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Integro-differential models from ecology and evolutionary biology

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Contents

General presentation

In this dissertation, I will present a large part of the research I did after my PhD on elliptic and parabolic integro-differential equations and Hamilton-Jacobi equations coming from ecology and evolutionary biology. This report is composed of four chapters. The first two chapters are devoted to the development of the basis of an asymptotic method based on Hamilton-Jacobi equations to study models from evolutionary biology and ecology. The last two chapters concern the development and the application of the method in the case of heterogeneous environments. At the end of the manuscript I will present comments and open questions for future research.

In Chapter 1, I will present the works [LMP11, MR15b, MR16] which concern the well-posedness of the Hamilton-Jacobi approach for a typical selection-mutation model. This approach has been introduced in [DJMP05] and has been developed during the last decade to study models from evolutionary biology (see [BP07, PB08] for the first results within this framework). A main part of my PhD thesis has also been devoted to the development of the basis of this approach [Mir11]. The main objective in such works is to provide an asymptotic analysis of the phenotypic density of a population which solves a parabolic (or elliptic) integro-differential equation, considering small diffusion term (modeling small effects of mutations). The solution to such equation concentrates, in the limit of vanishing diffusion and in long time, as a sum of Dirac masses corresponding to the dominant traits. The asymptotic analysis of the equation, via a logarithmic transformation of the solution, leads indeed usually to a Hamilton-Jacobi equation with constraint. The description of the phenotypic density is then reduced to the description of the solution to the corresponding Hamilton-Jacobi equation. While the derivation of such Hamilton-Jacobi equations from selection-mutation models is rather well-developed (see for instance [BP07, PB08, BMP09]), the asymptotic description of the phenotypic density, based on the analysis of the Hamilton-Jacobi equation with constraint, is less understood. In Chapter 1, I present a framework where such analysis of the Hamilton-Jacobi equation is provided and precise results on the phenotypic density are obtained. A main contribution in this chapter is the uniqueness of the viscosity solution to the Hamilton-Jacobi equation with constraint derived from a typical selection-mutation model. The uniqueness of the viscosity solution to such equation was an open question since the seminal work of Perthame and Barles [PB08]. In addition to the uniqueness property, within this framework, we show that the solution to the Hamilton-Jacobi equation is indeed smooth and classical and it has a unique maximum point. This allows us to describe the asymptotic phenotypic density as a single Dirac mass which evolves with time. Finally, this analysis leads to error estimates and an asymptotic expansion of the solution providing more quantitative results for biological applications.

In Chapter 2, I will focus on the asymptotic study of fractional reaction-diffusion equations [MM15, Mir, LMR]. A main objective in this chapter is to develop the Hamilton-Jacobi approach in the case of selection-mutation models where the mutation term is modeled by a fractional laplacian. The choice of a fractional laplacian rather than a classical laplacian or an integral kernel with thin tails, allows to take into account large mutation jumps with a high rate. The presence of such large mutations leads to drastically faster dynamics and the previous scalings are not adapted to the study of such problems. Note that a related problem is to provide an asymptotic analysis of the fractional Fisher-KPP equation which leads to propagation phenomena with exponential speed [CR13]. A variant of the asymptotic approach based on Hamilton-Jacobi equations has indeed been used in the 80's to study propagation phenomena in local reaction-diffusion equations [Fre85a, Fre85b, ES89, BES90]. As a first step, we first extend these results to the case of fractional Fisher-KPP equation [MM15]. By introducing an unconventional rescaling we derive indeed, via an asymptotic analysis, the exponential speed of propagation established by Cabré and Roquejoffre [CR13] (see also Section 2.4 where we extend this result to the case of periodically hostile environments in the framework of the PhD project of A. Léculier, a student that I supervise together with J.-M. Roquejoffre). Next, being inspired by such analysis we introduce a rescaling for the fractional selection-mutation model which leads to the concentration of the phenotypic density as a single Dirac mass, similarly to the case of classical selection-mutation models [MM15, Mir]. However, significant difficulties comparing to previous works arise from the fractional laplacian term which lead to considerably different analysis. In particular, the logarithmic transform of the phenotypic density does not converge anymore to a viscosity solution of a Hamilton-Jacobi equation, but to a viscosity supersolution which is minimal in a certain class of functions.

Chapter 3 is devoted to the study of the evolutionary dynamics of a population in a heterogeneous environment with a discrete spatial structure [Mir13, GM17, Mir17, MG]. In this chapter we characterize the phenotypic density of a population at equilibrium between selection, mutation and migration and provide analytic approximations for the moments of the phenotypic distribution. Note that such analytic approximations are closely related to an asymptotic expansion of the solution discussed above, at the end of the paragraph on the first chapter. A main part of the work presented in this chapter has been done in the framework of a collaboration project with S. Gandon who is a biologist. The objective of this project was to show, via the particular model considered in this work, how the Hamilton-Jacobi approach can be used to bring insight into current biological questions. This analysis improves the previous results in the biological literature and allows to consider less restrictive assumptions (see for instance [MCG97, Day00, YG09, DRG13, DYG15]). Furthermore, our work makes a connection between the theory of adaptive dynamics and moment based approaches in quantitative genetics. Adaptive dynamics and quantitate genetics, which focus respectively on the evolution of discrete and continuous characters (as a result, respectively, of rare and frequent mutations), are two theories which are widely used in theoretical evolutionary biology (see for instance [MHM+96, BÖ0, Die04, Ric04]). Finally, our method allows to go beyond the Gaussian approximation commonly used in the theory of quantitative genetics.

In Chapter 4, we study the evolutionary dynamics of populations in time varying environments [MPS15, FIM18, FIM, CEM]. While the understanding of the effect of the time variations of the environment, due for instance to seasonal changes, climate change or a time administration of drugs, on the adaptation of populations is an important problem in evolutionary biology [CLM10, PMLJ+13, KM14, BPnMGI17], the outcome of such heterogeneities is very rich and depends strongly on the speed of the environmental change, the size of the mutational effects, and on how the variations act on the growth rate of individuals. A main difficulty in the study of such problems comes from the combination of the nonlocal competition term with the time dependency of the growth rate. In chapter 4 we will study several types of time variations of the environment leading to different types of behaviors: time periodic environments [MPS15, FIM18], shifting and oscillating environments [FIM] and a piecewise constant environment with slow switch [CEM]. Several challenging mathematical questions emerge in the development of the Hamilton-Jacobi approach for these models. We apply our method to several illuminating biological examples leading to different outcomes on the phenotypic density. In particular, we show how our method can be used to provide a possible explanation for the outcome of a biological experiment [KMZ$^+$13, FIM18]. The articles [FIM18, FIM] are prepared in the framework of the PhD project of my student S. Figueroa Iglesisas. The result in [CEM] is obtained in the framework of the postdoctoral project of C. Etchegaray that I mentored together with M. Costa.

Some of the results that I have obtained after my PhD will not be addressed in this manuscript to maintain some homogeneity:

- The works [BCM$^+$12, LMM15, BM15, MP15, CHM$^+$] on evolutionary dynamics of populations in space-heterogeneous environments with continuous space structure. These works are closely related to the presented work in this dissertation. While I believe these results correspond to important contributions in this field, these articles are prepared less as a continuous project but more as independent contributions. This is why I chose not to present them in this dissertation.

- The work in [MPW14] where we derive, with B. Perthame and J. Wakano, a selection-mutation model, known as direct competition model, from a model taking into account the interaction of the population with resources.

- The work in [MS13] where we study, with P. Souganidis, a model for the motion of motor proteins.

List of publications

Here is the list of my publications. Papers marked with • are presented in this dissertation. Papers marked with ◇ are part of my PhD thesis. Those marked with ∗ were completed after my PhD but are not presented in this report.

• [CEM] M. Costa, C. Etchegaray, and S. Mirrahimi. *Survival criterion for a population subject to selection and mutations; application to temporally piecewise constant environments.* Preprint.

• [FIM] S. Figueroa Iglesias and S. Mirrahimi. *Selection and mutation in a shifting and fluctuating environment.* Preprint.

• [LMR] A. Léculier, S. Mirrahimi, and J.-M. Roquejoffre. *Propagation in a fractional reaction-diffusion equation in a periodically hostile environment.* Preprint.

∗ [CHM$^+$] V. Calvez, C. Henderson, S. Mirrahimi, O. Turanova and T. Dumont, *Non-local competition slows down front acceleration during dispersal evolution*, Preprint.

• [Mir] S. Mirrahimi, *Singular limits for models of selection and mutations with heavy tails*, accepted in J. Math. Pures Appl.

• [MG] S. Mirrahimi and S. Gandon, *Evolution of specialization in heterogeneous environments: equilibrium between selection, mutation and migration*, accepted in Genetics.

• [FIM18] S. Figueroa Iglesias and S. Mirrahimi, *Long time evolutionary dynamics of phenotypically structured populations in time-periodic environments*, SIAM J. Math. Anal, 50(5):5537–5568, 2018.

• [Mir17] S. Mirrahimi, *A Hamilton-Jacobi approach to characterize the evolutionary equilibria in heterogeneous environments*, Mathematical Models and Methods in Applied Sciences, 27(13):2425–2460, 2017.

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∗ [MPW14] S. Mirrahimi, B. Perthame and J. Y. Wakano, *Direct competition results from strong competition for limited resource*, Journal of mathematical biology, Vol. 68(4):931–949, 2014.

∗ [MS13] S. Mirrahimi and P. E. Souganidis, *A homogenization approach for the motion of motor proteins*, Nonlin. Diff. Eq. Appl. (NoDEA), 20(1):129–147, 2013.

• [Mir13] S. Mirrahimi, *Adaptation and migration of a population between patches*, Discrete Contin. Dyn. Syst. Ser. B, 18(3):753-768, 2013.

◇ [MR13] S. Mirrahimi and G. Raoul, *Population structured by a space variable and a phenotypical trait*, Theoretical Population Biology, 84:87–103, 2013.

∗ [BCM$^+$12] E. Bouin, V. Calvez, N. Meunier, S. Mirrahimi, B. Perthame, G. Raoul, and R. Voituriez, *Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration*, Comptes rendus - Mathématique 350:761-766, 2012.

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•◇ [LMP11] A. Lorz, S. Mirrahimi, and B. Perthame, *Dirac mass dynamics in multidimensional nonlocal parabolic equations*, Communications in Partial Differential Equations (CPDE), 36(6):1071-1098, 2011.

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Chapter 1

A Hamilton-Jacobi approach for models from evolutionary biology

1.1 Introduction

In this chapter we present the main elements of an approach based on Hamilton-Jacobi equations with constraint, and some recent results on the well-posedness of this approach, to study the evolutionary dynamics of populations structured by quantitative traits.
The ability of an individual to survive and to reproduce depends indeed on genetic or phenotypic parameters called traits. Several mechanisms contribute to the evolution of the living organisms: heredity, i.e. vertical transmission of the ancestral trait to the offspring, mutation which generates variability in the trait values, selection which results from the interaction of individuals with their environment, and horizontal gene transfer, i.e. horizontal exchange of genetic information between individuals during their life time. Is it possible to predict the survival or extinction of a population which is subject to such mechanisms? Can we characterize the phenotypic distribution of such population? Such types of questions emerge for instance in the study of the impact of an environmental change, e. g. climate change, on a population or in the investigation of an efficient therapy avoiding resistance of bacteria or cancer cells to medications [LMR10, CLM10, KM14, BPnMGI17].

Several mathematical formalisms are used to study the Darwinian evolution of phenotypically structured populations. Game theory is one of the first approaches to study evolution and remains one of the important tools in this field [MS74, HS88]. Adaptive dynamics, which is based on the study of the stability of differential systems, allows to study evolution under rare mutations (see for instance [MHM$^+$96, GKMM98, Die04]). Integro-differential models (usually elliptic, parabolic or kinetic equations) have also contributed a lot to the understanding of evolutionary dynamics of large populations (see for instance [MW00, CC04, DJMP05, DJMR08, JR11]). Finally, probabilistic approaches allow to study finite populations (see for instance [CL07]) and also to justify the above frameworks from individual based models by proper choices of scaling on the size of the population, birth, death and mutations (see for instance [CFM06, CFM08]).

Here, we are interested in the qualitative behaviour of parabolic Lotka-Volterra type integro-differential models describing populations with asexual reproduction. Such integro-differential equations have the property that in the limit of small diffusion, representing the mutations, and in long time the solution concentrates on one or several evolving points corresponding to dominant traits. A logarithmic transformation of the solutions to such equations lead to Hamilton-Jacobi equations with constraint. In this chapter, we present the main elements of an asymptotic approach based on the study of such Hamilton-Jacobi equations with constraint. This approach was first suggested in [DJMP05] and the first general results were provided in [BP07, PB08]. An important part of my work has also been devoted to the development of this approach for general selection-mutation models with possible heterogeneity. Note that related tools were already used to study the propagation phenomena for local reaction-diffusion equations (see for instance [Fre85a, ES89]).

A main contribution presented in this chapter corresponds to a uniqueness result for a Hamilton-Jacobi equation with constraint derived from a typical selection-mutation model. While the derivation of such Hamilton-Jacobi equations was obtained earlier in [PB08, BMP09], the uniqueness of the solution, being a more challenging question, was proved in a later work with J.-M. Roquejoffre in [MR16], under concavity assumptions on the growth rate. This result, in addition to the well-posedness of the Hamilton-Jacobi equation with constraint, provides a constructive existence result which was not available previously. In addition to the uniqueness property, within this framework, we show that the solution to the Hamilton-Jacobi equation with constraint is indeed smooth and classical and it has a unique maximum point. This allows us to describe the asymptotic phenotypic density as a single Dirac mass which evolves with time [LMP11]. Finally, this analysis leads to error estimates and an asymptotic expansion of the solution providing more quantitative results for biological applications [MR15b].

In Section 1.2 we introduce a typical selection-mutation model and our assumptions. In Section 1.3 we show how the asymptotic study of such selection-mutation equations leads to Hamilton-Jacobi equations with constraint. In Section 1.4 we introduce a particular framework, with concavity assumptions, where one can obtain concentration of n as a Dirac mass, using the limiting Hamilton-Jacobi equation with constraint [LMP11]. In Section 1.5 we present our uniqueness result for the Hamilton-Jacbi equation with constraint. In Section 1.6 we provide the main elements of the proof of the uniqueness result. These two sections are based on the works in [MR15b, MR16].

1.2 Model and assumptions

In this section we present a typical selection-mutation equation modeling populations structured by quantitative traits in a homogeneous environment.
We study the following equation:

$$\begin{cases} \partial_t n - \sigma \Delta n = n\, R(z,I), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ I(t) = \int_{\mathbb{R}^d} n(t,y)\psi(y)dy, \\ n(0,z) = n_0(z). \end{cases} \tag{1.1}$$

Here, t corresponds to time and z corresponds to a phenotypic trait. The function n represents the phenotypic density of a population. The term ψ models the consumption rate of the resources and $I(t)$ corresponds to the total consumption of the population. The growth rate of the individuals is denoted by $R(z,I)$ which is decreasing with respect to the total consumption I, taking into account in this way competition between the individuals. The Laplace term models the mutations and the term σ measures the effect of mutations. This type of model was first suggested by Kimura [Kim65] and was later derived from stochastic individual based models

[CFM06, CFM08].

A simple example with above type of growth rate is the chemostat model [Die04, DJMP05, MPBM11]. Chemostat is a laboratory device to culture micro-organisms like bacteria or algae. A standard equation for the chemostat is written

$$\begin{cases} \frac{d}{dt}S(t) = d(S_{\text{in}} - S(t)) - S(t)\int_{\mathbb{R}} \psi(y)n(t,y)dy, \\ \frac{\partial}{\partial t}n(t,z) - \sigma\Delta n(t,z) = -dn(t,z) + S(t)\psi(z)n(t,z). \end{cases} \tag{1.2}$$

Here we consider a population of micro-organisms, characterized by a parameter $z \in \mathbb{R}$ (it can be thought of as the logarithm of their size), which live in a bath containing a nutrient which is continuously renewed with a rate $d > 0$. The nutrient concentration is denoted by $S(t)$ and the fresh nutrient by $S_{\text{in}} > 0$. The population density is denoted by $n(t,z)$ and uptake rate for individuals of trait z is $\psi(z) > 0$. Finally, we model the mutations by a diffusion term.
We next suppose that the nutrients have fast dynamics compared to the time scale of the dynamics of the population and they reach quickly an equilibrium. Then, $S(t)$ is given by

$$S(t) = \frac{dS_{\text{in}}}{d + \int_{\mathbb{R}} \psi(y)n(t,y)dy}.$$

Replacing this in (1.2) we obtain an equation of type (1.1) with

$$R(z,I) = \frac{d\psi(z)S_{\text{in}}}{d + I(t)} - d.$$

Different variants of model (1.1) are used to model selection and mutation mechanisms. A well-known equation is the direct competition model where the growth rate $R(z,I)$ is replaced by a term $a(z) - \int c(z,y)n(t,y)dy$ (see for instance [BP97, DL00, CFM08]). Such growth rate considers more important competition between individuals with closer traits. In [DJMR08, JR11, CJR10] the long time behavior of the solutions to equations with such competition term, but without the diffusion term, are investigated. See also [LCS15, CJL15] for numerical analysis of such equations. [Rao11, CCDR13] provide also asymptotic analysis of the direct competition model, considering small rate of mutations, where the mutations are modeled via an integral kernel instead of a Laplace term. The Hamilton-Jacobi approach may also be applied to such models [BMP09, LMP11]. In the particular case where $a(x) \equiv 1$, the model is known as the nonlocal Fisher-KPP equation. For such model, the existence of traveling waves, pulsating waves and wave trains are widely investigated (see [GVA06, BNPR09, NTP10, NRRP13, HR14, FH15] and references therein). Models considering several resources are also studied [CJ11, CJM14]. In the case where $R(z,I) = \psi(z) - I$, such equation is known as the replicator-mutator equation [Kim65]. Note that in this case, the total population size is conserved (equal to 1). Then, considering particular forms of ψ, one can solve explicitly either the equation [AC14] or an equation verified by the cumulant generating function of the phenotypic distribution [GHGR17].

We are interested in the study of (1.1) in the case where the mutations have small effects. To this end, we take $\sigma = \varepsilon^2$, with ε a small parameter. We also make a change of variable in time:

$$t \mapsto \frac{t}{\varepsilon},$$

which accelerates the dynamics in order to observe the effect of small mutations. We hence define

$$n_\varepsilon(t,z) = n(\frac{t}{\varepsilon}, z),$$

which solves the following equation

$$\begin{cases} \varepsilon \partial_t n_\varepsilon - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon \, R(z, I_\varepsilon), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ I_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,y)\psi(y)dy, \\ n_\varepsilon(0,z) = n_{\varepsilon,0}(z). \end{cases} \tag{1.3}$$

The selection-mutation models have the property that, in the limit of small diffusion and in long time, the solution concentrates on one or several evolving points corresponding to dominant traits. In the case of (1.3) we expect that the solution concentrates as a single Dirac mass since there is a single limiting factor (the nutrient modeled via the term I_ε) in the model. The principle of competitive exclusion [Lev70, Sch74] in evolutionary biology states indeed that when there are k limiting factors for the population, no more than k distinct traits may coexist. See Figure 1.1 for an illustration of the solution of (1.3) for a choice of parameters, which is compatible with our assumptions below.

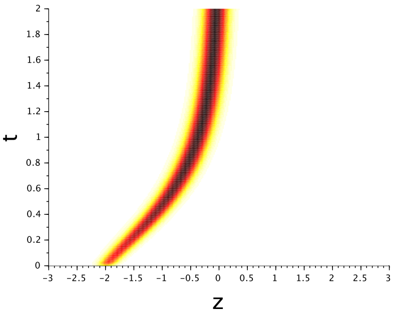

Figure 1.1: The dynamics of the phenotypic density. The colors represent different values of the phenotypic density $n_\varepsilon(t,z)$, the solution to (1.3). The population concentrates on a dominant trait which evolves with time. Here we consider the following parameters $R(z,I) = 7 - z^2 - I$, $\psi(z) \equiv 1$, $n_{\varepsilon,0}(z) = \frac{1}{\sqrt{\varepsilon\pi}} \exp(-\frac{(z+2)^2}{\varepsilon})$ and $\varepsilon = 0.02$.

Note that the main difficulties in the study of such problems come from the non-local term I_ε. Due to this term (1.3) does not admit a comparison principle. Moreover, as $\varepsilon \to 0$, the limit of I_ε is only of bounded variation and can be potentially discontinuous.

Assumptions:

To state more precise results on equation (1.3) we first present some assumptions. We assume that the growth rate R is a strictly decreasing function of the competition term I:

$$-K_1 \leq \frac{\partial}{\partial I} R(z,I) \leq -K_2. \tag{1.4}$$

We also assume that there is a certain threshold for the competition term I above which the growth rate is negative everywhere:

$$\max_{z \in \mathbb{R}^d} R(z, I_M) = 0. \tag{1.5}$$

This assumption means that the resources are limited. We also make the following technical assumptions on R:

$$R(\cdot,I)\in W^{2,\infty}_{\mathrm{loc}}(\mathbb{R}^d),\quad -K_4(1+|z|^2)\le R(z,I),\qquad \text{for all } z\in\mathbb{R}^d \text{ and } 0\le I\le 2I_M, \tag{1.6}$$

$$-K_3\le \Delta(\psi(z)R(z,I)),\qquad \text{for all } z\in\mathbb{R}^d \text{ and } 0\le I\le 2I_M. \tag{1.7}$$

We assume that the consumption rate ψ is a smooth function such that, for some positive constants ψ_m and ψ_M, we have

$$\psi_m\le\psi(z)\le\psi_M,\qquad \psi\in W^{2,\infty}(\mathbb{R}^d). \tag{1.8}$$

We then assume that the initial condition is well-prepared. We suppose indeed that there exist positive constants A_i such that

$$n_{\varepsilon,0}=\frac{1}{(2\pi\varepsilon)^{\frac{d}{2}}}\exp\big(\frac{u_{\varepsilon,0}}{\varepsilon}\big),\quad \text{with}\quad -A_1-A_2|z|^2\le u_{\varepsilon,0}(z)\le A_3-A_4|z|\quad \text{for all } z\in\mathbb{R}^d. \tag{1.9}$$

The left hand side inequality above is a technical assumption and may be relaxed. However, we keep it to simplify the presentation of the result. The right hand side inequality means that there is small size of population at infinity.
We also assume that the initial size of the population is non-negligeable:

$$I_\varepsilon(0)\to I_0>0,\qquad \text{as } \varepsilon\to 0. \tag{1.10}$$

Finally, we assume that the initial population is not maladapted to the environment so that we can guarantee the persistence of the population:

$$\frac{1}{\varepsilon}\int_{\mathbb{R}^d}\psi(z)R(z,I_\varepsilon(0))n_{\varepsilon,0}(z)dz\ge o(1),\qquad \text{as } \varepsilon\to 0. \tag{1.11}$$

1.3 Convergence to a Hamilton-Jacobi equation with constraint

In this section, we show that a Hamilton-Jacobi equation with constraint can be derived from (1.3). In order to study the limit of n_ε, as $\varepsilon\to 0$, we first introduce the following Hopf-Cole transformation

$$n_\varepsilon=\frac{1}{(2\pi\varepsilon)^{d/2}}\exp\big(\frac{u_\varepsilon}{\varepsilon}\big). \tag{1.12}$$

The reason why we introduce such transformation is that the solution n_ε to (1.3) will naturally have this form. While we expect that the limit of (n_ε), as $\varepsilon\to 0$, would be a measure, the limit of (u_ε) will be a continuous function that solves a Hamilton-Jacobi equation. The main idea of the approach is to first study u_ε and next obtain information on n_ε from the properties of u_ε.

Replacing (1.12) in (1.3) we obtain the following equation on u_ε:

$$\partial_t u_\varepsilon-\varepsilon\Delta u_\varepsilon=|\nabla u_\varepsilon|^2+R(z,I_\varepsilon).$$

We can then pass to the limit as $\varepsilon\to 0$ and obtain the following result:

Theorem 1.1 (Convergence to a Hamilton-Jacobi equation with constraint [PB08, BMP09])**.** *Assume* (1.4)–(1.11)*. Let* n_ε *be the solution of* (1.3)*, and* u_ε *be given by* (1.12)*. Then, as* $\varepsilon \to 0$ *and along subsequences,* (I_ε) *converges a.e. to* $I \in \mathrm{BV}(\mathbb{R}^+)$ *and* (u_ε) *converges locally uniformly to a function* $u \in \mathrm{C}((0,\infty)\times\mathbb{R}^d)$*, which solves the following equation in the viscosity sense*

$$\begin{cases} \partial_t u = |\nabla u|^2 + R(z,I), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ \max_{z\in\mathbb{R}^d} u(t,z) = 0, & t \in \mathbb{R}^+. \end{cases}$$

If additionally $(u_{\varepsilon,0})$ *is a sequence of uniformly continuous functions which converges locally uniformly to* u_0 *then* $u \in \mathrm{C}([0,\infty)\times\mathbb{R}^d)$ *and* $u(0,z) = u_0(z)$ *in* $\mathbb{R}^d$*.*

Here, I may be thought of as a sort of regulator, or a sort of Lagrange multiplier, to maintain the maximum of u equal to 0. Note that I is only of bounded variation and can be potentially discontinuous. The above theorem was proved in [PB08] with the uniform continuity assumption on the initial condition $(u_{\varepsilon,0})_\varepsilon$ and without such assumption in [BMP09].

Once we have identified the limit of (u_ε), we can then obtain some information on the limit phenotypic density n and in some cases to characterize n completely.

Theorem 1.2 (Convergence of (n_ε) [PB08])**.** *Assume* (1.4)–(1.11)*. Then, as* $\varepsilon \to 0$ *and along subsequences,* n_ε *converges in* $\mathrm{L}^\infty\left(\mathrm{w}*(0,\infty);\mathcal{M}^1(\mathbb{R}^d)\right)$ *to a measure* n *such that, for a.e.* t*,*

$$\int \psi(z) n(t,z) dz = I(t) \quad a.e.,$$

and

$$\operatorname{supp} n(t,z) \subset \{z \,|\, u(t,z) = 0\} \subset \{z \,|\, R(z, I(t)) = 0\}. \tag{1.13}$$

Note in particular that while $z \in \mathbb{R}$ and R is a monotonic function with respect to z, then (1.13) implies that n is a single Dirac mass., in the following form

$$n(t,z) = \rho(t)\delta(z - \overline{z}(t)),$$

with $(\overline{z}, \rho)$ uniquely determined by

$$R(\overline{z}(t), I(t)) = 0, \qquad \rho(t) = \frac{I(t)}{\psi(\overline{z}(t))}.$$

1.4 A concave framework and concentration as a Dirac mass

In this section, we introduce a particular framework, with concavity assumptions, where one can obtain concentration of n as a Dirac mass in the multi-d case. To this end, additionally to the above assumptions we also make the following concavity assumptions, for all $z \in \mathbb{R}^d$ and $0 \le I \le 2I_M$,

$$-2B_1 \le D^2 R(z,I) \le -2B_2, \quad -\underline{B}_0 - B_1|z|^2 \le R(z,I) \le -\overline{B}_0 - B_2|z|^2, \tag{1.14}$$

$$-2D_1 \le D^2 u_{\varepsilon,0}(z) \le -2D_2, \quad -\underline{D}_0 - D_1|z|^2 \le u_{\varepsilon,0}(z) \le -\overline{D}_0 - D_2|z|^2. \tag{1.15}$$

Here Df represents the derivative of the function f with respect to z. Under such assumptions, the limit function u has strong regularity properties and it is strictly concave with respect to z, and hence it has a unique maximum point. The property (1.13) then implies that n is indeed a single Dirac mass.
More precisely, we have

Theorem 1.3 (Convergence to a Dirac mass in the concave framework [LMP11])**.** *Assume* (1.4)–(1.11) *and* (1.14)–(1.15)*. Then, we have*

$$-E_1 \leq D^2 u_\varepsilon(t,z) \leq -E_2, \quad \textit{for all } (t,z) \in \mathbb{R} \times \mathbb{R}^d,$$

for some positive constants E_1 and E_2. Moreover, the limit function u belongs to $L^\infty_{\mathrm{loc}}\left(\mathbb{R}^+; W^{2,\infty}_{loc}(\mathbb{R}^d)\right) \cap W^{1,\infty}_{\mathrm{loc}}\left(\mathbb{R}^+; L^\infty_{loc}(\mathbb{R}^d)\right)$, and it is strictly concave with respect to z. As a consequence, we can identify n as follows

$$n(t,z) = \rho(t)\delta(z - \overline{z}(t)), \qquad \rho(t) = \frac{I(t)}{\psi(\overline{z}(t))},$$

with $\overline{z}(t) \in \mathbb{R}^d$ the unique maximum point of $u(t,\cdot)$.

If we make the following additional regularity assumptions,

$$\|D^3 R\|_{L^\infty(\mathbb{R}^d \times [0,2I_M])} \leq B_3, \tag{1.16}$$

$$\|D^3 u_{\varepsilon,0}\|_{L^\infty(\mathbb{R}^d)} \leq D_3, \tag{1.17}$$

we can then also provide a differential equation for the dominant trait $\overline{z}(t)$:

Theorem 1.4 (The canonical equation [LMP11])**.** *Assume* (1.4)–(1.11) *and* (1.14)–(1.17)*. Then, we have the following regularity properties*

$$(u, I) \in L^\infty_{\mathrm{loc}}\left(\mathbb{R}^+; W^{3,\infty}_{loc}(\mathbb{R}^d)\right) \cap C^1(\mathbb{R}^+ \times \mathbb{R}^d) \times C^1(\mathbb{R}^+).$$

Moreover, $\bar{z}(\cdot)$ belongs to $C^1(\mathbb{R}^+; \mathbb{R}^d)$ and satisfies

$$\dot{\bar{z}}(t) = \left(-D^2 u\big(t, \bar{z}(t)\big)\right)^{-1}.\nabla_z R\big(\bar{z}(t), I(t)\big). \tag{1.18}$$

1.5 A uniqueness result for the Hamilton-Jacobi equation with constraint

Together with Jean-Michel Roquejoffre in [MR15b, MR16] we provided a uniqueness result for the viscosity solution to the Hamilton-Jacobi equation with constraint

$$\begin{cases} \partial_t u = |\nabla u|^2 + R(z, I), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d \\ \max_{z\in\mathbb{R}^d} u(t,z) = 0, & t \in \mathbb{R}^+, \\ u(0,z) = u_0(z), \end{cases} \tag{1.19}$$

in the concave framework presented in the previous section, and showed that this result leads indeed to an asymptotic expansion for u_ε and hence to a more quantitative result for biological applications. Note that the uniqueness of the solution to (1.19) is a nonstandard problem because of the constraint $\max_{z\in\mathbb{R}^d} u(t,z) = 0$. The function I has to be chosen in a way such that this constraint holds. Such uniqueness property was indeed a missing element of the Hamilton-Jacobi approach for evolutionary biology since the seminal work of Perthame and Barles [PB08]. Our result allows to guarantee the well-posedness of this theory in the concave framework.

To present our main result we state the assumptions on u_0, which are analogous to the assumptions above on $u_{\varepsilon,0}$, and an additional regularity assumption on R.

Assumptions on u_0:
We assume the existence of positive constants $\overline{D}_0, \overline{D}_1, \overline{D}_2$ and $\overline{D}_3$ such that

$$-\overline{D}_0 - \overline{D}_1|z|^2 \leq u_0(z) \leq \overline{D}_0 - \overline{D}_2|z|^2, \tag{1.20}$$

$$-2\overline{D}_1 \leq D^2u_0 \leq -2\overline{D}_2, \tag{1.21}$$

$$\|D^3u_0\|_{L^\infty(\mathbb{R}^d)} \leq \overline{D}_3, \tag{1.22}$$

$$\max_z u_0(z) = u_0(\overline{z}_0) = 0, \qquad R(\overline{z}_0, I_0) = 0. \tag{1.23}$$

Additional regularity assumption on R:
We also assume that there exists a positive constant B_4 such that

$$|\frac{\partial^2 R}{\partial I \partial z_i}(z,I)| + |\frac{\partial^3 R}{\partial I \partial z_i \partial z_j}(z,I)| \leq B_4, \qquad \text{for } 0 \leq I \leq I_M, \text{ and } i,\, j = 1,2,\cdots,d. \tag{1.24}$$

Here is our main result:

Theorem 1.5 (Uniqueness for the Hamiton-Jacobi equation with constraint [MR16])**.** *Assume* (1.4)–(1.6)*,* (1.14)*,* (1.16) *and* (1.20)–(1.24)*. Then, the Hamilton-Jacobi equation with constraint* (1.19) *has a unique viscosity solution* $(u,I) \in \mathrm{C}(\mathbb{R}^+ \times \mathbb{R}^d) \times \mathrm{C}\big((0,+\infty)\big)$*, which is indeed a classical solution. Moreover we have*

$$(u,I) \in L^\infty_{\text{loc}}\big(\mathbb{R}^+; W^{3,\infty}_{\text{loc}}(\mathbb{R}^d)\big) \cap C^1(\mathbb{R}^+ \times \mathbb{R}^d) \times C^1(\mathbb{R}^+) \quad \textit{and} \quad \nabla u \in C^1(\mathbb{R}^+ \times \mathbb{R}^d).$$

The above theorem on the one hand provides the uniqueness of the solution to the Hamilton-Jacobi equation with constraint, in the concave framework. On the other hand it provides a constructive existence result while the previous existence result obtained by the vanishing viscosity limit of the viscous problem was not constructive. Moreover, this result implies that the convergence of (u_ε) to u is not only along subsequences and the whole sequence converges to the same limit.

The method used to prove such result is rather robust and can be generalized to study related models where for instance the competition term does not only depend on an integral with a weight of the phenotypic density n_ε but on a convolution term, as for the direct competition model:

$$\varepsilon\partial_t n_\varepsilon - \varepsilon^2\Delta n_\varepsilon = n_\varepsilon\big(r(z) - \int n(t,y)C(z,y)dy\big),$$

under some conditions presented in [LMP11].
Note also that such uniqueness result also allows to overcome some technical difficulties in the study of more complex heterogeneous models. In models with heterogeneity it is often harder to obtain regularity estimates in order to obtain the asymptotic convergence of the viscous problem. In such cases, one can indeed use a uniqueness result to pass to the limit (see for instance [MP15]).

The most important consequence of the uniqueness result is that it leads indeed to error estimates and an asymptotic expansion of u_ε in terms of ε ([MR15b] and work in progress with Jean-Michel Roquejoffre):

$$u_\varepsilon = u + \varepsilon v + o(\varepsilon), \qquad I_\varepsilon = I + \varepsilon J + o(\varepsilon).$$

The above expansion allows to obtain an interesting approximation of the phenotypic density n_ε:

$$n_\varepsilon(t,z) = \frac{1}{(2\pi\varepsilon)^{d/2}} \exp\big(\frac{u(t,z)}{\varepsilon} + v(t,z) + o(1)\big). \tag{1.25}$$

Such result goes further than the usual approximations used by biologists in the theory of quantitative genetics which is a theory in evolutionary biology that investigates the evolution of continuously varying traits (see for instance [Ric04]–chapter 7). Such approximations are usually based on an a priori assumption that the phenotypic distribution is a Gaussian.
We can go further in the approximations and use (1.25) and the Laplace's method of integration to obtain first order asymptotic expansions, in terms of ε, for the moments of the phenotypic distribution in terms of the derivatives of the functions u and v at the point $(t, \overline{z}(t))$, where $\overline{z}(t)$ is the unique maximum point of $u(t, \cdot)$. In particular, we can compute the covariance matrix of the phenotypic distribution as follows

$$\mathbf{V}_{\varepsilon,t} = \varepsilon(-D^2u)^{-1}(t, \overline{z}(t)) + o(\varepsilon),$$

where $\mathbf{V}_{\varepsilon,t} = (v_{i,j}(t))$ with $v_{i,j} = \int z_i z_j \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dx - (\int z_i \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dz)(\int z_j \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dz)$. Note that here we find again the term $(-D^2u)^{-1}(t, \overline{z}(t))$ which also appeared in equation (1.18). This property allows to provide a biological interpretation of this equation and in particular to compare it to the so-called canonical equation in the theory of adaptive dynamics [Die04, DL96] or to Lande's equation in the theory of quantitative genetics [Lus37, Lan79, LA83]. In these equations, which are very related equations under different formalisms, the change in the dominant/average trait is given by the product of the gradient of the fitness and a term that scales the rate of evolutionary change (proportional to mutational variance or genetic variance respectively in adaptive dynamics and quantitative genetics). In (1.18), the dynamics of the dominant trait $\dot{\overline{z}}(t)$ is also given by the product of the gradient of the fitness $\nabla_z R$ and the term $\left(-D^2u\left(t, \overline{z}(t)\right)\right)^{-1}$ which approximates well the phenotypic covariance matrix. In this way, (1.18) may be seen as a generalization of the canonical equation or Lande's equation to a case where the mutations are not assumed to be very rare (on the contrary to adaptive dynamics) and such that the evolution of the genetic variance is included in the dynamics.
In chapters 3 and 4 we will present some models with heterogeneous environments where such analytic approximations allow to bring insight into biological questions.

More recently, the uniqueness of the viscosity solutions of (1.19) in a more general setting was proved in [CL]. However, this more general result does not allow to describe the structure of the solutions, nor to prove the concentration of n on a single point. Furthermore this work does not lead to an asymptotic expansion of u_ε.

1.6 The main elements of the proof of Theorem 1.5

A first main element in the proof of Theorem 1.5 is the fact that under the assumptions of the theorem, any viscosity solution u to (1.19) is indeed smooth and strictly concave. We prove indeed such result for an unconstrained Hamilton-Jacobi equation where $R(z, I)$ is replaced by $R(t, z)$:

$$\begin{cases} u_t = |\nabla u|^2 + R(t, z) \quad (t > 0, z \in \mathbb{R}^d), \\ u(0, z) = u_0(z). \end{cases} \tag{1.26}$$

To present our results on (1.26) we provide our assumptions on $R(t, z)$ which are closely related to the ones on $R(z, I)$.

Assumptions on $R(t, z)$:
We choose R to be continuous in t and to have first and second derivatives with respect to z,

that are continuous both with respect to t and z. We suppose that

$$- \overline{B}_0 - \overline{B}_1|z|^2 \le R(t,z) \le \overline{B}_0 - \overline{B}_1|z|^2, \qquad \text{for } \ t \in \mathbb{R}^+, \tag{1.27}$$

$$- 2\overline{B}_1 \le D^2 R(t,z) \le -2\overline{B}_2 < 0 \text{ as symmetric matrices}, \tag{1.28}$$

$$\|D^3 R(t,\cdot)\|_{L^\infty(\mathbb{R}^d)} \le \overline{B}_3, \qquad \text{for } t \in \mathbb{R}^+. \tag{1.29}$$

Theorem 1.6 ([MR16])**.** *Assume* (1.20)–(1.22) *and* (1.27)–(1.29)*. Equation* (1.26) *has a unique viscosity solution u that is bounded from above. Moreover, it is a classical solution: $u \in L^\infty_{\mathrm{loc}}\big(\mathbb{R}^+; W^{3,\infty}_{\mathrm{loc}}(\mathbb{R}^d)\big) \cap C^1(\mathbb{R}^+ \times \mathbb{R}^d)$, $\nabla u \in C^1(\mathbb{R}^+ \times \mathbb{R}^d)$,*

$$- \max(2\,\overline{D}_1, \sqrt{\overline{B}_1}) \le D^2 u \le - \min(2\overline{D}_2, \sqrt{\overline{B}_2}) \quad \textit{and} \quad \|D^3 u\|_{L^\infty([0,T]\times\mathbb{R}^d)} \le C(T),$$

where $C(T)$ is a positive constant depending on $\overline{D}_1, \overline{B}_1, \overline{D}_3, \overline{B}_3$ and T.

The existence and uniqueness of viscosity solution to (1.26) is rather classical. The main ingredient to prove the regularity properties above is to use the fact that the viscosity solution to (1.26) is given by the dynamic programming principle:

$$u(t,z) = \sup_{\substack{(\gamma(s),s)\in\mathbb{R}^d\times[0,t] \\ \gamma(t)=x}} \left\{ F(\gamma) \ : \ \gamma \in C^1([0,t];\mathbb{R}^d) \right\},$$

with

$$F(\gamma) := \ u_0(\gamma(0)) + \int_0^t \left(- \frac{|\dot\gamma|^2}{4}(s) + R(s,\gamma(s)) \right) ds,$$

and the fact that u_0 and R are strictly concave functions.

The second step of the proof is to show that (1.19) is equivalent with the following slightly nonstandard differential system:

$$\begin{cases} R\left(\overline{z}(t), I(t)\right) = 0, & \text{for } t \in \mathbb{R}^+, \\ \dot{\overline{z}}(t) = \big(-D^2 u\big(t,\overline{z}(t)\big)\big)^{-1} \nabla R\big(\overline{z}(t), I(t)\big), & \text{for } t \in \mathbb{R}^+, \\ \partial_t u = |\nabla u|^2 + R(z,I), & \text{in } \mathbb{R}^+ \times \mathbb{R}^d, \end{cases} \tag{1.30}$$

with initial conditions

$$\begin{array}{c} I(0) = I_0, \qquad u(0,\cdot) = u_0(\cdot), \qquad \overline{z}(0) = \overline{z}_0, \\ \text{such that} \quad \max_z u_0(z) = u_0(\overline{z}_0) = 0 \quad \text{and} \quad R(\overline{z}_0, I_0) = 0. \end{array} \tag{1.31}$$

Note that (1.30) is really a differential system because the assumptions on R imply that $I(t)$ can implicitely be expressed in terms of $\overline{z}(t)$. And it is slightly nonstandard because $\overline{z}$ solves an ODE whose nonlinearity depends on u. The precise statement is the following

Theorem 1.7 ([MR16])**.** *Solving the constrained problem* (1.19) *is equivalent to solving the initial value ODE-PDE problem* (1.30)–(1.31)*.*

Finally the last step is to prove that (1.30)–(1.31) has a unique solution. This is obtained using a Banach fixed point argument, by defining an adapted mapping and proving, thanks to some technical computations, that such mapping is a strict contraction.

Chapter 2

Fractional reaction-diffusion equations

2.1 Introduction

In this chapter, we are interested in the study of the following selection-mutation model where the mutations are modeled by a fractional laplacian:

$$\begin{cases} \partial_t n + \sigma(-\Delta)^\alpha n = n\, R(z, \rho(t)), \quad (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d \\ n(t=0,\cdot) = n^0(\cdot), \quad \rho(t) = \int_{\mathbb{R}^d} n(t,z)dz, \end{cases} \tag{2.1}$$

with $0 < \alpha < 1$ and

$$(-\Delta)^\alpha n(t,z) = \text{p.v.} \int_{R^d} \big(n(t,z) - n(t,z+h)\big) \frac{dh}{|h|^{d+2\alpha}}.$$

Here, as in Chapter 1, z corresponds to a phenotypic trait and n represents the phenotypic density. The total size of the population is denoted by ρ. The function R represents the growth rate of individuals with trait z, and it is a decreasing function with respect to the total size of the population ρ, taking into account in this way competition between the individuals. The difference with (1.1) is that the mutations are modeled by a fractional laplacian instead of a classical laplacian. The choice of a fractional laplacian rather than a classical laplacian or an integral kernel with thin tails, allows to take into account large mutation jumps with a high rate. Such equation has been derived from stochastic individual based models, in the case where the mutation distribution has algebraic tails [JMW12].

We are interested in an asymptotic analysis of the above equation to understand the effect of large mutation jumps on the dynamics of the phenotypic density. Is there still a rescaling under which one would observe the concentration of the phenotypic density as a Dirac mass? Can the Hamilton-Jacobi approach be extended to study mutation integral kernels with thick tails? Models closely related to (2.1) but considering regular integral kernels with thin tails or with compact support, instead of the fractional laplacian, have been previously studied (see for instance [BMP09, Rao11, GHGR17]). However, not much is known for the models with heavy tailed integral kernels. The presence of large mutations with a high probabilty leads to drastically faster dynamics and the previous scalings are not adapted to the study of such problems.

With S. Méléard, in order to obtain a relevant rescaling and to perform an asymptotic analysis for the fractional selection-mutation equation, we first studied a fractional Fisher-KPP equation:

$$\partial_t n + (-\Delta)^\alpha n = n(1-n).$$

The level sets of the solution to such equation propagate with a speed that is exponential in time [CCR12, CR13]. Note that such propagation is much faster compared to the classical Fisher-KPP equation where the propagation has constant speed [Fis37, KPP37, AW78]. In [MM15] we provided an unconventional rescaling that allowed us to provide an asymptotic analysis of this equation and capture the exponential speed of propagation associated to this equation. This work extends previous works on the asymptotic analysis of propagation phenomena, related to large deviation principles [FW98], in classical reaction-diffusion equations to the case of diffusion kernels with fat tails (see for instance [Fre85a, Fre86, ES89]).

Next, being inspired by such analysis we introduced a rescaling for the fractional selection-mutation model which leads to the concentration of the phenotypic density as a single Dirac mass, similarly to the case of classical selection-mutation models [MM15, Mir]. However, significant difficulties comparing to previous works arise from the fractional laplacian term which lead to considerably different analysis. In particular, the logarithmic transform of the phenotypic density does not converge anymore to a viscosity solution of a Hamilton-Jacobi equation, but to a viscosity supersolution which is minimal in a certain class of functions. Moreover, the limiting Hamilton-Jacobi equation can take infinite values.

The result in [MM15] on the fractional KPP equation has been extended in several directions. With J.-M. Roquejoffre, we supervise a PhD student, A. Léculier, on reaction-diffusion equations with nonlocal diffusion operators. In a first work [LÍ19], he has extended the result in [MM15] on the fractional Fisher-KPP equation to more general stable operators and considering periodic media (see also [CCR12, ST19]). Together with A. Léculier and J.-M. Roquejoffre we also have expanded this approach to study fractional KPP type equations in a periodically hostile environment. Such model describes the nonlocal dispersion of a population in a domain with periodic presence of obstacles.

In [BGHP18], Bouin et al. extended also this method to other dispersion kernels without singularity but with other types of decay. It is expected that the more recent work [Mir] on the fractional selection-mutation model can also be extended to such integral kernels following the same type of adaptation.

In Section 2.2 we present the asymptotic analysis of the fractional Fisher-KPP equation, which is based on the work in [MM15]. In Section 2.3 we go back to the case of the fractional selection-mutation model (2.1) and provide our results on the derivation of a Hamilton-Jacobi equation with constraint and the concentration of n_ε as a Dirac mass. This part is based on the work in [Mir]. Finally, in Section 2.4 we present a result on the fractional Fisher-KPP equation in a periodically hostile environment [LMR].

2.2 Fractional Fisher-KPP equation

In this section we study the asymptotic behavior of the fractional Fisher-KPP equation:

$$\begin{cases} \partial_t n(t,x) + (-\Delta)^\alpha n = n\,(1-n), \\ n(0,x) = n^0(x), \ x \in \mathbb{R}^d, \end{cases} \tag{2.2}$$

with $\alpha \in (0,1)$. Note that, here x may correspond to a spatial position and n to a spatial density. Then (2.2) describes the spatial dispersion of a population under logistic growth. The fractional diffusion describes the situations where the individuals can jump (move rapidly) from one point to another with a high probability, for instance because of the wind for seeds or human transportation for animals.

It has been proved in [CCR12, CR13] that the level sets of n, the solution to (2.2), propagate with a speed that is exponential in time (see also [Eng10, BRR11, Gar11, CR12, RT17] for related works on the speed of propagation for reaction-diffusion equations with fractional laplacian or a diffusion term with heavy tails). In particular, in [CR13] it is proved that for any initial data such that

$$0 \le n_0(x) \le C\frac{1}{1+|x|^{d+2\alpha}}, \tag{2.3}$$

we have

$$\begin{cases} n(t,x) \to 0, & \text{uniformly in } \mathcal{A}_\sigma = \{|x| \ge e^{\sigma t}\}, \text{ if } \sigma > \frac{1}{d+2\alpha}, \text{ as } t \to \infty, \\ n(t,x) \to 1, & \text{uniformly in } \mathcal{B}_\sigma = \{|x| \le e^{\sigma t}\}, \text{ if } \sigma < \frac{1}{d+2\alpha}, \text{ as } t \to \infty. \end{cases} \tag{2.4}$$

Our objective is to understand this behavior using singular limits as for the KPP equation with a Laplace term (cf. [Fre85a, BES90]). The idea is to rescale the equation and to perform an asymptotic limit so that we forget the full and detailed behavior and capture only this propagation. In the case of the classical Fisher-KPP equation, where the speed of propagation is known to be constant [AW78], to study the asymptotic behavior of the solutions one should use the following rescaling [Fre85a, Fre85b, ES89, BES90]

$$x \mapsto \frac{x}{\varepsilon}, \qquad t \mapsto \frac{t}{\varepsilon}, \quad \text{and} \quad n_\varepsilon(t,x) = n(\frac{t}{\varepsilon}, \frac{x}{\varepsilon}).$$

In the case of the fractional Fisher-KPP equation, being inspired by (2.4) we use the following long-range/long-time rescaling

$$x \mapsto r^{\frac{1}{\varepsilon}}\nu, \qquad t \mapsto \frac{t}{\varepsilon}, \qquad \text{with } r = |x| \text{ and } \nu = \frac{x}{|x|}. \tag{2.5}$$

Note that with such rescaling the sets $\mathcal{A}_\sigma$ and $\mathcal{B}_\sigma$ remain unchanged. We then define

$$n_\varepsilon(t,x) = n(\frac{t}{\varepsilon}, r^{\frac{1}{\varepsilon}}\nu), \qquad \text{with } r = |x| \text{ and } \nu = \frac{x}{|x|},$$

which solves the following rescaled equation

$$\begin{cases} \varepsilon\partial_t n_\varepsilon = \mathcal{L}_\varepsilon n_\varepsilon + n_\varepsilon(1-n_\varepsilon), \\ \mathcal{L}_\varepsilon n_\varepsilon(t,x) = \text{p.v.} \int_{\mathbb{R}^d} \left(n_\varepsilon \left(t, \left| r^{\frac{1}{\varepsilon}}\nu + h \right|^\varepsilon \frac{r^{\frac{1}{\varepsilon}}\nu+h}{|r^{\frac{1}{\varepsilon}}\nu+h|} \right) - n_\varepsilon(t,x) \right) \frac{dh}{|h|^{d+2\alpha}}, \\ n_\varepsilon(0,x) = n_\varepsilon^0(x). \end{cases} \tag{2.6}$$

With this rescaling we are able to capture the exponential speed of propagation and obtain a result which is equivalent with the one given in [CR13]. To this end, we make the following assumption

$$0 \le n_\varepsilon(0,x) \le \frac{C}{1+|x|^{\frac{d+2\alpha}{\varepsilon}}}, \tag{2.7}$$

which is indeed equivalent with (2.3) after rescaling (2.5).
Here is our main result:

Theorem 2.1 (Exponential speed of propagation [MM15]). *Let n_ε be the solution of* (2.6). *Under assumption* (2.7)*, as $\varepsilon \to 0$, we have*

$$\begin{cases} n_\varepsilon \to 0, & \textit{locally uniformly in } \mathcal{A} = \{(t,x) \in (0,\infty) \times \mathbb{R}^d \,|\, t < (d+2\alpha)\log|x|\}, \\ n_\varepsilon \to 1, & \textit{locally uniformly in } \mathcal{B} = \{(t,x) \in (0,\infty) \times \mathbb{R}^d \,|\, t > (d+2\alpha)\log|x|\}. \end{cases}$$

Note that this result is equivalent with (2.4) proven in [CR13].

One may wonder why the rescaling (2.5) does not depend on α. Finding a relevant rescaling that would capture such exponential dynamics is indeed a major contribution of our work in [MM15]. Understanding the transition from exponential speed of propagation to constant speed of propagation as $\alpha \to 1$ is indeed very helpful to understand why our rescaling does not depend on α. In [CR12], A.-C. Coulon and J.-M. Roquejoffre studied such transition as $\alpha \to 1$. They proved that when $\alpha < 1$, the position of the front scales ultimately as $e^{\frac{t}{d+2\alpha}}$ for $t > t_\alpha$, with t_α a positive constant depending on α. At intermediate times, the position of the front scales as $2t^{1/\alpha}$. As $\alpha \to 1$, t_α tends to infinity and the front will ultimately move as $2t$.
With our asymptotic analysis, we fix α and we let $\varepsilon \to 0$. That is we study the large time behavior and in particular at the limit we only capture the dynamics corresponding to $t > t_\alpha$. This means that we capture only the exponential speed of propagation and our method does not allow to capture the transition from exponential speed to constant speed of propagation as $\alpha \to 1$.

In Subsection 2.2.1 we provide the main ingredients of the proof of our result. We also show that at the limit $\varepsilon = 0$ the only impact of the fractional laplacian is at the initial time when it determines the thickness of the tails of the solution. At positive times, the fractional laplacian does not have any impact on the dynamics of the solution which are determined uniquely by the reaction term. This is an important difference with the classical Fisher-KPP equation, where the Laplace term not only forces the solution to have an exponential tail but also it still influences in positive times the dynamics and modifies the speed of propagation.

2.2.1 The main ingredients of the proof and the impact of the fractional laplacian on the dynamics

A main ingredient in the proof of Theorem 2.1 is the fact that with the rescaling (2.5) the term $(\mathcal{L}_\varepsilon n_\varepsilon)n_\varepsilon^{-1}$ vanishes as $\varepsilon \to 0$. More precisely we find sub and supersolutions to (2.6) which are indeed sub and supersolutions to a perturbation of an ordinary differential equation derived from (2.6) by omitting the term coming from the fractional laplacian. They also have the property that when one applies the operator $(\mathcal{L}_\varepsilon f)f^{-1}$ to such functions, the outcome is very small.

To prove such results, we use the Hopf-Cole transformation. To show why such transformation is still relevant, we recall the following bounds on the transition probability function p associated with the fractional laplacian with coefficient α (see, e.g., Sato [Sat99] p.89 and p.202):

$$\frac{B_m}{t^{\frac{d}{2\alpha}}(1+|t^{\frac{-1}{2\alpha}}x|^{d+2\alpha})} \le p(t,x) \le \frac{B_M}{t^{\frac{d}{2\alpha}}(1+|t^{\frac{-1}{2\alpha}}x|^{d+2\alpha})}. \tag{2.8}$$

Note that the solution v to the following equation

$$\begin{cases} \partial_t v + (-\Delta)^\alpha v = 0, & \text{in } \mathbb{R} \times \mathbb{R}^+, \\ v(x,0) = v^0, & \text{in } \mathbb{R}, \end{cases}$$

satisfies

$$v(t,x) = \int_{\mathbb{R}} p(y,t)v^0(x-y)dy.$$

The inequality (2.8) is written after the rescaling (2.5) as

$$\frac{B_m}{(\frac{t}{\varepsilon})^{\frac{d}{2\alpha}}(1+|(\frac{t}{\varepsilon})^{\frac{-1}{2\alpha}}|x|^{\frac{1}{\varepsilon}}|^{d+2\alpha})} \leq p_\varepsilon(|x|,t) = p(|x|^{\frac{1}{\varepsilon}}, \frac{t}{\varepsilon}) \leq \frac{B_M}{(\frac{t}{\varepsilon})^{\frac{d}{2\alpha}}(1+|(\frac{t}{\varepsilon})^{\frac{-1}{2\alpha}}|x|^{\frac{1}{\varepsilon}}|^{d+2\alpha})}, \tag{2.9}$$

Being inspired now by (2.9) we use the classical Hopf-Cole transformation

$$n_\varepsilon = \exp\left(\frac{u_\varepsilon}{\varepsilon}\right), \tag{2.10}$$

and make the following assumption

$$\frac{C_m}{1+|x|^{\frac{d+2\alpha}{\varepsilon}}} \leq n_\varepsilon(x,0) \leq \frac{C_M}{1+|x|^{\frac{d+2\alpha}{\varepsilon}}}, \quad \text{with } C_m < 1 < C_M. \tag{2.11}$$

Note that this property can be obtained thanks to assumption (2.7), the estimates (2.8) on the heat kernel, and a translation in time. We then prove the following.

Theorem 2.2. *Let* n_ε *be the solution of* (2.6) *and* u_ε *be given by* (2.10)*. Under assumption* (2.11)*, as* $\varepsilon \to 0$*,* (u_ε) *converges locally uniformly to* u*, which is the unique solution to*

$$\begin{cases} \max(\partial_t u - 1, u) = 0, \\ u(0,x) = \min(0, -(1+\alpha)\log|x|). \end{cases} \tag{2.12}$$

Therefore, u *is given by*

$$u(t,x) = \min(0, -(1+\alpha)\log|x| + t).$$

This result is a main ingredient in the proof of Theorem 2.1. Note that it is immediate from (2.10) that in the set $\{u<0\}$, $n_\varepsilon \to 0$, as $\varepsilon \to 0$. We also prove, using an appropriate viscosity test function, that in the set $\{u = 0\}$, $n_\varepsilon \to 1$, as $\varepsilon \to 0$.

In view of (2.12), we notice that at the limit $\varepsilon = 0$, the fractional laplacian does not have any impact on the dynamics of u and the dynamics are determined only by the reaction term. The only role of the fractional laplacian in the limit is at the first initial time where the tail of the solution is forced to satisfy (2.11). The exponential propagation is hence derived only from the form of the solution at the initial layer. This is an important difference with the KPP equation with the classical laplacian where, the Laplace term not only forces the solution to have an exponential tail but also it still influences in positive times the dynamics and modifies the speed of propagation. To observe this property consider the following equation

$$\begin{cases} \partial_t m - \delta\Delta m = m(1-m), & \delta \in \{0,1\}, \\ m(x,0) = \exp\left(-\frac{x^2}{2}\right). \end{cases}$$

It is easy to verify that in long time the invasion front scales as $x \sim \sqrt{2t}$ for $\delta = 0$, while for $\delta = 1$ the invasion front scales as $x \sim 2t$. Therefore, the diffusion term speeds up the propagation. Next we consider an analogous equation but with fractional laplacian:

$$\begin{cases} \partial_t m + \delta(-\Delta)^\alpha m = m(1-m), & \delta \in \{0,1\} \quad \alpha \in [0,1], \\ m(x,0) = m^0(x), \quad \text{with } \frac{C_m}{1+|x|^{d+2\alpha}} \leq m^0 \leq \frac{C_M}{1+|x|^{d+2\alpha}}. \end{cases}$$

Then following the computations above, in long time and for both cases $\delta = 0, 1$, the invasion front scales as $x \sim e^{\frac{t}{d+2\alpha}}$.

2.3 Fractional selection-mutation equation

We now go back to the case of fractional selection-mutation model (2.1). In Subsection 2.3.1 we compare the behavior of (2.1) with classical selection-mutation models and discuss the choice of the rescaling, being inspired from the rescaling (2.5) for the fractional Fisher-KPP equation. In Subsection 2.3.2 we provide our assumptions and in Subsection 2.3.3 we present our main results. Finally in Subsection 2.3.4 we provide the main ideas of the proof.

2.3.1 The choice of the rescaling

Before providing our rescaling of the fractional selection-mutation model, we first compare the behavior of such equation with classical selection-mutation equations. To have an idea of the difference of selection-mutation models with fractional or classical Laplace terms, we compare the numerical resolutions of (2.1) and (1.1) in Figure 2.1, considering the following parameters

$$R(z,\rho) = 1 + \exp(2 - \frac{z^2}{5}) - \rho, \qquad \sigma = 1, \qquad n(0,z) = \exp\big(-\frac{(z+2)^2}{0.5}\big). \tag{2.13}$$

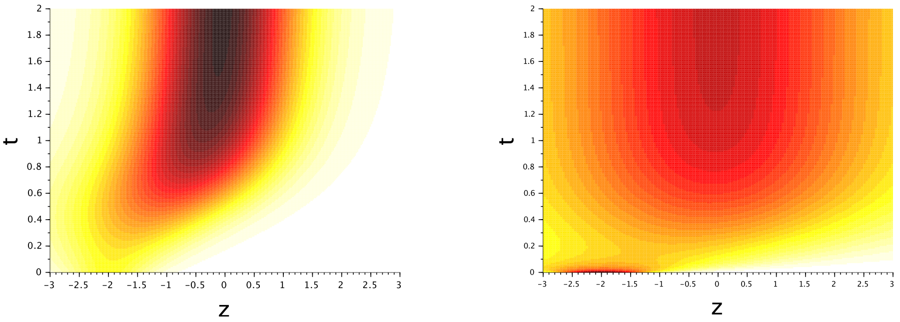

Figure 2.1: Left: the numerical resolution of (1.1) with the parameters given in (2.13) and with $I = \rho$. The colors represent the different values of the phenotypic density n. Right: the numerical resolution of (2.1) with the same parameters. We observe that in both cases the initial solution has a distribution centered around the point $z = -2$, and that this distribution moves gradually to the right and it will ultimately be centered around the point $z = 0$ which is the optimal trait corresponding to the growth rate given in (2.13). However, in the case with the fractional diffusion, i.e. the figure at the right hand side, the evolution of the phenotypic distribution is much faster and almost immediately the distribution becomes centered around the point $z = 0$. Moreover, this distribution is much wider because of the presence of large jumps with a high rate.

Note that here we have considered $\psi \equiv 1$ such that $\rho = I$. Moreover, with the above choice of R, assumptions (1.4)–(1.7) are satisfied.
We observe that in both cases the initial solution has a distribution centered around the point $z = -2$, and that this distribution moves gradually to the right and it will ultimately be centered around the point $z = 0$ which is the optimal trait corresponding to the growth rate given in (2.13). However, in the case with the fractional diffusion, the evolution of the phenotypic distribution is much faster and almost immediately the distribution becomes centered around the point $z = 0$.

Moreover, this distribution is much wider because of the presence of large jumps with a high rate.

It is also interesting to compare (2.1) with selection-mutation models where the mutations are described by an integral kernel with thin tails:

$$\begin{cases} \partial_t n = \int_{\mathbb{R}^d} \big(n(t,z+h) - n(t,z)\big) b(z) K(h) dh + R(z,\rho), \\ \rho(t) = \int_{\mathbb{R}^d} n(t,z) dz. \end{cases} \tag{2.14}$$

Here K corresponds to a mutation law, i.e. $K(h)$ is the probability of a mutation jump with size h. The other terms are as above.
Such selection-mutation model has been derived from stochastic individual based models, in the limit of large populations in [CFM06, CFM08]. In the case where K has thin tails, i.e. the decay of K is faster than exponential, an asymptotic study of (2.14), analogous to the one presented in Chapter 1, has been provided in [BMP09]. Such analysis, which assumes again small effect of mutations and long time, is based on the following rescaling

$$t \to \frac{t}{\varepsilon}, \qquad K(h) \to K(\frac{h}{\varepsilon})\frac{dh}{\varepsilon},$$

such that (2.14) becomes

$$\begin{cases} \varepsilon \partial_t n_\varepsilon = \int_{\mathbb{R}^d} \big(n_\varepsilon(t,z+\varepsilon h) - n_\varepsilon(t,z)\big) b(z) K(h) dh + R(z,\rho_\varepsilon), \\ \rho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,z) dz. \end{cases} \tag{2.15}$$

With this scaling, which is closely related to the one in (1.3), a Hamilton-Jacobi equation with constrained is derived which allows to capture a concentration phenomenon for n_ε, similarly to the one obtained for (1.3) in Chapter 1. However, this rescaling would not be adapted to study the fractional selection-mutation model (2.1). In particular, the limiting Hamilton-Jacobi equation derived in [BMP09], that is

$$\partial_t u(t,z) = \int e^{\nabla u(t,z)\cdot h} K(h) dh + R(z,\rho(t)),$$

will not be well-defined here, because of the algebraic decay of the integral kernel.

The above observations show that in order to capture concentration phenomena in fractional selection-mutations models a new rescaling is required. In [MM15], being inspired by the rescaling for the fractional Fisher-KPP equation introduced in Section 2.2, we provide a rescaling for (2.1) leading to the concentration of the phenotypic density as a Dirac mass. In what follows we show how such rescaling is derived.

Although, for the classical Fisher-KPP equation, the long range and long time rescaling coincides with the one with small diffusion steps and long time, this is not the case for the fractional Fisher-KPP equation. To understand this better, we rewrite (2.6) in a simple case, that is for $d=1$, $x \neq 0$ and assuming that the solution n is symmetric such that $n(x) = n(-x)$:

$$\begin{aligned} \varepsilon \partial_t n_\varepsilon(t,x) &= \int_0^\infty \Big(n_\varepsilon(t, ||x|^{1/\varepsilon} + h|^\varepsilon) - n_\varepsilon(t, ||x|^{1/\varepsilon} - h|^\varepsilon) - 2n_\varepsilon(t,x)\Big) \frac{dh}{|h|^{1+2\alpha}} \\ &\quad + n_\varepsilon(t,x)\,(1 - n_\varepsilon(x,t)) \\ &= |x|^{\frac{-2\alpha}{\varepsilon}} \int_0^\infty \left(n_\varepsilon\left(t, |x| + |x|((1+r)^\varepsilon - 1)\right) + n_\varepsilon\left(t, |x| + |x|(|1-r|^\varepsilon - 1)\right) - 2n_\varepsilon(t,x)\right) \frac{dr}{r^{1+2\alpha}} \\ &\quad + n_\varepsilon(t,x)\,(1 - n_\varepsilon(t,x)). \end{aligned}$$

Here we have used the following change of variable:

$$h = |x|^{\frac{1}{\varepsilon}} r, \quad \text{so that} \quad |x|^{\frac{1}{\varepsilon}} \pm h = |x|^{\frac{1}{\varepsilon}}(1 \pm r).$$

We observe that this rescaling is heterogeneous in x, and the diffusion steps are rescaled differently at different points.

Since in the context of selection-mutation models, the rescaling is on the size of the mutations and not on the variable z to consider the long range limit, the non homogeneity in the mutation kernel induced by (2.5) is not realistic. Therefore, in this case, we rescale the mutation step instead of the point z but following the same structure of rescaling. More precisely, we consider the following rescaling where the mutation kernel remains independent of z:

$$\begin{aligned} \varepsilon\partial_t n_\varepsilon(t,z) \quad &= \textstyle\int_0^\infty \int_{\nu \in S^{d-1}} \left(n_\varepsilon(t, z + ((1+r)^\varepsilon - 1)\nu) - n_\varepsilon(t,z)\right) \frac{dSdr}{r^{1+2\alpha}} \\ &+ n_\varepsilon(t,z)\, R(z, \rho_\varepsilon(t)). \end{aligned} \tag{2.16}$$

Here dS is the sphere element for the unit sphere. Note that the power of r in the above integral is now $1+2\alpha$ and does not depend on the dimension d anymore because of the change of variable. With this rescaling, where ε is a small parameter, we consider much smaller mutation steps than the scaling considered for the classical case (2.15). Here, the parameter ε appears as a power for the size of mutations, instead of a multiplicative constant. However, the mutation distribution has still algebraic law, but with a large power. Moreover, while the mutation distribution did not have a variance before rescaling, the rescaled mutation distribution has a small variance of order $O(\varepsilon^2)$, similarly to the case of classical selction-mutation (2.15). This property is an important element to obtain the concentration of the phenotypic density with a similar behavior to the one obtained for (2.14) or (1.1). We present in Figure 2.2 the numerical resolution of (2.16) with $\varepsilon = .01$ and compare it to the numerical resolution of (1.3) using the following parameters:

$$R(z,\rho) = 1 + \exp(2 - \frac{z^2}{5}) - \rho, \qquad \varepsilon = 0.01, \qquad n(0,z) = \exp\big(-\frac{(z+2)^2}{0.5\varepsilon}\big). \tag{2.17}$$

We observe that the dynamics of the solutions are qualitatively very close. The solution now concentrates at a dominant trait which evolves gradually and converges ultimately to the optimal trait $z = 0$.

For our analysis, it is helpful to rewrite the above equation with a change of variable:

$$r = e^k - 1,$$

which leads to

$$\begin{cases} \varepsilon\partial_t n_\varepsilon(t,z) = \int_0^\infty \int_{\nu\in S^{d-1}} \big(n_\varepsilon(t, z + (e^{\varepsilon k} - 1)\nu) - n_\varepsilon(t,z)\big) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dSdk + n_\varepsilon(t,z)\, R(z, \rho_\varepsilon(t)), \\ \rho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,z)dz, \\ n_e(x,0) = n_\varepsilon^0(x). \end{cases} \tag{2.18}$$

2.3.2 Assumptions

Our analysis is still based on the Hopf-Cole transformation

$$n_\varepsilon = \exp\left(\frac{u_\varepsilon}{\varepsilon}\right). \tag{2.19}$$

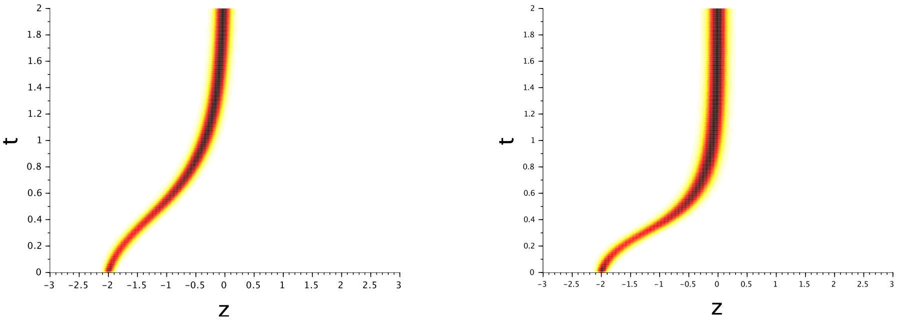

Figure 2.2: Left: the numerical resolution of (1.3) with the parameters given in (2.17) and with $I = \rho$. The colors represent the different values of the phenotypic density n. Right: the numerical resolution of (2.16) with the same parameters. In both figures, the population concentrates at a dominant trait which evolves with time. .

Our assumptions are analogous to the ones used in [BMP09] for the model with thin tailed mutation kernels:
We assume that there are two constants $0 < \rho_m < \rho_M < \infty$ such that

$$\min_{z\in\mathbb{R}^d} R(z,\rho_m) = 0, \qquad \max_{z\in\mathbb{R}^d} R(z,\rho_M) = 0. \tag{2.20}$$

The l.h.s. condition above means that all the traits are viable such that the growth rate of all individuals become positive when the competition is not strong. The r.h.s. condition means that the resources are limited such that the growth rate of all individuals become negative if the competition is too strong.
We also assume that the growth rate is a decreasing function of the competition term, that is there exists a constants $K_1 > 0$ such that, for any $z \in \mathbb{R}^d$, $\rho \in \mathbb{R}$,

$$-K_1 \leq \frac{\partial R}{\partial \rho}(z,\rho) \leq -K_1^{-1} < 0. \tag{2.21}$$

We also make the following technical assumption

$$\sup_{\frac{\rho_m}{2}\leq\rho\leq 2\rho_M} \| R(\cdot,\rho) \|_{W^{2,\infty}(\mathbb{R}^d)} < K_2. \tag{2.22}$$

Moreover, we make the following assumptions on the initial data:

$$(u_\varepsilon^0)_\varepsilon \text{ is a sequence of continuous functions which converge in } C_{\text{loc}}(\mathbb{R}^d) \text{ to } u^0, \text{ as } \varepsilon \to 0, \tag{2.23}$$

and there exists a constant $A < \alpha$ such that

$$n_\varepsilon^0(z) \leq \frac{C_0}{\big(C_1(1+|z|)\big)^{\frac{2A}{\varepsilon}}}, \tag{2.24}$$

$$\rho_m \leq \int_{\mathbb{R}^d} n_\varepsilon^0(z)dz \leq \rho_M. \tag{2.25}$$

2.3.3 Main results

Our main result is the following.

Theorem 2.3. *Let n_ε be the solution of* (2.18) *and* $u_\varepsilon = \varepsilon \log n_\varepsilon$*. Assume* (2.20)–(2.25)*. Then, along subsequences as $\varepsilon \to 0$, (ρ_ε) converges a.e. to ρ and (u_ε) converges locally uniformly to a function u which is Lipschitz continuous with respect to z and continuous in t, such that*

$$\|D_z u\|_{L^\infty(\mathbb{R}^d\times\mathbb{R}^+)} \le 2\alpha, \qquad u(t,z+h) - u(t,z) \le 2\alpha \log(1+|h|), \qquad \text{for all } z,h\in\mathbb{R}^d. \tag{2.26}$$

Moreover, u is a viscosity supersolution to the following equation

$$\begin{cases} \partial_t u - \int_0^\infty \int_{\nu\in S^{d-1}} \left(e^{kD_z u\cdot\nu} - 1\right) \frac{e^k dSdk}{|e^k-1|^{1+2\alpha}} = R(z,\rho), \\ u(z,0) = u^0(z). \end{cases} \tag{2.27}$$

For fixed ρ, u is indeed the minimal viscosity supersolution of (2.27) *satisfying* (2.26)*. Moreover, u satisfies the following constraint*

$$\max_{z\in\mathbb{R}^d} u(t,z) = 0, \qquad \text{for all } t>0. \tag{2.28}$$

It is also a viscosity subsolution of (2.27) *in the following weak sense. Let's $\varphi \in \mathrm{C}^2(\mathbb{R}^+\times\mathbb{R}^d)$ be a test function such that $u-\varphi$ takes a maximum at (t_0,z_0) and*

$$\varphi(t,z+h) - \varphi(t,z) \le (2\alpha-\xi)\log(1+|h|), \qquad \text{for all } (t,z)\in B_r(t_0,z_0) \text{ and } h\in\mathbb{R}^d,$$

with r and ξ positive constants. Then, we have

$$\partial_t\varphi(t_0,z_0) - \int_0^\infty \int_{\nu\in S^{d-1}} \left(e^{kD_z\varphi(t_0,z_0)\cdot\nu} - 1\right) \frac{e^k dSdk}{|e^k-1|^{1+2\alpha}} \le \limsup_{s\to t_0} R(z,\rho(s)).$$

A main difficulty in this convergence result is that the Hamiltonian in the above Hamilton-Jacobi equation can take infinite values and that the limit is not necessarily a viscosity solution to (2.27). Another difficulty comes from the fact that the term $\rho(t)$ is only BV and potentially discontinuous.

The above Hamilton-Jacobi equation can indeed take infinite values when $|D_z u| \ge 2\alpha$. This property leads to the Lipschitz regularity result in (2.26). The second regularity result in (2.26), which is stronger than the first one, is not a characteristic of a solution to (2.27) and it is not generally satisfied by a Hamilton-Jacobi equation of this type. This property comes from the original problem with ε. These regularity properties do not hold necessarily at the initial time, which means that a strong regularizing effect is associated with this problem.

Note that in Theorem 2.3 we do not characterize the limit u as a viscosity solution to a Hamilton-Jacobi equation with constraint, as was the case in the previous results on such selection-mutation models (see for instance [DJMP05, PB08, BMP09]). We only prove that u is the minimal viscosity supersolution to (2.27) satisfying (2.26) and a viscosity subsolution in a weak sense. One can wonder if u is indeed a viscosity solution to (2.27). We do not expect this assertion to be true in general. In [Mir], we provide an example of a Hamilton-Jacobi equation of similar type which has a solution that does not satisfy the second inequality in (2.26). Existence of such solutions together with the uniqueness of viscosity solutions to Hamilton-Jacobi equations of type (2.27), with fixed ρ, (see [BC13], Section 6) indicates that u might not be a viscosity solution of (2.27) in

general. Note that, of course, thanks to the comparison principle for fixed ρ, u is always greater than (or equal to) the unique viscosity solution of (2.27).
The information obtained in Theorem 2.3 still allows to obtain the concentration of the population's density as Dirac masses, analogously to the previous works [PB08, BMP09]:

Theorem 2.4. *Let* n_ε *be the solution of* (2.18)*. Assume* (2.20)*–*(2.25)*. Then, along subsequences as* $\varepsilon \to 0$*,* n_ε *converges in* $\mathrm{L}^\infty\left(\mathrm{w}{*}(0,\infty);\mathcal{M}^1(\mathbb{R}^d)\right)$ *to a measure* n*, such that,*

$$\mathit{supp}\, n(t,\cdot) \subset \{z \,|\, u(t,z) = 0\}, \qquad \textit{for a.e. } t.$$

Moreover, for all continuous points of $\rho(t)$*, we have*

$$\{z \,|\, u(t,z) = 0\} \subset \{z \,|\, R(z,\rho(t)) = 0\}.$$

In particular, if $z \in \mathbb{R}$ *and* R *is monotonic with respect to* z*, then for a.e.* $t > 0$*,*

$$n(t,z) = \rho(t)\,\delta(z - \overline{z}(t)).$$

2.3.4 The main elements of the proof

We replace the Hopf-Cole transformation (2.19) in (2.18):

$$\partial_t u_\varepsilon(t,z) = \int_0^\infty \int_{\nu \in S^{d-1}} (e^{\frac{u_\varepsilon(t,z+(e^{\varepsilon k}-1)\nu)-u_\varepsilon(t,z)}{\varepsilon}} - 1)\frac{e^k}{|e^k-1|^{1+2\alpha}} dSdk + R(z,\rho_\varepsilon(t)).$$

This equation converges formally to (2.27). The following properties would allow to obtain the convergence of the integral term:

$$\|D_z u_\varepsilon\|_{L^\infty(\mathbb{R}\times\mathbb{R}^+)} < 2\alpha, \qquad u_\varepsilon(t,z+h) - u_\varepsilon(t,z) < 2\alpha \log(1+|h|).$$

We prove these properties (with non-strict inequalities as given by (2.26)) and the convergence of (u_ε) simultaneously.

To prove the convergence of (u_ε) we use the method of semi-relaxed limits [BP88] in the theory of viscosity solutions. However, since the Hamiltonian in (2.27) takes infinite values and since the limit u is not in general a viscosity solution of (2.27), we cannot use this method in a classical manner and further work is required. This issue is indeed closely related to the work in [BC13] where a large deviation type result has been obtained for a Lévy type nonlocal operator where the integral kernel has at most exponential tails. In the case where the integral kernel has exponential tails, a Hamilton-Jacobi equation close to (2.27), without the growth term, is obtained at the limit. However, in that case the function obtained at the limit does not satisfy necessarily the second regularity result in (2.26) and it is indeed a viscosity solution to the Hamilton-Jacobi equation.

To provide a main idea in the proof, we first recall the classical method of semi-relaxed limits. We first define the semi-relaxed limits:

$$\overline{u}(t,x) = \limsup_{\substack{(s,y)\to(t,x)\\ \varepsilon\to 0}} u_\varepsilon(s,y), \qquad \underline{u}(t,x) = \liminf_{\substack{(s,y)\to(t,x)\\ \varepsilon\to 0}} u_\varepsilon(s,y).$$

With the classical method, one would prove that $\overline{u}$ and $\underline{u}$ are respectively sub and supersolution to the limit Hamilton-Jacobi equation (that is (2.27) here). Such properties usually hold because of the stability properties of the viscosity solutions. Then, if the problem admits a strong comparison principle (for discontinuous solutions), we can deduce that

$$\overline{u} \leq \underline{u}.$$

However, by definition, we also have

$$\underline{u} \leq \overline{u}.$$

Combining the above inequalities we deduce that $\underline{u} = \overline{u}$ and (u_ε) converges locally uniformly to $u := \underline{u} = \overline{u}$.

Here, since the Hamiltonian takes infinite values and since the limit u is not necessarily a subsolution to (2.27) we cannot expect to prove that $\overline{u}$ is a subsolution to (2.27). However, we can prove that $\underline{u}$ is a viscosity supersolution to (2.27) and it satisfies (2.26). We also prove that $\overline{u}$ is a viscosity subsolution to (2.27) in the weak sense as defined in Theorem 2.4. We then modify $\underline{u}$ to make it smooth and an admissible test function such that we can compare it with $\overline{u}$ to obtain that $\overline{u} \leq \underline{u}$.

2.4 Fractional Fisher-KPP equation in a periodically hostile environment

2.4.1 Model and motivations

We study the following equation

$$\begin{cases} \partial_t n + (-\Delta)^\alpha n = n(1-n) & \text{in } (0,\infty) \times \Omega, \\ n = 0 & \text{in } (0,\infty) \times \Omega^c, \\ n(0,x) = n_0(x), \end{cases} \tag{2.29}$$

with A a positive constant and

$$\Omega = \cup_{k\in\mathbb{Z}} (2kA, (2k+1)A).$$

Equation (2.29) models the growth and the invasion of a species subject to a non-local dispersion in a periodically hostile environment. The function n stands for the density of the population. The fractional Laplacian describes the motions of individuals, it takes into account the possibility of "jump" (move rapidly) of individuals from one point to another with a high probability, for instance because of the wind for seeds and polens or human transportation for animals. The logistic term $n(1-n)$ represents the growth rate of the population. The originality of this model is the following, we forbid our species to invade some periodic patches and thus the reachable areas are disconnected. This is for instance to consider the presence of obstacles as sees, lakes, or urban zones. Here, we assume that the regions where the species can develop itself are homogeneous. Thanks to the non-local diffusion (which models the "jumps"), the species will invade all the "good" patches and the solution will converge to a non-null stable stationary state with a speed which grows exponentially fast.

Many works deal with the case of a standard diffusion with homogenous or heterogeneous environment (see [Fis37, KPP37, AW78, GF79]). More close to this work, Guo and Hamel in [GH12] treat a Fisher-KPP equation with periodically hostile regions and a standard diffusion. The authors prove that the stable state will invade the unstable state in the connected component of the initial data. In our work, thanks to the non-local character of the fractional Laplacian, contrary to what happens in [GH12], we show that there exists a unique non-trivial positive bounded stationary state. Moreover this stationary state invades the unstable state 0 everywhere and not only on the connected component of the initial data. Existence and uniqueness of steady solutions to fractional KPP type equations in periodic media, without obstacles, was stablished in [BRR11]. Next, in [CCR12] it was proved that such steady solution invades the unstable state 0 with an exponential speed (see also [LÍ9, ST19] for alternative proofs). The work in this section extends those results to the case of periodically hostile environments.

2.4.2 Assumptions and main results

We assume that

$$A \geq A_0, \tag{2.30}$$

where A_0 is such that for all $A \geq A_0$ the principal eigenvalue λ_A of the Dirichlet operator $(-\Delta)^\alpha - Id$ in $(0, A)$ is negative (the existence of such A_0 is provided by [BRR11]). In other words, there exists a function φ_A and a constant λ_A such that

$$\begin{cases} ((-\Delta)^\alpha \varphi_A - \varphi_A = \lambda_A \varphi_A, & \text{in } (0, A), \\ \varphi_A = 0, & \text{in } \mathbb{R} \setminus (0, A), \\ \varphi_A \geq 0, \lambda_A < 0. \end{cases}$$

We also define λ_0 to be the principal eigenvalue to the problem in Ω:

$$\begin{cases} ((-\Delta)^\alpha \varphi_0 - \varphi_0 = \lambda_0 \varphi_0, & \text{in } \Omega, \\ \varphi_0 = 0, & \text{in } \Omega^c, \\ \varphi_0 \geq 0. \end{cases}$$

We prove the following.

Theorem 2.5. *Under the assumption* (2.30)*, there exists a unique positive and bounded stationary state* n_+ *to* (2.29)*. Moreover, we have* $0 \leq n_+ \leq 1$ *and* n_+ *is* $2A$*-periodic.*

The existence is due to the negativity of the principal eigenvalue of the Dirichlet operator $(-\Delta)^\alpha - Id$ in $(0, A)$ which allows to construct by an iterative method a stationary state. To prove the uniqueness, we first prove that thanks to the non-local character of the fractional Laplacian, all the bounded stationary states behave like

$$\delta(x) = \text{dist}(x, \partial\Omega)^\alpha 1_\Omega(x).$$

Hence, thanks to the maximum principle and the fractional Hopf Lemma (see [GS16]), we obtain the result. We should underline that the uniqueness is clearly due to the non-local diffusion operator and it does not hold in the case of a standard diffusion term ($\alpha = 1$).

We next focus on the propagation phenomena. Let's first recall the state of the art on related problems. The question of propagation in a Fisher-KPP type equation involving a fractional Laplacian in a constant environment was first treated by X. Cabré and J.-M. Roquejoffre in [CR13]. They proved that the front position is exponential in time. Next, X. Cabré, A. Coulon and J.-M. Roquejoffre proved in [CCR12] the convergence to a stationary state with an exponential speed in a periodic heterogeneous environment. Thanks to the asymptotic approach introduced in Subsection 2.2, in [MM15] with S. Méléard we proved the result of an exponential speed of propagation in a constant environment. More recently, [BGHP18, ST19, LÍ9] extended this approach to derive the speed of propagation for different non-local operators in the case of a homogeneous environment for [BGHP18] and a periodic environment for [ST19, LÍ9].

To study the present model we followed the general idea introduced in [MM15] and Section 2.2. We expect that in large time the propagation front is located in

$$\mathcal{B} = \{(t,x) \in \mathbb{R}^+ \times \mathbb{R} \,|\, (1+2\alpha)\log|x| < \lambda_0 t\}.$$

We then perform the long time-long range rescaling (2.5) to capture the effective behavior of the solution. We thus define

$$n_\varepsilon(t,x) = n(\frac{t}{\varepsilon}, |x|^{1/\varepsilon}\frac{x}{|x|}), \qquad n_{\varepsilon,+}(t,x) = n_+(\frac{t}{\varepsilon}, |x|^{1/\varepsilon}\frac{x}{|x|}).$$

To present our result we introduce the following notations, for $\nu, \varepsilon > 0$,

$$\Omega_\nu = \{x \in \Omega \,|\, \mathrm{dist}(x, \partial\Omega) > \nu\}, \qquad \Omega^\varepsilon = \{x \in \mathbb{R} \,|\, |x|^{1/\varepsilon}\frac{x}{|x|} \in \Omega\}.$$

We also make the following assumption on the initial condition

$$n_0 \in C^0(\mathbb{R}^+ \times \mathbb{R}) \cap C_c^\infty(\mathbb{R}^+ \times \Omega), \qquad n_0 \not\equiv 0. \tag{2.31}$$

This is our main result:

Theorem 2.6. *Assume* (2.30) *and* (2.31)*. Then, as* $\varepsilon \to 0$,
(i) n_ε *converges locally uniformly to* 0 *in* $\{(t,x) \in \mathbb{R}^+ \times \mathbb{R} \,|\, (1+2\alpha)\log|x| > \lambda_0 t\}$.
(ii) $\frac{n_\varepsilon}{n_{\varepsilon,+}}$ *converges locally uniformly to* 1 *in* $\big((0,\infty) \times \Omega^\varepsilon\big) \cap B$.

A direct consequence of this result is the invasion of the unstable state by the stable state:

Corollary 2.7. *Assume* (2.30) *and* (2.31)*. Then, for all* $\nu > 0$,
(i) $\lim\limits_{t\to+\infty} n(t,x) = 0$ *uniformly in* $\{(t,x) \,|\, |x| \geq e^{Ct}\}$, *for all* $C > \frac{|\lambda_0|}{1+2\alpha}$.
(ii) $\lim\limits_{t\to+\infty} n(t,x) = n_+(x)$ *uniformly in* $\{(t,x) \,|\, |x| \leq e^{ct}\} \cap\ (0,\infty) \times \Omega_\nu$, *for all* $c < \frac{|\lambda_0|}{1+2\alpha}$.

Note that the main new difficulty to study this problem comes from the Dirichlet boundary condition. We modify the previous sub and supersolutions introduced for the KPP equation in Section 2.2 carefully and in particular by multiplying by the principal eigenfunction associated to the operator $(-\Delta)^\alpha - Id$ in $\Omega_{\pm\nu}$. Note that these sub and supersolutions have algebraic decay at infinity. Obviously, we cannot put the subsolution below n_0. However, using heat kernel estimates, we are able to put the subsolution below the solution n for $t \geq 1$. Finally, to prove the convergence of n_ε, we use the method of perturbed test functions from the theory of viscosity solutions and homogenization (introduced by Evans [Eva89, Eva92]).

Chapter 3

Evolutionary adaptation in space-heterogeneous environments

3.1 Introduction

This chapter is devoted to the study of the evolutionary dynamics of a population in a heterogeneous environment with a discrete spatial structure. Spatially heterogeneous selection is ubiquitous and constitutes a potent evolutionary force that promotes the emergence and the maintenance of biodiversity. Spatial variation in selection can yield adaptation to local environmental conditions, however, other evolutionary forces like migration and mutation tend to homogenize the spatial patterns of differentiation and thus to impede the build up of local adaptation. Understanding the balance between these contrasted evolutionary forces is a major objective of evolutionary biology theory [Sla78, Whi15, SLM13]) and could lead to a better understanding of the speciation process and the evolutionary response to global change [DD03, LDD08].

In the previous chapters we saw that an approach based on Hamilton-Jacobi equations with constraint allows to describe the evolutionary dynamics of phenotypically structured populations in homogeneous environments. Is it possible to extend this approach to study heterogeneous environments? Are the limiting solutions still in the form of sums of Dirac masses? Does the heterogeneity lead to polymorphic situations? In this chapter we extend the Hamilton-Jacobi approach to the case of spatially heterogeneous environments. In chapter 4 we will focus on time heterogeneous environments.

A main part of the work presented in this chapter has been done in the framework of a collaboration project with S. Gandon who is a biologist. The objective of this project was to show, via the particular model considered in this work, how the Hamilton-Jacobi approach can be used to bring insight into current biological questions.

We study the following system, for $z \in \mathbb{R}^d$,

$$\begin{cases} -\varepsilon^2 \Delta n_{\varepsilon,1}(z) = n_{\varepsilon,1}(z) R_1(z, \rho_{\varepsilon,1}) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\ -\varepsilon^2 \Delta n_{\varepsilon,2}(z) = n_{\varepsilon,2}(z) R_2(z, \rho_{\varepsilon,2}) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z), \\ \rho_{\varepsilon,i} = \int_{\mathbb{R}^d} n_{\varepsilon,i}(z) dz, \qquad \text{for } i = 1, 2. \end{cases} \tag{3.1}$$

This system represents the equilibrium of a population that is structured by a phenotypic trait

z, and which is subject to selection, mutation and migration between two habitats. We denote by $n_{\varepsilon,i}(z)$ the phenotypic density, and by $\rho_{\varepsilon,i}$ the total population size in habitat i. The term $R_i(z,\rho_{\varepsilon,i})$ represents the growth rate of the individuals with trait z in habitat i and it is a decreasing function of the total population size $\rho_{\varepsilon,i}$ taking into account in this way a local competition between individuals. The nonnegative constants m_i are the migration rates between the habitats. The diffusion terms correspond to the mutations and ε is an effective size of the mutations.

In this work, we study the asymptotic behavior of (3.1), as $\varepsilon \to 0$. Using the Hamilton-Jacobi approach, we characterize the solution of (3.1) for ε small. we show that the population's phenotypical distribution has at most two peaks and we give explicit conditions under which the population will be monomorphic (unimodal distribution) or dimorphic (bimodal distribution). More importantly, we determine the dominant terms of the population's distribution in each case. This analysis improves the previous results in the biological literature and allows to consider less restrictive assumptions (see for instance [MCG97, Day00, YG09, DRG13, DYG15]). Furthermore, our work makes a link between the theory of adaptive dynamics and moment based approaches in quantitative genetics. Adaptive dynamics and quantitate genetics, which focus respectively on the evolution of discrete and continuous characters, are two theories which are widely used in theoretical evolutionary biology (see for instance [MHM$^+$96, B0̈0, Die04, Ric04]). Finally, our method allows to go beyond the Gaussian approximation commonly used in the theory of quantitative genetics.

Closely related models describing the balance between selection, mutation and migration between habitats have indeed been studied using the theories of adaptive dynamics (see for instance [MCG97, Day00, FMP$^+$]) and quantitative genetics (see for instance [HDT01, RK01]). In the adaptive dynamics approach, one considers that the mutations are very rare such that the population has time to attain its equilibrium between two mutations and hence the population's distribution has discrete support (one or two points in a two habitats model). The quantitative genetics approach allows more frequent mutations and does not separate the evolutionary and the ecological time scales so that the population's distribution is continuous (see [Ric04]–chapter 7). In this class of works, models closely related to (3.1) are studied based on a main assumption that one considers that the population's distribution is a gaussian [HDT01, RK01] or, to take into account the possibility of dimorphic populations, a sum of one or two gaussian distributions [YG09, DRG13].

In our work, as in the quantitative genetics framework, we also consider continuous phenotypic distributions. However, we don't assume any a priori gaussian assumption. We compute directly the population's distribution and in this way we correct the previous approximations. The asymptotic analysis of (3.1) is closely related to the identification of the evolutionary stable strategy (ESS) (see Section 3.2.1 for the definition) in adaptive dynamics. To perform such asymptotic analysis, we indeed provide also some new results in the framework of adaptive dynamics and in particular, we generalize previous results on the identification of the ESS to the case of non-symmetric habitats.

In [Mir13] a general convergence result (allowing also more than two habitats) has been provided and a Hamilton-Jacobi equation has been derived at the limit considering general form of growth rate R. However, to provide more precise results, in [Mir17, MG] we restricted the study to $z \in \mathbb{R}$ and to the following particular form of growth rate:

$$R_i(z,\rho_i) = r_i - g_i(z-\theta_i)^2 - \kappa_i\rho_i, \qquad \text{with } \theta_1 = -\theta \text{ and } \theta_2 = \theta. \tag{3.2}$$

Here, r_i represents the maximum intrinsic growth rate, the positive constant g_i is the strength of the selection, θ_i is the optimal trait in habitat i and the positive constant κ_i represents the intensity of the competition.
In this chapter we will present the results for this particular form of growth rate to provide the most precise results.

Assumptions:
To guarantee that the population does not get extinct, we assume that

$$\max(r_1 - m_1, r_2 - m_2) > 0. \tag{3.3}$$

Moreover, in the first part of this work, we assume that there is positive migration rate in both directions, i.e.

$$m_i > 0, \qquad \text{i=1,2}. \tag{3.4}$$

The source and sink case, where for instance $m_2 = 0$, will also be analyzed.

The main elements of the method:
To describe the solutions $n_{\varepsilon,i}(z)$ we use a WKB transformation

$$n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{\varepsilon,i}(z)}{\varepsilon}\right). \tag{3.5}$$

Note that a first approximation that is commonly used in the theory of 'quantitative genetics', is a gaussian distribution of the following form

$$n_{\varepsilon,i}(z) = \frac{\rho_i}{\sqrt{2\pi\varepsilon}\sigma} \exp\left(\frac{-(z-z^*)^2}{\varepsilon\sigma^2}\right) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{-\frac{1}{2\sigma^2}(z-z^*)^2 + \varepsilon \log\frac{\rho_i}{\sigma}}{\varepsilon}\right).$$

Here, we try to go further than this a priori gaussian assumption and to approximate directly $u_{\varepsilon,i}$. To this end, we write an expansion for $u_{\varepsilon,i}$ in terms of ε:

$$u_{\varepsilon,i} = u_i + \varepsilon v_i + O(\varepsilon^2). \tag{3.6}$$

By replacing (3.6) and (3.5) in (3.1), we first prove that $u_1 = u_2 = u$ is the unique viscosity solution to a Hamilton-Jacobi equation with constraint which can be computed explicitly. The uniqueness of solution of such Hamilton-Jacobi equation with constraint is related to the uniqueness of the ESS and to the weak KAM theory ([Lio82a], Chapter 5 and [Fat16]). Such function u indeed satisfies

$$\max_{\mathbb{R}} u(z) = 0,$$

with the maximum points attained at one or two points corresponding to the ESS points of the problem. We next compute formally the next order terms v_i. Note that once u and v_i are known we have already a good approximation of the population's distribution with an error of order $O(\sqrt{\varepsilon})$. We then notice that, while $u(z) < 0$, $n_{\varepsilon,i}(z)$ is exponentially small. Therefore, to estimate the moments of the population's distribution only the values of u and v_i at the points which are close to the zero level set of u matter, i.e. the ESS points. Using the Laplace's method of integration and the Taylor expansions of the terms u and v_i around the ESS points we provide indeed some analytic approximations of the moments of the population's distribution with an error of order ε^2 as $\varepsilon \to 0$.

An asymptotic expansion for $u_{\varepsilon,i}$ of type (3.6) can be rigorously derived in the homogeneous case without spatial structure (see [MR15b] and Chapter 1). In the case of heterogeneous environment such rigorous derivation is more technical but do not seem inaccessible. The computation of the correctors allows us to complete our method and to characterize the dominant terms of the population's distribution and to estimate it's moments.

Using the method presented in this chapter, a detailed biological study of this model has been provided in [MG]. This analysis allows to observe new features. In particular, the computation of the correctors, v_i is important to estimate the mean phenotypic trait. This computation allows indeed to capture a gap between the mean phenotypic traits in the two habitats in presence of mutations, in a case where in absence of the mutations the population is monomorphic, i.e. the distribution concentrates on a same single point in the two habitats (see Subsection 3.5 for more details). Moreover, the analytical approximation of the moments is of particular interest in the biological community and there have been several attempts to provide such approximations (see for instance [YG09, DRG13, DYG15]). Our work provides a more mathematically rigorous method for such computations and improves some previous results. In particular, we precise the impact of the migration rate, and other parameters of the model, on the variance of the population's distribution (see [MG] and Subsection 3.5). This is specially interesting since in classical quantitative genetics models, it is not clear how to include the influence of migration in the variance of the population's distribution that one generally assumes to be fixed. In such models the variance is usually under estimated (see for instance [DRG13]).

Note that the part of the method where one proves the convergence of $(u_{\varepsilon,i})_\varepsilon$ to a viscosity solution of a Hamilton-Jacobi equation is very robust and can be generalized to the case of several habitats with multi-dimensional trait and general growth rates R_i (see [Mir13]). However, we use the particular structure of the model to obtain the uniqueness and the identification of the ESS. This is the reason why in [Mir17, MG] we consider a particular growth rate (3.2), so that we can highlight the usefulness of the Hamilton-Jacobi approach for the cases where the adaptive dynamics framework is well-understood. Note however that although with this choice of model, in absence of migration, the asymptotic analysis in each habitat is rather simple (in each habitat the population will concentrate on the fittest trait in the patch), the presence of the migration makes the qualitative study non-trivial. The migration can indeed lead to dimorphism in each of the habitats. In particular a Gaussian approximation would not be adapted.

In Section 3.2 we present our main results in the case where there is migration in both directions, that is under assumption (3.4). In Section 3.3 we provide our main results in a source and sink scenario, that is with $m_2 = 0$. The works presented in Section 3.2 and in Section 3.3 are based on the results in [Mir13, Mir17]. In Section 3.4 we provide some heuristic computations that allow to understand our main results but also to compute formally the corrector terms and to provide analytic approximations of the moments of the phenotypic distribution. Finally in Section 3.5 we provide our analytic approximations of the moments of the phenotypic distribution for two biological examples and discuss the biological results [MG].

3.2 Migration in both directions

In this section, we study the case where there is migration in both directions, that is we assume (3.4). In Subsection 3.2.1 we provide some notions from the theory of adaptive dynamics. Note that our objective is not to study the framework of adaptive dynamics where the mutations are assumed to be very rare. However, these notions appear naturally from our asymptotic computations. Our analysis of the integro-differential model (3.1) is indeed based on a preliminary analysis in the adaptive dynamics framework. In Subsection 3.2.2 we present the main results in the adaptive dynamics framework. Finally, in Subsection 3.2.3 we provide our main results on the derivation of the zero order term u.

3.2.1 Some notions from the theory of adaptive dynamics

In this subsection, we introduce some notions from the theory of adaptive dynamics [MCG97] that we will be using in the next subsections.

Effective fitness: The effective fitness $W(z;\rho_1,\rho_2)$ is the largest eigenvalue of the following matrix:

$$\mathcal{A}(z;\rho_1,\rho_2)=\begin{pmatrix} R_1(z;\rho_1)-m_1 & m_2 \\ m_1 & R_2(z;\rho_2)-m_2 \end{pmatrix}, \tag{3.7}$$

that is

$$\begin{aligned} W(z;\rho_1,\rho_2) &= \tfrac{1}{2}\Big[(R_1(z;\rho_1)+R_2(z;\rho_2)-m_1-m_2) \\ &\quad + \sqrt{(R_1(z;\rho_1)-R_2(z;\rho_2)-m_1+m_2)^2+4m_1m_2)}\Big]. \end{aligned}$$

This indeed corresponds to the *effective* growth rate associated with trait z in the whole metapopulation when the total population sizes are given by (ρ_1,ρ_2).

Demographic equilibrium: Consider a set of points $\Omega=\{z_1,\cdots z_m\}$. The demographic equilibrium corresponding to this set is given by $(n_1(z),n_2(z))$, with the total population sizes (ρ_1,ρ_2), such that

$$n_i(z)=\sum_{j=1}^{m}\alpha_{i,j}\delta(z-z_j),\quad \rho_i=\sum_{j=1}^{m}\alpha_{i,j},\quad W(z_j,\rho_1,\rho_2)=0,\quad i=1,2,\ j=1,\cdots,m,$$

and such that $(\alpha_{1,j},\alpha_{2,j})^T$ is the right eigenvector associated with the largest eigenvalue $W(z_j,\rho_1,\rho_2)=0$ of $\mathcal{A}(z_j;\rho_1,\rho_2)$.

Invasibility: We say that a mutant trait z_m can invade a resident strategy $\{\overline{z}\}$ at its demographic equilibrium $(\overline{\rho}_1,\overline{\rho}_2)$ if $W(z_m,\overline{\rho}_1,\overline{\rho}_2)>0$.

Evolutionary stable strategy: A set of points $\Omega^*=\{z_1^*,\cdots,z_m^*\}$ is called an evolutionary stable strategy (ESS) if

$$W(z,\rho_1^*,\rho_2^*)=0,\quad \text{for } z\in\mathcal{A} \text{ and},\quad W(z,\rho_1^*,\rho_2^*)\le 0,\quad \text{for } z\notin\mathcal{A},$$

where ρ_1^* and ρ_2^* are the total population sizes corresponding to the demographic equilibrium associated with the set Ω^*. Note that this definition corresponds indeed to globally evolutionary stable strategies. Here, we are interested only in such global ESS (see for instance [Die04] for the definition of local ESS).

Notation: We will use the star sign * whenever we talk about an evolutionary stable strategy Ω^* (and similarly for the corresponding demographic equilibrium (n_1^*,n_2^*) and the total population sizes (ρ_1^*,ρ_2^*)). We add an index M when the strategy is monomorphic (a set of a single trait $\{z^{M*}\}$ with the corresponding demographic equilibrium (n_1^{M*}, n_2^{M*}), and the total population sizes $(\rho_1^{M*}, \rho_2^{M*}))$ and an index D when the strategy is dimorphic (a set of two traits $\{z_{\mathrm{I}}^{D*}, z_{\mathrm{II}}^{D*}\}$ with the corresponding demographic equilibrium (n_1^{D*}, n_2^{D*}), and the total population sizes $(\rho_1^{D*}, \rho_2^{D*}))$.

3.2.2 The main results in the adaptive dynamics framework

Our main result in the adaptive dynamics framework is that there exists a unique ESS which is whether monomorphic (a single Dirac mass) or dimorphic (a sum of two Dirac masses). We determine indeed under which conditions the ESS is monomorphic or dimorphic. To state our result, we first define

$$z^{D*} = \sqrt{\theta^2 - \frac{m_1 m_2}{4\theta^2 g_1 g_2}}, \qquad \rho_1^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 g_2} + r_1 - m_1}{\kappa_1}, \qquad \rho_2^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 g_1} + r_2 - m_2}{\kappa_2}.$$

Theorem 3.1. *Assume* (3.3)–(3.4). *Then, there exists a unique set of points* Ω^* *which is an ESS.*
(i) The ESS is dimorphic if and only if

$$\frac{m_1 m_2}{4 g_1 g_2 \theta^4} < 1, \tag{3.8}$$

$$0 < m_2 \rho_2^{D*} + (R_1(-z^{D*}; \rho_1^{D*}) - m_1)\rho_1^{D*}, \tag{3.9}$$

and

$$0 < m_1 \rho_1^{D*} + (R_2(z^{D*}; \rho_2^{D*}) - m_2)\rho_2^{D*}. \tag{3.10}$$

Then the dimorphic equilibrium is given by

$$n_i^{D*} = \nu_{\mathrm{I},i}\delta(z + z^{D*}) + \nu_{\mathrm{II},i}\delta(z - z^{D*}), \quad \nu_{\mathrm{I},i} + \nu_{\mathrm{II},i} = \rho_i^{D*}, \quad i = 1, 2. \tag{3.11}$$

(ii) If the above conditions are not satisfied then the ESS is monomorphic. In the case where condition (3.8) *is verified but the r.h.s. of* (3.9) *(respectively* (3.10)*) is negative, the fittest trait belongs to the interval* $(-\theta, -z^{D*})$ *(respectively* (z^{D*}, θ)*). If* (3.8) *is satisfied but* (3.9) *(respectively* (3.10)*) is an equality then the monomorphic ESS is given by* $\{-z^{D*}\}$ *(respectively* $\{z^{D*}\}$*).*

Note that one can compute the weights $\nu_{k,i}$, for $k = \mathrm{I}, \mathrm{II}$ and $i = 1, 2$:

$$\begin{pmatrix} \nu_{\mathrm{I},1} \\ \nu_{\mathrm{I},2} \end{pmatrix} = \frac{m_1\rho_1^{D*} + (R_2(z^{D*};\rho_2^{D*}) - m_2)\rho_2^{D*}}{m_1 m_2 - \left(R_1(-z^{D*};\rho_1^{D*}) - m_1\right)\left(R_2(z^{D*};\rho_2^{D*}) - m_2\right)} \begin{pmatrix} m_2 \\ -R_1(-z^{D*}; \rho_1^{D*}) + m_1 \end{pmatrix},$$
$$\begin{pmatrix} \nu_{\mathrm{II},1} \\ \nu_{\mathrm{II},2} \end{pmatrix} = \frac{m_2\rho_2^{D*} + (R_1(-z^{D*};\rho_1^{D*}) - m_1)\rho_1^{D*}}{m_1 m_2 - \left(R_1(-z^{D*};\rho_1^{D*}) - m_1\right)\left(R_2(z^{D*};\rho_2^{D*}) - m_2\right)} \begin{pmatrix} -R_2(z^{D*}; \rho_2^{D*}) + m_2 \\ m_1 \end{pmatrix}.$$

The above theorem leads to the following corollary which will be helpful thereafter.

Corollary 3.2. *Assume that*

$$m_2\rho_2^{D*} + (R_1(-z^{D*}; \rho_1^{D*}) - m_1)\rho_1^{D*} \neq 0, \qquad m_1\rho_1^{D*} + (R_2(z^{D*}; \rho_2^{D*}) - m_2)\rho_2^{D*} \neq 0, \tag{3.12}$$

and let the set Ω^* *be the unique ESS of the model and* (ρ_1^*, ρ_2^*) *be the total population sizes at the demographic equilibrium of this ESS. Then,*

$$W(z, \rho_1^*, \rho_2^*) < 0, \qquad \textit{for all } z \in \mathbb{R} \setminus \Omega^*.$$

Note also that when the habitats are symmetric, then conditions (3.9) and (3.10) always hold under condition (3.8), and hence

Corollary 3.3. *Assume that the habitats are symmetric:*

$$r = r_1 = r_2, \quad g = g_1 = g_2, \quad \kappa = \kappa_1 = \kappa_2, \quad m = m_1 = m_2. \tag{3.13}$$

(i) Then the unique ESS is dimorphic if and only if

$$\frac{m}{2g} < \theta^2. \tag{3.14}$$

The dimorphic ESS is determined by (3.11)*.*
(ii) When condition (3.14) *is not satisfied, then the ESS is monomorphic and the corresponding monomorphic equilibrium is given by*

$$n_1^{M*}(z) = n_2^{M*}(z) = N^{M*}\,\delta(z), \quad \textit{with } N^{M*} = \frac{1}{\kappa}\left(r - g\theta^2\right).$$

The next proposition gives an interpretation of conditions (3.9) and (3.10).

Proposition 3.4. *Assume that condition* (3.8) *is satisfied and that* $r_i - m_i > 0$*, for* $i = 1, 2$*. Then,*
(i) condition (3.9) *holds if and only if a mutant trait of type* z^{D*} *can invade a monomorphic resident population of type* $-z^{D*}$ *which is at it's demographic equilibrium.*
(ii) condition (3.10) *holds if and only if a mutant trait of type* $-z^{D*}$ *can invade a monomorphic resident population of type* z^{D*} *which is at it's demographic equilibrium.*

One can indeed rewrite conditions (3.9) and (3.10) respectively as below

$$C_1 < \alpha_2 r_2 - \alpha_1 r_1, \qquad C_2 < \beta_1 r_1 - \beta_2 r_2,$$

with C_i, α_i and β_i constants depending on m_1, m_2, g_1, g_2, κ_1, κ_2 and θ. These conditions are indeed a measure of asymmetry between the habitats. They appear from the fact that even if condition (3.8), which is the only condition for dimorphism in symmetric habitats, is satisfied, while the quality of the habitats are very different, the ESS cannot be dimorphic. In this case, the population will be able to adapt only to one of the habitats and it will be maladapted to the other one.

3.2.3 Derivation of the zero order terms u_i

The identification of the zero order terms u_i is based on the following result.

Theorem 3.5. *Assume* (3.3)–(3.4)*.*
(i) As $\varepsilon \to 0$*,* $(n_{\varepsilon,1}, n_{\varepsilon,2})$ *converges to* (n_1^*, n_2^*)*, the demographic equilibrium of the unique ESS of the model. Moreover, as* $\varepsilon \to 0$*,* $\rho_{\varepsilon,i}$ *converges to* ρ_i^**, the total population size in habitat i corresponding to this demographic equilibrium.*
(ii) As $\varepsilon \to 0$*, both sequences* $(u_{\varepsilon,i})_\varepsilon$*, for* $i = 1, 2$*, converge along subsequences and locally uniformly in* $\mathbb{R}$ *to a continuous function* $u \in \mathrm{C}(\mathbb{R})$*, such that* u *is a viscosity solution to the following equation*

$$\begin{cases} -|u'(z)|^2 = W(z, \rho_1^*, \rho_2^*), & \textit{in } \mathbb{R}, \\ \max_{z\in\mathbb{R}} u(z) = 0. \end{cases} \tag{3.15}$$

Moreover, we have the following condition on the zero level set of u*:*

$$\operatorname{supp} n_1^* = \operatorname{supp} n_2^* \subset \{z \,|\, u(z) = 0\} \subset \{z \,|\, W(z, \rho_1^*, \rho_2^*) = 0\}.$$

(iii) Under condition (3.12) *we have* $\operatorname{supp} n_1^* = \operatorname{supp} n_2^* = \{z \,|\, W(z, \rho_1^*, \rho_2^*) = 0\}$ *and hence*

$$\{z \,|\, u(z) = 0\} = \{z \,|\, W(z, \rho_1^*, \rho_2^*) = 0\}. \tag{3.16}$$

The solution of (3.15)–(3.16) *is indeed unique and hence the whole sequence* $(u_{\varepsilon,i})_\varepsilon$ *converge locally uniformly in* $\mathbb{R}$ *to* u*.*

Note that statement (iii) above is a consequence of the results in the adaptive dynamics framework and in particular of Corollary (3.2). Hamilton-Jacobi equations of type (3.15) in general might admit several viscosity solutions. Here, the uniqueness is obtained thanks to (3.16) and a property from the weak KAM theory, which is the fact that the viscosity solutions are completely determined by one value taken on each static class of the Aubry set ([Lio82a], Chapter 5 and [Con01]). Here, this set corresponds to the maximum points of W. In what follows we assume that (3.12) and hence (3.16) always hold. We then give an explicit formula for u considering two cases (one can indeed verify easily that the functions below are viscosity solutions to (3.15)–(3.16)):

(i) **Monomorphic ESS :** We consider the case where there exists a unique monomorphic ESS z^{M*} such that the corresponding demographic equilibrium is given by $(\rho_1^{M*}\delta(z^*), \rho_2^{M*}\delta(z^{M*}))$. Then u is given by

$$u(z) = -\Big| \int_{z^{M*}}^{z} \sqrt{-W(x; \rho_1^{M*}, \rho_2^{M*})}dx \Big|.$$

(ii) **Dimorphic ESS :** We next consider the case where there exists a unique dimorphic ESS $(z_{\mathrm{I}}^{D*}, z_{\mathrm{II}}^{D*})$ with the demographic equilibrium: $n_i = \nu_{\mathrm{I},i}\delta(z - z_{\mathrm{I}}^{D*}) + \nu_{\mathrm{II},i}\delta(z - z_{\mathrm{II}}^{D*})$, and $\nu_{\mathrm{I},i} + \nu_{\mathrm{II},i} = \rho_i^{D*}$. Then u is given by

$$u(z) = \max\Big(-\Big| \int_{z_{\mathrm{I}}^*}^{z} \sqrt{-W(x; \rho_1^{D*}, \rho_2^{D*})}dx \Big|, -\Big| \int_{z_{\mathrm{II}}^*}^{z} \sqrt{-W(x; \rho_1^{D*}, \rho_2^{D*})}dx \Big| \Big).$$

3.3 A source and sink case

In this section, we consider a particular case where there is migration only from one habitat to the other, that is

$$m_1 > 0, \qquad m_2 = 0. \tag{3.17}$$

In this case, one population (the source) does not receive any migrant from the second population (the sink). We also assume that

$$r_1 - m_1 > 0. \tag{3.18}$$

Following similar arguments to the case of migration in both directions, one can characterize the mutation, selection and migration equilibria. However, since the migration is only in one direction, we should study the equilibria in the two habitats separately.

Note that since $m_2 = 0$, there is no influence of the second habitat on the first habitat. One can indeed compute explicitly $n_{\varepsilon,1}$:

$$n_{\varepsilon,1}(z) = \frac{g_1^{\frac{1}{4}}\rho_{\varepsilon,1}}{\sqrt{2\pi\varepsilon}} \exp\Big(-\frac{\sqrt{g_1}(z+\theta)^2}{2\varepsilon}\Big), \qquad \rho_{\varepsilon,1} = \frac{r_1 - m_1 - \varepsilon\sqrt{g_1}}{\kappa_1}.$$

Note that as $\varepsilon \to 0$, $n_{\varepsilon,1}$ converges in the sense of measures to n_1^{M*} with

$$n_1^{M*}(z) = \rho_1^{M*}\delta(z+\theta), \qquad \rho_1^{M*} = \frac{r_1 - m_1}{\kappa_1}.$$

Here, $\{-\theta\}$ is indeed the unique ESS in the first habitat and n_1^* corresponds to the demographic equilibrium at the ESS.

In the second habitat however, there is an influence of the population coming from the first habitat. The natural quantity that appears in this case as the effective fitness in the second habitat is still the principal eigenvalue of (3.7) which is, in this case, given by

$$\begin{aligned} W(z,\rho_2) &= \max(r_1 - g_1(z+\theta)^2 - \kappa_1\rho_1^{M*} - m_1, r_2 - g_2(z-\theta)^2 - \kappa_2\rho_2) \\ &= \max(-g_1(z+\theta)^2, r_2 - g_2(z-\theta)^2 - \kappa_2\rho_2). \end{aligned}$$

Then one can introduce the notion of the ESS for this habitat similarly to Section 3.2.1.

In Subsection 3.3.1 we present our results for the source and sink model in the adaptive dynamics framework. In Subsection 3.3.2 we provide our main result on the derivation of the zero order term u_2.

3.3.1 The results in the adaptive dynamics framework

We can indeed always identify the unique ESS:

Theorem 3.6. *Assume* (3.17)–(3.18)*. In each habitat there exists a unique ESS. In habitat* 1 *the ESS is always monomorphic and it is given by* $\{-\theta\}$ *with the following demographic equilibrium:*

$$n_1^{M*} = \rho_1^{M*}\,\delta(z+\theta), \quad \rho_1^{M*} = \frac{r_1 - m_1}{\kappa_1}.$$

In habitat 2 *there are two possibilities:*
(i) the ESS is dimorphic if and only if

$$\frac{m_1(r_1 - m_1)}{\kappa_1} < \frac{4g_2\theta^2 r_2}{\kappa_2}. \tag{3.19}$$

The dimorphic ESS is given by $\{-\theta, \theta\}$ *with the following demographic equilibrium:*

$$n_2^{D*} = \alpha\delta(z+\theta) + \beta\delta(z-\theta), \quad \rho_2^{D*} = \alpha+\beta = \frac{r_2}{\kappa_2}, \quad \alpha = \frac{m_1(r_1-m_1)}{4g_2\theta^2\kappa_1}, \quad \beta = \frac{r_2}{\kappa_2} - \frac{m_1(r_1-m_1)}{4g_2\theta^2\kappa_1}.$$

(ii) If condition (3.19) *is not satisfied then the ESS in the second habitat is monomorphic. The ESS is given by* $\{-\theta\}$ *with the following demographic equilibrium:*

$$n_2^{M*} = \rho_2^{M*}\,\delta(z+\theta), \quad \rho_2^{M*} = \frac{1}{2\kappa_2}\Big(r_2 - 4g_2\theta^2 + \sqrt{(r_2 - 4g_2\theta^2)^2 + 4\frac{\kappa_2}{\kappa_1}m_1(r_1 - m_1)}\Big).$$

3.3.2 The computation of the zero order term u_2

We next identify the zero order term u_2 (introduced in (3.5)–(3.6)):

Theorem 3.7. *Assume* (3.17)–(3.18).
(i) As $\varepsilon \to 0$, $(n_{\varepsilon,1}, n_{\varepsilon,2})$ *converges to* (n_1^{M*}, n_2^*), *the demographic equilibrium of the unique ESS of the metapopulation, given by Theorem 3.6. Moreover, as* $\varepsilon \to 0$, $(\rho_{\varepsilon,1}, \rho_{\varepsilon,2})$ *converges to* (ρ_1^{M*}, ρ_2^*), *the total population sizes in habitats* 1 *and* 2 *corresponding to this demographic equilibrium.*
(ii) As $\varepsilon \to 0$, $(u_{\varepsilon,1})_\varepsilon$ *converges locally uniformly in* $\mathbb{R}$ *to* $u_1(z) = -\frac{\sqrt{g_1}}{2}(z+\theta)^2$. *As* $\varepsilon \to 0$, $(u_{\varepsilon,2})_\varepsilon$ *converges along subsequences and locally uniformly in* $\mathbb{R}$ *to a function* $u_2 \in \mathrm{C}(\mathbb{R})$ *which satisfies*

$$-|u_2'|^2 \leq \max(R_1(z,\rho_1^{M*})-m_1, R_2(z,\rho_2^*)), \quad -|u_2'|^2 \geq R_2(z,\rho_2^*), \quad u_1(z) \leq u_2(z), \quad \max_{z\in\mathbb{R}} u_2(z) = 0,$$

where the first two inequalities are in the viscosity sense. Moreover, we have the following condition on the zero level set of u_2*:*

$$\operatorname{supp} n_2^* \subset \{z \,|\, u_2(z) = 0\} \subset \{z \,|\, \max(R_1(z,\rho_1^{M*}) - m_1, R_2(z,\rho_2^*)) = 0\}.$$

Theorem 3.7 allows us to identify u in a neighborhood of the ESS points:

Proposition 3.8. *(i) There exists a connected and open set* $\gamma_{\mathrm{I}} \subset \mathbb{R}$, *with* $-\theta \in \gamma_{\mathrm{I}}$, *such that*

$$u_2(z) = -\frac{\sqrt{g_1}}{2}(z+\theta)^2.$$

(ii) Assume that (3.19) *holds. Then, there exists a connected and open set* $\gamma_{\mathrm{II}} \subset \mathbb{R}$, *with* $\theta \in \gamma_{\mathrm{II}}$, *such that*

$$u_2(z) = -\frac{\sqrt{g_2}}{2}(z-\theta)^2.$$

(iii) Assume that

$$\frac{4g_2\theta^2 r_2}{\kappa_2} < \frac{m_1(r_1-m_1)}{\kappa_1}.$$

Then $u_2(\theta) < 0$.

3.4 Heuristics and approximation of the moments of the phenotypic distribution

In order to apply our results to the study of some biological case studies, which will be done in the next section, we will provide two analytic approximations. Our *first approximation* is provided by the computation of the global values of the terms u and v_i and using (3.5) and (3.6). In order to provide more explicit formula for the moments of order $k \geq 1$ of the population's distribution in terms of the parameters of the model, we also provide a *second approximation*. This *second approximation*, instead of using the values of u and v_i in the whole domain, is based on the computation of Taylor expansions of u and v_i around the ESS points.

Our *second approximation* is by definition less accurate than the first one. It still provides convincing results when the parameters are such that we are far from the transition zone from monomorphic to dimorphic distribution (see for instance Figure 3.2). This approximation is indeed based on an integral approximation (see Subsection 3.4.2) which is relevant only when the population's distribution is relatively sharp around the ESS points. This is not the case in the transition zone unless the effect of the mutations, i.e. ε, is very small.

In this section, we show how to derive these approximations in the case where $m_i > 0$ (see [MG] for the derivations in the source and sink scenario). First, we provide some heuristic computations which allow us to derive terms u and v_i and hence our *first approximation* (subsection 3.4.1). In particular, such computations allow us to derive the Hamilton-Jacobi equation (3.15) . Next, we show how to derive analytic approximations for the moments of the phenotypic distribution, that is our *second approximation* (subsection 3.4.2).

3.4.1 Derivation of our *first approximation*

In this subsection we can provide the elements to obtain an approximation of the population's total density $\rho_{\varepsilon,i}$ and the phenotypic density $n_{\varepsilon,i}(z)$ in the following form

$$\rho_{\varepsilon,i} \approx \rho_i + \varepsilon K_i, \qquad n_{\varepsilon,i}(z) \propto \frac{1}{\sqrt{2\pi\varepsilon}} \exp\big(\frac{u_i(z) + \varepsilon v_i(z)}{\varepsilon}\big).$$

Computation of the zero order term u_i:

We first provide some heuristic arguments leading to the Hamilton-Jacobi equation (3.15). Note that the equilibrium $(n_{\varepsilon,1}, n_{\varepsilon,2})$ solves

$$\begin{cases} 0 = \varepsilon^2 \frac{\partial^2 n_{\varepsilon,1}(z)}{\partial z^2} + n_{\varepsilon,1}(z) R_1(z;\rho_{\varepsilon,1}) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\ \\ 0 = \varepsilon^2 \frac{\partial^2 n_{\varepsilon,2}(z)}{\partial z^2} + n_{\varepsilon,2}(z) R_2(z;\rho_{\varepsilon,2}) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z). \end{cases} \tag{3.20}$$

We first let $\varepsilon \to 0$ in the above equation to obtain formally that $n_{\varepsilon,i}(z) \to n_i(z)$ and $\rho_{\varepsilon,i} \to \rho_i$ with

$$\begin{cases} 0 = n_1(z) R_1(z;\rho_1) + m_2 n_2(z) - m_1 n_1(z), \\ \\ 0 = n_2(z) R_2(z;\rho_2) + m_1 n_1(z) - m_2 n_2(z), \\ \\ \rho_i = \int_{\mathbb{R}} n_i(z) dz, \end{cases}$$

which is equivalent with

$$\mathcal{A}(z,\rho_1,\rho_2) \begin{pmatrix} n_1(z) \\ n_2(z) \end{pmatrix} = 0, \qquad \rho_i = \int_{\mathbb{R}} n_i(z) dz,$$

with $\mathcal{A}(z,\rho_1,\rho_2)$ given by (3.7). This means that (ρ_1,ρ_2) corresponds to the sizes of the populations 1 and 2 at the demographic equilibrium $(n_1(z), n_2(z))$, in absence of mutations. We will show that this equilibrium corresponds indeed to an evolutionary stable strategy. To this end, we replace (3.5) in (3.20) and obtain

$$\begin{cases} 0 = \varepsilon \frac{\partial^2 u_{\varepsilon,1}(z)}{\partial z^2} + |\frac{\partial}{\partial z} u_{\varepsilon,1}(z)|^2 + R_1(z;\rho_1) + m_2 \exp(\frac{u_{\varepsilon,2}(z) - u_{\varepsilon,1}(z)}{\varepsilon}) - m_1, \\ \\ 0 = \varepsilon \frac{\partial^2 u_{\varepsilon,2}(z)}{\partial z^2} + |\frac{\partial}{\partial z} u_{\varepsilon,2}(z)|^2 + R_2(z;\rho_2) + m_1 \exp(\frac{u_{\varepsilon,1}(z) - u_{\varepsilon,2}(z)}{\varepsilon}) - m_2. \end{cases} \tag{3.21}$$

We can determine $u_i(z)$, $v_i(z)$ from the above equation and (3.6).
Note that the exponential terms in (3.21) suggest that, when $m_i > 0$ for $i = 1, 2$, as $\varepsilon \to 0$ $u_{\varepsilon,1}(z)$ and $u_{\varepsilon,2}(z)$ converge to the same limit $u(z)$. Otherwise, one of these exponential terms tends to infinity while the other terms are bounded. Keeping the zero order terms we obtain

$$\begin{cases} 0 = |\frac{\partial}{\partial z}u(z)|^2 + R_1(z;\rho_1) + m_2\exp(v_2(z) - v_1(z)) - m_1, \\ 0 = |\frac{\partial}{\partial z}u(z)|^2 + R_2(z;\rho_2) + m_1\exp(v_1(z) - v_2(z)) - m_2. \end{cases} \tag{3.22}$$

We then multiply the first line by $\exp(v_1(z))$ and the second line by $\exp(v_2(z))$ and write the system in the matrix form to obtain

$$\begin{pmatrix} R_1(z;\rho_1) - m_1 & m_2 \\ m_1 & R_2(z;\rho_2) - m_2 \end{pmatrix} \begin{pmatrix} \exp(v_1(z)) \\ \exp(v_2(z)) \end{pmatrix} = -|\frac{\partial}{\partial z}u(z)|^2 \begin{pmatrix} \exp(v_1(z)) \\ \exp(v_2(z)) \end{pmatrix}.$$

Note that the matrix in the l.h.s. is nothing but $\mathcal{A}(z,\rho_1,\rho_2)$ given by (3.7). The equality above means that $-|\frac{\partial}{\partial z}u(z)|^2$ is indeed the principal eigenvalue of $\mathcal{A}(z;\rho_1,\rho_2)$, that is (see Section 3.2.1):

$$-|\frac{\partial}{\partial z}u(z)|^2 = W(z;\rho_1,\rho_2).$$

Moreover, since the total population size is bounded, we have

$$\max_{z\in\mathbb{R}} u(z) = 0.$$

Similarly we obtain

$$\operatorname{supp} n_i \subset \{z \,|\, u(z) = 0\}. \tag{3.23}$$

Let $\bar{z}$ be such that $u(\bar{z}) = 0$ which means that it is a maximum point of $u(z)$. Then, $\frac{\partial}{\partial z}u(\bar{z}) = 0$ and hence

$$W(\bar{z};\rho_1,\rho_2) = 0.$$

Moreover in all the points $z \in \mathbb{R}$, we have

$$W(z;\rho_1,\rho_2) = -|\frac{\partial}{\partial z}u(z)|^2 \le 0.$$

This implies that

$$\begin{array}{l} \text{if } z \in \operatorname{supp} n_1 = \operatorname{supp} n_2 \text{ then } W(z;\rho_1,\rho_2) = 0, \\ \text{if } z \notin \operatorname{supp} n_1 = \operatorname{supp} n_2 \text{ then } W(z;\rho_1,\rho_2) \le 0. \end{array}$$

In other words $(n_1(z), n_2(z))$ corresponds to the demographic equilibrium corresponding to the global ESS and hence $n_i(z) = n_i^*(z)$ and $\rho_i = \rho_i^*$, with $n_i^*(z)$ and ρ_i^* given in Subsection 3.2.2. We gather the informations that we obtained on $u(z)$:

$$\begin{cases} -|\frac{\partial}{\partial z}u(z)|^2 = W(z;\rho_1^*,\rho_2^*), \\ \max_{z\in\mathbb{R}} u(z) = 0, \end{cases}$$

which is nothing but (3.15).

Such Hamilton-Jacobi equation may admit several viscosity solutions in general. However, any nonpositive viscosity solution of (3.15) can be determined by its values at the maximum points of W ([Lio82a], Chapter 5 and [Con01]). The maximum points of W are given by the set $\{z \in \mathbb{R} \,|\, W(z;\rho_1^*,\rho_2^*) = 0\}$. Under condition (3.12), we obtain that

$$\text{if } z \notin \operatorname{supp} n_1 = \operatorname{supp} n_2 \text{ then } W(z;\rho_1^*,\rho_2^*) < 0,$$

which implies that

$$\operatorname{supp} n_1 = \operatorname{supp} n_2 = \{z \in \mathbb{R} \,|\, W(z;\rho_1^*,\rho_2^*)\}.$$

Combining this equality with (3.23) we deduce that $u = 0$ at the maximum points of W. This property leads to the uniqueness of u and allows us to derive the explicit formula for u, given in Section 3.2.3.

Computation of the next order terms $v_i(z)$: Next, we provide the main elements to compute formally the next order term $v_i(z)$.

From (3.22) and (3.15) we can compute $v_2(z) - v_1(z)$ thanks to the following formula

$$v_2(z) - v_1(z) = \log\Big(\frac{1}{m_2}\big(W(z,\rho_1^*,\rho_2^*) - R_1(z,\rho_1^*) + m_1\big)\Big).$$

We next keep the first order terms in (3.21). To do so, we need to go further in the approximation of $u_{\varepsilon,i}(z)$ in (3.6) and also keep the term of order ε^2:

$$u_{\varepsilon,i}(z) = u(z) + \varepsilon v_i(z) + \varepsilon^2 l_i(z) + O(\varepsilon^3).$$

Then, keeping the first order terms in (3.21) we obtain

$$\begin{cases} 0 = \frac{\partial^2}{\partial z^2}u(z) + 2\frac{\partial}{\partial z}u(z)\frac{\partial}{\partial z}v_1(z) - \kappa_1 K_1 + m_2\exp(v_2(z) - v_1(z))(l_2(z) - l_1(z)), \\ 0 = \frac{\partial^2}{\partial z^2}u(z) + 2\frac{\partial}{\partial z}u(z)\frac{\partial}{\partial z}v_2(z) - \kappa_2 K_2 + m_2\exp(v_1(z) - v_2(z))(l_1(z) - l_2(z)). \end{cases}$$

Using the above equalities and by evaluating them at the ESS points we can compute $v_i(z)$ and K_i for $i = 1, 2$. See [Mir17]–Section 3.3 for the details of such computations.

3.4.2 Derivation of our *second approximation*

In this subsection, we prove the main elements to derive analytic approximations for the moments of the phenotypic distribution. We only present the method in the case of monomorphic population. See [MG] for the case of dimorphic population.

Let's suppose that we are in the case where the ESS is monomorphic and given by z^{M*} In order to provide an explicit approximation of the moments of the population's distribution, we compute the third order approximation of $u(z)$ around z^{M*}:

$$u(z) = -\frac{A}{2}(z - z^{M*})^2 + B(z - z^{M*})^3 + O(z - z^{M*})^4. \tag{3.24}$$

and the first order approximation of $v_i(z)$ around z^{M*}:

$$v_i(z) = \log(\sqrt{A}\rho_i^{M*}) + D_i(z - z^{M*}) + O(z - z^{M*})^2. \tag{3.25}$$

To obtain the zero order term in the expansion for $v_i(z)$ we use the fact that, as the mutation's variance vanishes ($\varepsilon \to 0$), the total population size $\rho_{\varepsilon,i}$ tends to ρ_i^{M*} which corresponds to the demographic equilibrium at the ESS.

The above expansions allow us to estimate the moments of the population's distribution:

$$\begin{cases}\mu_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}} \int z n_{\varepsilon,i}(z) dz = z^{M*} + \varepsilon(\frac{3B}{A^2} + \frac{D_i}{A}) + O(\varepsilon^2),\\ \sigma^2_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}} \int (z-\mu_{\varepsilon,i})^2 n_{\varepsilon,i}(z) dz = \frac{\varepsilon}{A} + O(\varepsilon^2),\\ \psi_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}} \int (z-\mu_{\varepsilon,i})^3 n_{\varepsilon,i}(z) dz = \frac{6B}{A^3}\varepsilon^2 + O(\varepsilon^3).\end{cases}$$

We next show how to compute such approximations. We can indeed use the expressions in (3.24) and (3.25) to compute for any integer $k \geq 1$,

$$\begin{aligned}\int (z-z^{M*})^k n_{\varepsilon,i}(z) dz &= \frac{\varepsilon^{\frac{k}{2}} \sqrt{A} \rho_i^{M*}}{\sqrt{2\pi}} \int_{\mathbb{R}} (y^k e^{-\frac{A}{2}y^2} \big(1 + \sqrt{\varepsilon}(By^3 + D_i y) + O(\varepsilon)\big) dy\\ &= \varepsilon^{\frac{k}{2}} \rho_i^{M*} \Big(\omega_k(\tfrac{1}{A}) + \sqrt{\varepsilon}\big(B\omega_{k+3}(\tfrac{1}{A}) + D_i \omega_{k+1}(\tfrac{1}{A})\big)\Big) + O(\varepsilon^{\frac{k+2}{2}}),\end{aligned}$$

where $\omega_k(\sigma^2)$ corresponds to the k-th order central moment of a Gaussian distribution with variance σ^2. Note that to compute the integral terms above we have performed a change of variable $z - z^{M*} = \sqrt{\varepsilon} y$, therefore each term $z - z^{M*}$ can be considered as of order $\sqrt{\varepsilon}$ in the integrations. The above integrations are the main ingredients to obtain the approximations of the moments given above, i.e. our *second approximation.*

3.5 Some examples and biological applications

In this section, we consider two particular case studies: a first case with symmetric habitats (that is under assumption (3.13)), and a second case with source and sink scenario (that is with $m_2 = 0$). For both examples, we will compare the numerical value of the phenotypic density $n_{\varepsilon,i}$ and its moments (obtained by the numerical approximation of the solution to (3.1)) with our two analytic approximations and discuss the biological applications of our results.

See [MG] for more detailed results and discussion on the biological application of this method.

3.5.1 Symmetric fitness landscapes

We focus first on a symmetric scenario where, apart from the position of the optimum, the two habitats are identical: $m_1 = m_2 = m, \kappa_1 = \kappa_2 = \kappa, g_1 = g_2 = g, r_1 = r_2 = r$. In this special case it is possible to fully characterize the evolutionary equilibrium.

When migration rate is higher than critical migration threshold $m > m_c = 2g\theta^2$ migration prevents the differentiation of the trait between the two habitats (see Corollary 3.3). The only evolutionary equilibrium, when the mutation rate is vanishingly small, is monomorphic and satisfies $z^{M*} = 0$ and $n_1^{M*}(z) = n_2^{M*}(z) = \rho^{M*}\delta(z)$, where $\delta(.)$ is the Dirac delta function and $\rho^{M*} = \frac{1}{\kappa}\left(r - g\theta^2\right)$.

Monomorphic case: Let's suppose that $m_c = 2g\theta^2 \leq m$. Then $z^{M*} = 0$ is the only ESS and $\rho^{M*} = \frac{1}{\kappa}\left(r - g\theta^2\right)$. Then, we can provide our *first approximation* of the phenotypic density $n_{\varepsilon,i}(z)$ following the method introduced above (Figure 3.1). Moreover, defining $\phi = \sqrt{1 - 2g\theta^2/m}$, we can use the *second approximation* to obtain analytic formula for the moments of the stationary state

$$\begin{cases}\rho_{\varepsilon,1} = \rho_{\varepsilon,2} = \int n_{\varepsilon,i}(z)dz = \frac{1}{\kappa}\left(r - g\theta^2\right) - \varepsilon\,\frac{\sqrt{g}\phi}{\kappa} + O(\varepsilon^2),\\ \mu_{\varepsilon,1} = \frac{1}{\rho_{\varepsilon,1}}\int z n_{\varepsilon,1}(z)dz = -\varepsilon\frac{\sqrt{g}\theta}{m\phi} + O(\varepsilon^2),\\ \mu_{\varepsilon,2} = \frac{1}{\rho_{\varepsilon,2}}\int z n_{\varepsilon,2}(z)dz = \varepsilon\frac{\sqrt{g}\theta}{m\phi} + O(\varepsilon^2),\\ \sigma^2_{\varepsilon,1} = \sigma^2_{\varepsilon,2} = \frac{1}{\rho_{\varepsilon,i}}\int(z-\mu_{\varepsilon,i})^2 n_{\varepsilon,i}(z)dz = \frac{\varepsilon}{\sqrt{g}\phi} + O(\varepsilon^2),\\ \psi_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}}\int(z-\mu_{\varepsilon,i})^3 n_{\varepsilon,i}(z)dz = O(\varepsilon^3).\end{cases}$$

In what follows 'differentiation' refers to the following quantity:

$$D_\varepsilon = \mu_{\varepsilon,2} - \mu_{\varepsilon,1}.$$

Note that the variance $\sigma^2_{\varepsilon,i}$ is larger than the case with no heterogeneity between the habitats, where we recover the well-known equilibrium variance $\frac{\varepsilon}{\sqrt{g}}$ of Quantitative Genetics [Lan75, BÖ0, Ric04]. This increase in the equilibrium variance comes from ϕ which depends on dispersion and the heterogeneity between the two habitats. The variance of the distribution increases as ϕ decreases. When $\phi = 0$ the approximation for the variance becomes infinitely large. Indeed, this corresponds to the threshold value of migration below which the above approximation collapses because the distribution becomes bimodal. In this case we have to switch to the analysis of the dimorphic case. Note that the differentiation between habitats depends also on ϕ. Some differentiation start to emerge even when the migration rate is above the critical migration rate, m_c. In Figure 3.2 we provide a comparison of the results from the *first* and the *second approximations*. Our *second approximation* provides convincing results when the parameters are such that we are far from the transition zone from monomorphic to dimorphic distribution as expected.

Dimorphic case: When $m < m_c$, the only stable evolutionary equilibrium is dimorphic which yields the following ESS: $\{z_{\mathrm{I}}^{D*},\ z_{\mathrm{II}}^{D*}\}$ with $z_{\mathrm{I}}^{D*} = -z_{\mathrm{II}}^{D*} = -z^{D*}$ and $z^{D*} = \frac{\sqrt{4g^2\theta^4 - m^2}}{2g\theta}$. When $\varepsilon = 0$ this yields the following phenotypic densities at equilibrium : $n_i^{D*}(z) = \nu_{\mathrm{I},i}\delta(z - z_{\mathrm{I}}^{D*}) + \nu_{\mathrm{II},i}\ \delta(z - z_{\mathrm{II}}^{D*})$ (analytic expressions for $\nu_{\mathrm{I},j}$ and $\nu_{\mathrm{II},j}$ are given in [MG]). When $\varepsilon > 0$ we can use the *second approximation* to obtain analytic expressions for the local moments of the stationary distribution in each habitat (see [MG]).

3.5.2 The source-sink scenario

We next focus on the source-sink scenario, assuming that $m_1 > 0$ and $m_2 = 0$. In this case, we are not able to compute the first order corrector v_2 in the whole domain. However, a local approximation of v_2 gives already convincing results (Figure 3.3).

The evolutionary outcome in the first habitat is obvious because it depends only on selection acting in habitat 1: the ESS is $-\theta$ and

$$\rho_1^* = \frac{r_1 - m_1}{\kappa_1}. \tag{3.26}$$

Moreover, the population's phenotypic density $n_{\varepsilon,1}$ can be computed explicitly: $n_{\varepsilon,1} = \rho_{\varepsilon,1} f_\varepsilon$, where $\rho_{\varepsilon,1} = \frac{r_1 - m_1 - \varepsilon\sqrt{g_1}}{\kappa_1}$ and f_ε is the probability density of a normal distribution $\mathcal{N}(-\theta, \frac{\varepsilon}{\sqrt{g_1}})$.

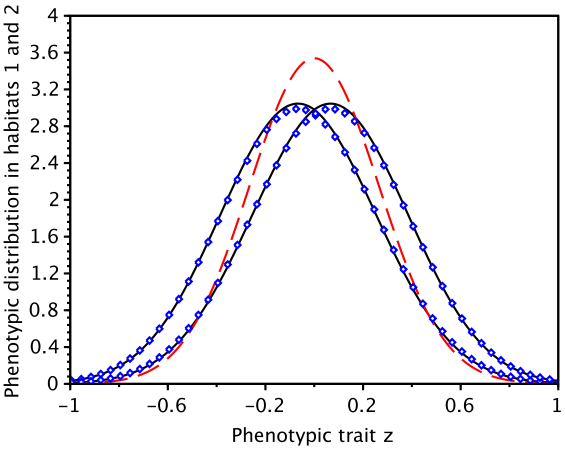

Figure 3.1: Selection-mutation-migration equilibrium of the phenotypic densities $n_{\varepsilon,i}(z)$ in the two habitats in a symmetric scenario. We plot the exact phenotypic densities at equilibrium obtained from numerical computations (blue dots) together with our *first approximation* (full black line) in a case where the distribution is unimodal in each habitat. We also plot the approximation given in [DRG13] (red dashed line). Note that our approximation captures the emergence of some differentiation even though we are above the critical migration rate leading to the evolution of a dimorphic population. In presence of mutations, the population's distribution is indeed shifted to the left(respectively right) in the first(respectively second) habitat, while [DRG13] provided the same approximation for both habitats. Our calculation yields also better approximations for the variance of the distribution in each habitat ([DRG13] underestimates this variance). In this figure and in the following ones, to compute numerically the equilibrium, we have solved numerically a time-dependent version of equation (3.1) and kept the solution obtained after long time when the equilibrium has been reached. Parameter values: $m = 1.5$, $r = 3$, $g = 2$; $\theta = 0.5$, $\kappa = 1$, $U = 1$, $\varepsilon = 0.1$.

In habitat 2, the evolutionary outcome results from the balance between migration from habitat 1 and local selection. Interestingly, migration has a non-monotonous effect on adaptation in the sink (See Figure 3.3). Indeed, Figure 3.3A shows that the population size in the sink is maximized for intermediate values of migration. More migration from the source has a beneficial effect on the demography of the sink but it prevents local adaptation. Yet, when migration from the source becomes very large it limits the size of the population in the source (see (3.26)). This limits the influence of the source on the sink and can even promote adaptation to the sink. In fact it is worth noting that differentiation between the two habitats can actually increase with migration (Figure 3.3B). The level of migration from the source that prevents local adaptation in the sink is given by the condition:

$$\frac{4g_2\theta^2 r_2}{\kappa_2} \leq \frac{m_1(r_1 - m_1)}{\kappa_1}, \tag{3.27}$$

Indeed, when condition (3.27) is verified, the migration from the source overwhelms local selection and the evolutionary stable strategy in the sink is $z^* = -\theta$. In contrast, when condition (3.27) does not hold, the effective growth rate of the optimal trait θ in the sink habitat is high enough

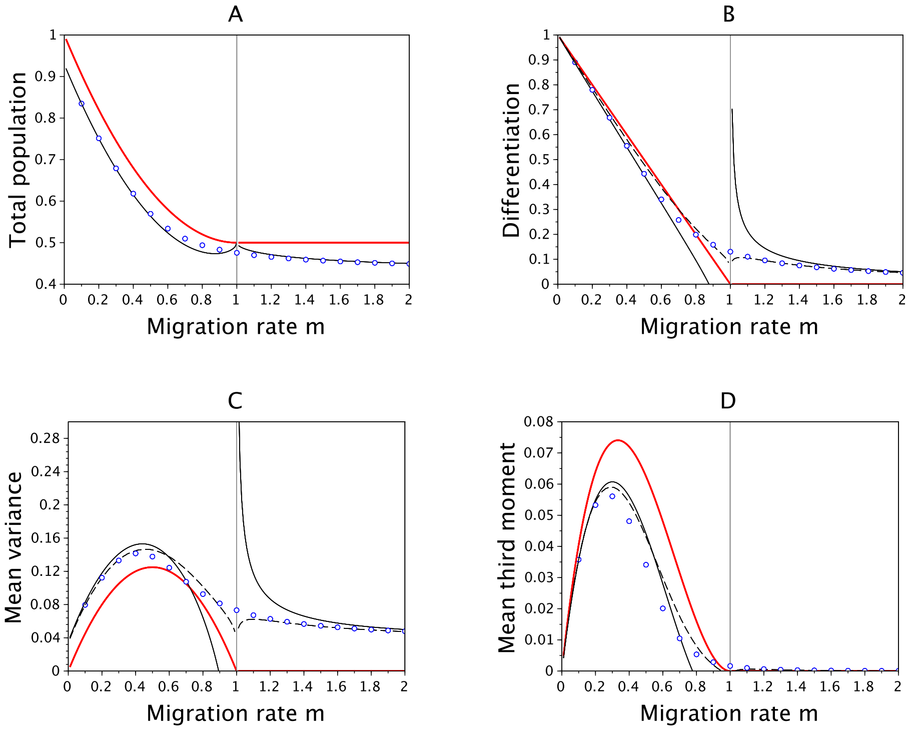

Figure 3.2: Effects of migration in a symmetric scenario on (A) the total population size ($\rho_{\varepsilon,1}$) in habitat 1, (B) the differentiation between habitats ($\mu_{\varepsilon,2} - \mu_{\varepsilon,1}$), (C) the variance ($\sigma^2_{\varepsilon,1}$) and (D) the third central moment of the phenotypic distribution ($\psi_{\varepsilon,1}$) in habitat 1. The dots refer to the numerical resolutions of the problem with $\varepsilon = 0.05$, the red line indicates the case where $\varepsilon = 0$ while the lines in black refer to our two approximations when $\varepsilon = 0.05$ (the dashed line for the *first approximation* and the full line for the *second approximation*). The vertical gray line indicates the critical migration rate below which dimorphism can evolve in the Adaptive Dynamics scenario. Other parameter values: $r = 1$, $g = 2$, $\theta = 0.5$, $\kappa = 1$.

to compete with the trait $-\theta$ coming from the source, allowing coexistence between the two strategies. Note again that our two approximations (see [MG] for more details) provide very good predictions for the moments of the phenotypic distribution in the sink (Figure 3.3).

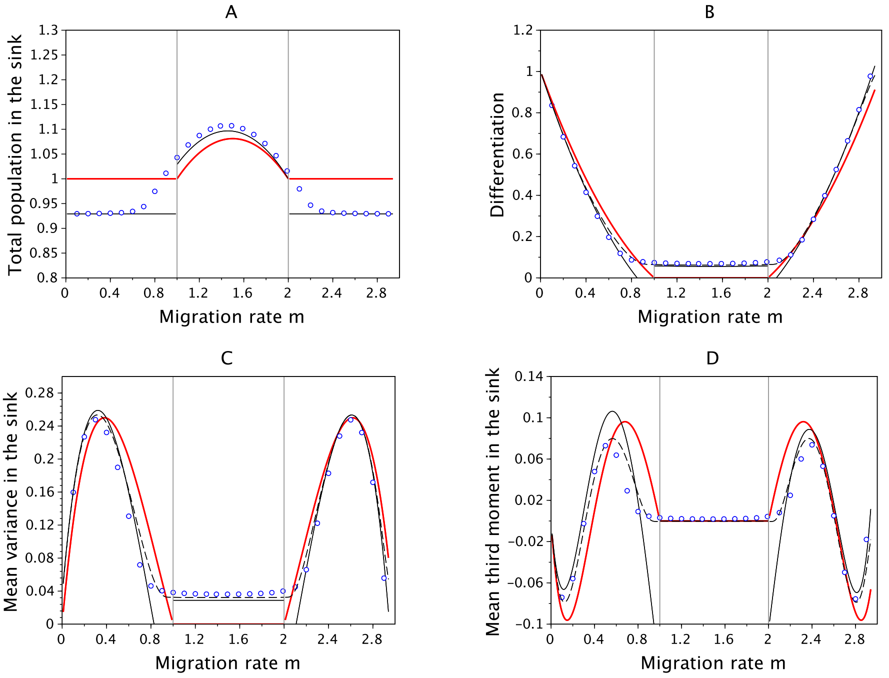

Figure 3.3: Effects of migration in a source-sink scenario on (A) the total population size in the sink habitat, (B) the differentiation between habitats, (C) the variance and (D) the third central moment of the phenotypic distribution in sink. The dots refer to exact numerical computations when $\varepsilon = 0.05$, the red line indicates the case where $\varepsilon = 0$ while the lines in black refer to our two approximations when $\varepsilon = 0.05$ (dashed line for the *first approximation* and the full line for the *second approximation*). The vertical gray lines, at $m = 1$ and $m = 2$, indicate the critical migration rates where transition occurs between monomorphism and dimorphism in the Adaptive Dynamics framework (see condition (3.27)). Other parameter values: $r_1 = 3$, $r_2 = 1$, $g_1 = 3$, $g_2 = 2$, $\kappa_1 = \kappa_2 = 1$, $\theta = 0.5$.

Chapter 4

Evolutionary adaptation in time-heterogeneous environments

4.1 Introduction

In this chapter, we study the evolutionary dynamics of populations in time varying environments. Natural populations experience environmental change due for instance to seasonal changes, climate change and interaction with other species. Cancer tumors and bacterial infections, when treated, are subject to a time heterogeneous selection thanks to the time dependent administration of the medications. Several questions arise with regard to time heterogeneous selection. How the time variations of an environment modify the evolutionary dynamics of a population? Can a population survive under the environmental change? How the size of the population would be affected? What would be the impact of time heterogeneous selection on the phenotypic distribution of the population? The better understanding of such phenomena is a major topic in the evolutionary biology theory and may help the understanding of several important questions [LMR10, CLM10, PMLJ$^+$13, KM14, BPnMGI17]. What is the role of adaptation in the preservation of the biodiversity in the context of climate change? Is it possible to find optimal drug delivery schedules or optimal ways of combining drugs to avoid resistance in the treatment of cancer and bacterial infections?

An example of biological experiment addressing the above questions is given in [KMZ$^+$13]. In this experiment, initially genetically identical populations of bacterial pathogen Serratia marcescens were kept in two different environments with constant or fluctuating temperatures for several weeks. Then, these populations were sampled and their growth rates were measured in different environments. The authors compared the performance of these two populations in different environments and observed in particular that the population evolved in periodically fluctuating temperature (daily variation between 24°C and 38°C, mean 31°C) outperformed the strains that evolved in constant temperature (31°C), when both strains were allowed to compete in a constant environment with temperature 31°C (see Figure 4.1). This is surprising at the first glance, since one could expect that the population evolved in a constant environment would select for the best traits in such environment, while the population evolved in a changing environment would have better performance when it is exposed to different types of environments but not necessarily at temperature 31°C which is the original environment of the first population. In Section 4.3 we will investigate, based on a mathematical model, in which situations such phenomenon may arise and provide some possible explanation for the outcome of this experiment.

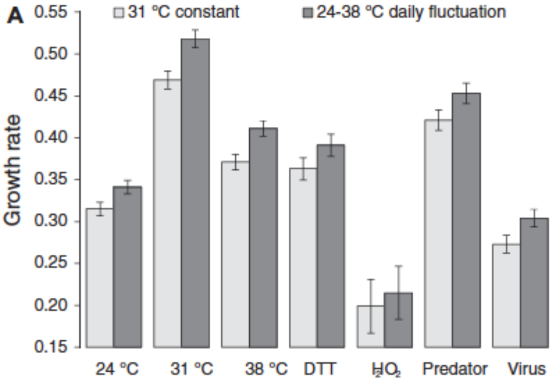

Figure 4.1: The comparison of the performances of the populations of bacterial pathogen Serratia marcescens evolved in environments with constant or fluctuating temperature, when they are placed at different environments. Figure from [KMZ+13].

A typical selection-mutation model in a time heterogeneous environment is written

$$\begin{cases} \frac{\partial}{\partial t} n(t,z) - \sigma \Delta n(t,z) = n(t,z) R(e(t), z, I(t)), \qquad (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ I(t) = \int_{\mathbb{R}^d} n(t,y)\psi(y)dy, \\ n(0,z) = n_0(z). \end{cases} \tag{4.1}$$

Here, as in the above chapters, z represents a phenotypic trait and $n(t,z)$ corresponds to the density of individuals with phenotype z at time t. The diffusion term corresponds to the mutations. We denote by $\psi(z)$ the resource consumption rate of individuals with trait z and by $I(t)$ the total resource consumption of the population. The main difference with the previous models is that the growth rate R depends, in addition to the trait z and the environmental feedback I, on the environmental state $e(t)$. A main difficulty in the study of such problems comes from the combination of the nonlocal competition term with the time dependency of the growth rate.

The outcome of such models is very rich. We will observe in the next sections that, depending on how the environment variations act on the growth rate and depending on the speed of the environment change, different types of behaviors may be observed. In Section 4.2 we will study the dynamics of the phenotypic density under periodically oscillating growth rate, in a concave framework closely related to [LMP11], when the effect of the mutations is much smaller than the frequency of the oscillations [MPS15]. In Section 4.3 we study a model where the fitness landscape varies with a linear trend but in an oscillatory manner, that is we consider a growth rate of the form $R(e(t), z - ct) - I(t)$ [FIM18, FIM]. In this section similarly to Section 4.2, we assume that the effect of the mutations are much smaller than the frequency of the oscillations. However, on the contrary to the model in Section 4.2, we do not make any concavity assumption on R but we consider a linear dependence of the growth rate on the nonlocal competition term I. This model is motivated by the study of the adaptation of a population to a climate change. Note that many natural populations are subject both to directional change of phenotypic optimum and random fluctuations of the environment [CVT15]. Such analysis provides also new results in the case of oscillating environments, without linear change ($c = 0$) [FIM18]. While the work in Section 4.2 allows to study the dynamics of a population under fluctuating selection, the work in [FIM18], corresponding to the case $c = 0$ in Section 4.3, focuses on the long time outcome of such fluctuating selection. In particular, this analysis allows us to provide some possible explanation for the outcome of the experience in [KMZ+13] presented above. Finally in Section 4.4, we study a case where the environmental change occurs very slowly [CEM]. More precisely, we consider a piecewise constant environmental state with slow switch.

The adaptation of populations in time varying environments is a major topic in evolutionary biology (see for instance [BL95, LS96, CLM10, KM14]). In [LCDH15, LCC16, ABF+19] models closely related to (4.1) are studied. These works focus mostly, in the context of cancer therapy optimization, on the numerical study of the problem or on the study of particular forms of growth rate R where semi-explicit solutions or explicit solutions may be obtained. In the case of a directional environment change, that is by replacing z by $z - ct$ in the growth rate R, closely related equations, but with a local reaction term and no fluctuation, have been widely studied (see for instance [BDNZ08, BR08, BR09, BDD14, BF18]). Such models are introduced to study dynamics of populations structured by a space variable neglecting evolution. It is shown in particular that there exists a critical speed of environment change c^*, such that the population survives if and only if the environment change occurs with a speed less than c^*. We also refer to [BL16] where an integro-difference model has been studied for the spatial dynamics of a population in the case of a randomly changing environment. Moreover, in [ABR17] both spatial and evolutionary dynamics of a population in an environment with linearly moving optimum has been studied. While here we don't include any spatial structure, in Section 4.3 we take into account an oscillatory change of the environment in addition to a change with linear trend.

The work in Section Section 4.2 is based on the result in [MPS15] in collaboration with B. Perthame and P. E. Souganidis. The work in Section 4.3 is based on the articles [FIM18, FIM] which are prepared in the framework of the PhD project of my student S. Figueroa Iglesias. Finally, Section 4.3 is based on the results in [CEM] which are obtained in the framework of the postdoctoral project of C. Etchegaray, who I mentored with M. Costa.

4.2 The evolutionary dynamics of a population in an oscillating environment

In this section, we extend the Hamilton-Jacobi approach to the case of oscillatory environments using homogenization tools. We study (4.1) considering an oscillating environment, with $e(\cdot)$ a 1-periodic function, and assuming small effect of the mutations $\sigma = \varepsilon^2$, with ε a small parameter. Being interested in the dynamics of the solution, we perform a change of variable in time $t \to \frac{t}{\varepsilon}$ and define

$$n_\varepsilon(t,z) = n(\frac{t}{\varepsilon}, z), \qquad I_\varepsilon(t) = I(\frac{t}{\varepsilon}),$$

to accelerate the dynamics and observe the effect of small mutations, similarly to Chapter 1. Then, (4.1) becomes

$$\begin{cases} \varepsilon \frac{\partial}{\partial t} n_\varepsilon(t,z) - \varepsilon^2 \Delta n_\varepsilon(t,z) = n_\varepsilon(t,z) R(e(\frac{t}{\varepsilon}), z, I_\varepsilon(t)), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ I_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,y)\psi(y)dy, \\ n_\varepsilon(0,z) = n_{\varepsilon,0}(z). \end{cases} \tag{4.2}$$

Our objective is to describe the limit of the solution n_ε as the effect of the mutations, measured by ε, vanishes. The major difficulty in the asymptotic analysis of this problem comes from the fast oscillatory function $e(\frac{t}{\varepsilon})$ combined with the nonlocal term $I_\varepsilon(t)$.

To provide an asymptotic analysis of this model we consider a concave framework closely related to [LMP11]. We prove that, as $\varepsilon \to 0$, the phenotypic density concentrates on an evolving point $\overline{z}(t)$ corresponding to a dominant trait. The dynamics of this dominant trait is given by a canonical equation, indicating that $\overline{z}(t)$ follows the gradient of an effective growth rate $\mathcal{R}$, obtained after a homogenization process from the growth rate $R(e, z, I)$. The size of the population $\rho_\varepsilon(t) = \int n_\varepsilon(t, z)dz$ and the competition term $I_\varepsilon(t)$ may still have oscillations at the limit $\varepsilon \to 0$ and they converge only in a weak sense. For some particular forms of the growth rate R we also provide the long time behavior of the dominant trait $\overline{z}(t)$. Finally, we provide an example where our method allows to show that periodic fluctuations may increase the population size.

In subsection 4.2.1 we present our assumptions and in subsection 4.2.2 we provide our main results. In subsection 4.2.3 we provide an example where fluctuations may increase the population size.

4.2.1 Assumptions

We assume that

$$R : \mathbb{R} \times \mathbb{R}^d \times [0, \infty) \to \mathbb{R} \quad \text{is smooth and} \qquad e : \mathbb{R}^+ \to \mathbb{R} \text{ is 1-periodic.} \tag{4.3}$$

To ensure the survival and the boundedness of the population we assume that R takes positive values for “small enough populations” and negative values for “large enough populations" , i.e., there exist a value $I_M > 0$ such that

$$\max_{0 \le s \le 1,\ z \in \mathbb{R}^d} R(e(s), z, I_M) = 0 \quad \text{and} \quad \mathcal{Z} := \{z \in \mathbb{R}^d, \int_0^1 R(e(s), z, 0)ds > 0\} \neq \emptyset. \tag{4.4}$$

In addition the growth rate R satisfies, for some positive constants K_i, $i = 1, \dots, 7$, and all $(e, z, I) \in \mathbb{R} \times \mathbb{R}^d \times [0, I_M]$ and $A > 0$, the following decay and concavity assumptions:

$$-2K_1 \le D_z^2 R(e, z, I) \le -2K_2, \qquad -K_3 - K_1|z|^2 \le R(e, z, I) \le K_4 - K_2|z|^2, \tag{4.5}$$

$$-K_5 \le D_I R(e, z, I) \le -K_6, \tag{4.6}$$

$$D_z^3 R \in L^\infty\big(\mathbb{R} \times \mathbb{R}^d \times [0, A]\big) \quad \text{and} \quad |D_{z,I}^2 R| \le K_7. \tag{4.7}$$

The "uptake coefficient” $\psi : \mathbb{R}^d \to \mathbb{R}$ must be regular and bounded from above and below, i.e., there exist positive constants ψ_m, ψ_M and K_8 such that

$$0 < \psi_m \le \psi \le \psi_M \quad \text{and} \quad \|\psi\|_{C^2} \le K_8. \tag{4.8}$$

We also assume that the initial datum is "asymptotically monomorphic”, i.e., it is close to a Dirac mass in the sense that there exist $z_0 \in \mathcal{Z}$, $\rho_0 > 0$ and a smooth $u_{\varepsilon,0} : \mathbb{R}^d \to \mathbb{R}$ such that

$$n_{\varepsilon,0} = e^{u_{\varepsilon,0}/\varepsilon} \quad \text{and, as } \varepsilon \to 0, \tag{4.9}$$

$$n_\varepsilon(0,\cdot) \underset{\varepsilon\to 0}{\longrightarrow} \varrho_0\delta(\cdot - z_0) \quad \text{weakly in the sense of measures.} \tag{4.10}$$

In addition there exist constants $L_i > 0, i = 1, \dots, 4$, and a smooth $u_0 : \mathbb{R}^d \to \mathbb{R}$ such that, for all $z \in \mathbb{R}^d$,

$$-2L_1 I \le D_z^2 u_{\varepsilon,0} \le -2L_2 I, \quad -L_3 - L_1|z|^2 \le u_{\varepsilon,0}(z) \le L_4 - L_2|z|^2, \quad \max_{z\in\mathbb{R}^d} u_0(z) = 0 = u_0(z_0), \tag{4.11}$$

and, as $\varepsilon \to 0$,

$$u_{\varepsilon,0} \longrightarrow u_0 \quad \text{locally uniformly in } \mathbb{R}^d. \tag{4.12}$$

4.2.2 Main results

To state our results we first need, as usual in homogenization, a cell problem given by the following Lemma:

Lemma 4.1. *Assume* (4.4), (4.5) *and* (4.8). *For all* $z \in \mathcal{Z}$, *there exists a unique* 1*-periodic positive solution* $\mathcal{I}(z,s) : [0,1] \to (0, I_M)$ *to*

$$\begin{cases} \frac{d}{ds}\mathcal{I}(z,s) = \mathcal{I}(z,s)\ R\big(e(s), z, \mathcal{I}(z,s)\big), \\ \mathcal{I}(z,0) = \mathcal{I}(z,1). \end{cases} \tag{4.13}$$

Moreover, as $\mathcal{Z} \ni z \to z_0 \in \partial\mathcal{Z}$,

$$\max_{0\le s\le 1} \mathcal{I}(z,s) \to 0. \tag{4.14}$$

In view of (4.14), for $z \in \partial\mathcal{Z}$, we define, by continuity, $\mathcal{I}(z,s) = 0$. The function $\mathcal{I}(z,s)$ helps us to identify the weak limit of $I_\varepsilon(t)$. Moreover it helps us to derive, using a homogenization process, an effective growth rate $\mathcal{R}$ which will replace R (see Theorem 4.2). This effective growth rate is defined, for all $y \in R^d$ and $z \in \overline{\mathcal{Z}}$ (here $\overline{\mathcal{Z}}$ stands for the closure of $\mathcal{Z}$), as below

$$\mathcal{R}(y,z) := \int_0^1 R(e(s), y, \mathcal{I}(z,s))ds.$$

Notice also that, dividing (4.13) by $\mathcal{I}(z,s)$ and integrating in s and using the periodicity, we always have, for $z \in \overline{\mathcal{Z}}$,

$$\mathcal{R}(z,z) \equiv 0.$$

Example of effective growth rate: if the growth rate R has the following form

$$R(e,z,I) = a(e,z) - \kappa I,$$

then the effective growth rate $\mathcal{R}$ is given by

$$\mathcal{R}(y,z) = \overline{a}(y) - \kappa\overline{\mathcal{I}}(z),$$

with

$$\overline{a}(y) = \int_0^1 a(e(s), y)ds, \qquad \overline{\mathcal{I}}(z) = \int_0^1 \mathcal{I}(z,s)ds.$$

Our first result is about the behavior of (n_ε) as $\varepsilon \to 0$. It asserts the existence of a fittest trait $\overline{z}(t)$ and a total population size $\overline{\rho}(t)$ at time t and provides a "canonical equation" for the evolution in time of $\overline{z}$ in terms of the "effective fitness" $\mathcal{R}(y,z)$. In the sequel, $D_1\mathcal{R}$ denotes the derivative of $\mathcal{R}$ with respect to the first argument.

Theorem 4.2 (Limit as $\varepsilon \to 0$ [MPS15]). *Assume* (4.3)–(4.12). *There exist a fittest trait* $\overline{z} \in \mathrm{C}^1([0,\infty);\mathcal{Z})$ *and a total population size* $\overline{\rho} \in \mathrm{C}^1([0,\infty);(0,\infty))$ *such that, along subsequences as* $\varepsilon \to 0$,

$$n_\varepsilon(t,\cdot) \rightharpoonup \overline{\varrho}(t)\delta(\cdot - \overline{z}(t)) \quad \textit{weakly in the sense of measures,}$$

$$I_\varepsilon(\cdot) \rightharpoonup \overline{I}(\cdot) = \int_0^1 \mathcal{I}(\overline{z}(\cdot),s)ds = \overline{\varrho}(\cdot)\psi(\overline{z}) \qquad \textit{in} \ \ L^\infty(0,\infty) \ \textit{weak-}\star,$$

and

$$R(e(\frac{t}{\varepsilon}),z,I_\varepsilon(t)) \rightharpoonup \mathcal{R}(z,\overline{z}(t)) \quad \textit{weakly in the sense of measures in } t \textit{ and strongly in } z.$$

Moreover, $\overline{z}$ *satisfies the canonical equation*

$$\dot{\overline{z}}(t) = \left(-D_z^2 u(t,\overline{z}(t))\right)^{-1} \cdot D_1\mathcal{R}(\overline{z}(t),\overline{z}(t)). \tag{4.15}$$

We note that, even if we are not in the framework of adaptive dynamics with rare mutations, we can still interpret the above terms in the language of adaptive dynamics: $\mathcal{R}(y,z)$ can be interpreted as the effective fitness of a mutant y in a resident population with a dominant trait z, while $D_1\mathcal{R}$ is usually called the selection gradient, since it represents the capability of invasion. The extra term $\left(-D_z^2 u(t,\overline{z}(t))\right)^{-1}$, as in Section 1.5, approximates the covariance matrix of the phenotypic distribution and is an indicator of the diversity around the dominant trait in the resident population.

The second issue is the identification of the long time limit of the fittest trait $\overline{z}$. We prove that, in the limit $t \to \infty$, the population converges to a, so called, Evolutionary Stable Strategy (ESS) corresponding to a distribution of population which is stable under introduction of small mutations (see [MSP73, Esh83, JR11] and Section 3.2.1 for a more detailed definition). See also for instance [DJMR08, Rao11] for studies of the local and global stability of stationary solutions of integro-differential population models in constant environments.

Theorem 4.3 (Limit as $t \to \infty$ [MPS15]). *In addition to* (4.3)–(4.12) *assume that either* $d = 1$ *or, if* $d > 1$, R *is given, for some smooth* $a, b, A, B : \mathbb{R}^d \to (0,\infty)$ *by*

$$R(e,z,I) = a(z)A(e,I) - b(z)B(e,I). \tag{4.16}$$

Then, as $t \to \infty$, *the population reaches an Evolutionary Stable Distribution* $\overline{\varrho}_\infty\delta(\cdot - \overline{z}_\infty)$, *i.e.,* $\overline{\varrho}(t) \longrightarrow \overline{\varrho}_\infty$ *and* $\overline{z}(t) \longrightarrow \overline{z}_\infty$, *where* $\overline{\varrho}_\infty > 0$ *and* $\overline{z}_\infty$ *are characterized by (*$\mathcal{I}$ *is defined in* (4.13)*)*

$$\mathcal{R}(\overline{z}_\infty,\overline{z}_\infty) = 0 = \max_{z\in\mathbb{R}^d}\mathcal{R}(z,\overline{z}_\infty) \quad \textit{and} \ \ \overline{\varrho}_\infty = \frac{1}{\psi(\overline{z}_\infty)}\int_0^1 \mathcal{I}(\overline{z}_\infty,s)ds. \tag{4.17}$$

The proof of the above result for a growth rate R given by (4.16), is based on a Lyapunov functional defined by

$$L(t) := \frac{a(\overline{z}(t))}{b(\overline{z}(t))}.$$

Notice that we do not claim the uniqueness of the Evolutionary Stable Strategy. Indeed there may exist several $(\rho_\infty,\overline{z}_\infty)$ satisfying (4.17). Here we only prove that there exists $(\rho_\infty,\overline{z}_\infty)$

satisfying (4.17) such that, as $t \to \infty$, the phenotypic density converges to $\varrho_\infty \delta(\cdot - \overline{z}_\infty)$.

The difference between our conclusions and the results for time homogeneous environments in [LMP11] is that, in the canonical equation (4.15), the growth rate R is replaced by an effective growth rate $\mathcal{R}$ which is derived after a homogenization process. Moreover, we are only able to prove that (I_ε) converges in L^∞ weak-$*$ and not a.e., which is the case for constant environments in [BMP09, LMP11] (see also Section 1.3). One can wonder whether the convergence of (I_ε) towards $\overline{I}$ is indeed in the strong sense as in the case with constant environment. The numerical resolution of the problem suggests that I_ε oscillates with period of order ε, with non-vanishing amplitude and hence such convergence is indeed only in the weak sense (see Figure 4.2). This adds a difficulty in Theorem 4.3 and it is the reason why we are not able to describe, without additional assumptions, the long-time limit behavior of the fittest trait $\overline{z}$ for general growth rate R when $d > 1$. This remains an open question.

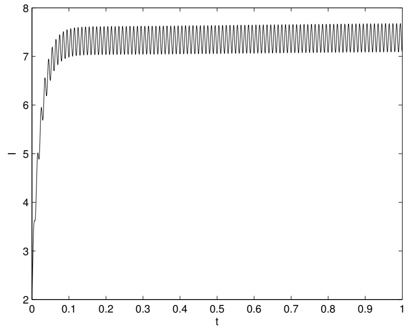

Figure 4.2: Dynamics of the total resource consumption $I_\varepsilon(t)$ for $R(e, z, I) = (2 + e)\frac{2-z^2}{I+.5} - .5$, $e(s) = \sin(2\pi s)$, $\psi(z) = 1$ and $\varepsilon = 0.01$. The function I_ε oscillates with period of order ε around a monotone curve $\overline{I}$.

In [MPS15], we give an example of $\mathcal{R}$ not satisfying the assumptions of Theorem 4.3 for which $\overline{z}(t)$ exhibits a periodic behavior. This example fits the structure (4.18) below with general concavity properties on $\mathcal{R}$ but it is not necessarily derived from a homogenization limit.

The proofs use in a fundamental way the classical Hopf-Cole transformation

$$u_\varepsilon = \varepsilon \ln n_\varepsilon,$$

which yields the following Hamilton-Jacobi equation for u_ε :

$$\begin{cases} \partial_t u_\varepsilon = R\big(e(\tfrac{t}{\varepsilon}), z, I_\varepsilon(t)\big) + |\nabla u_\varepsilon|^2 + \varepsilon \Delta u_\varepsilon, & \text{in } (0,\infty) \times \mathbb{R}^d, \\ u_\varepsilon(0,\cdot) = u_{\varepsilon,0}(\cdot), & \text{in } \mathbb{R}^d. \end{cases}$$

The next theorem describes the behavior of (u_ε), as $\varepsilon \to 0$.

Theorem 4.4. *Assume* (4.3)–(4.12). *Along subsequences as $\varepsilon \to 0$, $u_\varepsilon \to u$ locally uniformly in $[0,\infty) \times \mathbb{R}^d$, where $u \in \mathrm{C}([0,\infty) \times \mathbb{R}^d)$ is a viscosity solution of*

$$\begin{cases} \partial_t u = \mathcal{R}(z, \overline{z}(t)) + |\nabla u|^2 & \textit{in } \mathbb{R}^d \times (0,\infty), \\ \max_{z \in \mathbb{R}^d} u(t,z) = 0 = u(t, \overline{z}(t)) & \textit{in } (0,\infty), \\ u(0,\cdot) = u_0 & \textit{in } \mathbb{R}^d. \end{cases} \tag{4.18}$$

In the case of time homogeneous environments, one can derive such Hamilton-Jacobi equation without any concavity assumption on R and u_0 (see [PB08, BMP09] and Section 1.3). In order to extend our result beyond the concave framework, the major difficulty is to determine the effective growth rate $\mathcal{R}$. We need indeed assumptions (4.5) and (4.11) to ensure a priori that n_ε goes to a single Dirac mass at the point $\overline{z}(t)$. This information is needed in order to write (4.18). We point out that it is also known for such models that, while $z \in \mathbb{R}$ and R is monotonic with respect to z and making no concavity assumption, n_ε still converges to a single Dirac mass. This suggests that we could relax the concavity assumptions in this latter case or in similar situations where such information is known a priori.
It is also possible to obtain such type of results, in the multi-d case and beyond the concave framework, for particular forms of R without using the concentration of n_ε as a Dirac mass. In [MPS15] we give indeed an example of a non-concave R, that is

$$R(e,z,I) = a(z)A(e,I) - B(e,I),$$

for which the effective growth rate $\mathcal{R}$ can be computed independently of $\overline{z}(t)$ and equivalent results can be obtained. This example is all the more interesting since the corresponding effective growth rate $\mathcal{R}$ has a natural form that can be computed explicitly, while in general not much is known about the structure of $\mathcal{R}$.

4.2.3 A qualitative effect: fluctuations may increase the population size

We conclude with an example that shows that the time-oscillations may lead to a strict increase of the population size at the evolutionary stable state, a conclusion which also holds in the context of physiologically structured populations [CGP07]. Note that the positive or negative impact of time-oscillations on the population size depends on the choice of the growth rate R. In Section 4.3 we will provide other examples of growth rate where on the contrary the fluctuations have a negative impact on the population size.

We consider, the rate function

$$R(e,z,I) = a(z) - B_1(e)B_2(I),$$

with $e(\cdot)$ a 1-periodic function and a, B_1 and B_2 smooth functions such that

$$0 < B_i, \qquad 0 < a_m \le a(z) \le a_M, \qquad 0 < \frac{\partial}{\partial I} B_2(I), \qquad \frac{\partial^2}{\partial I^2} B_2(I) < 0, \qquad \text{for } i = 1,2,$$

and

$$\lim_{I \to 0} \min_{0 \le s \le 1} \big(a_m - B_1(e(s))B_2(I)\big) > 0, \qquad \lim_{I \to +\infty} \max_{0 \le s \le 1} \big(a_M - B_1(e(s))B_2(I)\big) < 0.$$

We also take $\psi \equiv 1$. Note that in [MPS15] we have shown that the analysis in Section 4.2.2 can be applied to such type of growth rate without any concavity assumption on a. Such analysis is obtained via an effective growth rate which is defined independently of the dominant trait $\overline{z}$. Here, we don't go through the details of such analysis. We only focus on the longtime outcome that can be determined using the same effective growth rate $\mathcal{R}$ as above and under the assumption that there exists a unique $z_m \in \mathbb{R}^d$ such that

$$\max_{z \in \mathbb{R}^d} a(z) = a(z_m).$$

The goal is to compare the long time limit of the total population size for the model with fluctuations ($\overline{\rho}_\infty$) given by (4.17) to the one (ρ^c_∞) obtained from the model with the "averaged rate":

$$R_{\text{av}}(z, I) = a(z) - B_{1,\text{av}} B_2(I) \quad \text{with } B_{1,\text{av}} = \int_0^1 B_1(e(s))ds.$$

Later, we write f_{av} for the average of the 1-periodic map $f : \mathbb{R} \to \mathbb{R}$, i.e., $f_{\text{av}} = \int_0^1 f(s)ds$. In the constant case, the outcome can be obtained from the previous results [PB08, LMP11]: as $t \to \infty$ the dominant trait is given by $z^c_\infty = z_m$ and the total population size is given by

$$\rho^c_\infty = I^c_\infty, \qquad \text{such that} \qquad a(z_m) = B_{1,\text{av}} B_2(\rho^c_\infty). \tag{4.19}$$

In the periodic case, the outcome is given by Theorem 4.3: as $t \to \infty$ the dominant trait is given by $z^c_\infty = z_m$ and the total population size is given by

$$\rho^p_\infty = I^p_\infty, \qquad \text{such that} \qquad \rho^p_\infty = \int_0^1 \mathcal{I}(z_m, s)ds,$$

where $\mathcal{I}$ solves (4.13). Multiplying (4.13) by suitable functions of $\mathcal{I}$ and integrating with respect to s, we obtain that

$$a(z_m) = \int_0^1 B_1(e(s))B_2(\mathcal{I}(z_m, s))ds \ \text{ and } \ \int_0^1 B_2(\mathcal{I}(z_m, s))ds \; a(z_m) = \int_0^1 B_1(e(s))B_2^2(\mathcal{I}(z_m, s))ds. \tag{4.20}$$

A straightforward application of the Cauchy-Schwarz inequality in (4.20), since $B_2(\mathcal{I}(z_m, s))$ is not constant, yields

$$a(z_m)^2 < B_{1,\text{av}} \; a(z_m) \int_0^1 B_2(\mathcal{I}(z_m, s))ds,$$

and thus

$$a(z_m) < B_{1,\text{av}} \int_0^1 B_2(\mathcal{I}(z_m, s))ds. \tag{4.21}$$

Combining (4.19) and (4.21) we obtain that

$$B_2(\rho^c_\infty) < \int_0^1 B_2(\mathcal{I}(z_m, s))ds.$$

Using the concavity and the monotonicity of B_2 we obtain that

$$\rho^c_\infty < \int_0^1 \mathcal{I}(z_m, s)ds = \overline{\rho}_\infty,$$

which substantiates our claim about the possible effect of the time oscillations.

4.3 Adaptation to a shifting and oscillating environment

In this section, we study the evolutionary dynamics of a phenotypically structured population in an environment where the fitness landscape varies with a linear trend but in an oscillatory manner. We study the following non-local parabolic equation

$$\begin{cases} \partial_t \widetilde{n} - \sigma \partial_{zz} \widetilde{n} = \widetilde{n}[a(e(t), z - \widetilde{c}t) - \kappa \widetilde{\rho}(t)], \quad (t,z) \in [0, +\infty) \times \mathbb{R}, \\ \widetilde{\rho}(t) = \displaystyle\int_{\mathbb{R}} \widetilde{n}(t,z) dz, \\ \widetilde{n}(t=0, z) = \widetilde{n}_0(z). \end{cases} \tag{4.22}$$

This equation models the dynamics of a population which is structured by a phenotypic trait $z \in \mathbb{R}$. Here, $\widetilde{n}(t,z)$ corresponds to the density of individuals with trait z at time t. We denote by $a(e(t), z - \widetilde{c}t)$ the intrinsic growth rate of an individual with trait z at time t. The term $-\widetilde{c}t$ has been introduced to consider a variation of the fitness landscape with a linear trend. The term e is an environment state which varies periodically to consider fluctuations of the environment. The term $\widetilde{\rho}$ which corresponds to the total size of the population represents a competition term. Here, we assume indeed a uniform competition between all the individuals with intensity κ. The diffusion term models the mutations, with σ a measure of the effect of the mutations.

A natural motivation to study such type of problem is the fact that many natural populations are subject both to directional change of phenotypic optimum and random fluctuations of the environment or seasonal changes ([BL95, CVT15]). Here, we consider a deterministic growth rate that varies with a linear trend but in an oscillatory manner as a first step to study such situations. Will the population be able to adapt to the environmental change? Is there a maximum speed above which the population will get extinct? How is such maximal speed modified due to the fluctuations? Such questions have been studied in the biological literature using related quantitative genetics models under simplifying assumptions and in particular considering Gaussian distributions (see for instance [BL95, LS96, GH09]).

In this work we prove indeed that there exists a critical speed of linear change above which the population will get extinct. When the speed of linear change is less than this critical speed we prove that the population persists and we characterize the long time behavior of the solution to (4.22) assuming small effect of mutations (σ small). We also provide an asymptotic expansion for the critical speed in terms of σ. These results allow us to provide analytic approximations for the moments of the phenotypic density. We provide such analytic approximations for several case studies leading to different biological behaviors. In particular, we investigate the role of the fluctuations in the ability of the population to follow the environment linear change.

The analysis in this section provides also new results in the case of pure environmental oscillations without change with linear trend (the case with $c = 0$) [FIM18]. Note that the work in Section 4.2 allows to study the dynamics of a population under fluctuating selection, while the work in [FIM18], corresponding to the case $c = 0$ in this section, focuses on the long time outcome of such fluctuating selection. In particular, this analysis allows us to provide some possible explanation for the outcome of the experience in [KMZ$^+$13] presented above (see subsection 4.3.4.2). Note also that the results in Section 4.2 were obtained under concavity assumptions on the growth rate R. Here, we don't make any concavity assumption but we consider a linear dependence of the growth rate on the competition term I.

The work in [FIM18], corresponding to the case $c = 0$, is performed in the multi-d case, that is

$z \in \mathbb{R}^d$. In [FIM] we assume $z \in \mathbb{R}$. However, we believe that the results may be extended to the multi-d case with no significant difficulty. Here, we present our results in the framework of [FIM] considering $z \in \mathbb{R}$. In subsection 4.3.1 we provide our assumptions and our preliminary results. In subsection 4.3.2 we present our main results. In subsection 4.3.3 we provide some heuristic computations which show on the one hand where the corresponding Hamilton-Jacobi equation comes from. On the other hand these computations lead to a system of equations for the next order term. The computation of the next order term allows us, as in subsection 3.4.2, to provide analytic approximations of the moments of the phenotypic distribution. Such analytic approximations are provided in 4.3.4 considering several case studies and show that depending on how the fluctuations modify the growth rate R different biological behaviors may be observed.

4.3.1 Assumptions and preliminary results

To introduce our assumptions, we first define

$$\overline{a}(y) = \frac{1}{T}\int_0^T a(e(t), y)dt.$$

We then assume that $e : \mathbb{R}^+ \to \Omega \subset \mathbb{R}$ is a periodic function and that, for all $t \in \mathbb{R}^+$ and $e_0 \in \Omega$,

$$e(t) = e(t+T), \qquad \|a\|_{L^\infty(\Omega\times\mathbb{R})} \leq C_0, \qquad a(e_0, \cdot) \in C^3(\mathbb{R}). \tag{4.23}$$

In addition, the averaged function $\overline{a}$ attains its maximum and

$$\max_{z\in\mathbb{R}} \overline{a}(z) > 0, \tag{4.24}$$

which means that there exist at least some traits with strictly positive average growth rate. Moreover, for some of our results we assume that there exists a unique optimal trait z_m in the average environment, that is

$$\exists!\ z_m \in \mathbb{R} : \max_{z\in\mathbb{R}} \overline{a}(z) = \overline{a}(z_m), \tag{4.25}$$

and also

$$\exists!\ \overline{z} \leq z_m;\ \overline{a}(\overline{z}) + \frac{\widetilde{c}^2}{4\sigma} = \overline{a}(z_m). \tag{4.26}$$

Furthermore, we make the following assumption on the initial condition which means that the density of individuals with large trait in the initial population is exponentially small:

$$0 \leq \widetilde{n}_0(z) \leq e^{C_1 - C_2|z|}, \quad \forall z \in \mathbb{R}, \tag{4.27}$$

for some positive constants C_1, C_2.

To avoid the shift in the growth rate a, we transform our problem with a change of variable. We introduce indeed $n(t,z) = \widetilde{n}(t, z + \widetilde{c}t)$ which satisfies:

$$\begin{cases} \partial_t n - \widetilde{c}\partial_z n - \sigma\partial_{zz} n = n[a(e(t), z) - \rho(t)], \quad (t,z) \in [0,+\infty)\times\mathbb{R}, \\ \rho(t) = \displaystyle\int_{\mathbb{R}} n(t,y)dy, \\ n(t=0,z) = n_0(z) = \widetilde{n}_0(z). \end{cases} \tag{4.28}$$

Next, we introduce the linearized problem associated to (4.28). Let $m(t,z) = n(t,z)e^{\int_0^t \rho(s)ds}$, for n the solution of (4.28), then m satisfies

$$\begin{cases} \partial_t m - \widetilde{c}\partial_z m - \sigma\partial_{zz} m = a(e(t),z)m, & (t,z) \in [0,+\infty) \times \mathbb{R}, \\ m(t=0,z) = n_0(z), & z \in \mathbb{R}. \end{cases}$$

We also introduce the corresponding parabolic eigenvalue problem as follows

$$\begin{cases} \partial_t p_{\tilde{c}} - \tilde{c}\partial_z p_{\tilde{c}} - \sigma\partial_{zz} p_{\tilde{c}} - a(e(t),z)p_{\tilde{c}} = \lambda_{\tilde{c},\sigma} p_{\tilde{c}}, & (t,z) \in [0,+\infty) \times \mathbb{R}, \\ 0 < p_{\tilde{c}}(t,z);\ p_{\tilde{c}}(t,z) = p_{\tilde{c}}(t+T,z), & (t,z) \in [0,+\infty) \times \mathbb{R}. \end{cases} \tag{4.29}$$

We also define the eigenvalue problem in the bounded domain $[-R,R]$, for some $R > 0$,

$$\begin{cases} \partial_t p_R - \widetilde{c}\partial_z p_R - \sigma\partial_{xx} p_R - a(e(t),z)p_R = \lambda_R p_R, & (t,z) \in [0,+\infty) \times [-R,R], \\ p_R(t,z) = 0, & (t,z) \in [0,+\infty) \times \{-R,R\}, \\ 0 < p_R(t,z);\ p_R(t,z) = p_R(t+T,z), & (t,z) \in [0,+\infty) \times [-R,R]. \end{cases} \tag{4.30}$$

It is known that problem (4.30) has a unique eigenpair (λ_R, p_R) with p_R a strictly positive eigenfunction such that $\|p_R(0,\cdot)\|_{L^\infty([-R,R])} = 1$ (see [Hes91]). Another fundamental result (see for instance [HP08]), for our purpose is that the function $R \mapsto \lambda_R$ is decreasing and $\lambda_R \to \lambda_{\tilde{c},\sigma}$ as $R \to +\infty$.

We next assume that there exist positive constants δ and R_0 such that

$$a(e(t),z) + \lambda_{\tilde{c},\sigma} \leq -\delta, \quad \text{for all } 0 \leq t, \text{ and } R_0 \leq |z|, \tag{4.31}$$

which means that large traits have negative enough growth rates. Under the above additional assumption, there exists a unique principal eigenpair $(\lambda_{\tilde{c},\sigma}, p_{\tilde{c}})$ for (4.29) [HP08]:

Proposition 4.5. *Assume* (4.23), (4.27) *and* (4.31). *Then for problem* (4.29) *there exists a unique principal eigenfunction* $p_{\tilde{c}}$ *associated to* $\lambda_{\tilde{c},\sigma}$, *with* $\|p_{\tilde{c}}(0,\cdot)\|_{L^\infty(\mathbb{R})} = 1$. *Moreover, we have* $p_{\tilde{c}} = \lim_{R\to\infty} p_R$ *and*

$$p_{\tilde{c}}(t,z) \leq \|p_{\tilde{c}}\|_{L^\infty} e^{-\nu(|z|-R_0)}, \qquad \forall (t,z) \in [0,+\infty) \times \mathbb{R},$$

for $\nu = -\frac{\widetilde{c}}{2\sigma} + \sqrt{\frac{\delta}{\sigma} + \frac{1}{2}\left(\frac{\widetilde{c}}{\sigma}\right)^2}$.
Finally, the eigenfunction $p_{\tilde{c}}(t,z)$ *is exponentially stable, in the following sense; there exists* $\alpha > 0$ *such that:*

$$\|m(t,z)e^{t\lambda_{\tilde{c},\sigma}} - \alpha p_{\tilde{c}}(t,z)\|_{L^\infty(\mathbb{R})} \to 0 \quad \textit{exponentially fast as } t \to \infty.$$

We next define the $T-$periodic functions $Q_{\tilde{c}}(t)$ and $P_{\tilde{c}}(t,z)$ as follows:

$$Q_{\tilde{c}}(t) = \frac{\int_{\mathbb{R}} a(e(t),z)p_{\tilde{c}}(t,z)dz}{\int_{\mathbb{R}} p_{\tilde{c}}(t,z)dz}, \quad P_{\tilde{c}}(t,z) = \frac{p_{\tilde{c}}(t,z)}{\int_{\mathbb{R}} p_{\tilde{c}}(t,z)dz},$$

Finally we state a Lemma which will be useful for the next section.

Lemma 4.6. *There exists a positive solution* $\widehat{\rho}(t)$ *to the problem*

$$\begin{cases} \dfrac{d\widehat{\rho}}{dt} = \widehat{\rho}\left[Q_{\tilde{c}}(t) - \widehat{\rho}\right], & t \in (0,T), \\ \widehat{\rho}(0) = \widehat{\rho}(T), \end{cases} \tag{4.32}$$

if and only if $\displaystyle\int_0^T Q_{\tilde{c}}(t)dt > 0$. *Moreover, this solution is unique.*

4.3.2 Main results

First, we determine conditions on the environment shift speed $\widetilde{c}$ which lead to extinction or survival of the population. Next, in the case of the population survival, we characterize asymptotically the population density considering small effect of the mutations.

To present our result on the survival criterion, we define the "critical speed".

Definition 4.7. *We define the critical speed* $\widetilde{c}_\sigma^*$ *as follows*

$$\widetilde{c}_\sigma^* = \begin{cases} 2\sqrt{-\sigma\lambda_{0,\sigma}}, & \text{if } \lambda_{0,\sigma} < 0, \\ 0, & \text{otherwise}, \end{cases}$$

where $\lambda_{0,\sigma}$ *corresponds to the principal eigenvalue introduced by Proposition 4.5, in the case* $c = 0$.

The next result shows that $\widetilde{c}_\sigma^*$ is indeed a critical speed of climate change above which the population goes extinct.

Proposition 4.8 (Survival criterion [FIM])**.** *Let* $n(t, z)$ *be the solution of* (4.28)*. Assume* (4.23), (4.24), (4.27) *and* (4.31)*. Then the following statements hold:*

(i) if $\widetilde{c} \geq \widetilde{c}_\sigma^*$, *then the population will go extinct, i.e.* $\rho(t) \to 0$, *as* $t \to \infty$,

(ii) if $\widetilde{c} < \widetilde{c}_\sigma^*$, *then* $|\rho(t) - \widehat{\rho}(t)| \to 0$, *as* $t \to \infty$, *with* $\widehat{\rho}$ *the unique solution to* (4.32).

(iii) Moreover, $\left\| \frac{n(t,z)}{\rho(t)} - P_{\widetilde{c}}(t,z) \right\|_{L^\infty} \longrightarrow 0$, *as* $t \to \infty$. *Consequently we have, as* $t \to \infty$:

$$\|n(t,\cdot) - \widehat{\rho}(t)P_{\widetilde{c}}(t,\cdot)\|_{L^\infty} \to 0, \text{ if } \widetilde{c} < \widetilde{c}_\sigma^* \quad \text{and} \quad \|n\|_{L^\infty} \to 0, \text{ if } \widetilde{c} \geq \widetilde{c}_\sigma^*.$$

Remark 4.9. *Note that if* $\lambda_{0,\sigma} \geq 0$, *then* $\widetilde{c}_\sigma^* = 0$ *which means that the population goes extinct even without climate change, that is with* $\widetilde{c} = 0$.

Proposition 4.8 shows that if the environment change occurs "too fast" the population will not be able to follow the environment change and will get extinct. However, if the change speed is "moderate" the phenotypic density n converges to the periodic function $n_{\widetilde{c}}(t, z) = \widehat{\rho}(t)P_{\widetilde{c}}(t, z)$, which is in fact the unique periodic solution of (4.28).

Next, we are interested in describing this periodic solution $n_{\widetilde{c}}$, asymptotically as the effect of the mutations is small. To this end, we take $\sigma = \varepsilon^2$ and $\widetilde{c} = \varepsilon c$, with ε small, and we study asymptotically the solution $(n_{\varepsilon c}, \widehat{\rho}_{\varepsilon c})$ as ε vanishes. For better legibility, we also define $c_\varepsilon^* := \frac{\widetilde{c}_{\varepsilon^2}^*}{\varepsilon}$ where $\widetilde{c}_{\varepsilon^2}^*$ stands for the critical speed $\widetilde{c}_\sigma^*$ with $\sigma = \varepsilon^2$. Note that, in view of Proposition 4.8, to provide an asymptotic analysis considering $\sigma = \varepsilon^2$ small, a rescaling of the climate shift speed as $\widetilde{c} = \varepsilon c$ is necessary. The population can tolerate only a climate change with small speed if the mutations have small effect. Otherwise the phenotypic variability is not high enough for the population to adapt to the climate change.

In order to keep the notations simpler we denote $(n_{\varepsilon c}, \widehat{\rho}_{c\varepsilon}) = (n_\varepsilon, \rho_\varepsilon)$, which is the unique periodic solution of the problem:

$$\begin{cases} \partial_t n_\varepsilon - \varepsilon c \partial_z n_\varepsilon - \varepsilon^2 \partial_{zz} n_\varepsilon = n_\varepsilon [a(e(t), z) - \rho_\varepsilon(t)], & (t,z) \in [0, +\infty) \times \mathbb{R}, \\ \rho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,z) dz, \\ n_\varepsilon(0,z) = n_\varepsilon(T,z). \end{cases} \tag{4.33}$$

To study asymptotically this problem we perform a Hopf-Cole transformation

$$n_\varepsilon = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_\varepsilon}{\varepsilon}\right). \tag{4.34}$$

Here is our first main result:

Theorem 4.10 (Limit as $\varepsilon \to 0$ [FIM]). *Assume* (4.23), (4.24) *and* (4.31) *and also that* $c < \liminf_{\varepsilon \to 0} c_\varepsilon^*$. *Then the following statements hold:*

(i) As $\varepsilon \to 0$, *we have* $\|\rho_\varepsilon(t) - \widetilde{\varrho}(t)\|_{L^\infty} \to 0$, *with* $\widetilde{\varrho}(t)$ *a* $T-$*periodic function.*

(ii) Moreover, as $\varepsilon \to 0$, $u_\varepsilon(t,z)$ *converges locally uniformly to a function* $u(z) \in C(\mathbb{R})$, *a viscosity solution to the following equation:*

$$\begin{cases} -\left|\partial_z u + \frac{c}{2}\right|^2 & = & \overline{a}(z) - \overline{\rho} - \frac{c^2}{4}, \quad z \in \mathbb{R}, \\ \max_{z \in \mathbb{R}} u(z) & = & 0, \\ -A_1|z|^2 - \frac{c}{2}z - A_2 & \le u \le & c_1 - c_2|z|, \end{cases} \tag{4.35}$$

with

$$\overline{\rho} = \int_0^T \widetilde{\varrho}(t) dt,$$

and some positive constants A_1, A_2, c_1 *and* $c_2 = -\frac{c}{2} + \sqrt{\delta + \frac{c^2}{2}}$.

The prove of the theorem above is based on appropriate regularity estimates on u_ε. A main difficulty to obtain such estimates, comparing to the previous related works (see for instance [BMP09]), comes from the time periodicity condition in this problem.

Next, under the additional assumptions (4.26)–(4.31) we provide the uniqueness and the identification of the limit:

Theorem 4.11 (Uniqueness and identification of the limit [FIM]). *Asssume* (4.23)–(4.26), (4.31) *and that* $c < \liminf_{\varepsilon \to 0} c_\varepsilon^*$. *Then the following statements hold:*

(i) The viscosity solution of (4.35) *is unique and it is indeed a classical solution given by*

$$u(z) = \frac{c}{2}(\overline{z} - z) + \int_{\overline{z}}^{z_m} \sqrt{\overline{a}(z_m) - \overline{a}(y)} dy - \left| \int_{z_m}^{z} \sqrt{\overline{a}(z_m) - \overline{a}(y)} dy \right|,$$

where $\overline{z} < z_m$ *is given in* (4.26).

(ii) Furthermore, let n_ε solve (4.33), *then*

$$n_\varepsilon(t,z) - \widetilde{\varrho}(t)\delta(z-\overline{z}) \rightharpoonup 0, \quad \text{as } \varepsilon \to 0,$$

pointwise in time, weakly in z in the sense of measures, with $\widetilde{\varrho}$ the unique periodic solution of the following equation

$$\begin{cases} \dfrac{d\widetilde{\varrho}}{dt} = \widetilde{\varrho}\left[a(e(t),\overline{z}) - \widetilde{\varrho}\right], \quad t \in (0,T), \\ \widetilde{\varrho}(0) = \widetilde{\varrho}(T). \end{cases}$$

Remark 4.12. *The statement (ii) in Theorem 4.11 implies for the solution $\widetilde{n}_\varepsilon$ to the original problem* (4.22) *with $\sigma = \varepsilon^2$ and $\widetilde{c} = c\varepsilon$ that*

$$\widetilde{n}_\varepsilon(t,z) - \widetilde{\varrho}(t)\delta(x-\overline{z}-ct) \rightharpoonup 0, \quad \text{as } \varepsilon \to 0,$$

pointwise in time, weakly in z in the sense of measures. This implies that the phenotypic density of the population concentrates on a dominant trait which follows the optimal trait with the same speed but with a constant lag $z_m - \overline{z}$.

Note that the proof of the uniqueness of the viscosity solution to (4.35) is not straight forward. To prove such result, we first introduce a new function $\widetilde{u}(x) = u(x) + \frac{c}{2}x$ which solves

$$\begin{cases} -|\partial_z \widetilde{u}|^2 = \overline{a}(z) - \overline{\rho} - \frac{c^2}{4}, \quad z \in \mathbb{R}, \\ \\ -A_1|z|^2 - A_2 \leq \widetilde{u}(z) \leq c_1 - c_2|z| + \frac{c}{2}z, \end{cases} \tag{4.36}$$

where the constants A_1, A_2, c_1, c_2 are the same as in (4.35). Then a main ingredient comes from the fact that any viscosity solution to a Hamilton-Jacobi equation of type (4.36) but in a bounded domain Γ can be uniquely determined by its values on the boundary points of Γ and by its values at the maximum points of the r.h.s of the Hamilton-Jacobi equation [Lio82b]. However, here we have an unbounded domain. To control the trajectories coming from infinity we use indeed the bounds above on $\widetilde{u}(z)$ and prove that the solution to (4.36) is indeed determined by its value at the maximum point of $\overline{a}$ that is z_m. Finally the constraint $\max_z u(z) = 0$ allows us to identify u.

Finally, to present our last result, let us consider the eigenproblem (4.29) for $\sigma = \varepsilon^2$ and $\widetilde{c} = c\varepsilon$, that is:

$$\begin{cases} \partial_t p_{c\varepsilon} - \varepsilon c \partial_z p_{c\varepsilon} - \varepsilon^2 \partial_{zz} p_{c\varepsilon} - a(e(t),z)p_{c\varepsilon} = p_{c\varepsilon}\lambda_{c,\varepsilon}, & (t,z) \in [0,+\infty) \times \mathbb{R}, \\ \qquad 0 < p_{c\varepsilon};\ p_{c\varepsilon}(t,z) = p_{c\varepsilon}(t+T,z), & (t,z) \in [0,+\infty) \times \mathbb{R}. \end{cases} \tag{4.37}$$

Here $\lambda_{c,\varepsilon}$ denotes the eigenvalue $\lambda_{\widetilde{c},\sigma}$ with $\sigma = \varepsilon^2$ and $\widetilde{c} = c\varepsilon$ for better legibility. We next provide an asymptotic expansion for λ_ε and consequently for $\overline{\rho}_\varepsilon$ and c_ε^*:

Theorem 4.13. *(Asymptotic expansions [FIM]) Let $\lambda_{c,\varepsilon}$ be the principal eigenvalue of problem* (4.37) *and assume* (4.23), (4.25) *and* (4.31). *Assume in addition that $c < \liminf_{\varepsilon \to 0} c_\varepsilon^*$, then the following asymptotic expansions hold*

$$\overline{\rho}_\varepsilon = -\lambda_{c,\varepsilon} = \overline{a}(z_m) - \frac{c^2}{4} - \varepsilon\sqrt{-\overline{a}_{zz}(z_m)/2} + o(\varepsilon),$$

$$c_\varepsilon^* = 2\sqrt{\overline{a}(z_m)} - \varepsilon\sqrt{-\frac{\overline{a}_{zz}(z_m)}{2\,\overline{a}(z_m)}} + o(\varepsilon).$$

Such expansion is indeed related to the harmonic approximation of the energy of the ground state of the Shrödinger operator ([Hel04]). However, here we have a parabolic, non self-adjoint operator.

4.3.3 Heuristics and the next order term

We next provide some heuristic computations which allow us to derive the Hamilton-Jacobi equation (4.35) but also to identify the corrector term v, with the ansatz

$$u_\varepsilon(t,z) = u(t,z) + \varepsilon v(t,z) + \varepsilon^2 w(t,z) + o(\varepsilon^2), \quad \rho_\varepsilon(t) = \widetilde{\rho}(t) + \varepsilon\kappa(t) + o(\varepsilon), \tag{4.38}$$

where the coefficients of the developments are time periodic. We also define

$$\overline{\rho} = \frac{1}{T}\int_0^T \widetilde{\rho}(t)dt, \qquad \overline{\kappa} = \frac{1}{T}\int_0^T \kappa(t)dt.$$

Replacing (4.34) in (4.33), we first notice that u_ε solves

$$\begin{cases} \frac{1}{\varepsilon}\partial_t u_\varepsilon - c\partial_z u_\varepsilon - \varepsilon\partial_{zz}u_\varepsilon &= |\nabla u_\varepsilon|^2 + a(e(t),z) - \rho_\varepsilon(t), \quad (t,z) \in [0,+\infty)\times\mathbb{R}^d, \\ u_\varepsilon(t=0,z) &= u_\varepsilon^0(z) = \varepsilon \ln n_\varepsilon^0(z). \end{cases} \tag{4.39}$$

We then substitute (4.38) into (4.39) and obtain:

$$\frac{1}{\varepsilon}\partial_t u + \partial_t v - c\partial_z u - c\varepsilon\partial_z v - \varepsilon\partial_{zz}u - \varepsilon^2\partial_{zz}v = |\partial_z u + \varepsilon\partial_z v|^2 + a(e(t),z) - \widetilde{\rho} - \varepsilon\kappa + o(\varepsilon).$$

We keep respectively the ε^{-1} and ε^0 order terms to obtain

$$\partial_t u(t,z) = 0 \Leftrightarrow u(t,z) = u(z),$$

and

$$\partial_t v - c\partial_z u = |\nabla u|^2 + a(e(t),z) - \widetilde{\rho}.$$

Integrating this latter equation in $t \in [0,T]$ and using the $T-$periodicity of v, leads to the first equation in (4.35).

Finally, the corrector terms v and $\overline{\kappa}$ can be determined by the equations obtained by keeping respectively the ε^0 and ε order terms:

$$\begin{cases} \partial_t v = \left|\partial_z u + \dfrac{c}{2}\right|^2 + a(e(t),z) - \dfrac{c^2}{4} - \widetilde{\rho}, \\ \\ -\partial_{zz}u = [2\partial_z u + c]\dfrac{1}{T}\displaystyle\int_0^T \partial_z v(t,z)dt - \overline{\kappa}. \end{cases} \tag{4.40}$$

Once u and v are known, one can provide analytic approximations for the moments of the phenotypic distribution following similar arguments as in Section 3.4.2.

4.3.4 Biological applications

In this section we discuss the effect of the periodic fluctuations on the critical speed of survival and the dynamics of the phenotypic density considering the following particular form of growth rate, taking into account a quadratic stabilizing selection ([BÖ0]– pages 117-121 and chapter VI),

$$a(e,x) = r - g(e)(z-\theta(e))^2. \tag{4.41}$$

Here, r is a positive constant corresponding to the maximal intrinsic growth rate. The function θ represents the optimal trait and the positive function g represents the pressure of the selection, both being functions of the environment state e.

In subsection 4.3.4.1 we will provide some preliminary computations considering above growth rate which will be helpful in the following subsections.

In subsection 4.3.4.2 we will consider the above growth rate with $c = 0$, that is the case where we have pure oscillations. Being motivated by the experiment of [KMZ+13] we investigate in which situations a population that has evolved in a periodic environment will outperform a population that has evolved in an average constant environment when both populations are placed at the same constant environment. We show indeed that when the fluctuations act on the pressure of the selection, that is when g is a function of the periodic environment state e but when θ is constant, then such property may be observed.

In subsection 4.3.4.3 we will consider the same growth rate but with $c > 0$. We show in this case that, when the population persists, the phenotypic mean follows the dominant trait with the same speed but with a constant lag. We also show that when the fluctuations act on the pressure of the selection, the periodic fluctuations may help the population to follow the linear environment change. More precisely, we show that in presence of periodic fluctuations, the critical speed of survival may be greater than the case without fluctuations of the environment.

4.3.4.1 Preliminary computations

In this subsection, using our method we provide some preliminary computations that we will use in the following subsections. We compute the mean of $a(e,z)$

$$\overline{a}(z) = \int_0^1 a(e(t),z)dt = r - z^2\overline{g} + 2zg_1 - g_2,$$

where

$$\overline{g} = \int_0^1 g(e(t))dt, \quad g_1 = \int_0^1 g(e(t))\theta(e(t))dt, \quad g_2 = \int_0^1 g(e(t))\theta^2(e(t))dt,$$

and we observe that the maximum of $\overline{a}(z)$ is attained at $z_m = \frac{g_1}{\overline{g}}$, with

$$\bar{a}(z_m) = r + \frac{g_1^2}{\overline{g}} - g_2.$$

From Theorem 4.11-(ii) we obtain that $u(z)$ is given by

$$u(z) = -\frac{\sqrt{\overline{g}}}{2}\left(z-\overline{z}\right)^2, \qquad \overline{z} = z_m - \frac{c}{2\sqrt{\overline{g}}} = \frac{g_1}{\overline{g}} - \frac{c}{2\sqrt{\overline{g}}}.$$

To present our results we introduce the following notations:

$$\begin{cases} \overline{\rho}_{\varepsilon,p} = \frac{1}{T}\int_0^T \rho_\varepsilon(t)dt, \\ \mu_{\varepsilon,p}(t) = \dfrac{1}{\rho_{\varepsilon,p}(t)}\displaystyle\int_{\mathbb{R}^d} z\; n_\varepsilon(t,z)dz, \\ \sigma^2_{\varepsilon,p}(t) = \dfrac{1}{\rho_\varepsilon(t)}\displaystyle\int_{\mathbb{R}^d} (z-\mu_\varepsilon(t))^2 n_\varepsilon(t,z)dz, \\ F_{\varepsilon,p}(e_0) = \displaystyle\int_{\mathbb{R}^d} a(e_0,z)\frac{1}{T}\int_0^T \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)}dtdz. \end{cases}$$

Here, $\overline{\rho}_{\varepsilon,p}$ corresponds to the average population size of a population evolved for a long time in the periodic environment. The terms $\mu_{\varepsilon,p}(t)$ and $\sigma^2_{\varepsilon,p}(t)$ correspond respectively to the mean phenotypic trait and the phenotypic variance of such population. The last term $F_{\varepsilon,p}(e_0)$ corresponds to the average growth rate of such population when it is placed at environment state e_0. This quantity corresponds to what was measured in the experiment of [KMZ$^+$13].

The asymptotic expansions in Theorem 4.13 imply that

$$\overline{\rho}_{\varepsilon,p} = r + \frac{g_1^2}{\bar{g}} - g_2 - \frac{c^2}{4} - \varepsilon\sqrt{\bar{g}} + o(\varepsilon), \quad c^*_{\varepsilon,p} = 2\sqrt{r + \frac{g_1^2}{\bar{g}} - g_2} - \varepsilon\sqrt{\frac{\bar{g}}{r + \frac{g_1^2}{\bar{g}} - g_2}} + o(\varepsilon).$$

Furthermore, following the arguments in Section 3.4.2, we can also obtain formally an approximation of order ε for the phenotypic mean $\mu_{\varepsilon,p}$ and the variance $\sigma^2_{\varepsilon,p}$ of the phenotypic distribution, that is:

$$\mu_{\varepsilon,p}(t) = \frac{g_1}{\bar{g}} - \frac{c}{2\sqrt{\bar{g}}} + \varepsilon D(t) + o(\varepsilon), \qquad \sigma^2_{\varepsilon,p}(t) = \frac{\varepsilon}{\sqrt{\bar{g}}} + o(\varepsilon),$$

where $D(t) = \partial_z v(\bar{z},t)$ for v the solution of the system (4.40). One can verify that for this growth rate, and choosing the period $T = 1$, we have

$$D(t) = -c\sqrt{\bar{g}}\left(t - \frac{1}{2}\right) + 2\int_0^1\int_0^\tau g(s)(\bar{z} - \theta(s))dsd\tau - 2\int_0^t g(s)(\bar{z} - \theta(s))ds.$$

4.3.4.2 No environment change with linear trend ($c = 0$); A comparison with the experiment of [KMZ$^+$13].

In this subsection, we apply our analysis to two biological case studies considering $c = 0$. This analysis is motivated by the experiment in [KMZ$^+$13] (see the introduction of Chapter 4 for the presentation of this biological experiment). We are interested in the comparison of the phenotypic distributions of populations evolved for a long time whether in a periodic environment or in a constant environment at an average state. We seek in particular to determine conditions under which the population evolved in a time periodic environment, with a T-periodic state $e(t)$ (e corresponding for instance to the temperature), will outperform a population evolved in a constant environment (with state $\overline{e} = \frac{1}{T}\int_0^T e(s)ds$) when both strains are placed at the constant environment $\overline{e}$.

We will consider the quadratic stabilizing selection (4.41) presented above, in two particular cases. First, we will assume that the variations of the environment modify the optimal trait but have no influence on the pressure of the selection ($g(e) = g > 0$ is constant). Next, we will assume that the environment variations modify the pressure of the selection but have no influence on the optimal trait ($\theta(e) = 0$).

Oscillations on the optimal trait. For this case study, we take

$$g(e) = g > 0, \qquad \theta(e) = e, \qquad e(t) = l \sin\big(\frac{2\pi}{b} t\big). \tag{4.42}$$

Then, considering a population evolved in such a periodic environment, the average size of the population, the mean phenotypic trait, the phenotypic variance and the mean fitness of the population in an environment with state $\overline{e} = 0$, are given by

$$\overline{\rho}_{\varepsilon,p} = r - \frac{gl^2}{2} - \varepsilon\sqrt{g} + o(\varepsilon), \quad \mu_{\varepsilon,p}(t) = \frac{\varepsilon l b\sqrt{g}}{\pi} \sin\left(\frac{2\pi}{b}(t - \frac{b}{4})\right) + o(\varepsilon),$$

$$\sigma^2_{\varepsilon,p}(t) = \frac{\varepsilon}{\sqrt{g}} + o(\varepsilon), \quad F_{\varepsilon,p}(e_0 = 0) = r - \varepsilon\sqrt{g} + o(\varepsilon).$$

We observe indeed that the mean trait $\mu_{\varepsilon,p}(t)$ oscillates with the same period as the optimal trait but with a delay $\frac{b}{4}$ and a small amplitude (such property was obtained for a related model in [LS96]).
We next compare these approximations with the ones obtained for a population evolved in a constant environment with $\theta(e) = \theta(\overline{e} = 0) = 0$ and $g(e) = g$:

$$\rho_{\varepsilon,0} = r - \varepsilon\sqrt{g}, \quad \mu_{\varepsilon,0} = 0, \quad \sigma^2_{\varepsilon,0} = \frac{\varepsilon}{\sqrt{g}}, \quad F_{\varepsilon,0}(e_0 = 0) = r - \varepsilon\sqrt{g}. \tag{4.43}$$

Note that these quantities correspond to the approximations obtained in subsection 4.3.4.1 with $\theta(e) = 0$ and $g(e) = g$. However, here these are exact values and not only approximations for ε small, since the problem with constant g and θ can indeed be solved explicitly.
We deduce that both populations (the one evolved in the constant environment $e_0 = 0$ and the other evolved in the fluctuating environment) have the same mean fitness, up to order ε, when they are placed at the same constant environment $e_0 = 0$.

Oscillations on the pressure of the selection. For this case study, we take

$$\theta(e) = 0, \qquad g(e) \text{ a positive function of } e \text{ and } e(t) \text{ a 1-periodic function of time.} \tag{4.44}$$

We also define

$$\overline{g} = \int_0^1 g(e(s))ds.$$

Then, considering a population evolved in such a periodic environment, the average size of the population, the mean phenotypic trait, the phenotypic variance and the mean fitness of the population in an environment with state $\overline{e}$, are given by

$$\overline{\rho}_{\varepsilon} = r - \varepsilon\sqrt{\overline{g}} + o(\varepsilon), \quad \mu_{\varepsilon,p} = o(\varepsilon), \quad \sigma^2_{\varepsilon,p} = \frac{\varepsilon}{\sqrt{\overline{g}}} + o(\varepsilon), \qquad F_{\varepsilon,p}(e_0 = \overline{e}) = r - \varepsilon\frac{g(\overline{e})}{\sqrt{\overline{g}}} + o(\varepsilon).$$

We next compare these quantities with the ones corresponding to a population evolved in a constant environment with average state $\overline{e}$, given by (4.43). We remark that if we choose $g(e)$ such that

$$g(\overline{e}) < \overline{g}, \tag{4.45}$$

then we obtain that, for ε small,

$$\overline{\rho}_{\varepsilon,p} < \rho_{\varepsilon,0}, \quad \mu_{\varepsilon,p} \approx \mu_{\varepsilon,0} = 0, \quad \sigma^2_{\varepsilon,p} < \sigma^2_{\varepsilon,0} \quad \text{and} \quad F_{\varepsilon,0}(\overline{e}) < F_{\varepsilon,p}(\overline{e}).$$

We hence obtain that, depending on the choice of g, the population which evolved in a fluctuating environment may have a larger fitness than the one evolved in a constant environment $\overline{e}$, when they are both placed at the same constant environment $\overline{e}$. This property corresponds to what was observed in the biological experiment in [KMZ$^+$13]. Note that both of these environments select for populations with the same mean phenotypic trait $z = 0$. However, the population evolved in a periodic environment has a smaller variance comparing to the one evolved in a constant environment. This makes the population evolved in the periodic environment more performant.

Discussion. The above approximations show that, when the mutational effect ε is small, and when the environment variations modify the pressure of the selection, the population evolved in a time periodic environment may outperform a population evolved in a constant environment (with average state $\overline{e}$) when both strains are placed at the constant environment $\overline{e}$. By contrast, when the environment variations modify the optimal trait, the two environments select for populations with approximately similar performance. S. Figuera, in her PhD thesis [FI19], extends these results to the case where the mutations have larger effects using numerical simulations and also by obtaining semi-explicit solutions for the case studies above, following the method of [ABF$^+$19]. She shows on the one hand that, when the environment variations modify the optimal trait (case (4.42)) and when the mutations have large effects, the mean fitness of the population evolved in a periodic environment is smaller than the mean fitness of the population evolved in a constant environment. Larger rate of mutations increases indeed the cost of fluctuations in this case. On the other hand, when the environment variations modify the pressure of the selection (case (4.44)), then the fluctuating environment may still select for a more performant population.

4.3.4.3 Environment change with linear trend ($c > 0$); the population follows the optimum with a constant lag

In this subsection, we provide our results for the case $c > 0$, in the two case studies where the oscillations act whether on the optimal trait or on the pressure of the selection. We show on the one hand, in both cases, that the average phenotypic mean follows the average optimal trait with a constant lag. On the other hand, we show that when the environment variations modify the pressure of the selection, the periodic fluctuations may help the population to follow the environment change.

Oscillations on the optimal trait. We take $g(e) = g$ constant and $\theta(e)$ a function of the environment state $e(t)$, which is itself 1-periodic. We also define

$$\bar{\theta} = \int_0^1 \theta(e(t))dt.$$

We next compute the average population size, the average mean phenotypic trait and the critical speed $c^*_{\varepsilon,p}$ following the method presented above:

$$\overline{\rho}_{\varepsilon,p} = r + g\left[\bar{\theta}^2 - \int_0^1 \theta^2(e(t))dt\right] - \frac{c^2}{4} - \varepsilon\sqrt{g} + o(\varepsilon), \qquad \overline{\mu}_{\varepsilon,p} = \int_0^1 \mu_{\varepsilon,p}(t)dt = \bar{\theta} - \frac{c}{2\sqrt{g}} + o(\varepsilon),$$

$$c^*_{\varepsilon,p} = 2\sqrt{r + g\left[\bar{\theta}^2 - \int_0^1 \theta^2(e(t))dt\right]} - \varepsilon\sqrt{\frac{g}{r + g\left[\bar{\theta}^2 - \int_0^1 \theta^2(e(t))dt\right]}} + o(\varepsilon).$$

Note in view of Remark 4.12 that, the above approximation of the average phenotypic mean indicates that the population follows the average optimal trait with a constant lag which is

approximated by $\frac{c}{2\sqrt{g}}$.
In order to study the effect of the fluctuations on the adaptation of the population to the environment change we consider two sub-cases where e is constant or periodic.

a) If $e(t) \equiv e_0$ is constant we obtain that

$$\overline{\rho}_{\varepsilon,0} = r - \frac{c^2}{4} - \varepsilon\sqrt{g}, \quad \overline{\mu}_{\varepsilon,0} = \theta(e_0) - \frac{c}{2\sqrt{g}}, \quad c^*_{\varepsilon,0} = 2\sqrt{r} - \varepsilon\sqrt{\frac{g}{r}} + o(\varepsilon).$$

b) If $e(t)$ is a 1−periodic function then, $\bar{\theta}^2 < \int_0^1 \theta^2(e(t))dt$ and we obtain that, for ε small,

$$\overline{\rho}_{\varepsilon,p} < r - \frac{c^2}{4} - \varepsilon\sqrt{g}, \quad \big\langle \mu_{\varepsilon,p}(t) \big\rangle \approx \bar{\theta} - \frac{c}{2\sqrt{g}}, \quad c^*_{\varepsilon,p} < 2\sqrt{r} - \varepsilon\sqrt{\frac{g}{r}}.$$

Thus, by keeping the pressure of selection constant, we deduce that, for ε small,

$$\overline{\rho}_{\varepsilon,p} < \overline{\rho}_{\varepsilon,0} \quad \text{and} \quad c^*_{\varepsilon,p} < c^*_{\varepsilon,0}.$$

This means that having an oscillating optimal trait is not beneficial for the population, in the sense that the mean total size of the population decreases with respect to the case with a constant optimal trait and the critical speed which leads the population to extinction is smaller in the periodic case.

Oscillations on the pressure of the selection. We take $\theta(e) = \theta$ constant and $g(e)$ a function of the environment state $e(t)$, which is itself 1-periodic. Note that, in such a case $g_1 = \bar{g}\theta$ and $g_2 = \bar{g}\theta^2$. We compute

$$\overline{\rho}_{\varepsilon,p} = r - \frac{c^2}{4} - \varepsilon\sqrt{\bar{g}} + o(\varepsilon), \qquad \overline{\mu}_{\varepsilon,p}(t) = \theta - \frac{c}{2\sqrt{\bar{g}}} + o(\varepsilon), \qquad c^*_{\varepsilon,p} = 2\sqrt{r} - \varepsilon\sqrt{\frac{\bar{g}}{r}} + o(\varepsilon).$$

We compare then, the sub-cases where e is constant or periodic.

a) If $e(t) \equiv e_0$ is constant, we obtain that

$$\overline{\rho}_{\varepsilon,0} = r - \frac{c^2}{4} - \varepsilon\sqrt{g(e_0)}, \quad \overline{\mu}_{\varepsilon,0}(t) = \theta - \frac{c}{2\sqrt{g(e_0)}}, \quad c^*_{\varepsilon,0} \approx 2\sqrt{r} - \varepsilon\sqrt{\frac{g(e_0)}{r}}.$$

b) If $e(t)$ is a 1−periodic function then we obtain

$$\overline{\rho}_{\varepsilon,p} = r - \frac{c^2}{4} - \varepsilon\sqrt{\bar{g}} + o(\varepsilon), \quad \overline{\mu}_{\varepsilon,p}(t) = \theta - \frac{c}{2\sqrt{\bar{g}}} + o(\varepsilon), \quad c^*_{\varepsilon,p} = 2\sqrt{r} - \varepsilon\sqrt{\frac{\bar{g}}{r}} + o(\varepsilon).$$

In this case we deduce that if we choose the functions g and e such that

$$\bar{g} < g(e_0), \tag{4.46}$$

then we obtain that, for ε small,

$$\overline{\rho}_{\varepsilon,0} < \overline{\rho}_{\varepsilon,p} \quad \text{and} \quad c^*_{\varepsilon,0} < c^*_{\varepsilon,p}.$$

This means that the mean total size of the population increases with respect to the case with a constant selection pressure. Moreover, the critical speed above which the population

goes extinct is larger in the periodic case. This means that the periodic fluctuations can help the population to follow the environment change.
Note that the condition (4.46) imposed to g is the opposite to the one imposed by (4.45) leading to more performant populations. There, we saw that in presence of the mutations and while the fluctuations act on the pressure of the selection (that is with a similar growth rate, however with $c = 0$ and under the condition $\bar{g} > g(e_0)$), a fluctuating environment can select for a population with smaller variance and in this way lead to more performant populations. What is beneficial in a (in average) constant environment may indeed be disadvantageous in a changing environment.

4.4 Evolutionary dynamics of a population in a piecewise constant environment with slow switch

In this section we study another type of time varying environment where the environment state is a piecewise constant function. The model is the same as (4.1), that we rewrite as below, taking $\sigma = \varepsilon^2$,

$$\begin{cases} \dfrac{\partial}{\partial t}\widetilde{n}_\varepsilon - \varepsilon^2\Delta\widetilde{n}_\varepsilon = \widetilde{n}_\varepsilon R(\widetilde{e}(t), z, \widetilde{\rho}_\varepsilon), \qquad z \in \mathbb{R}^d, \\ \widetilde{\rho}_\varepsilon(t) = \displaystyle\int_{\mathbb{R}^d} \widetilde{n}_\varepsilon(t,y)\psi(y)\,dy, \\ \widetilde{n}_\varepsilon(0,z) = \widetilde{n}_{\varepsilon,0}(z). \end{cases}$$

The meaning of the terms are the same as in (4.1). The environment state $\widetilde{e}(t)$ is a piecewise constant environment, that is there exists an increasing sequence of times $(t_k)_{k\geq 0}$, with $t_k \to \infty$ as $k \to \infty$, such that

$$\widetilde{e}(t) = e_k, \quad \text{for } t \in [\widetilde{t}_{k-1}, \widetilde{t}_k).$$

With such choice of $\widetilde{e}$, on the contrary to the previous models the environment is not subject to a gradual change but it experiences sudden changes. In the models in the previous sections, the frequency of the environment oscillations was much larger than the effect of the mutations (measured by ε). In those models the population adapted to an average environment since the population did not have the time to adapt to the environment changes ponctually. Here we consider a smaller frequency for the environment change which is comparable with the effect of the mutations. That is we choose

$$\widetilde{t}_k = \frac{t_k}{\varepsilon}.$$

In this way the switch between the environment states occurs slowly such that the population has the time to follow the punctual environment state before the switch. This work is motivated by the study of the prey and predator interactions, where the prey has a much slower dynamics than the predator (for instance trees and insects) [Cos16]. However, the model studied in this section is a very simplified version of such problem.

In order to take into account the slow switch between the environment states and to study the effect of small mutations and slow change of the environment we make a change of variable in time, and define

$$n_\varepsilon(t,z) = \widetilde{n}_\varepsilon(\frac{t}{\varepsilon}, z), \qquad \rho_\varepsilon(t) = \widetilde{\rho}_\varepsilon(\frac{t}{\varepsilon}), \qquad e(t) = \widetilde{e}(\varepsilon t).$$

The above rescaling leads to

$$\begin{cases} \varepsilon\frac{\partial}{\partial t}n_\varepsilon - \varepsilon^2\Delta n_\varepsilon = n_\varepsilon R(e(t),z,\rho_\varepsilon), \\ \rho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,y)\,dy, \\ n_\varepsilon(0,z) = n_{\varepsilon,0}(z). \end{cases} \tag{4.47}$$

In the case of constant environment state e the asymptotic analysis of such equation is well-known (see [PB08, BMP09, LMP11] and Chapter 1). However, all the known results suppose some initial conditions which guarantee that the initial population is well-adapted to the environment such that the population will not get extinct asymptotically at the initial time. The study of the case with piecewise constant environment requires however to understand the dynamics of the solution for general initial condition. In particular, we look for a criterion on the initial population which leads to extinction or survival of the population.

As explained above the asymptotic study of the problem reduces to the understanding of the asymptotic dynamics of the solutions considering a constant environment but general initial condition. In subsection 4.4.1 we study such problem and provide criteria on the initial condition leading to persistence or extinction of the population. In subsection 4.4.2 we deduce the asymptotic dynamics of the phenotypic density thanks to the results of subsection 4.4.1 and in the concavity framework of Section 1.4.

4.4.1 Persistence and extinction criterion on the initial condition

In this subsection, we provide persistence and extinction criteria for the selection-mutation model (4.47) in the case of constant environments but under general conditions. Once the survival of the population is guaranteed, then similar results as in [PB08, BMP09] on the asymptotic analysis of the equation apply. Note that in the case of constant environment, (4.47) is nothing but equation (1.3) in Chapter 1, that we recall below:

$$\begin{cases} \varepsilon\frac{\partial}{\partial t}n_\varepsilon - \varepsilon^2\Delta n_\varepsilon = n_\varepsilon R(z,\rho_\varepsilon), \\ \rho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,y)\,dy, \\ n_\varepsilon(0,z) = n_{\varepsilon,0}(z). \end{cases}$$

Here, we use similar assumptions as in Section 1.2, however we relax Assumption (1.11) which is a sufficient condition on the initial population guaranteeing that it is well adapted and that the population does not get extinct.

Before providing our main result, we assume that the WKB transformation of the initial condition $u_{\varepsilon,0}$, given by

$$n_{\varepsilon,0} = \exp\big(\frac{u_{\varepsilon,0}}{\varepsilon}\big),$$

converges, as $\varepsilon \to 0$, to u_0 and we define

$$\Gamma_0 := \{z \in \mathbb{R}^d,\, u_0(z) = 0\}. \tag{4.48}$$

Theorem 4.14. *[CEM] Assume* (1.4)–(1.10).

i) If

$$Supp\ n(0,\cdot) \cap \{z \in \mathbb{R}^d,\, R(z,0) > 0\} \neq \emptyset\,,$$

then the population persists, that is for every $T > 0$, there exists $\underline{I}(T) > 0$ and $\varepsilon(T) > 0$ such that

$$I_\varepsilon(t) \geq \underline{I}(T), \qquad \forall t \in [0,T), \forall \varepsilon \leq \varepsilon(T)\,,$$

and $(I_\varepsilon)_\varepsilon$ *converges up to a subsequence a.e in* $t \in \mathbb{R}^+$ *towards a BV function* I. *In this case the results of Theorems 1.1 and 1.2 are valid.*

ii) If

$$\exists C > 0 \text{ such that } \Gamma_0 \subseteq \{z \in \mathbb{R}^d,\, R(z,0) \leq -C\}\,,$$

then the population goes extinct asymptotically, that is there exists a finite and positive constant $0 < T_0 < +\infty$, *such that* $\lim_{\varepsilon \to 0} I_\varepsilon(t)|_{(0,T_0)} = 0$.

iii) If

$$\Gamma_0 \subseteq \{z \in \mathbb{R}^d,\, R(z,0) \leq 0\}\,,$$

then the population goes extinct asymptotically and punctually, that is $\forall \delta > 0,\, \exists \varepsilon_\delta > 0,\, \forall \varepsilon < \varepsilon_\delta,\, \exists t_\varepsilon \in [0,T]$, *such that*

$$I_\varepsilon(t_\varepsilon) < \delta.$$

Note that these conditions are based on the viability of the traits initially present in the population, and not on the growth rate of the individuals at initial time, since we look at $R(\cdot,0)$ rather than at $R(\cdot, I_\varepsilon(0))$. A main difficulty in the proof of the persistence, is indeed to show that when the competition term I_ε drops below a threshold such that some viable traits have positive growth rates, such viable traits are still present in the population so that they can rescue the population from extinction.

Remark 4.15. *Note that in the condition for asymptotic persistence in i) the set Supp* $n(0,\cdot)$ *is involved, which is a smaller set than* Γ_0, *the set involved in the condition for asymptotic extinction in ii), iii). Therefore, one situation is not described, namely when*

$$\text{Supp } n(0,\cdot) \subseteq \{z \in \mathbb{R}^d,\, R(z,0) \leq 0\} \text{ and } \Gamma_0 \cap \{z \in \mathbb{R}^d,\, R(z,0) > 0\} \neq \emptyset\,.$$

We illustrate this situation numerically in [CEM]. The numerical resolution of the problem indicates indeed that in this case the mass drops immediately as the population carrying traits with negative growth rates disappears, but it quickly increases again thanks to the viable traits in the set Γ_0.

4.4.2 The dynamics of the population in a piecewise constant environment in the concave framework

In this section we go back to the case of piecewise constant environments. Thanks to Theorem 4.14 and similarly to Section 1.4, additional concavity assumptions on R and u_0 allow us to identify the phenotypic density as an evolving Dirac mass, as long as the population persists.

To identify the asymptotic dynamics of the phenotypic density, we recall that, thanks to Theorem 4.14-(i) and as long as the population persists, a Hamilton-Jacobi equation with constraint is derived from the Hopf-Cole transformation of the problem, that is

$$\begin{cases} \partial_t u = |\nabla u|^2 + R(e,z,I), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ \max_{z \in \mathbb{R}^d} u(t,z) = 0, & t \in \mathbb{R}^+, \\ u(0,z) = u_0(z). \end{cases}$$

The dynamics of the phenotypic density is then identified by the following proposition.

Proposition 4.16. *[CEM] Assume* (1.4)–(1.10) *and* (1.14)–(1.15).
(i) As long as the population persists, as $\varepsilon \to 0$*, the population concentrates on a dominant trait which follows the gradient of the environment:*

$$n_\varepsilon(t,z) \rightharpoonup \rho(t)\,\delta(z-\overline{z}(t)), \quad \dot{\overline{z}} = (-D^2u)^{-1}(t,\overline{z}(t))\nabla R(e,\overline{z},I).$$

(ii) If the environment switches from e_k *to* e_{k+1} *at time* t_k*. Then, the population goes extinct, asymptotically as* $\varepsilon \to 0$*, if*

$$R(e_{k+1},\overline{z}(t_k),0) \leq 0.$$

Otherwise, the population persists until the next switch.

Perspectives

I will formulate here some questions related to the works presented in this manuscript.

Hamilton-Jacobi equations with constraint and concentration of the phenotypic density

In chapter 1, we studied the following selection-mutation model:

$$\begin{cases} \varepsilon\partial_t n_\varepsilon - \varepsilon^2\Delta n_\varepsilon = n_\varepsilon R(z, I_\varepsilon), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ I_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t,z)\psi(z)dz, \\ n_\varepsilon(0,z) = n_{\varepsilon,0}(z). \end{cases} \tag{5.1}$$

We showed that a Hopf-Cole transformation of the problem, that is,

$$n_\varepsilon(t,z) = \frac{1}{(2\pi\varepsilon)^d}\exp\big(\frac{u_\varepsilon(t,z)}{\varepsilon}\big), \tag{5.2}$$

leads to the following Hamilton-Jacobi equation with constraint [PB08, BMP09]:

$$\begin{cases} \partial_t u = |\nabla u|^2 + R(z,I), & (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d, \\ \max_{z\in\mathbb{R}^d} u(t,z) = 0, & t \in \mathbb{R}^+, \\ u(0,z) = u_0(z), \end{cases}$$

with $I : \mathbb{R}^+ \to \mathbb{R}^+$ and $u \in \mathrm{C}(\mathbb{R}^+ \times \mathbb{R}^d)$ a solution in the viscosity sense. Here, I may be thought of as a sort of regulator, or a sort of Lagrange multiplier, to maintain the maximum of u equal to 0. Such result would then allow to determine the limit of n_ε as $\varepsilon \to 0$. As $\varepsilon \to 0$, n_ε converges indeed in $\mathrm{L}^\infty\big(\mathrm{w}{*}(0,\infty); \mathcal{M}^1(\mathbb{R}^d)\big)$ to a measure n which has the following property

$$\operatorname{supp} n(t,z) \subset \{z | u(t,z) = 0\} \subset \{z | R(z, I(t)) = 0\}, \qquad \text{a.e. } t.$$

We expect that the solution of (5.1), in the limit as $\varepsilon \to 0$, concentrates as a single Dirac mass corresponding to a dominant trait. In Chapter 1, we derived such concentration phenomenon under concavity assumptions on u_0 and R [LMP11]. Within this framework, we also provided uniqueness and regularity of the solution (u, I) to the Hamilton-Jacobi equation with constraint [MR16]. In a work in preparation with J.-M. Roquejoffre, we prove that this result leads to error estimates and asymptotic expansions for u_ε and I_ε in terms of ε [MR15b]:

$$u_\varepsilon = u + \varepsilon v + O(\varepsilon^2), \qquad I_\varepsilon = I + \varepsilon J + O(\varepsilon^2).$$

Such asymptotic expansion would then allow to obtain an approximation of the phenotypic density n_ε for ε small but nonzero. Such approximation is particularly interesting for the biological applications, since in many biological situations it is more relevant to consider small but nonvanishing effect of mutations. These approximations lead indeed to more quantitative results which allow to bring insight into current biological questions. In chapters 3 and 4 we provided several examples of applications of such approximations.

In a second current project, with J.-M. Roquejoffre and C. Quininao, we try to extend our result in [MR16] to the case where R and u_0 are only locally concave. This would allow us to obtain concentration of the solution on a single point in a more general range of situations. Note indeed that while the derivation of the Hamilton-Jacobi equation from the selection-mutation model above is well-known under general assumptions [PB08, BMP09], the identification of the phenotypic density n as a Dirac mass, which is equivalent with the identification of the maximum points of the viscosity solution u to the corresponding Hamilton-Jacobi equation, is only obtained in particular cases. Such concentration is indeed proved whether in 1-d and under monotony assumption on R with respect to z [PB08], or under concavity assumptions on R and u_0 [LMP11, MR16]. However, we expect that such concentration property would hold under general assumptions. This is indeed related to the principle of competitive exclusion [Lev70, Sch74] in evolutionary biology which states that when there are k limiting factors for the population, no more than k distinct traits may coexist. In this model there is only one limiting factor which is the resource taken into account via the competition term I.
We expect indeed that the current project with J.-M. Roquejoffre and C. Quininao would allow us to consider the cases where u has several maxima, which means that n is a sum of Dirac masses. Such polymorphic situations may arise in more complex models where for instance several integral terms are considered corresponding to several nutrients [DJMP05]. While the study of polymorphic populations and in particular the emergence of evolutionary branching (the creation of two Dirac masses from one) is an important question in evolutionary biology, there are not many results describing the dynamics of such polymorphic populations (see however [CJ11] where a Hamilton-Jacobi equation with constraint is derived in the case of several competition terms I_k and considering a particular form of the growth rate R). Note however that the study of polymorphic populations at equilibrium is an easier question (see for instance [Mir17] and chapter 3 where dimorphic populations are described in the case of spatially heterogeneous environments).

Fractional reaction-diffusion equations

In Chapter 2, we studied the following selection-mutation model, where the mutations are modeled with an integral kernel with thick tails:

$$\begin{cases} \varepsilon \partial_t n_\varepsilon(t,z) = \int_0^\infty \int_{\nu \in S^{d-1}} \big(n_\varepsilon(t, z + (e^{\varepsilon k} - 1)\nu) - n_\varepsilon(t,z) \big) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dS dk + n_\varepsilon(t,z)\, R(z, \rho_\varepsilon(t)), \\ \rho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,z) dz, \\ n_e(x,0) = n_\varepsilon^0(x). \end{cases}$$

We showed that a Hopf-Cole transformation, similar to (5.2), leads to the following Hamilton-Jacobi equation with constraint

$$\begin{cases} \partial_t u - \int_0^\infty \int_{\nu \in S^{d-1}} \big(e^{k D_z u \cdot \nu} - 1 \big) \frac{e^k dS dk}{|e^k - 1|^{1+2\alpha}} = R(z, I), \\ u(z,0) = u^0(z). \end{cases} \tag{5.3}$$

We prove indeed that the function u_ε converges to a viscosity supersolution of (5.3) which is minimal in a certain class of supersolutions. Similarly to the case of classical laplacian, we also obtain that

$$\max_z u(t,z) = 0, \qquad \operatorname{supp} n(t,z) \subset \{z | u(t,z) = 0\} \subset \{z | R(z, I(t)) = 0\}, \text{ a.e. } t.$$

Such property allows then to conclude, in the case where $z \in \mathbb{R}$ and R is monotonous with respect to z, that n is indeed a single Dirac mass for a.e. t. A question that I am interested in, is whether in the general multi-d case there exists a framework similar to the concave framework in Chapter 1 (see also [LMP11, MR16]) where we can obtain such concentration property for n and provide more precise description of the limit n. To this end, a natural first step is to study the properties of the Hamilton-Jacobi equation (5.3), where the Hamiltonian can take infinite values, and the corresponding minimal viscosity supersolution. Note however that since such minimal viscosity supersolution u has logarithmic decay according to Theorem 2.3, it cannot be strictly concave. Therefore, we do not expect that the theory in Chapter 1 would apply directly to such problem.

Another direction of study is to investigate whether the asymptotic analysis performed in Chapter 2 for the fractional Fisher-KPP equation and for the fractional selection-mutation model is related to a large deviation principle. Note that in the case of classical KPP equation, such asymptotic analysis, dealing with Hamilton-Jacobi equations, was first performed using stochastic tools and large deviation type estimates in the works of Friedlin [Fre85a, Fre85b, Fre86]. Similarly, an asymptotic analysis of the classical selection-mutation model using probabilistic tools has been provided recently [CH19] (see also [Fre87]). In the case of fractional reaction-diffusion equations, up to my knowledge, such stochastic analysis is not provided. I am interested in the understanding of the stochastic interpretation of our results and in investigating whether this is related to a large deviation principle for Lévy type operators.

In Section 2.4 in the framework of the PhD thesis of A. Léculier, a student that I supervise with J.-M. Roquejoffre, we presented a work on the following fractional Fisher-KPP type problem with obstacles

$$\begin{cases} \partial_t n + (-\Delta)^\alpha n = R(n), & (t,x) \in (0,\infty) \times \Omega, \\ n(t,x) = 0, & (t,x) \in [0,\infty) \times \Omega^c, \\ n(0,x) = n_0(x), & x \in \Omega, \end{cases} \tag{5.4}$$

with $\Omega \subset \mathbb{R}$ an open set. The function $R(n)$ is a reaction term of KPP type : one can consider for instance $R(n) = n(1-n)$. Here, x is the position in space and n corresponds to the population density as a function of time and position in space. Such study allows to investigate the impact of obstacles, as urban zones or rivers and seas, in the propagation of populations with nonlocal dispersion.

In a case where Ω is a periodic set of intervals of equal sizes, we prove that when such intervals are large enough, there exists a unique nonzero steady solution to (5.4) and that such steady state invades the unstable steady state 0 in the whole domain Ω with an exponential speed. Note that the uniqueness of the steady state is due to the nonlocal diffusion operator and it does not hold for the case with the classical diffusion $\alpha = 1$. Additionally, A. Léculier attempts to obtain a survival criterion, as a function of the domain or α, considering more general domains where the size of the obstacles are not fixed or considering for instance only two connected intervals in Ω (see [BCV16] for a related work).

As a second step, we plan to study a model with trait dependence as follows

$$\begin{cases} \partial_t n + \sigma_1(-\Delta)_x^\alpha n - \sigma_2 \Delta_z n = n(R(z,x) - \rho(t,x)), & (t,x,z) \in (0,\infty)\times\Omega\times\mathbb{R}, \\ \rho(t,x) = \int_{\mathbb{R}} n(t,x,z)dz, & \\ n(t,x,z) = 0, & (t,x,z) \in [0,\infty)\times\Omega^c\times\mathbb{R}, \\ n(0,x,z) = n_0(x,z), & (x,z) \in \Omega\times\mathbb{R}. \end{cases} \tag{5.5}$$

Such analysis would allow to investigate the impact of nonlocal dispersion on the genetic adaptation of a population to its environment in presence of obstacles. The role of long distance dispersal is for instance important in the study of adaptation of forest trees to climate change [KRRA$^+$12]. Note that models structured with trait and space with a local dispersion term are studied widely recently (see for instance [ACR13, BM15, Tur15, BJS16, BHR17, BMR] and [CM07] where such models were derived from stochastic individual based models and [ADP12] where the mathematical properties of such equations were first studied). In such models the reaction term has generally an integral term with respect to only one variable as above. Such problems do not admit comparison principle. Moreover, it is usually hard to obtain regularity estimates for such problems due to the nonlocal term only with respect to one variable. Note also that the non-local term may lead to different behaviors compared to an analogous local model (see for instance [CHM$^+$] where we prove that the nonlocal competition may slow down the propagating front compared to an analogous model with local competition).
As a first step, we are interested in the asymptotic study of the equilibrium of (5.5) considering small effect of mutations ($\sigma_2 = \varepsilon^2$). Such analysis would be closely related to the work in Chapter 3, where several habitats are considered. However, here we consider a continuous space structure in each habitat. For instance in the case where Ω is a set of two distinct intervals, by an analogy to model (3.1) we expect that the equilibrium population would be monomorphic or dimorphic. A first step is to investigate the validity of such claim and to identify the conditions leading to polymorphic populations. Note that the analysis of models with continuous space structure in presence of obstacle, compared to the case of discrete space structured models, allows to consider more realistic models for instance to study the role of adaptation in response to climate change. The scaling $\sigma_2 = \varepsilon^2$ is also similar to the scaling used in articles [PS16, LL17]. However those articles consider a connected domain and local dispersion where the trait z models the dispersal rate and has no influence on the growth rate.

More complex reproduction mechanisms

A major problem in evolutionary biology is to take into account the sexual mechanisms of reproduction. Most of my previous works coming from selection-mutation models focused on the study of asexual reproduction, leading to nonlocal reaction-diffusion equations or systems. More recently, I have become interested in the study of sexual mechanisms which lead to some nonlinear integral terms adding significant difficulty to the previous analysis.

A first problem that I am interested in is the extension of the work presented in chapter 3 to the case of sexual reproduction:

$$\begin{cases} \left(-R_1(z) + \rho_{\varepsilon,1}\right) n_{\varepsilon,1}(z) = r_1 \mathcal{B}(n_{\varepsilon,1})(z) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\ \left(-R_2(z) + \rho_{\varepsilon,2}\right) n_{\varepsilon,2}(z) = r_2 \mathcal{B}(n_{\varepsilon,2})(z) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z), \\ \rho_{\varepsilon,i} = \int n_{\varepsilon,i}(z)dz, \quad i = 1,2. \end{cases} \tag{5.6}$$

Here, z corresponds to the phenotypic trait, and $n_{\varepsilon,i}$ is the phenotypic density in habitat i, for $i = 1, 2$. The term $R_i(z)$ is an intrinsic mortality rate that depends on the trait and on the habitat. We take into account a mortality term due to competition, through the total size of the population in each habitat $\rho_{\varepsilon,i}$. We also assume migration between patches, with migration rates m_i. The difference with the model in Chapter 3, that is (3.1), is in the term $r_i\mathcal{B}$ which corresponds to sexual reproduction. The rates of reproduction are denoted by r_i. New offsprings appear following Fisher's infinitesimal model [Fis19]. The trait of each offspring is the average of parental traits plus a random variable normally distributed with variance $\epsilon^2/2$. This translates into the following expression:

$$\mathcal{B}(n)(z) = \iint_{\mathbb{R}^2} G_\epsilon \left(z - \frac{z_1 + z_2}{2} \right) n(z_1) \left(\frac{n(z_2)}{\int_{\mathbb{R}} n(z_2')\, dz_2'} \right) dz_1 dz_2.$$

Note that Fisher's infinitesimal model is derived considering infinitely many genes each of which having a small contribution to the phenotype z [Fis19, BEV17]. The study of models with such sexual reproduction term has gained recent attention from the mathematical community. In [BCGL] the existence of equilibria to such equations without space heterogeneity was studied. In [CGP] an asymptotic analysis of such problem was provided using a similar scaling as in (5.6). In [Rao], another model with continuous space heterogeneity but with the same sexual reproduction term $\mathcal{B}$ was studied with a different approach using the Wasserstein distance (see also [MR13]).

In the framework of the master's project and PhD thesis of L. Dekens, a student that I supervise with V. Calvez, we are interested in an asymptotic study of the selection-mutation-migration model (5.6) as $\varepsilon \to 0$. Note that in the case of the model with sexual reproduction (5.6) we expect to observe very different behaviors comparing to the results obtained for the asexual reproduction [Mir17]. In particular, it is known thanks to numerical simulations that in the case of sexual reproduction, non-symmetric steady solutions may exist even if we consider symmetric habitats [RK01].

The sexual reproduction term $\mathcal{B}$ adds significant difficulty to the problem and even the case of one habitat is not entirely understood. In particular, even in the one habitat model, there may exist multiple steady solutions [CGP]. This is in contrast with the case of a sexual reproduction, where generally the Krein-Rutman Theorem guarantees the uniqueness of the solution. In the case of one habitat, it is shown heuristically in [BBC$^+$] that a different rescaling, replacing ε by ε^2 in (5.2), allows to obtain a limiting problem indicating that the dominant term of the solution is a Gaussian. Then, again in the case of one habitat, in [CGP] it is proved using a perturbative analysis that there exist strong solutions of the selection-mutation model, for ε small, near the solutions of the limiting problem. Such limiting problem may have multiple solutions leading to multiple steady solutions of the selection-mutation model. Note however that this result does not imply that all the solutions of the selection-mutation model are well-approximated by the solutions of the limiting problem.

A second problem that I plan to study is a model with asexual reproduction but taking into account horizontal gene transfer:

$$\begin{cases} \varepsilon \partial_t n_\varepsilon - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon (R(z) - \rho_\varepsilon) + \tau n_\varepsilon \int_{\mathbb{R}} \frac{n_\varepsilon(t,y)}{\rho_\varepsilon(t)} \beta(z-y) dy, \\ \rho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,x) dx. \end{cases}$$

This model is derived from stochastic individual based models [BCF$^+$18] in the limit of large populations. The meanings of the terms in the equations are as above. The new integral term corresponds to the horizontal gene transfer in form of conjugation, where genetic material is replicated and transferred from a cell to another. This form of genetic exchange is particularly important for instance in the case of plasmids which have a major role in the emergence of bacterial resistance to antibiotics [NHS09]. Horizontal gene transfer is not usually taken into account in the models in evolutionary biology. See however [HLFMW09, MR15a] where some integro-differential models including this phenomenon are studied.

I am interested in the study of the impact of this additional integral term on the asymptotic behavior of the population density n_ε, as $\varepsilon \to 0$. In [BCF$^+$18, CFIH$^+$19] numerical simulations reveal that surprising behaviors may arise due to the horizontal gene transfer compared to scenarios where one considers only selection and mutations (see also [CMT] for the theoretical analysis of a stochastic model with a finite number of traits). Depending on the rate or the form of the transfer, in addition to the expected scenarios, one can for instance observe periodic evolution of the dominant trait or evolutionary suicide, i.e. the process of adaptation leads to the extinction of the population. Note that this additional integral term leads to significant difficulties. In particular, it is not easy to identify the limit of n_ε, as $\varepsilon \to 0$, which may be concentrated on one or several points, which may go extinct for certain values of transfer rate τ or have a periodic behavior. Moreover, from a technical point of view it is not easy to obtain a priori regularity estimates.

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