1 and 4.3), in the sense that

$$\begin{aligned} \lim_{t\to+\infty} w(t,c't) &= 0 \quad \text{for all } c' > c^*, \\ \lim_{t\to+\infty} w(t,c''t) &= 1 \quad \text{for all } c'' \in (0,c^*). \end{aligned} \tag{9.5}$$

The speed c^* which satisfies (9.5) is called the *critical speed*. A *travelling wave* of speed c is a solution w of the local equation which can be written in the form $w(t,x) := W(x-ct)$, where $W : \mathbb{R} \to [0,1]$ satisfies $W(-\infty) = 1$ and $W(+\infty) = 0$. The function W is called the profile of the travelling wave, and has the shape of an interface between the *invaded zone*, where $W \simeq 1$, and the *non-invaded zone*, where $W \simeq 0$. The solution of the Cauchy problem (9.2) converges "in shape" to the unique positive travelling wave of critical speed c^* [143, 217]. We thus say that an *invasion front* appears in the solution.

Now, we might wonder where exactly the invasion front is: is it really "near" the travelling wave? More precisely, given any level $\rho \in (0,1)$, let $\theta^\rho_{loc}(t)$ be the largest position such that $w(t,\theta^\rho_{loc}(t)) = \rho$. The goal is to compare $\theta^\rho_{loc}(t)$, which represents the position of the invasion front, to c^*t, which is the position of the travelling wave with minimal speed.

The *KPP condition* on the reaction term f is defined by

$$\forall u \in [0,1], \qquad f(u) \leqslant f'(0)u. \tag{9.6}$$

The KPP condition means that the per-capita growth rate $f(u)/u$ is maximal at 0. In biological models, it implies that there is no Allee effect (e.g., [215]). When the KPP condition is satisfied, the critical speed is known to be $c^* = 2\lambda$, with $\lambda = \sqrt{f'(0)}$ [143]. Bramson, in [53], showed that if $f'(u)$ is maximal at $u = 0$ (which implies that the KPP condition is satisfied), and if the initial condition is $\mathbb{1}_{(-\infty,0]}$, then the invasion front is located well behind the position $x = c^*t$. More precisely, he showed

$$\theta^\rho_{loc}(t) = c^*t - s\ln(t) + O_{t\to+\infty}(1) \qquad \text{with} \qquad s = \frac{3}{2\lambda}, \tag{9.7}$$

where $\lambda = \sqrt{f'(0)}$. The term $-s\ln(t)$ is called the (Bramson) logarithmic delay. The same year, Uchiyama [217] proved a slightly less precise result, but for much more general initial conditions and more general reaction term: the KPP condition is almost sufficient. A few years later, keeping the assumption that $f'(u)$ is maximal at $u = 0$, Bramson [52] showed that in fact the term $O(1)$ can be turned into a term $C + o(1)$ for some constant $C \in \mathbb{R}$ (which depends on the initial condition). Moreover, he extended again the class of initial conditions for which (9.7) holds, and for which the solution converges to a travelling wave. His proofs use the so-called McKean representation with a branching Brownian motion [166, 212]. Lau [148] gave another proof of the convergence of the solution to a travelling wave, with the same assumptions as [52], but using analytic techniques. Likewise, more recently, the emergence of the logarithmic delay in (9.7) has been proved thanks to interesting analytic techniques [120], for initial conditions with a support bounded from above and for reaction terms satisfying the KPP condition. For example, the techniques of [120] have been used in [177, 178] to prove refinements of (9.7) up to order $\frac{1}{\sqrt{t}}$ (which before had been found formally in [79]).

Bramson and Uchiyama's results, with their extensions, induce that in the local equation, when the KPP condition is satisfied and when the initial condition decreases sufficiently fast,

the shift between the position θ^{ρ}_{loc} of the invasion front and the position c^*t is unbounded. Such a situation does not always occur. See the works of Rothe [204] and of Fife and McLeod [92] for the study of reaction terms which give rise to bounded shifts. See also the work of Giletti [108] for the study of general monostable reaction terms (that is, satisfying (9.4) but not necessarily (9.6)), which always give rise to unbounded shifts.

Much fewer articles have focused on nonlocal equations. The emergence of a logarithmic delay has been shown for other nonlocal variants of the classical Fisher-KPP equation. The case of a competition which is nonlocal in space has been studied in [188] (using probabilistic arguments) and in [42] (using analytic arguments). In the latter, the authors also showed that for a slowly-decaying competition kernel, the delay takes an algebraic form. The case of a phenotype-dependent equation with a competition which is nonlocal in phenotype and a diffusion rate which depends on the phenotype, the "cane-toad equation", has been studied in [43].

We now turn our attention to the results we have at hand for the nonlocal Cauchy problems of interest (9.1) and (9.3). Here, the nonlocality is on the movements, not on the competition. Throughout this chapter, we let J be a measure on $\mathbb{R}$ and we assume that J satisfies the assumptions:

$$J((0,+\infty)) > 0, \qquad J(\mathbb{R}) = 1, \tag{9.8}$$

together with the assumption:

$$\text{There exists } L > 0 \text{ such that} \qquad \int_{\mathbb{R}} e^{L|x|} J(\mathrm{d}x) < +\infty. \tag{9.9}$$

Assumption (9.9) means that the dispersal kernel is *thin-tailed*. It means that individuals usually do not move too far away from their origin, and it implies that travelling waves do exist. If the tail of J is too heavy, the invasion is accelerating [100, 144]. When the invasion is accelerating, self-similar travelling waves cannot exist due to a flattening of the solutions [102].

Under those assumptions (9.8) and (9.9) on the dispersal kernel J and the monostability assumptions (9.4) on the reaction term f, the Cauchy problem is well-posed (see e.g. the argument at the beginning of [225]). If we assume further that J is continuous, then there exists, as in the local case, a minimal speed for travelling waves, called the *critical speed* [67, 68, 207]. For the nonlocal equation, we denote by c the critical speed. When the KPP condition (9.6) is satisfied, the expression for c is explicit:

$$c = \inf_{\lambda>0} \frac{M(\lambda)+r-1}{\lambda} \qquad \text{with} \qquad M(\lambda) := \int_{\mathbb{R}} e^{\lambda x} J(\,\mathrm{d}x). \tag{9.10}$$

By Proposition 1.1 in [113], under Assumptions (9.8) and (9.9), there exists a unique $\lambda_r > 0$ at which the infimum is reached:

$$c = \frac{M(\lambda_r)+r-1}{\lambda_r}. \tag{9.11}$$

Under mild additional assumptions on the kernel J, the critical speed c satisfies the propagation property (9.5) for all nonzero solutions v with an initial support bounded from above (replacing w by v in (9.5)). See [157], Theorem 3.2.

Recently, Graham [113] showed that the logarithmic delay (9.7) can also arise for the *nonlocal* equation (9.1). He assumes that f satisfies the KPP condition. He also makes the

following slightly technical assumption on the kernel J: there exist $M > 0$ and $B > 0$ such that for all $x \geqslant 0$,

$$J([x, x+M]) \geqslant BJ((x+M, +\infty)). \tag{9.12}$$

This assumption holds if J has a compact support, is exponential or Gaussian, but may fail for other thin-tailed kernels. For example, let

$$J := \alpha \sum_{k=1}^{+\infty} e^{-|k|} \left(\delta_{k^2} + \delta_{-k^2}\right),$$

where $\alpha > 0$ is a normalisation constant such that $J(\mathbb{R}) = 1$. Then, for all $M > 0$, there exists $x \geqslant 0$ such that $J([x, x+M]) = 0$ and $J([x+M, +\infty)) > 0$; thus (9.12) cannot be satisfied. Roquejoffre [197], assuming that J has a compact support, was able to turn the term $O(1)$ into $C + o(1)$ (for some $C \in \mathbb{R}$). The techniques in both works are close to those of [120] (Graham combines them with a probabilistic argument, and Roquejoffre uses a refinement as in [177]). Our goal is to relax their conditions on J and to treat the general case of thin-tailed kernels. A first step towards this goal is to work on the *linear* Cauchy problem and, using the maximum principle, to find an upper bound for the position of the invasion front for the nonlinear Cauchy problem.

One specificity of this chapter is the use of the large deviation theory. In the works cited above, there are essentially two kinds of proofs: those which use analytic tools, as in [92, 94, 108, 120, 143, 148, 178, 197, 204] and those which use probabilistic tools, as in [52, 53, 166, 188, 217]. Graham and Uchiyama combine both kinds of proofs. The methods here are probabilistic. We shall use a Feynman-Kac representation of the solution. Then, we shall use the large deviation theory to estimate precisely the terms of the sum which will arise. In fact, it seems natural to use the large deviation theory in the problem we have raised, because we are mainly concerned with the extreme behaviour of individuals modelled by the solution of the Cauchy problem – much as the large deviation theory is concerned with the extreme values of random processes.

Note however that the use of the large deviation theory is not new in the study of local or nonlocal Fisher-KPP equations. Freidlin [98] uses a large deviation principle over the paths of a Brownian motion to determine the area covered by the solution in a heterogeneous environment; Evans and Souganidis [87] used a Hamilton-Jacobi version of the large deviation principle to get the same results as Freidlin with analytic methods. A recent article [5] deals with an equation close to ours, but with bistable or ignition reaction. The authors use the same Feynman-Kac representation as we do, the terms of which are also estimated thanks to the large deviation theory. With such estimates they are able to derive requirements on the initial condition so that the population persists. Their problem, therefore, is different from ours but their methods are very close.

Finally, it is worth to mention [2], in which Addario-Berry and Reed deal with branching random walks in discrete time. In his work, Graham [113] explains quickly how, from Addario-Berry and Reed's main result, one can deduce the emergence of the logarithmic delay (9.7) for the solution of the nonlinear nonlocal Cauchy problem (9.1) for a *restricted* class of monostable reaction terms and general dispersal kernels (he does not enter much into the details because he focuses on *general* monostable reaction term). The connection between Addario-Berry and Reed's work and the Cauchy problem (9.1) follows from a McKean-like representation of the solution of (9.1) using a well-chosen branching random walk (instead of a branching Brownian motion). The jump law of the branching random walk is the

kernel J, and the branching law depends on the nonlinear reaction term. In the classical McKean representation, which holds for the local equation (9.2), the branching random walk is replaced by a branching Brownian motion.

9.2 Main results

The first result is a proposition which gives a representation of the solution $u(t,x)$ of the linear Cauchy problem (9.3). Let J be a kernel which satisfies the hypotheses (9.8) and (9.9). The kernel J is therefore a probability law. We consider a sequence $(X_k)_{k\geqslant 1}$ of real independent and identically distributed random variables, following the law J. We define the random walk

$$S_n := \sum_{k=1}^{n} X_k.$$

The following proposition is a Feynman-Kac representation of the solution of the linear Cauchy problem (9.3).

Proposition 9.2.1. *Let $(S_n)_{n\geqslant 1}$ be the random walk defined above. Let $u(t,x)$ be a solution of the linear Cauchy problem* (9.3)*. Then, for all $t \in [0,+\infty)$, for all $x \in \mathbb{R}$,*

$$u(t,x) = e^{(r-1)t} \sum_{n=0}^{+\infty} \frac{t^n}{n!} \mathbb{P}\left(S_n \geqslant x\right). \tag{9.13}$$

As we look closely at each term of the sum (9.13), we observe that when x is near the position ct, there is a trade-off between the two factors $\frac{t^n}{n!}$ and $\mathbb{P}\left(S_n \geqslant x\right)$:

- for $t \simeq n$ and $t \gg n$, the factor $\frac{t^n}{n!}$ is large, but the probability $\mathbb{P}\left(S_n \geqslant x\right)$ is small;
- for $t \ll n$, the probability $\mathbb{P}\left(S_n \geqslant x\right)$ is large but the factor $\frac{t^n}{n!}$ is small.

In fact, we shall understand in the following that for $x = ct + o(\sqrt{t})$, the dominant terms of the sum (9.13) are located around a position $n \simeq \alpha t$ proportional to t. Therefore, when we study $u(t,ct)$, we will have to deal with probabilities of the form $\mathbb{P}\left(\frac{S_n}{n} \geqslant \frac{c}{\alpha}\right)$, where $\frac{c}{\alpha}$ is a constant. The theory of large deviations provides a useful framework to estimate precisely those very small probabilities as $n \to +\infty$, see e.g. the introduction of [75]. These observations will allow us to prove the main result.

Theorem 9.2.2. *Let J be a kernel which satisfies the hypotheses* (9.8) *and* (9.9)*. Let u be a solution of the linear Cauchy problem* (9.3)*. Take $\rho \in (0,1)$ and denote by*

$$\sigma^\rho(t) := \sup\left\{x \in \mathbb{R} \ / \ u(t,x) \geqslant \rho\right\}$$

the position of the level ρ of u at time t. We have

$$\sigma^\rho(t) = ct - s\ln(t) + O_{t\to+\infty}(1) \qquad \textit{with} \qquad s = \frac{1}{2\lambda_r},$$

where λ_r is defined by (9.11)*.*

Remark 9.2.3. Naturally, as we are currently considering the linear equation, we are not expecting to find exactly the same result as in Equation (9.7). However, we do get the same result with the local counterpart of the linear Cauchy problem (9.3),

$$\partial_t z = \partial_{xx} z + rz, \qquad r = f'(0), \tag{9.14}$$

together with the initial condition $z(1,x) = \frac{1}{4\pi} e^{-x^2/4}$. We then have a simple explicit expression for the solutions of Equation (9.14), $z(t,x) = \frac{e^{rx}}{\sqrt{4\pi t}} e^{-x^2/4t}$. We now look for the position $\sigma^\rho_{loc}(t)$ such that $z(t, \sigma^\rho_{loc}(t)) = \rho$. A short computation yields, as $t \to +\infty$,

$$\sigma^\rho_{loc}(t) = 2\sqrt{r}t - \frac{1}{2\sqrt{r}} \ln(t) + O(1) = c^* t - \frac{1}{2\lambda} \ln(t) + O(1),$$

which implies the same result as in Theorem 9.2.2 but for the local equation. Note also that the values $\lambda = \sqrt{f'(0)}$ and λ_r play a symmetric role for, respectively, the local equation and the nonlocal equation.

Thanks to the maximum principle, we then deduce the following corollary about the nonlinear equation.

Corollary 9.2.4. *Let J be a kernel which satisfies the hypotheses* (9.8) *and* (9.9). *Let f be a reaction term which satisfies the monostability conditions* (9.4) *and the KPP condition* (9.6). *Let v be a solution of the nonlinear Cauchy problem* (9.1). *Take $\rho \in (0,1)$ and denote by*

$$\theta^\rho(t) := \sup \{x \in \mathbb{R} \ / \ v(t,x) \geqslant \rho\}$$

the position of the level ρ of v at time t. We have

$$\theta^\rho(t) \leqslant ct - s \ln(t) + O_{t \to +\infty}(1) \qquad \textit{with} \qquad s = \frac{1}{2\lambda_r},$$

where λ_r is defined by (9.11).

Remark 9.2.5. This corollary is consistent with the main results of Graham and Roquejoffre [113, 197], which include the situation when J has compact support (see above).

Section 9.3 gives preliminary results about the theory of large deviations; we shall use these results in Subsection 9.4.2 to prove Theorem 9.2.2. Subsection 9.4.1 is devoted to the proof of Proposition 9.2.1. Finally, Subsection 9.4.3 is devoted to the proof of Corollary 9.2.4.

9.3 Preliminary results about large deviations

We first focus on the useful notions from large deviations theory. Let J be a dispersal kernel satisfying the hypotheses (9.8) and (9.9) and let X be a real random variable following the law J. Let $D = \left\{\zeta \in \mathbb{R} \ / \ \mathbb{E}\left[e^{\zeta X}\right] < +\infty\right\}$. The *cumulant generating function* of the law J is defined at all $\zeta \in D$ by

$$\Lambda(\zeta) := \ln\left(\mathbb{E}\left[e^{\zeta X}\right]\right).$$

As J decreases at least exponentially fast at $\pm\infty$, the set D contains a neighbourhood of 0. The Legendre-Fenchel transform of Λ is denoted by Λ^* and plays a fundamental role in the

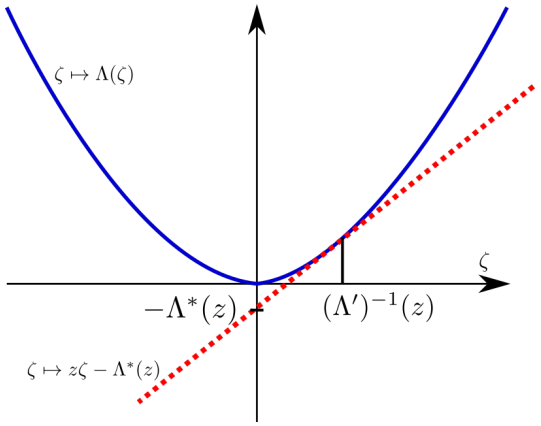

Figure 9.1: Graphical interpretation of the Legendre-Fenchel transform of Λ (inspired from [75]). The curve in blue looks like Λ, the dotted line in red is *the* line tangent to the blue curve and with slope z. The dotted line in red crosses the vertical axis at $-\Lambda^*(z)$, the opposite of the Legendre-Fenchel transform of Λ at z.

statement of the theorem of Bahadur-Rao. It is defined, for all $z \in \mathbb{R}$, by

$$\Lambda^*(z) = \sup_{\zeta \in D} [\zeta z - \Lambda(\zeta)] \in [0, +\infty].$$

Figure 9.1 gives a graphical interpretation of the Legendre-Fenchel transform of a (symmetric) convex function.

The following lemma contains general properties of the functions Λ and Λ^* (see [75], Lemma 2.2.5).

Lemma 9.3.1. *Assume that J satisfies the hypotheses (9.8) and (9.9). We then have:*

1. *The function Λ is smooth (i.e. C^∞) over D. Let $A = \sup\{\text{supp}(J)\}$. The function Λ^* is finite and smooth over $D^* = (-A, A)$;*
2. *The functions Λ and Λ^* are nonnegative and strictly convex on, respectively, D and D^*. Moreover, $\Lambda(0) = \Lambda^*(0) = 0$;*
3. *The function Λ' is a bijection from D to D^*. We define, for $z \in D^*$: $\zeta_m(z) := (\Lambda')^{-1}(z)$. We have, for all $z \in D^*$,*
$$\Lambda^*(z) = \zeta_m(z) z - \Lambda(\zeta_m(z)) \tag{9.15}$$
and
$$(\Lambda^*)'(z) = \zeta_m(z).$$

Proof. We sketch the proof of these classical properties (see also [75], Lemma 2.2.5).

- The nonnegativity of Λ comes from Jensen's inequality. Since J is thin-tailed, Λ is smooth in D;

- The strict convexity of Λ follows: for $\zeta \in D$,

$$\Lambda''(\zeta) = \frac{\mathbb{E}\left[X^2 e^{\zeta X}\right]\mathbb{E}\left[e^{\zeta X}\right] - \mathbb{E}\left[X e^{\zeta X}\right]^2}{\mathbb{E}\left[e^{\zeta X}\right]^2}$$
$$= \frac{\mathbb{E}\left[(Xe^{\zeta X/2})^2\right]\mathbb{E}\left[(e^{\zeta X/2})^2\right] - \mathbb{E}\left[(Xe^{\zeta X/2})(e^{\zeta X/2})\right]^2}{\mathbb{E}\left[e^{\zeta X}\right]^2} > 0,$$

  by the Cauchy-Schwarz inequality (the inequality is strict because X is nonconstant);

- We have

$$\Lambda'(\zeta) = \frac{\mathbb{E}\left[Xe^{\zeta X}\right]}{\mathbb{E}\left[e^{\zeta X}\right]} \underset{\zeta \to +\infty}{\to} \sup\{\mathrm{supp}(J)\},$$

  thus: $\sup_{\zeta \in D} \Lambda'(\zeta) = \sup\{\mathrm{supp}(J)\}$. Moreover, Λ' is strictly increasing and smooth. Therefore, Λ' is a smooth bijection from D to D^* with smooth converse $(\Lambda')^{-1}$;

- For $z \in D^*$, the supremum in the definition of $\Lambda^*(z)$ is reached when $\Lambda'(\zeta) = z$. We get (9.15). We then deduce that Λ^* is finite and smooth over D^*. Using (9.15), we get: $(\Lambda^*)'(z) = \zeta_m(z)$. Finally, $\zeta_m(z)$ is increasing, so Λ^* is convex.

□

Let $(X_k)_{k \geqslant 1}$ be a sequence of independent and identically distributed random variables, following the law J, and define the corresponding random walk $(S_n)_{n \geqslant 1}$ as in the introduction. We are now ready to state, in our particular case, the theorem of Bahadur-Rao [16]. This theorem will be useful in the proof of Theorem 9.2.2. Recall that, for $z \in D^*$, we have defined $\zeta_m(z) = (\Lambda')^{-1}(z)$.

Theorem 9.3.2 (Bahadur-Rao [16])**.** *Assume that J is nonlattice. Take $M_1, M_2 \in D^*$ with $M_2 > M_1 > 0$. The random walk defined above satisfies*

$$\mathbb{P}(S_n \geqslant nz) = \frac{e^{-n\Lambda^*(z)}}{\zeta_m(z)\sqrt{2n\pi\Lambda''(\zeta_m(z))}}(1 + o(1)) \quad \text{as } n \to +\infty, \tag{9.16}$$

uniformly in $z \in [M_1, M_2]$.

The uniformity is not present in the original paper of Bahadur and Rao, but it has been proved by Petrov in [189]. If J is lattice (i.e. X_1 is almost surely of the form $a + kb$, $k \in \mathbb{Z}$, for some fixed $a, b \in \mathbb{R}$), then the form is slightly different, but the proofs of the main results do not change.

9.4 Proofs of the main results

9.4.1 Proof of Proposition 9.2.1

Proof of Proposition 9.2.1. If u is a solution of the linear Cauchy problem (9.3), and if we set $\tilde{u} := e^{-rt}u$, then $\tilde{u}$ is a solution of the linear equation $\partial_t \tilde{u} = J * \tilde{u} - \tilde{u}$ with the same initial condition. Therefore, we may assume $r = 0$.

Let $(Z_t)_{t\geqslant 0}$ be a Poisson process with rate 1 and jump law J, and such that $Z_0 = 0$ almost surely. The infinitesimal generator of the process $(Z_t)_{t\geqslant 0}$ is

$$\mathcal{G}f = J * f - f$$

and, therefore, the function

$$u(t,x) := \mathbb{E}\left[Z_t \geqslant x\right]$$

solves $\partial_t u = J * u - u$ with initial condition $u(0,\cdot) = \mathbb{1}_{(-\infty,0]}$. Upon partitioning events according to the number of jumps made by the process in $[0,t]$, we conclude

$$u(t,x) = \sum_{n=0}^{+\infty} \frac{e^{-t}t^n}{n!}\mathbb{P}\left(X_1 + \ldots + X_n \geqslant x\right),$$

where $\frac{e^{-t}t^n}{n!}$ is the probability that exactly n jumps occurred in $[0,t]$. This yields the result for $r = 0$. The conclusion follows by multiplying by e^{rt}. □

Remark 9.4.1. An important feature of Proposition 9.2.1 is that it allows us to work on the discrete-time random walk $(X_1 + \ldots + X_n)_{n\geqslant 0} = (S_n)_{n\geqslant 0}$ rather than on the continuous-time random walk $(Z_t)_{t\geqslant 0}$. In this situation, the theory of large deviations applies more easily. Another method to do the transformation from continuous time to discrete time is to consider the continuous-time random walk $(Z_t)_{t\geqslant 0}$ restricted to integer times, which gives the discrete-time random walk $(Z_n)_{n\geqslant 0}$. The jump law of the process $(Z_n)_{n\geqslant 0}$ is found by conditioning on the number of jumps made by the process $(Z_t)_{t\geqslant 0}$ between the times 0 and 1. Hence the sum arising in Proposition 9.2.1 is directly incorporated into the jump law of $(Z_n)_{n\geqslant 0}$. This second method, which is inspired from the introduction of [2], should lead to easier computations: one simply has to estimate the probabilities $\mathbb{P}\left(Z_n \geqslant cn - \frac{1}{2\lambda_r}\ln(n)\right)$, and no more sum is involved. We shall rather concentrate on the first method, which seems more interesting from the point of view of modelling: indeed, it explicitly counts the jumps, i.e. the generations. Such a record can be helpful if one wants to take into account the fact, for example, that mutations can arise at each generation.

9.4.2 Proof of Theorem 9.2.2

Throughout Subsection 9.4.2, we assume for convenience that $\sup\{\mathrm{supp}J\} = +\infty$, so that Λ^* is defined on $D^* = \mathbb{R}$ (the proof is almost the same if $\sup\{\mathrm{supp}J\} < +\infty$). We consider a nonnegative function $m(t) = o(\sqrt{t})$, and we note

$$x_t = ct - m(t).$$

The function m is intended to represent the delay, while x_t is intended to represent the position of the front at time t. Our goal is to estimate $u(t,x_t)$ as t grows to infinity. The idea of the proof is to cut the sum expressing $u(t,x_t)$ given by Proposition 9.2.1,

$$u(t,x_t) = e^{(r-1)t}\sum_{n=0}^{+\infty}\frac{t^n}{n!}\mathbb{P}\left(S_n \geqslant x_t\right) \tag{9.17}$$

into partial sums $S_{a,b}(t,x_t)$ of the form

$$S_{a,b}(t,x_t) := e^{(r-1)t} \sum_{n=\lfloor at\rfloor+1}^{\lfloor bt\rfloor} \frac{t^n}{n!}\mathbb{P}\left(S_n \geqslant x_t\right),$$

and to estimate each partial sum independently. We will show that there exists a value $\alpha > 0$ such that the dominant terms of the total sum are located around $\lfloor \alpha t\rfloor$. A large part of the proof is devoted to the estimation of those terms, that is, to the estimation of $S_{\alpha-\varepsilon,\alpha+\varepsilon}(t,x_t)$.

We begin with a lemma which estimates the partial sums $S_{a,b}(t,x_t)$. We use a version of the theorem of Bahadur-Rao (Theorem 9.3.2) to turn the probability $\mathbb{P}\left(S_n \geqslant x_t\right)$ into a more tractable expression. In the proofs, we will sometimes use the notation

$$p(t) = \Theta(q(t))$$

to say that there exist $0 < K_- < K_+$ and $t_0 > 0$ such that for all $t \geqslant t_0$, $K_- q(t) \leqslant p(t) \leqslant K_+ q(t)$.

Lemma 9.4.2. *Let $b > a > 0$. Define*

$$g(y) := y\left(\ln\left(\frac{e}{y}\right) - \Lambda^*\left(\frac{c}{y}\right)\right) + r - 1$$

and

$$h(t,y) := \frac{e^{(\Lambda^*)'(c/y)m(t)}}{t} e^{tg(y)}.$$

There exist $K_-(a,b), K_+(a,b) > 0$ such that for t large enough,

$$K_-(a,b) \sum_{n=\lfloor at\rfloor+1}^{\lfloor bt\rfloor} h\left(t,\frac{n}{t}\right) \leqslant S_{a,b}(t,x_t) \leqslant K_+(a,b) \sum_{n=\lfloor at\rfloor+1}^{\lfloor bt\rfloor} h\left(t,\frac{n}{t}\right).$$

Proof. We shall use the following property, resulting from Theorem 9.3.2: for every subset $V \subset (0,+\infty)$, there exists $n_0(V)$ such that for all $n \geqslant n_0(V)$, for all $z \in V$,

$$\frac{e^{-n\Lambda^*(z)}}{2\zeta_m(z)\sqrt{2n\pi\Lambda''(\zeta_m(z))}} \leqslant \mathbb{P}\left(S_n \geqslant nz\right) \leqslant 2\frac{e^{-n\Lambda^*(z)}}{\zeta_m(z)\sqrt{2n\pi\Lambda''(\zeta_m(z))}}. \tag{9.18}$$

Recall that $\zeta_m(z)$ is defined in Lemma 9.3.1.

Step 1: Application of (9.18)**.** Take $V = \left[\frac{c}{2b}, \frac{2c}{a}\right]$. Recall that $x_t = ct - m(t)$ where $m(t) = o(\sqrt{t})$ is nonnegative. Therefore, for t large enough and for all integer n between $\lfloor at\rfloor + 1$ and $\lfloor bt\rfloor$, we have $x_t/n \in V$. Let $n_0(V)$ be the index given by Property (9.18). Consider $t_0 \geqslant 0$ such that for all $t \geqslant t_0$, both $\lfloor at\rfloor + 1 \geqslant n_0(V)$ and $x_t/n \in V$ hold. Take $t \geqslant t_0$ and apply Property (9.18) to each integer n between $\lfloor at\rfloor + 1$ and $\lfloor bt\rfloor$, each time with $z_n = \frac{x_t}{n} \in V$. We find that there exist two constants $0 < K_0 < K_1$ independent of t such that for each integer n between $\lfloor at\rfloor + 1$ and $\lfloor bt\rfloor$,

$$K_0 \frac{e^{-n\Lambda^*\left(\frac{x_t}{n}\right)}}{\zeta_m(x_t/n)\sqrt{2n\pi\Lambda''(\zeta_m(x_t/n))}} \leqslant \mathbb{P}\left(S_n \geqslant x_t\right) \leqslant K_1 \frac{e^{-n\Lambda^*\left(\frac{x_t}{n}\right)}}{\zeta_m(x_t/n)\sqrt{2n\pi\Lambda''(\zeta_m(x_t/n))}}.$$

By Lemma 9.3.1, the function ζ_m is continuous and positive over $(0,+\infty)$. Since V is a compact subset of $(0,+\infty)$, we have

$$0 < \inf_{z\in V} \frac{1}{\zeta_m(z)\sqrt{2\pi\Lambda''(\zeta_m(z))}} \leqslant \sup_{z\in V} \frac{1}{\zeta_m(z)\sqrt{2\pi\Lambda''(\zeta_m(z))}} < +\infty.$$

Thus, summing over n, as $t \to +\infty$,

$$S_{a,b}(t,x_t) = \Theta\left(T_{a,b}(t,x_t)\right) \tag{9.19}$$

where

$$T_{a,b}(t,x_t) := e^{(r-1)t} \sum_{n=\lfloor at\rfloor+1}^{\lfloor bt\rfloor} \frac{t^n}{n!\sqrt{n}} e^{-n\Lambda^*\left(\frac{x_t}{n}\right)}.$$

Our goal is now to estimate the sum $T_{a,b}(t,x_t)$.

Step 2: Estimation of Λ^*. Take $t \geqslant t_0$ and an integer n such that $\lfloor at\rfloor + 1 \leqslant n \leqslant \lfloor bt\rfloor$. Recall that $x_t = ct - m(t)$ where $m(t) = o(\sqrt{t})$. We have

$$\Lambda^*\left(\frac{x_t}{n}\right) = \Lambda^*\left(\frac{ct}{n} - \frac{m(t)}{n}\right) = \Lambda^*\left(\frac{ct}{n}\right) - (\Lambda^*)'\left(\frac{ct}{n}\right)\frac{m(t)}{n} + O_{m/n\to 0}\left(\frac{m(t)^2}{n^2}\right).$$

Thus there exists a time $t_1 \geqslant t_0$ and a constant $K_2 > 0$ such that for all $t \geqslant t_1$ and for every integer n such that $\lfloor at\rfloor + 1 \leqslant n \leqslant \lfloor bt\rfloor$, we have

$$\left|\Lambda^*\left(\frac{x_t}{n}\right) - \left(\Lambda^*\left(\frac{ct}{n}\right) - (\Lambda^*)'\left(\frac{ct}{n}\right)\frac{m(t)}{n}\right)\right| \leqslant K_2\frac{m(t)^2}{n^2}.$$

We rewrite this as

$$\begin{aligned}
&\Lambda^*\left(\frac{ct}{n}\right) - (\Lambda^*)'\left(\frac{ct}{n}\right)\frac{m(t)}{n} - K_2\frac{m(t)^2}{n^2} \\
&\quad\leqslant \Lambda^*\left(\frac{x_t}{n}\right) \\
&\quad\leqslant \Lambda^*\left(\frac{ct}{n}\right) - (\Lambda^*)'\left(\frac{ct}{n}\right)\frac{m(t)}{n} + K_2\frac{m(t)^2}{n^2}.
\end{aligned} \tag{9.20}$$

Step 3: Estimation of each single term of the sum $T_{a,b}(t,x_t)$. By Stirling's formula, as $n \to +\infty$,

$$n! = \Theta\left(\sqrt{n}\exp(n\ln(n/e))\right).$$

Using the second inequality in (9.20), we obtain a constant $K_3 > 0$ and a time $t_2 \geqslant t_1$ such that, for all $t \geqslant t_2$, for all integer n such that $\lfloor at \rfloor + 1 \leqslant n \leqslant \lfloor bt \rfloor$,

$$\begin{aligned}
&\frac{e^{(r-1)t} t^n}{n!\sqrt{n}} e^{-n\Lambda^*(x_t/n)} \\
&\quad \geqslant \frac{K_3}{n} \exp\left[n\left(\ln\left(e\frac{t}{n} \right) - \Lambda^*(ct/n) \right) + (r-1)t \right] \exp\left[(\Lambda^*)'(ct/n) m(t) - K_2 \frac{m(t)^2}{n} \right] \\
&\quad = \frac{K_3}{n} \exp\left[tg\left(\frac{n}{t} \right) \right] \exp\left[(\Lambda^*)'(ct/n) m(t) - K_2 \frac{m(t)^2}{n} \right].
\end{aligned}$$

Since $m(t) = o(\sqrt{t})$, we have $m(t)^2 = o(t)$. Therefore there exist $K_4 > 0$ and $t_3 \geqslant t_2$ such that for all $t \geqslant t_3$, for all integer n such that $\lfloor at \rfloor + 1 \leqslant n \leqslant \lfloor bt \rfloor$,

$$\frac{e^{(r-1)t} t^n}{n!\sqrt{n}} e^{-n\Lambda^*(x_t/n)} \geqslant \frac{K_4}{n} \exp\left[tg\left(\frac{n}{t} \right) \right] \exp\left[(\Lambda^*)'(ct/n) m(t) \right] \geqslant \frac{K_4}{b} h\left(t, \frac{n}{t} \right).$$

Thus, summing on all n between $\lfloor at \rfloor + 1$ and $\lfloor bt \rfloor$, we obtain an estimation of $T_{a,b}(t, x_t)$ which yields, together with Equation (9.19), the existence of a constant $K_-(a,b)$ such that for all $t \geqslant t_3$,

$$S_{a,b}(t, x_t) \geqslant K_-(a,b) \sum_{n=\lfloor at \rfloor + 1}^{\lfloor bt \rfloor} h\left(t, \frac{n}{t} \right).$$

Using the first inequality in (9.20), we proceed to the same reasoning with reversed inequalities, and we obtain the existence of a constant $K_+(a,b)$ and a time $t_3' \geqslant t_2$ such that for all $t \geqslant t_3'$,

$$S_{a,b}(t, x_t) \leqslant K_+(a,b) \sum_{n=\lfloor at \rfloor + 1}^{\lfloor bt \rfloor} h\left(t, \frac{n}{t} \right).$$

The lemma is proved. □

Now, we introduce the value α, which is constructed so that the most important terms of the sum (9.17) expressing $u(t, x_t)$ are located around the position $n \simeq \alpha t$.

Lemma 9.4.3. *Set*

$$\alpha = c\lambda_r - (r-1).$$

Then $\alpha > 0$ *and*

$$\lambda_r = (\Lambda^*)'\left(\frac{c}{\alpha} \right). \tag{9.21}$$

Moreover, the function g *defined in Lemma 9.4.2 is strictly concave on* $(0, +\infty)$ *and is maximal at* α. *Finally, we have* $g(\alpha) = 0$, $g'(\alpha) = 0$, *and, for* $y > 0$, $y \neq \alpha$, *we have* $g(y) < 0$.

Remark 9.4.4. We can write $h(t,y)$ in the form $h(t,y) = C(t,y)e^{tg(y)}$, where $C(t,y)$ is not too large as $t \to +\infty$. Hence, Lemmas 9.4.2 and 9.4.3 entail that when $a < b < \alpha$ or $b > a > \alpha$, the partial sum $S_{a,b}(t, x_t)$ contains only terms which are exponentially small in t, thus the partial sum $S_{a,b}(t, x_t)$ is also exponentially small in t. Therefore, the dominant terms of the whole sum (9.17) expressing $u(t, x_t)$ are located around $n \simeq \alpha t$.

Proof of Lemma 9.4.3. Let $M(\lambda) = \mathbb{E}\left[e^{\lambda X}\right]$. Let $A(\lambda) = \frac{M(\lambda)+r-1}{\lambda}$. With this notation, $c = \inf_{\lambda>0} A(\lambda) = A(\lambda_r)$ and

$$\alpha = c\lambda_r - (r-1) = M(\lambda_r).$$

Hence $\alpha > 0$. Since λ_r is positive and A is smooth and minimal at λ_r, we have $A'(\lambda_r) = 0$, that is

$$\frac{1}{\lambda_r^2}\left(\lambda_r M'(\lambda_r) - M(\lambda_r) - (r-1)\right) = 0.$$

Recall $\Lambda = \ln M$. Thus, differentiating,

$$\lambda_r \Lambda'(\lambda_r) = \lambda_r \frac{M'(\lambda_r)}{M(\lambda_r)} = 1 + \frac{r-1}{M(\lambda_r)},$$

which implies

$$\Lambda'(\lambda_r) = \frac{1}{\lambda_r} + \frac{r-1}{\lambda_r M(\lambda_r)} = \frac{M(\lambda_r)+r-1}{\lambda_r M(\lambda_r)} = \frac{c}{M(\lambda_r)} = \frac{c}{\alpha}.$$

Lemma 9.3.1 tells us that $(\Lambda^*)' = \zeta_m = (\Lambda')^{-1}$. Equality (9.21) follows.

We also have

$$\Lambda^*\left(\frac{c}{\alpha}\right) = \zeta_m\left(\frac{c}{\alpha}\right)\frac{c}{\alpha} - \Lambda\left(\zeta_m\left(\frac{c}{\alpha}\right)\right) = \lambda_r \frac{c}{\alpha} - \Lambda(\lambda_r)$$

so, using the fact that $\alpha = M(\lambda_r)$,

$$\Lambda^*\left(\frac{c}{\alpha}\right) + \ln(\alpha) - \frac{c\lambda_r}{\alpha} = 0. \tag{9.22}$$

With equalities (9.21) and (9.22) at hand, we are ready to conclude. Recall that

$$g(y) = y\left(\ln\left(\frac{e}{y}\right) - \Lambda^*\left(\frac{c}{y}\right)\right) + r - 1.$$

We have, by (9.22),

$$g(\alpha) = \alpha\left(1 - \ln(\alpha) - \Lambda^*(c/\alpha)\right) + r - 1 = \alpha\left(1 - \frac{c\lambda_r}{\alpha}\right) + r - 1.$$

Hence, since $\alpha = c\lambda_r - (r-1)$, we conclude that $g(\alpha) = 0$. Furthermore,

$$g'(y) = -\ln(y) - \Lambda^*\left(\frac{c}{y}\right) + \frac{c}{y}(\Lambda^*)'\left(\frac{c}{y}\right).$$

Therefore, by (9.21) and (9.22), we get $g'(\alpha) = 0$. Finally, we have, for all $y > 0$,

$$g''(y) = -\frac{1}{y} - \frac{c^2}{y^3}(\Lambda^*)''\left(\frac{c}{y}\right) < 0.$$

These elements allow us to conclude. □

Lemma 9.4.5. *The following asymptotic properties hold as $t \to +\infty$.*

1. *For $0 < a < b < \alpha$, there exists $\chi > 0$ such that*
$$S_{a,b}(t, x_t) = o(e^{-\chi t});$$
2. *For $B > A > \alpha$, there exists $\chi > 0$ such that*
$$S_{A,B}(t, x_t) = o(e^{-\chi t});$$
3. *There exists $\varepsilon > 0$, two constants $K_-, K_+ > 0$ and a time $t_0 > 0$ such that for all $t \geqslant t_0$,*
$$K_- \frac{e^{\lambda_r m(t)}}{\sqrt{t}} \leqslant S_{\alpha-\varepsilon,\alpha+\varepsilon}(t, x_t) \leqslant K_+ \frac{e^{\lambda_r m(t)}}{\sqrt{t}}.$$

Proof. Let $0 < a < b < \alpha$ and let $\chi = -\frac{1}{2}\sup_{y\in[a,b]} g(y)$. Then, by Lemma 9.4.3, χ is positive. From Lemma 9.4.2 and the fact that $m(t) = o(\sqrt{t})$, we deduce that the first point holds for this value of χ. The same reasoning is valid for the second point as well. Now we prove the third point, which is more involved due to the equality $g(\alpha) = 0$.

Step 1: Estimation of the partial sum $S_{\alpha-\varepsilon,\alpha+\varepsilon}(t, x_t)$; simple integrals arise. Take $\varepsilon \in (0, \alpha/2)$. By Lemma 9.4.2, there exist $K_0, K_1 > 0$ such that for t large enough,

$$K_0 t \left(\frac{1}{t} \sum_{n=\lfloor(\alpha-\varepsilon)t\rfloor+1}^{\lfloor(\alpha+\varepsilon)t\rfloor} h\left(t, \frac{n}{t}\right) \right) \leqslant S_{\alpha-\varepsilon,\alpha+\varepsilon}(t, x_t) \leqslant K_1 t \left(\frac{1}{t} \sum_{n=\lfloor(\alpha-\varepsilon)t\rfloor+1}^{\lfloor(\alpha+\varepsilon)t\rfloor} h\left(t, \frac{n}{t}\right) \right).$$

By Lemma 9.4.3, for $t > 0$ sufficiently large, there exists $\varepsilon > 0$ sufficiently small such that $y \mapsto h(t, y)$ is increasing on $[\alpha - 2\varepsilon, \alpha]$ and decreasing on $[\alpha, \alpha + 2\varepsilon]$. We obtain that there exist $K_2, K_3 > 0$ such that for t large enough,

$$K_2 t \int_{-\varepsilon}^{\varepsilon} h(t, \alpha + y)\,\mathrm{d}y \leqslant S_{\alpha-\varepsilon,\alpha+\varepsilon}(t, x_t) \leqslant K_3 t \int_{-\varepsilon}^{\varepsilon} h(t, \alpha + y)\,\mathrm{d}y. \tag{9.23}$$

Step 2: Estimation of the integral arising in (9.23) and conclusion. At the light of Equation (9.23), we wish to estimate $h(t, \alpha + y)$ for y close to 0. By Lemma 9.4.3, we have $g''(\alpha) < 0$ and

$$g(\alpha + y) = O(y^2).$$

Therefore we can take $A', A'' > 0$, and reduce $\varepsilon > 0$ if necessary, so that for all $y \in (-\varepsilon, \varepsilon)$,

$$-A'y^2 \leqslant g(\alpha + y) \leqslant -A''y^2.$$

Then, we have for some constants $K_5, K_6 > 0$ and for t large enough,

$$K_5 \int_{-\varepsilon}^{\varepsilon} \frac{e^{(\Lambda^*)'\left(\frac{c}{\alpha+y}\right)m(t)}}{t} e^{-tA'y^2}\,\mathrm{d}y \leqslant \int_{-\varepsilon}^{\varepsilon} h(t, y)\,\mathrm{d}y \leqslant K_6 \int_{-\varepsilon}^{\varepsilon} \frac{e^{(\Lambda^*)'\left(\frac{c}{\alpha+y}\right)m(t)}}{t} e^{-tA''y^2}\,\mathrm{d}y. \tag{9.24}$$

Now, note that

$$(\Lambda^*)'\left(\frac{c}{\alpha+y}\right)m(t) = \lambda_r m(t) + O_{y\to 0}(y m(t)).$$

Thus, there are random variables $Z_t \sim \mathcal{N}\left(O\left(\frac{m(t)}{t}\right), \frac{1}{2tA'}\right)$ such that as t goes to infinity,

$$\begin{aligned}\int_{-\varepsilon}^{\varepsilon} \frac{e^{(\Lambda^*)'\left(\frac{c}{\alpha+y}\right)m(t)}}{t} e^{-tA'y^2}\,\mathrm{d}y &= \Theta\left(\frac{e^{\lambda_r m(t)}}{t}\int_{-\varepsilon}^{\varepsilon}\exp\left[-tA'\left(y+O\left(\frac{m(t)}{t}\right)\right)^2\right]\mathrm{d}y\right)\\ &= \Theta\left(\frac{e^{\lambda_r m(t)}}{t\sqrt{t}}\times \mathbb{P}\left(-\varepsilon < Z_t < \varepsilon\right)\right)\\ &= \Theta\left(\frac{e^{\lambda_r m(t)}}{t\sqrt{t}}\right).\end{aligned}$$

The last line holds because $m(t) = o(t)$, so that Z_t converges to 0 in probability, as $t \to +\infty$. Injecting twice this estimation into (9.24) (once as such and once replacing A' by A''), we deduce that there exist constants $K_7, K_8 > 0$ such that for t large enough,

$$K_7 \frac{e^{\lambda_r m(t)}}{t\sqrt{t}} \leqslant \int_{-\varepsilon}^{\varepsilon} h(t,y)\,\mathrm{d}y \leqslant K_8 \frac{e^{\lambda_r m(t)}}{t\sqrt{t}}. \tag{9.25}$$

Equation (9.25), together with Equation (9.23), proves that the third point of the statement holds for the values of ε that we have selected in the beginning of Step 2. □

We are now ready to conclude the proof of the main theorem.

Proof of Theorem 9.2.2. Let $\varepsilon > 0$ be defined as in Lemma 9.4.5. Take a, B such that $0 < a < \alpha < B$. By Proposition 9.2.1, we have

$$u(t,x_t) = e^{(r-1)t}\sum_{n=0}^{+\infty}\frac{t^n}{n!}\mathbb{P}\left(S_n \geqslant x_t\right),$$

so, cutting the sum into five parts, we have

$$\begin{aligned}u(t,x_t) = \Bigg(&\sum_{n=0}^{\lfloor at\rfloor} + \sum_{n=\lfloor at\rfloor+1}^{\lfloor(\alpha-\varepsilon)t\rfloor} + \sum_{n=(\alpha-\varepsilon)+1}^{\lfloor(\alpha+\varepsilon)t\rfloor}\\ &+ \sum_{n=\lfloor(\alpha+\varepsilon)t\rfloor+1}^{\lfloor Bt\rfloor} + \sum_{n=\lfloor Bt\rfloor+1}^{+\infty}\Bigg)\frac{e^{(r-1)t}t^n}{n!}\mathbb{P}\left(S_n \geqslant x_t\right).\end{aligned} \tag{9.26}$$

Now, we estimate the first and last part of the sum (the other three will be estimated thanks to Lemma 9.4.5). First, for $a > 0$ small enough and $\chi_1 > 0$ small enough, we have, as $t \to +\infty$,

$$\begin{aligned}\sum_{n=0}^{\lfloor at\rfloor}\frac{e^{(r-1)t}t^n}{n!}\mathbb{P}\left(S_n \geqslant x_t\right) &\leqslant e^{rt}\mathbb{P}\left(\max_{n=1,\dots,\lfloor at\rfloor} S_n \geqslant x_t\right)\\ &\leqslant \lfloor at\rfloor\, e^{rt}\mathbb{P}\left(\max(S_1,\ S_{\lfloor at\rfloor}) \geqslant x_t\right) = o(e^{-\chi_1 t}).\end{aligned}$$

The last estimation is obtained thanks to the Theorem 9.3.2 with $z = c/a$ (which becomes

large when $a > 0$ becomes small), as well as the exponential decay of J in (9.9). Second, we have, as $t \to +\infty$,

$$\sum_{n=\lfloor Bt \rfloor+1}^{+\infty} \frac{e^{(r-1)t} t^n}{n!} \mathbb{P}\left(S_n \geqslant x_t\right) \leqslant \sum_{n=\lfloor Bt \rfloor+1}^{+\infty} \frac{e^{(r-1)t} t^n}{n!}$$
$$\leqslant \frac{e^{(r-1)t} t^{\lfloor Bt \rfloor}}{\lfloor Bt \rfloor!} \sum_{n=0}^{+\infty} \frac{t^n}{n!} = e^{rt} \frac{t^{\lfloor Bt \rfloor}}{\lfloor Bt \rfloor!} = o(e^{-\chi_2 t})$$

for $B > 0$ large enough and $\chi_2 > 0$ small enough.

Therefore, thanks to Lemma 9.4.5 and the decomposition (9.26), we conclude that there exist constants $K_-, K_+ > 0$ and $\chi_3 > 0$ such that for t large enough,

$$K_- \frac{e^{\lambda_r m(t)}}{\sqrt{t}} \leqslant u(t, x_t) \leqslant K_+ \frac{e^{\lambda_r m(t)}}{\sqrt{t}} + o(e^{-\chi_3 t}).$$

Hence, there exists $t_0 > 0$ such that for all $t \geqslant t_0$,

$$\frac{1}{2} K_- \frac{e^{\lambda_r m(t)}}{\sqrt{t}} \leqslant u(t, x_t) \leqslant 2K_+ \frac{e^{\lambda_r m(t)}}{\sqrt{t}}.$$

Hence, upon choosing $m(t) = \frac{1}{2\lambda_r} \ln(t) \pm C$ for a large C, we have:

$$u\left(t, ct - \frac{1}{2\lambda_r} \ln(t) + C\right) \ll \rho,$$
$$u\left(t, ct - \frac{1}{2\lambda_r} \ln(t) - C\right) \gg \rho,$$

as $t \to +\infty$. (Recall that ρ is the level in which we are interested). Thus for t large enough, $\left|\sigma^\rho(t) - \frac{1}{2\lambda_r} \ln(t)\right| < C$. The conclusion of the theorem follows. □

9.4.3 Proof of Corollary 9.2.4

Proof of Corollary 9.2.4. We denote by v the solution of the nonlinear Cauchy problem (9.1) and by u the solution of the linear Cauchy problem (9.3) with $r = f'(0)$. As the reaction term satisfies the KPP condition (9.6), the function v is a subsolution of the linear Cauchy problem (9.3). As u and v have the same initial condition, the maximum principle tells us that $v \leqslant u$. Finally, when we apply Theorem 9.2.2 to the function u, we get the conclusion of Corollary 9.2.4. □

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Chapter 10

How to analyse the loss of neutral diversity?

Abstract

In this chapter, we are interested in the effect, on the dynamics of neutral diversity, of a physical barrier to dispersal. Through the measurement of diversity at different positions, we wish to estimate the "strength" of the barrier. The origin of this chapter is an experiment performed by N. Peeters and S. Vicente, in which they followed the dynamics of 120 neutral tags (given by DNA bar-coding) during the invasion of *Ralstonia solanacearum* bacteria in tomato plants. In this chapter, we study the barrier between the soil and the root of the plants.

We describe several models for the barrier: a "one-step bottleneck" model, a "constant-rate crossing" model, and models based on the Kingman coalescent and the Bolthausen-Sznitman coalescent. Next, we provide a method to compare these models with one another, and apply this method to experimental data.

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10.1 Introduction

Once an environment is colonised by a population, how to get information on how the colonisation took place? If one merely looks at population sizes at different positions of the environment, one loses much information, because population size is a mix of colonisation, migrations and local growth. For example, one cannot make the distinction between an isolated place that was colonised by a single founder and in which all current individuals descend from this founder, and a very connected place to which and from which individuals constantly migrate.

Much more information can be obtained if one looks at the dynamics of neutral diversity. Then, isolated places will show low diversity (as the local population will all descend from the same few individuals), while connected places will show high diversity. However, studying neutral diversity experimentally is a technical challenge. First, one needs to ensure that diversity is indeed neutral, in order to avoid bias due to selection; second, to get precise information, one needs the initial population to be *sufficiently diverse*.

Using techniques of DNA bar-coding to create artificial neutral diversity, Kaiser et al. [131] and Grant et al. [114] were able to get insight into the mechanisms of the invasion of *Salmonella* bacteria in mice after an oral infection, by looking at where diversity was conserved and where diversity was lost. Abel et al. [1] went further and provided an analytical framework, called STAMP (for "Sequence Tag-based Analysis of Microbial Population dynamics") to analyse the data provided by such DNA bar-coding experiments. Using this framework, they studied the infection of rabbits by *Vibrio cholerae* bacteria, and showed, for example, the unexpected fact that bacteria could go against the intestinal flow.

In this chapter, we are interested in the effect, on the dynamics of neutral diversity, of a physical barrier to dispersal. Through the measurement of diversity at different positions, we will try to estimate the "strength" of the barrier. The origin of this chapter is an experiment performed by N. Peeters and S. Vicente, in which they followed the dynamics of $K := 120$ neutral tags (given by DNA bar-coding) during the invasion of *Ralstonia solanacearum* bacteria in tomato plants. As we will see, the STAMP framework provided by [1] is ill-adapted to describe the structure of diversity after the invasion. An adaptation of the STAMP framework was proposed by [129]; we will go further and construct three additional models, and describe a method to compare these models to the real data.

Description of the experiment. The experiment of N. Peeters and S. Vicente is designed to follow the dynamics of neutral diversity during an invasion of bacteria in a tomato plant. Neutral diversity is artificially created by giving to each bacteria a selectively neutral tag. Their techniques allow them to use $K := 120$ tags, which are assumed to be evenly distributed in the original population.

Once these tags are given, bacteria are inoculated in the soil where the tomato plants grow. After a few days, bacteria have infected most plants: they first entered the root, and then entered the stem. Once a deterioration of the plants is detected (which means that a large population of bacteria has entered), the plants are dissected and the experimenters can measure the frequencies of the different tags in each compartment of the plants (root and stem). For each plant, we know:

- the time of sampling;
- the frequency of each tag in each compartment at the time of sampling;
- the total bacterial load in each compartment at the time of sampling.

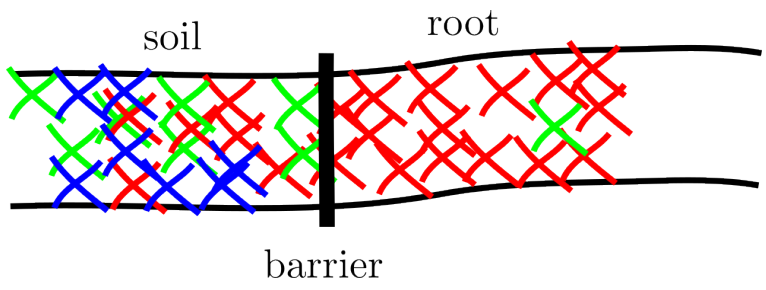

Figure 10.1: A representation of the barrier. Bacteria move from left to right. They are represented by coloured crosses, and their colours correspond to the tags that they carry. Before the barrier, there is a large diversity. After the barrier, diversity is lost, owing to the fact that only the descendants of the very first bacteria that crossed the barrier are present.

It is hypothesised that bacteria must cross two barriers during the infection of the plant: one barrier between the soil and the root and one barrier between the root and the stem. The questions are:

How do the barriers work? How strong are the barriers? What is the influence of the experimental conditions?

In this chapter, we will focus only on the barrier from the soil to the root. On the one hand, we would like to understand how the barrier works. We shall focus on the following models:

- The barrier works as a "one-step bottleneck": when sufficiently many bacteria are close to the barrier, all of these bacteria cross the barrier instantly. This is the model provided by the STAMP framework. The name "bottleneck" comes from the metaphor of a population going through a bottleneck and thereby reducing drastically its size;
- The barrier is crossed, at a constant rate, by a single bacteria;
- The population is described by a noisy monostable or bistable Fisher-KPP equation, and the barrier is a zone where the diffusion coefficient is very low.

On the other hand, we would like to know how strong the barrier is. It is expected, indeed, that for different experimental conditions (e.g. temperature), the barrier might be more or less strong. The hope is to be able to address these questions by looking at how neutral diversity is affected by the crossing of a barrier.

Layout. In Section 10.2, we shall describe several models for the barrier. Next, we shall provide a method to compare these models with one another, and apply this method to partial (not yet released) experimental data. Last, Section 10.3 is devoted to the derivation and the definition of two models. A Python code for simulation and comparison of the different models is available in a Jupyter notebook at DOI: 10.5281/zenodo.15083456.

10.2 Modelling a barrier

The goal of this section is to construct different models for the barrier and to provide a method to compare them. Last, we will say a few words about the application of this method to partial experimental data.

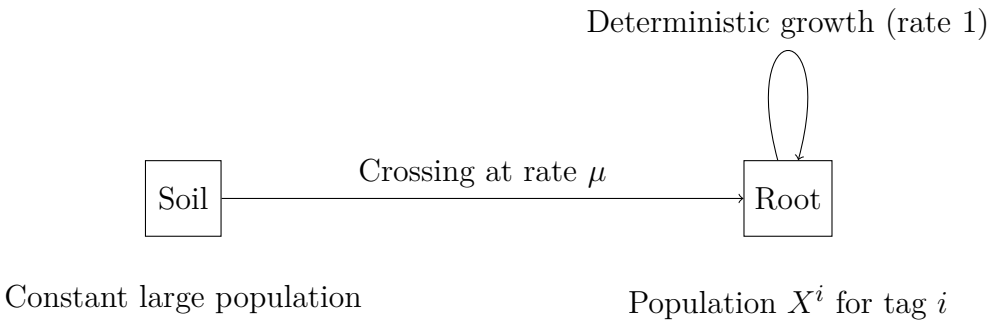

Figure 10.2: The "constant-rate crossing" model. A crossing involves exactly one bacteria. The experimenters observe the quantities X^i $(i = 1, \ldots, K)$, which correspond to the population size for tag i after the barrier.

10.2.1 Different models for the barrier

For short, the models that we will consider in this chapter are:

1. A "one-step bottleneck" model, parameterised by a quorum threshold $N_b \in \mathbb{N}$. The smaller N_b, the stronger the barrier.
2. A "constant-rate crossing" model, which is parameterised by a crossing rate μ. The smaller μ, the stronger the barrier.
3. Two models based on the genealogies taking place in travelling waves of noisy Fisher-KPP equations. The parameter will be the time t during which the genealogy runs. The higher t, the stronger the barrier.

The "one-step bottleneck" model $\mathcal{M}_{STAMP}(N_b)$.

First, we describe the "one-step bottleneck" model, which is the model used in the STAMP framework [1, 129]. We fix a threshold $N_b \in \mathbb{N}$ and we assume that when at least N_b bacteria are close to the barrier, all of these bacteria cross the barrier instantly. Therefore, the frequencies of the different tags in the root are the same as in a population of N_b individuals where each individual chooses uniformly one of the $K = 120$ tags. For this first model, therefore, the frequencies $(f_1, \ldots, f_K)$ (where f_i corresponds to the frequency of tag i) follow the multinomial law

$$(f_1, \ldots, f_K) \sim \frac{1}{N_b} \text{Multinomial}\left(N_b; \frac{1}{K}, \ldots, \frac{1}{K}\right).$$

To summarise, in the "one-step bottleneck" model, the founding population after the barrier consists of exactly N_b bacteria that cross the barrier simultaneously, selected from the initial population according to a multinomial distribution. This leads to a stronger barrier effect as N_b decreases.

The "constant-rate crossing" model $\mathcal{M}_{CR}(\mu, r)$.

The second model is a simple model where the environment is made up of two compartments: one compartment corresponds to the soil, and one compartment corresponds to the root. See Figure 10.2.

The population in the soil is assumed to be constant and very large. The population in the root is initially 0. At rate $\mu > 0$, a new bacteria migrates from the soil to the root. The new bacteria carries a tag, which is chosen uniformly between 1 and $K = 120$. Once it is in the root, a bacteria stays there and its offspring grows deterministically as e^t. The offspring of the bacteria carries the same tag as the bacteria.

In this simple model, there exists an explicit analytic estimator on the barrier parameter μ (however, we will *not* use this estimator for comparison of models, because it is specific to this model). After some computations, one can find that

$$\mu = K\mathbb{E}[X]\left(2\frac{Var(X)}{\mathbb{E}[X]} - 2\right)^{-1},$$

where X is the population, at the time of observation, of individuals carrying a given tag.

Let us now comment on some of the assumptions and consequences of the model. The model assumes that growth in the compartment of the root is deterministic and exponential. In particular, it assumes that no interactions between individuals occur. This is a strong assumption, which may not be realised in the experiment. On the other hand, independence implies that a single replicate of the experiment is in fact equivalent to $K = 120$ replicates of independent experiments. Therefore, on simulated data, the estimations of $\mathbb{E}[X]$ and $Var[X]$ – and then of μ – are very precise even with few replicates.

Two "coalescent-based" models $\mathcal{M}_K(v)$ and $\mathcal{M}_{BS}(v)$.

Last, we will focus on two barrier models based on *coalescents*. The starting point for the derivation of these coalescent models is the idea of the spreading of a population modelled by a noisy Fisher-KPP equation. Noise allows one to account for finite population effects, and, as a consequence of noise, the dynamics of neutral tags within the wave is affected. We emphasise that the effect of noise is distinct from the phenomena occurring in (deterministic) pulled and pushed waves presented in Subsection 1.1.1 of the general introduction.

A convenient way to understand this dynamics is the backward-in-time framework of coalescents, or genealogies. Namely, if we sample n individuals in the current population, how old is their most recent common ancestor? The answer to this question is crucial: if their ancestor is "recent", then these n individuals carry the same tag.

We shall focus on two standard models of genealogies. The first is the Kingman coalescent [141], which occurs in noisy bistable Fisher-KPP equations. The second is the Bolthausen-Sznitman coalescent [38], which is conjectured to occur in some noisy monostable Fisher-KPP equations. These notions will be precised in Section 10.3.

The time t during which the coalescents run – and, therefore, the available time for individuals to find common ancestors and lose diversity – is proportional to the time t spent to cross the barrier. Therefore, we will measure the strength of such a barrier by t; the higher t, the stronger the barrier.

10.2.2 Comparison of models

We now construct a method to *compare* the different models. We shall encode the data given by an experiment (simulated or not) in a frequency vector F:

$$F = (f_1, \dots, f_K), \qquad \text{with} \qquad f_i \geqslant 0, \qquad \sum_{i=1}^{K} f_i = 1.$$

Recall that K is the number of tags. In order to compare two given frequency vectors, we will use the *Hill numbers*.

Hill numbers.

The Hill number of order q for the frequency vector $F = (f_1, \dots, f_K)$ is given by:

$$H_q(F) := \left(\sum_{i=1}^{K} f_i^q \right)^{\frac{1}{1-q}}, \qquad q \neq 1,$$

and

$$H_1(F) := \lim_{q \to 1, q \neq 1} H_q(F) = \exp\left(-\sum_{i=1}^{K} f_i \ln(f_i) \right).$$

Some values of q correspond to standard diversity indices: $H_0(F)$ is the species richness (number of types); $H_1(F)$ is the exponential of the Shannon entropy; $H_2(F)$ is related to the inverse Simpson index. For all values of $q \geqslant 0$, the maximum diversity is reached when $f_i = 1/K$ for all $i \in \{1, \dots, K\}$; in this case, $H_q(F) = K$ for all $q \geqslant 0$. More generally, for each fixed q, a lower $H_q(F)$ corresponds to lower diversity, and the parameter q controls the relative emphasis placed on common tags (large q) or rare tags (small q).

Here, as proposed by [152], we describe the distribution of the frequencies through the full *diversity profile* $q \mapsto H_q(F)$ over a continuum of values of q. As observed in [152, Proposition A22], the diversity profile fully characterises the frequencies, as two frequency vectors cannot lead to the same profile unless they are equal up to a permutation.

Distance between models.

Observing the diversity profiles $q \mapsto H_q(F)$ allows us to directly visualise the effect of the barrier on the frequency vector. These profiles will also enable us to compare models and data. Consider two frequency vectors $F^1 = (f_1^1, \dots, f_K^1)$ and $F^2 = (f_1^2, \dots, f_K^2)$. We define the distance between F^1 and F^2 as the average relative difference between the diversity profiles of F^1 and F^2 over a range of values of q:

$$d(F_1, F_2) := \int_Q \frac{|H_q(F_1) - H_q(F_2)|}{H_q(F_1) + H_q(F_2)} \, \mathrm{d}q, \tag{10.1}$$

where Q is a representative set of values of q. Here, we took $Q = [0, 4]$. This choice of the set Q seems quite arbitrary; it stems from the visual study of the functions $q \mapsto H_q$, which usually show most variations for $q \in [0, 4]$.

Now, consider a stochastic model $\mathcal{M}(\theta)$, parameterised by $\theta \in \mathbb{R}$, and describing frequencies F after the barrier, starting from known initial frequencies F_0 (before the barrier).

Here, we assume that $F_0 = \left(\frac{1}{K}, \ldots, \frac{1}{K}\right)$. Given observed experimental frequencies $\hat{F}$, for each fixed θ, we define the performance $P[\mathcal{M}(\theta)]$ of $\mathcal{M}(\theta)$ as the 0.05 quantile of the distribution of $d(F, \hat{F})$ over replicate simulations. Then, the performance $P[\mathcal{M}]$ of the model $\mathcal{M}$ is obtained by choosing the parameter θ that leads to the smallest value of $P[\mathcal{M}(\theta)]$. Said otherwise, we let $P[\mathcal{M}(\theta)]$ be the 0.05 quantile of

$$\Big\{ d(F_i[\mathcal{M}(\theta)], \hat{F}),\ i = 1, \ldots, N \Big\}$$

where $F_i[\mathcal{M}(\theta)] \in [0,1]^K$, $i = 1, \ldots, N$, are the final frequencies for N replicate simulations simulated with model $\mathcal{M}$ and parameter θ. We then let

$$P[\mathcal{M}] := \min_{\theta} P[\mathcal{M}(\theta)], \qquad \theta[\mathcal{M}] := \operatorname*{argmin}_{\theta} P[\mathcal{M}(\theta)],$$

be, respectively, the performance of the model $\mathcal{M}$ and the estimated parameter for the model $\mathcal{M}$.

If we have several experimental frequency vectors $\hat{F}_1$, ..., $\hat{F}_N$, observed under the same experimental conditions, there are at least two relevant possibilities to estimate the model performance and the best parameter:

1. Consider independently the vectors $\hat{F}_1$, ..., $\hat{F}_N$. For $i = 1, \ldots, N$, let θ_i be the parameter that leads to the smallest value of $P[\mathcal{M}(\theta_i); F_i]$. The model performance is then the average of the $P[\mathcal{M}(\theta_i); F_i]$, $i = 1, \ldots, N$, and the output parameter $\widehat{\theta}$ is the average of the θ_i.
2. Consider jointly the vectors $\hat{F}_1$, ..., $\hat{F}_N$. The output parameter $\widehat{\theta}$ is the parameter that leads to the smallest average value of $P[\mathcal{M}(\widehat{\theta}); F_i]$ over $i = 1, \ldots, N$. The model performance is the average of $P[\mathcal{M}(\theta_i); F_i]$.

In Subsection 10.2.3, we will present results that used the first method. However, if the parameter is assumed to be constant over all replicates, the second method should be better adapted. See the associated Jupyter notebook (where we worked on the second method).

10.2.3 First results

Simulated data.

First, we tested our method on simulated data. Empirically, the procedure described in Subsection 10.2.2 worked very well, even though it induced arbitrary choices for the definition of the distance and for the choice of the quantile. For data generated by each of the four models that we defined above, the algorithm was able to find from which model these data were simulated, and to give a fairly good approximation of the parameter. See Table 10.1 and the associated Jupyter notebook.

Experimental data.

Second, we applied the same method to the data provided by N. Peeters and S. Vicente. Here, we will consider two different experimental conditions: in the first, the root of the plants are intact, and the barrier is expected to be stronger; in the second, the root of the plants are cut, and the barrier is expected to be weaker (as it is physically easier for bacteria to go from the soil to the root). For the sake of example, we drew on Figure 10.3 the frequency

Model (parameter)	$\mathcal{M}_{STAMP}$	$\mathcal{M}_{CR}$	$\mathcal{M}_{K}$	$\mathcal{M}_{BS}$
$\mathcal{M}_{STAMP}(N_b = 150)$	**154 (0.013)**	218 (0.101)	0.012 (0.585)	0.061 (0.345)
$\mathcal{M}_{CR}(\mu = 10)$	26.5 (0.393)	**10.1 (0.107)**	0.045 (0.232)	0.434 (0.413)
$\mathcal{M}_{K}(t = 0.1)$	12.4 (0.300)	4.65 (0.317)	**0.112 (0.095)**	0.745 (0.422)
$\mathcal{M}_{BS}(t = 0.2)$	27.0 (0.989)	12.7 (0.686)	0.140 (0.763)	**0.247 (0.211)**

Table 10.1: Estimation of the parameter of each model, and associated performances in parentheses.
(First column) Models and parameters that were used for simulations and that we tried to recognise. **(First line)** Models against which we compared the output of the simulations, and for which we estimated a parameter and the performance.
For example, the box "218 (0.101)" means that when we tried to fit a "constant-rate crossing" model with the output of a "one-step bottleneck" model with parameter $N_b = 150$, we estimated $\widehat{\theta} = \widehat{\mu} = 218$ and the performance was 0.101.
The nature and scale of the parameter depend on the model.

vector corresponding to one of the replicates for the "Intact" experiment, and some frequency vectors simulated by each model. For each model, we chose a simulated replicate according to the method that we describe now.

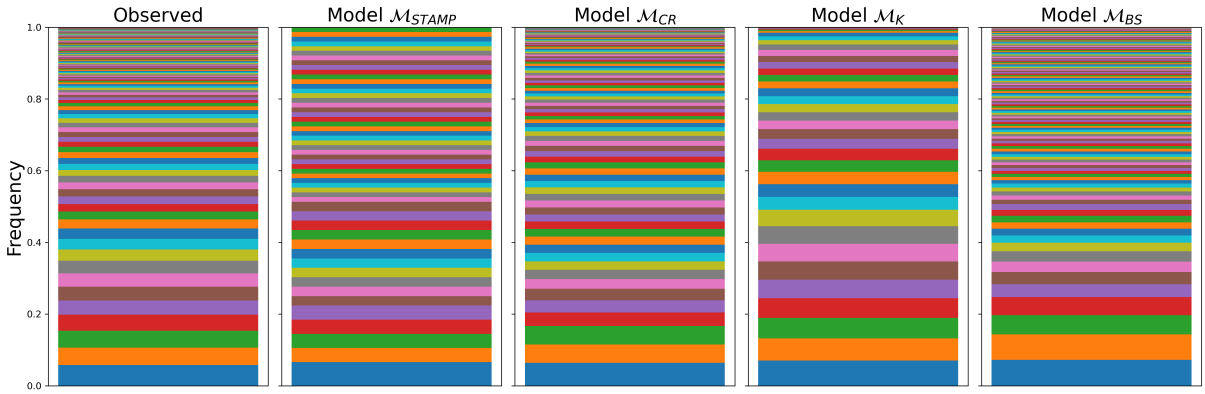

Figure 10.3: (Leftmost column) Frequencies of the different tags corresponding to one of the replicates for the "Intact" experiment; **(Other columns)** Frequencies of the different tags corresponding to each model, for the parameter estimate with the replicate represented in the first column.

For each model $\mathcal{M}$, for each of the 24 replicates of the experiment, we computed independently a best parameter $\theta_j[\mathcal{M}]$, $j = 1, \ldots, 24$, according to the method described in Subsection 10.2.2. Next, we ran 100 simulations of the model $\mathcal{M}$ with the parameter $\theta_j[\mathcal{M}]$, and computed the Hill curves $H^{i,j}[\mathcal{M}]$, $i = 1, \ldots, 100$, $j = 1, \ldots, 24$, resulting from these simulations. On Figure 10.4, we drew, on the first column, the Hill curves $\widehat{H^j}$, $j = 1, \ldots, 24$, for each replicate of the experiment; on the other columns, we drew, for each model $\mathcal{M}$, for each replicate $j = 1, \ldots, 24$, the simulated Hill curve $H^{i,j}[\mathcal{M}]$, $i = 1, \ldots, 100$, that was closest to the Hill curve $\widehat{H^j}$ of the replicate.

On the one hand, Figure 10.4 suggests that the "one-step bottleneck" model and the Kingman coalescent are unable to reproduce the structure of diversity observed in the experiments. The first point is very interesting, as the "one-step bottleneck" model is the only one that was considered so far in the STAMP literature.

On the other hand, Figure 10.4 suggests that the "constant-rate crossing" model and the Bolthausen-Sznitman coalescent are able to reproduce quite well the structure of diversity observed in the experiments. In fact, if we look at the numerical distances between the Hill curves, we observe that the Bolthausen-Sznitman coalescent behaves much better than the "constant-rate crossing" model. Further, we show in the notebook that for a fixed parameter, the Hill curves obtained with "constant-rate crossing" are very similar to one another, whereas the Hill curves obtained with the Bolthausen-Sznitman coalescent show a large variety of behaviours. The latter is more similar to the Hill curves obtained thanks to the experimental data. Therefore, if the parameter is assumed to be constant over all replicates, the Bolthausen-Sznitman coalescent is better able to reproduce the observations.

Last, we mention that all models are able to detect that for the "Intact" condition, the Hill curves are smaller than for the "Cut" condition, as is apparent on the Hill curves obtained from the experiment. This confirms the intuition that the barrier is stronger when the root is intact.

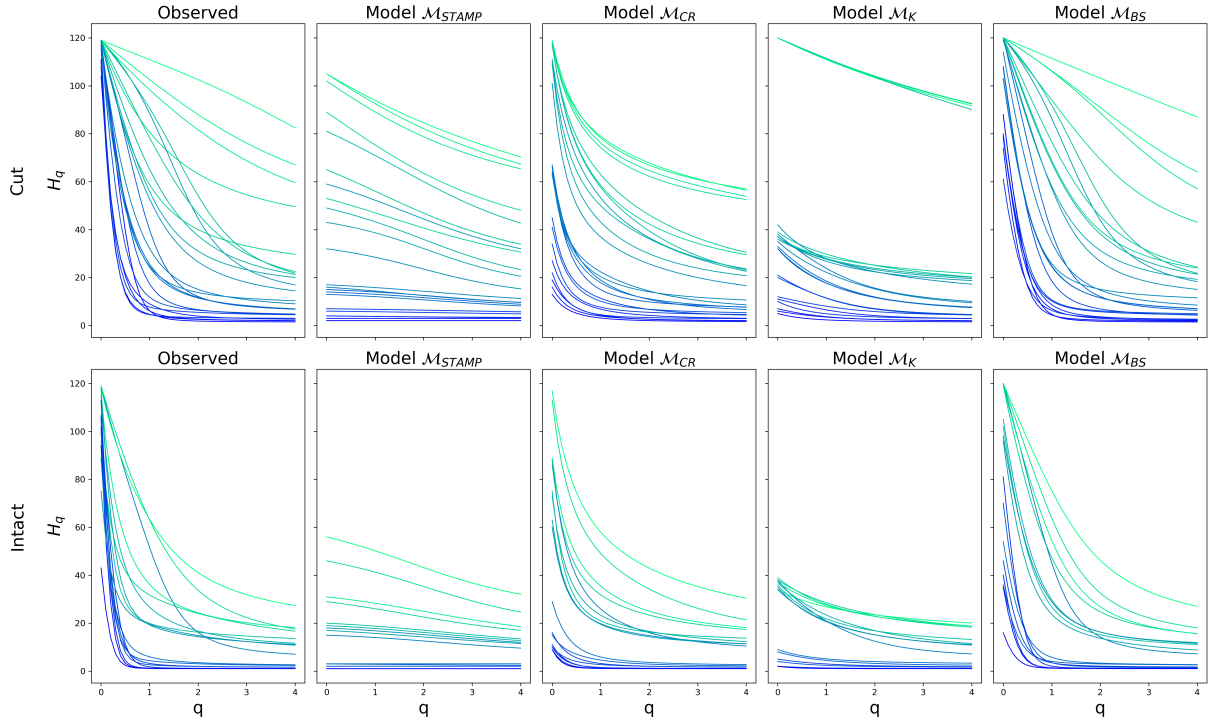

Figure 10.4: **(Leftmost column)** Hill curves for the experimental data; **(Other columns)** Hill curves for the simulated data with the estimated parameter.
(Upper line) The root is cut, leading to a weak barrier; **(Lower line)** The root is intact, leading to a strong barrier.

10.3 Definition and derivation of the two "coalescent-based" models

Let us now define and derive the two models based on coalescents. The motivation for these models comes from the dynamics of neutral fractions (as defined in [101, 202]) in noisy

Fisher-KPP equations. Before defining the two coalescents, let us see, heuristically, how they arise.

The noisy Fisher-KPP equation.

The starting point to define the models is the derivation of the Fisher-KPP equations in Subsection 1.2.1 of the general introduction. There, the Fisher-KPP equation is obtained by making a parameter N, corresponding to population size, go to infinity. In the finite population with size N, it is possible to sample $n \geqslant 2$ individuals and to see, backward in time, what their genealogies are, i.e. who their common ancestors are. If these individuals are sampled at a fixed time $T \gg 1$ large enough, with high probability, they are the descendants of a single individual at time 0, and therefore the full knowledge of their genealogy is contained in the interval $[0,T]$.

However, as $N \to +\infty$, the probability that $n \geqslant 2$ individuals sampled at time T share a common ancestor goes to 0 (as there are more and more potential ancestors for each individual). In the branching Brownian motion representation, which corresponds to a deterministic equation, this is translated through the fact that particles split (to account for potential ancestors) but never merge again. Thus, two different particles never find a common ancestor. This can also be understood by using neutral fractions: in a deterministic Fisher-KPP equation, if the initial population is structured into different tags located at the same position, then nothing happens: all tags remain equivalent as time goes by.

In our study, we need to ensure that a sample of n individuals can find a common ancestor in finite time. This can be done by a change of time scales: let us accelerate time and replace T by NT, where N is a scaling parameter accounting for the total population size. With this acceleration of time, when the local growth rate gives rise to a reaction term equal to $f(u) = u(1-u)$, the empirical measure converges to the solution of a noisy Fisher-KPP equation, see [78, Theorem 1]:

$$\mathrm{d}u(t,x) = \left[\frac{1}{2}\partial_{xx}u(t,x) + f(u(t,x))\right]\mathrm{d}t + \sqrt{u(t,x)(1-u(t,x))}\,\mathrm{d}W(t), \tag{10.2}$$

where W is a cylindrical Wiener process. With this change of scales, if we go back long enough in time, we will find common ancestors to current individuals.

In fact, when $f(u) = u(1-u)(u-\rho)$ for some $0 < \rho < 1/2$, the "genealogy" of these individuals converges, up to another rescaling involving acceleration of time and reduction of noise, as $N \to +\infty$, to what is known as the *Kingman coalescent* [84]. When $f(u) = u(1-u)$, the "genealogy" of these individuals is conjectured to converge, up to another rescaling, to the *Bolthausen-Sznitman coalescent* [34, 55]. See also [36] for nonrigorous arguments suggesting that some monostable pushed reaction terms (termed "fully-pushed") also lead to the Kingman coalescent, and some monostable pushed reaction terms (termed "semi-pushed") can lead to *Beta-coalescents*. Regarding fully-pushed reaction terms, see also [96] for another heuristic of why such reaction terms should lead to the Kingman coalescent.

Before we define the Kingman coalescent and Bolthausen-Sznitman coalescent, let us go back to our problem of modelling a barrier and see how it is related to these coalescents. We think of the barrier as an area where the population must remain very low with respect to the outside population. In the experiment, n individuals are sampled shortly after the population has crossed the barrier. *What are their genealogies?* No common ancestor can be found outside the barrier, since the population is very large in these areas. However, inside

the barrier, common ancestors can be found, so genealogies can merge.

The connection to our problem is that if two individuals located after the barrier are sampled, then they will necessarily carry the same tag if they have a common ancestor that lived after the tags were attributed. If no such common ancestor exists, the tags of the two sampled individuals are independent and uniformly chosen among $1,\dots,K$. Similarly, if we know the genealogies of a sample of $n \geqslant 3$ individuals, then we perfectly know the joint law of their tags. Therefore, understanding how genealogies go inside the barrier is sufficient to understand the frequencies of the different tags that we observe at the present time after the barrier. As explained above, the genealogies are described by the Kingman coalescent (for bistable reaction) and by the Bolthausen-Sznitman coalescent (for Fisher-KPP reaction). The time t during which these genealogies run can reasonably be approximated by the time spent by the population to cross the barrier; the larger t, the stronger the barrier.

Let us now define the Kingman and the Bolthausen-Sznitman coalescents.

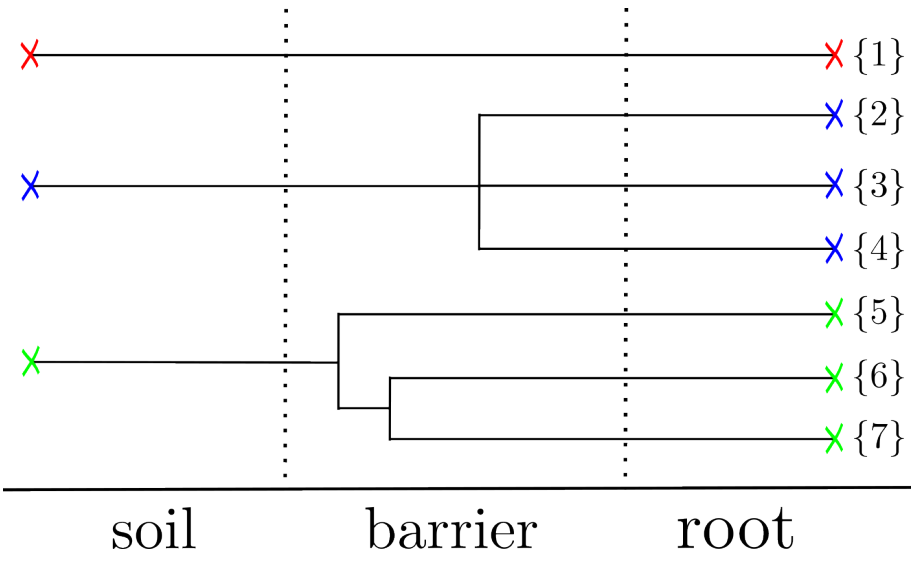

Figure 10.5: Common ancestors can only be found inside the barrier, where the population is not macroscopic.
The crosses to the right are individuals sampled at the present time, after the barrier. The lines issuing from these crosses are the genealogies of these individuals. Outside the barrier, no common ancestor exists, so the lines are independent. On this figure, the seven current individuals are in fact descendants of only three individuals, which are represented by the crosses to the left of the barrier (in the formalism of coalescents, they will be denoted by $\{1\}$, $\{2,3,4\}$, and $\{5,6,7\}$). The descendants carry the tags (colours) of their ancestors.

The Kingman coalescent.

The Kingman coalescent is an object that follows the "genealogy" of current individuals. Let us describe the n-coalescent, which is the restriction of the Kingman coalescent to $\{1,\dots,n\}$. Let n current individuals be labelled by $1,\dots,n$. The n-Kingman coalescent is a process going backward in time, which, at time t, contains the ancestors of the n current individuals living at time t *before* the present time. More specifically:

1. The initial state, denoted by Π_0, is the set of blocks $\{1\},\dots,\{n\}$. Each block corresponds to a single individual living at the present time;

2. Each $t > 0$ corresponds to a time *in the past*. Then Π_t is made of blocks of families of individuals living at the present time. For example, if $\Pi_t = \{1,2\},\{3\},\{4\}$, this means that individuals 1 and 2 have a common ancestor that lived between $-t$ and the present time (thus are close cousin); and 3 and 4 share no common ancestor with $1,2$ that lived between $-t$ and 0;
3. The evolution of Π_t is as follows: for each given pair of block, this pair merges at rate 1. For example, at rate 1, $\{1,2\}$ and $\{3\}$ will try to merge to form $\{1,2,3\}$. A merger means that the two families have found their common ancestor.

Figure 10.5 does not represent a Kingman coalescent, because there is a merger involving three blocks. However, the restriction of the process represented on Figure 10.5 to the individuals $\{1,5,6,7\}$ could be generated by a Kingman coalescent.

The Bolthausen-Sznitman coalescent.

The Bolthausen-Sznitman coalescent, similarly to the Kingman coalescent, is a process that goes backward in time and that, at time t, contains the families living at time t *before* the present time. However, the mechanism for the merging of blocks is different from that of the Kingman coalescent. While in the Kingman coalescent, only two blocks can merge at the same time, the Bolthausen-Sznitman coalescent allows *multiple mergers*. For example, in Figure 10.5, the structure of the genealogy inside the barrier could be generated by a Bolthausen-Sznitman coalescent.

There are several constructions of the Bolthausen-Sznitman coalescent. It can be seen as the Λ-coalescent with $\Lambda(\mathrm{d}x) = \mathrm{d}x$ [35]. However, we shall define it in another way, which seems apter to simulations, using the construction of [112] (see also the description in [35]).

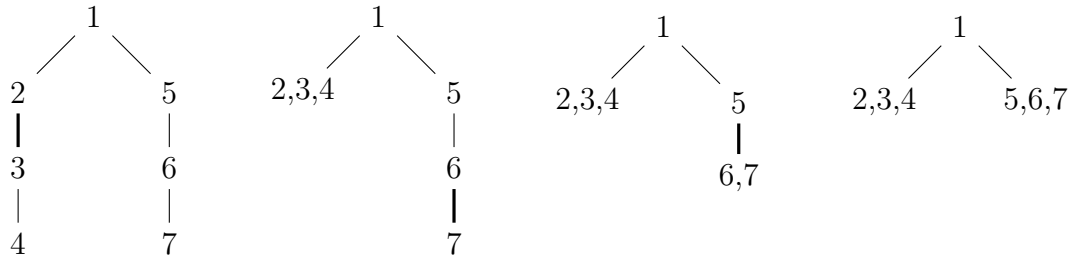

Figure 10.6: The construction of the Bolthausen-Sznitman coalescent of [112]. Each vertex corresponds to an individual. The initial tree is a random tree where the individual $n+1$ chooses its parent uniformly at random among $1,\dots,n$. At each step, an edge (drawn thick on the picture) is "lifted".
The steps represented here correspond to the mergers in Figure 10.5.

First, construct a tree recursively in the following way. The root is indexed by 1. Once n vertices are positioned on the tree, the $(n+1)^{th}$ vertex chooses its parent uniformly at random among the n vertices of the tree. Each vertex of the tree corresponds to a block; initially, all blocks contain only a singleton.

The merging procedure is as follows. Each edge of the tree carries an exponential clock with rate 1. If the clock of an edge rings, the edge is "lifted"; namely, all descendants of the edge are absorbed by the parent of the edge. See Figure 10.6.

Appendix

Appendix A

Proofs of some results stated in the introduction

The branching Brownian motion representation for the equation with phenotype.

Proof of Theorem 1.2.2. The proof follows the original argument of McKean [166]. The assumptions are: $\Theta = \mathbb{R}^P$, $r \in \mathcal{C}(\mathbb{R}^P)$ and $0 \leqslant r \leqslant 1$. It is proved in Chapter 5 that, under these assumptions, there exists exactly one solution of the Cauchy problem

$$\partial_t u(t,x,\theta) = \frac{1}{2}\Delta_x u + \frac{1}{2}\Delta_\theta u + r(\theta)u - \rho u, \qquad u(0,x,\theta) = u_0(x,\theta), \tag{A.1}$$

with

$$\rho(t,x) := \int_{\mathbb{R}^P} u(t,x,\theta)\,\mathrm{d}\theta.$$

We let $\kappa_t(x) \in \mathbb{R}^P \cup \{\emptyset\}$ be defined by Definition 1.2.1, and we let $((X_s^i)_{1\leqslant i\leqslant N_s})_{0\leqslant s\leqslant t}$ be the branching Brownian motion used to construct $\kappa_t(x)$. Recall that N_s is the number of particles of the branching Brownian motion at time s.

By uniqueness, it is sufficient for our purpose to prove that the law of the random variable $\kappa_t(x)$ restricted to $\mathbb{R}^P$ has a density $u(t,x,\cdot)$, and that u is sufficiently regular and satisfies (A.1). For $t = 0$, we have $N_0 = 1$, and $\kappa_0(x)$ coincides with ξ_0^1, which is sampled according to (1.13) (with $u_0(X_0^1,\cdot)$ instead of $v_0(\cdot)$). Thus the law of $\kappa_0(x)$ has a density u_0. Therefore, the initial condition of (A.1) is satisfied.

Next, we fix $t > 0$. We first prove that for $t > 0$, the density $u(t,\cdot,\cdot)$ exists and is regular.

Step 1. Density of $\kappa_t(x)$ and regularity. First, for $A \subset \mathbb{R}^P$ such that the Lebesgue measure of A is $Leb(A) = 0$, we have:

$$\mathbb{P}(\kappa_t(x) \in A) \leqslant \sum_{n=1}^{+\infty} \left(\mathbb{P}(N_t = n) \sum_{i=1}^{n} \mathbb{P}(\xi_t^i \in A) \right) = 0.$$

Therefore, for all $t > 0$, $x \in \mathbb{R}$, the random variable $\kappa_t(x)$ has a density $u(t,x,\cdot)$ with respect to Lebesgue measure. Now, let us prove that $u(t,\cdot,\cdot)$ is of class $\mathcal{C}^\infty$ on $\mathbb{R} \times \mathbb{R}^P$. Let $\tau_1 > 0$ be the random time of the first branching of X (thus, τ_1 is an exponential variable with

parameter 1). We have, for $x \in \mathbb{R}$ and $\theta \in \mathbb{R}^P$,

$$\begin{aligned} u(t,x,\theta) &= \int_0^t \mathbb{P}\left(\tau_1 \in \mathrm{d}s\right) \int_{\mathbb{R}} \int_{\mathbb{R}^P} u(t-s, x-y, \theta-\sigma) \mathbb{P}\left(\xi^1_{t-s} - \xi^1_t \in \mathrm{d}\sigma\right) \mathbb{P}\left(X^1_{t-s} - X^1_t \in \mathrm{d}y\right) \\ &\quad + \mathbb{P}\left(\tau_1 > s\right) \left(\Gamma_t * u_0\right)(x,\theta) \\ &= \int_0^t e^{-s} (\Gamma_s * u(t-s,\cdot,\cdot))(x,\theta)\, \mathrm{d}s + \mathbb{P}\left(\tau_1 > s\right) \left(\Gamma_t * u_0\right)(x,\theta), \end{aligned}$$

where $\Gamma_s(y,\sigma) := \frac{1}{\sqrt{2\pi s^2}} e^{-(y^2+\|\sigma\|^2)/2s}$, and

$$(\Gamma_s * U)(x,\theta) := \int_{\mathbb{R}} \int_{\mathbb{R}^P} \Gamma_s(y,\sigma) U(x-y, \theta-\sigma)\, \mathrm{d}\sigma\, \mathrm{d}y.$$

For each $s \in (0,t)$, the function $(x,\theta) \mapsto (\Gamma_s * u(t-s,\cdot,\cdot))(x,\theta)$ is of class $\mathcal{C}^\infty$. Therefore, for all $t > 0$, the density $u(t,\cdot,\cdot)$ is of class $\mathcal{C}^\infty(\mathbb{R})$.

In particular, $\Delta_x u$ and $\Delta_\theta u$ exist. In Step 2, we will prove that $\partial_t u$ exists and prove that (A.1) is satisfied.

Step 2. A weak equation satisfied by the law of $\kappa_t(x)$. Let $0 < \tau_1 < \tau_2$ be the random times of, respectively, the first and second branching of $((X^i_s)_{1 \leqslant i \leqslant N_s})_{0 \leqslant s \leqslant t}$. For $0 \leqslant h < \tau_1$, we have $N_s = 1$ and for $\tau_1 \leqslant h < \tau_2$, we have $N_s = 2$. Two types $\xi, \xi' \in \mathbb{R}^P \cup \{\emptyset\}$ being given, we let $G[\xi,\xi'] \in \mathbb{R}^P \cup \{\emptyset\}$ be a random variable giving the resulting type according to the rules (1.14)–(1.16).

For $h \in (0,t)$ and $f \in \mathcal{C}^2(\mathbb{R}^P \cup \{\emptyset\})$ with $f(\emptyset) = 0$, we have:

$$\begin{aligned} \mathbb{E}\left[f(\kappa_t(x))\right] - \mathbb{E}\left[f(\kappa_{t-h}(x))\right] &= \mathbb{E}\left[f\left(\kappa_t(x)\right) \mathbb{1}_{\{\tau_1 > h\}}\right] - \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] \\ &\quad - \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 < h\}}\right] \\ &\quad + \mathbb{E}\left[f\left(\kappa_t(x)\right) \mathbb{1}_{\{\tau_1 \leqslant h < \tau_2\}}\right] + O\left(h^2\right). \end{aligned} \tag{A.2}$$

Let us compute this expression term by term. On the one hand, we have:

$$\begin{aligned} &\mathbb{E}\left[f(\kappa_t(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] - \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] \\ &\quad = \mathbb{E}\left[f(\kappa_t(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] - \mathbb{E}\left[f(\kappa_{t-h}(X^1_h)) \mathbb{1}_{\{\tau_1 > h\}}\right] \\ &\qquad + \mathbb{E}\left[f(\kappa_{t-h}(X^1_h)) \mathbb{1}_{\{\tau_1 > h\}}\right] - \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 > h\}}\right]. \end{aligned}$$

The process $(X^1_h)_{h \geqslant 0}$ is a Brownian motion. Therefore,

$$\mathbb{E}\left[f(\kappa_{t-h}(X^1_h)) \mathbb{1}_{\{\tau_1 > h\}}\right] - \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] = \frac{h}{2} \Delta_x \mathbb{E}\left[f(\kappa_{t-h}(x)) \mathbb{1}_{\{\tau_1 > h\}}\right] + O(h^2).$$

(The existence of the right-hand side is ensured by the smoothness of the density u.) Moreover, conditionally on $\{\tau_1 > h\}$, we can couple the variables $\kappa_{t-u}(X^1_u)$, for all $u \in [0,h)$, in such a way that the process

$$\left(\kappa_{t-u}(X^1_u) - \kappa_t(x)\right)_{0 \leqslant u \leqslant h}$$

is a Brownian motion. Therefore,

$$\mathbb{E}\left[f(\kappa_t(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]-\mathbb{E}\left[f(\kappa_{t-h}(X_h^1))\,\mathbb{1}_{\{\tau_1>h\}}\right]=h\mathbb{E}\left[\frac{1}{2}\Delta f(\kappa_{t-h}(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]+O(h^2).$$

Summing up, we can compute the first line of the right-hand side of (A.2):

$$\begin{aligned}
&\mathbb{E}\left[f(\kappa_t(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]-\mathbb{E}\left[f(\kappa_{t-h}(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]\\
&\quad=h\mathbb{E}\left[\frac{1}{2}\Delta f(\kappa_{t-h}(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]+\frac{h}{2}\Delta_x\mathbb{E}\left[f(\kappa_{t-h}(x))\,\mathbb{1}_{\{\tau_1>h\}}\right]+O(h^2)\\
&\quad=\mathbb{E}\left[\frac{h}{2}\Delta f(\kappa_t(x))\right]+\frac{h}{2}\Delta_x\mathbb{E}\left[f(\kappa_t(x))\right]+O(h^2).
\end{aligned}$$

On the other hand, let $\kappa_t'(x)$ be a random variable with the same law as $\kappa_t(x)$ and independent. We have:

$$\mathbb{E}\left[f\left(\kappa_t(x)\right)\mathbb{1}_{\{\tau_1\leqslant h<\tau_2\}}\right]=h\mathbb{E}\left[f\left(G\left[\kappa_t(x),\kappa_t'(x)\right]\right)\right]+O(h^2).$$

Applying the rules (1.14)–(1.16), we have (recall that $f(\emptyset)=0$):

$$\begin{aligned}
\mathbb{E}\left[f\left(G\left[\kappa_t(x),\kappa_t'(x)\right]\right)\right]&=\frac{1}{2}\mathbb{E}\left[\left(r(\kappa_t(x))f(\kappa_t(x))+r(\kappa_t'(x))f(\kappa_t'(x))\right)\mathbb{1}_{\kappa_t(x),\kappa_t'(x)\neq\emptyset}\right]\\
&\quad+\frac{1}{2}\mathbb{E}\left[\left(1+r(\kappa_t(x))f(\kappa_t(x))\right)\mathbb{1}_{\kappa_t(x)\neq\emptyset,\kappa_t'(x)=\emptyset}\right]\\
&\quad+\frac{1}{2}\mathbb{E}\left[\left(1+r(\kappa_t'(x))f(\kappa_t'(x))\right)\mathbb{1}_{\kappa_t(x)=\emptyset,\kappa_t'(x)\neq\emptyset}\right].
\end{aligned}$$

Since κ and κ' are independent and have the same law, we obtain:

$$\begin{aligned}
\mathbb{E}\left[f\left(G\left[\kappa_t(x),\kappa_t'(x)\right]\right)\right]&=\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)\neq\emptyset)\\
&\quad+\mathbb{E}\left[(1+r(\kappa_t(x))f(\kappa_t(x)))\right]\mathbb{P}(\kappa_t(x)=\emptyset).
\end{aligned}$$

Last, we have

$$\mathbb{E}\left[f(\kappa_{t-h}(x))\,\mathbb{1}_{\{\tau_1<h\}}\right]=h\mathbb{E}\left[f(\kappa_t(x))\right]+O(h^2).$$

All in all, we obtain:

$$\begin{aligned}
&\mathbb{E}\left[f(\kappa_t(x))\right]-\mathbb{E}\left[f(\kappa_{t-h}(x))\right]\\
&\quad=\mathbb{E}\left[\frac{h}{2}\Delta f(\kappa_t(x))\right]+\frac{h}{2}\Delta_x\mathbb{E}\left[f(\kappa_t(x))\right]-h\mathbb{E}\left[f(\kappa_t(x))\right]\\
&\qquad+h\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)\neq\emptyset)+h\mathbb{E}\left[(1+r(\kappa_t(x))f(\kappa_t(x)))\right]\mathbb{P}(\kappa_t(x)=\emptyset)+O(h^2).
\end{aligned}$$

Dividing by h and taking $h\to 0$, we obtain that $\partial_t\mathbb{E}\left[f(\kappa_t(x))\right]$ exists and:

$$\begin{aligned}
\partial_t\mathbb{E}\left[f(\kappa_t(x))\right]&=\mathbb{E}\left[\frac{1}{2}\Delta f(\kappa_t(x))\right]+\frac{1}{2}\Delta_x\mathbb{E}\left[f(\kappa_t(x))\right]-\mathbb{E}\left[f(\kappa_t(x))\right]\\
&\quad+\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)\neq\emptyset)\\
&\quad+\mathbb{E}\left[\left(1+r(\kappa_t(x))\right)f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)=\emptyset).
\end{aligned}$$

We point out that

$$\begin{aligned}&-\mathbb{E}\left[f(\kappa_t(x))\right]+\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)\neq\emptyset)+\mathbb{E}\left[(1+r(\kappa_t(x)))\,f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)=\emptyset)\\&\quad=-\mathbb{E}\left[(1-r(\kappa_t(x)))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)\neq\emptyset)+\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}(\kappa_t(x)=\emptyset).\end{aligned}$$

Therefore, the above display becomes

$$\begin{aligned}\partial_t\mathbb{E}\left[f(\kappa_t(x))\right]=\mathbb{E}\left[\frac{1}{2}\Delta f(\kappa_t(x))\right]+\frac{1}{2}\Delta_x\mathbb{E}\left[f(\kappa_t(x))\right]\\+\mathbb{E}\left[r(\kappa_t(x))f(\kappa_t(x))\right]\mathbb{P}\left(\kappa_t(x)=\emptyset\right)-\mathbb{E}\left[(1-r(\kappa_t(x)))\,f(\kappa_t(x))\right]\mathbb{P}\left(\kappa_t(x)\neq\emptyset\right).\end{aligned}$$

Step 3. Conclusion. Translating the last expression by using the density u defined in Step 1, we get, for all $t>0$ and $x\in\mathbb{R}$,

$$\begin{aligned}\partial_t\int f(\theta)u(t,x,\theta)\,\mathrm{d}\theta=\frac{1}{2}\Delta_x\int f(\theta)u(t,x,\theta)\,\mathrm{d}\theta+\frac{1}{2}\int(\Delta_\theta f(\theta))u(t,x,\theta)\,\mathrm{d}\theta\\+\left(\int r(\theta)f(\theta)u(t,x,\theta)\,\mathrm{d}\theta\right)\left(1-\int u(t,x,\theta)\,\mathrm{d}\theta\right)\\-\left(\int(1-r(\theta))f(\theta)u(t,x,\theta)\,\mathrm{d}\theta\right)\int u(t,x,\theta)\,\mathrm{d}\theta,\end{aligned}$$

where the integrals are taken on $\mathbb{R}^P$. Define $\rho(t,x):=\int u(t,x,\theta)\,\mathrm{d}\theta$. We rearrange the terms and integrate by parts. We obtain:

$$\begin{aligned}\partial_t\int fu&=\int f\left[\frac{1}{2}\Delta_x u+\frac{1}{2}\Delta_\theta u+ru(1-\rho)-(1-r)u\rho\right]\\&=\int f\left[\frac{1}{2}\Delta_x u+\frac{1}{2}\Delta_\theta u+ru-\rho u\right].\end{aligned}$$

As this equality holds for all $f\in\mathcal{C}^2(\mathbb{R}^P\cup\{\emptyset\})$ with $f(\emptyset)=0$, we conclude that u is a classical solution of (A.1).

□

Proof of the Feynman-Kac formula.

Let $u(t,x)$ solve the linear equation

$$\partial_t u=\frac{1}{2}\Delta u+r(x)u.$$

Let $(B_t)_{t\geqslant 0}$ be a Brownian motion. Fix $t>0$ and, for $s\in[0,t]$, let

$$M_s:=u(t-s,B_s)\exp\left(\int_0^s r(B_u)\,\mathrm{d}u\right).$$

We have:

$$\begin{aligned}\mathrm{d}M_s&=\mathrm{d}(u(t-s,B_s))\exp\left(\int_0^s r(B_u)\,\mathrm{d}u\right)+u(t-s,B_s)\,\mathrm{d}\left(\exp\left(\int_0^s r(B_u)\,\mathrm{d}u\right)\right)\\&=\mathrm{d}(u(t-s,B_s))\exp\left(\int_0^s r(B_u)\,\mathrm{d}u\right)+r(B_s)u(t-s,B_s)\exp\left(\int_0^s r(B_u)\,\mathrm{d}u\right)\mathrm{d}s.\end{aligned}$$

Moreover, applying Itô's formula, we have:

$$\begin{aligned}\mathrm{d}(u(t-s,B_s)) &= -\partial_t u(t-s,B_s) + \partial_x u(t-s,B_s)\,\mathrm{d}B_s + \frac{1}{2}\partial_{xx} u(t-s,B_s)\,\mathrm{d}s \\ &= \partial_x u(t-s,B_s)\,\mathrm{d}B_s - r(B_s)u(t-s,B_s).\end{aligned}$$

Summing up, we get:

$$\mathrm{d}M_s = \partial_x u(t-s,B_s)\,\mathrm{d}B_s,$$

so $(M_s)_{0\leqslant s\leqslant t}$ is a local martingale. Further, $(M_s)_{0\leqslant s\leqslant t}$ is bounded. Therefore, $(M_s)_{0\leqslant s\leqslant t}$ is a martingale, so $\mathbb{E}[M_0] = \mathbb{E}[M_t]$. This means:

$$u(t,x) = \mathbb{E}_x\left[u_0(t,x)\exp\left(\int_0^t r(B_u)\,\mathrm{d}u\right)\right].$$

This is the Feynman-Kac formula stated in Section 1.2 of the introduction.

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