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Dynamics of concentration in a population model structured by age and a phenotypical trait

Samuel Nordmann*[‡] Benoît Perthame^{†‡} Cécile Taing^{†‡}

March 20, 2017

Abstract

We study a mathematical model describing the growth process of a population structured by age and a phenotypical trait, subject to aging, competition between individuals and rare mutations. Our goals are to describe the asymptotic behaviour of the solution to a renewal type equation, and then to derive properties that illustrate the adaptive dynamics of such a population. We begin with a simplified model by discarding the effect of mutations, which allows us to introduce the main ideas and state the full result. Then we discuss the general model and its limitations.

Our approach uses the eigenelements of a formal limiting operator, that depend on the structuring variables of the model and define an effective fitness. Then we introduce a new method which reduces the convergence proof to entropy estimates rather than estimates on the constrained Hamilton-Jacobi equation. Numerical tests illustrate the theory and show the selection of a fittest trait according to the effective fitness. For the problem with mutations, an unusual Hamiltonian arises with an exponential growth, for which we show existence of a global viscosity solution, using an uncommon a priori estimate and a new uniqueness result.

Key-words: Adaptive evolution; Asymptotic behaviour; Dirac concentrations; Hamilton-Jacobi equations; Mathematical biology; Renewal equation; Viscosity solutions.

AMS Class. No: 35B40, 35F21, 35Q92, 49L25.

1 Introduction

The mathematical description of competition between populations and selection phenomena leads to the use of nonlocal equations that are structured by a quantitative trait. A mathematical way to express the selection of the fittest trait is to show that the population density concentrates as a Dirac mass (or a sum of Dirac masses) located on this trait. This result has been obtained for various models with parabolic ([8, 5, 25]) and integro-differential equations ([7, 15]). The question that we pose in the present paper is the long time behaviour of the population density when the growth rate depends both on phenotypical fitness and age. This question brings up to consider the aging parameter and to use renewal type equations. Accordingly, the aim of this paper is to

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study the asymptotic behaviour of the solutions, as $\epsilon \rightarrow 0$, to the following model, with $x \geq 0$ and $y \in \mathbb{R}^n$:

$$\begin{cases} \epsilon \partial_t m_\epsilon(t, x, y) + \partial_x [A(x, y)m_\epsilon(t, x, y)] + (\rho_\epsilon(t) + d(x, y)) m_\epsilon(t, x, y) = 0, \\ A(x = 0, y)m_\epsilon(t, x = 0, y) = \frac{1}{\epsilon^n} \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} M(\frac{y'-y}{\epsilon}) b(x', y') m_\epsilon(t, x', y') dx' dy', \\ \rho_\epsilon(t) = \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} m_\epsilon(t, x, y) dx dy, \\ m_\epsilon(t = 0, x, y) = m_\epsilon^0(x, y) > 0. \end{cases} \quad (1)$$

We choose $m_\epsilon(t, x, y)$ to represent the population density of individuals which, at time t , have the age x and the trait y . The function $A(x, y)$ is the speed of aging for individuals with age x and trait y . We denote with $\rho_\epsilon(t)$ the total size of the population at time t . Here the mortality effect features the nonlocal term $\rho_\epsilon(t)$, which represents competition, and an intrinsic death rate $d(x, y) > 0$. The condition at the boundary $x = 0$ describes the birth of newborns that happens with rate $b(x, y) > 0$ and with the probability kernel of mutation M . The terminology of "renewal equation" comes from this boundary condition. It is related to the McKendrick-von Foerster equation which is only structured in age (see [32] for a study of the linear equation). This model has been extended with other structuring variables as size for example (see [26, 31]) and then with more variables (representing DNA content, maturation, etc.) to illustrate biological phenomena, among many others, like cell division (see [18, 27]), proliferative and quiescent states of tumour cells (see [1, 21]). Space structured problems have also been extensively studied (see [24, 29, 30, 33]).

The parameter $\epsilon > 0$ is used for a time rescaling, since we consider selection-mutation phenomena that occur in a longer time scale than in an individual life cycle. It is also introduced to consider rare mutations. This rescaling is a classical way to give a continuous formulation of the adaptive evolution of a phenotypically structured population, in particular to analyze the dynamics of " $\bar{y}_\epsilon(t)$ ", the fittest trait at time t .

Here we observe two different time scales for our model. The first one is the individual life cycle time scale, i.e. the time for the population to reach the dynamical equilibrium for a fixed y . The second one is the evolutionary time scale, corresponding to the evolution of the population distribution with respect to the variable y . The mathematical expression of these two time scales is the property of variable separation

$$m_\epsilon(t, x, y) \simeq \bar{\rho}(t) Q(x, y) \delta_{y=\bar{y}(t)},$$

when ϵ is close to 0, where $Q(x, y)$ is a normalized equilibrium distribution over age for a fixed y . In order to observe the asymptotic behaviour of the solution to (1), the key point is to prove convergence results when ϵ vanishes, that is when the two time scales become totally separated. In other words, as ϵ vanishes, the life cycle time scale becomes smaller, whereas the evolutionary time scale becomes larger.

As a first step, we ignore mutations, i.e. we take $M(z) = \delta_0$. Equation (1) becomes

$$\begin{cases} \epsilon \partial_t m_\epsilon(t, x, y) + \partial_x [A(x, y)m_\epsilon(t, x, y)] + (\rho_\epsilon(t) + d(x, y)) m_\epsilon(t, x, y) = 0, \\ A(x = 0, y)m_\epsilon(t, x = 0, y) = \int_{\mathbb{R}_+} b(x', y) m_\epsilon(x', y) dx', \\ \rho_\epsilon(t) = \iint m_\epsilon(t, x, y) dx dy, \\ m_\epsilon(t = 0, x, y) = m_\epsilon^0(x, y) > 0. \end{cases} \quad (2)$$

The analysis of this simplified model allows us to introduce the main ideas of our work. In order to study the asymptotic behaviour of the solution to (2), we consider the associated eigenproblem, that is to find, for each $y \in \mathbb{R}^n$, the solution $(\Lambda(y), Q(x, y))$ to

$$\begin{cases} \partial_x [A(x, y)Q(x, y)] + d(x, y)Q(x, y) = \Lambda(y)Q(x, y), \\ A(x = 0, y)Q(x = 0, y) = \int_{\mathbb{R}_+} b(x', y)Q(x', y)dx', \\ Q(x, y) > 0, \quad \int_{\mathbb{R}_+} b(x', y)Q(x', y)dx' = 1. \end{cases} \quad (3)$$

We also define Φ , solution of the dual problem

$$\begin{cases} A(x, y)\partial_x \Phi(x, y) + [\Lambda(y) - d(x, y)]\Phi(x, y) = -b(x, y)\Phi(0, y), \\ \int Q(x, y)\Phi(x, y)dx = 1. \end{cases} \quad (4)$$

The purpose of this paper is to introduce an alternative to the usual WKB method (see [8, 17]) to prove the concentration phenomenon in the y variable for the model (2). Indeed we propose a new approach that consists in firstly introducing the exponential concentration singularity and secondly in estimating the corresponding age profile. The main idea is to define a function $u_\epsilon(t, y)$ independent of x , and an "age profile" $p_\epsilon(t, x, y)$, such that we can write $m_\epsilon(t, x, y) = p_\epsilon(t, x, y)e^{\frac{u_\epsilon(t, y)}{\epsilon}}$. Then we prove that u_ϵ converges uniformly to a function u , which zeros correspond to the potential concentration points of the population density when ϵ vanishes. Moreover, following earlier works, we prove that $p_\epsilon(t, x, y)$ converges to the first eigenvector of the stationary problem introduced in (3) using the general relative entropy (GRE) principle (see [28] for an introduction).

This convergence result does not apply for the model (1) with mutations. Because of several technical obstructions we cannot prove the full result. However, we are able to derive some estimates resulting from the study of the formal limiting problem. Then we derive an approximation problem with a Hamilton-Jacobi equation satisfied by a sequence u_ϵ that we build and we prove its convergence to the solution to the constrained Hamilton-Jacobi equation coming from the formal limiting problem. This constrained Hamilton-Jacobi formally determines the locations of the concentration points.

Recently, the asymptotic behavior of an age-structured equation with spatial jumps has been determined in [11] when the death rate vanishes and with a slowly decaying birth rate b ; then the eigenproblem (3) does not have a solution.

The Hamilton-Jacobi approach to prove the concentration of the population density goes back to [17] and has been extensively used in works on the similar issue (see [12] for example). It also has been used in the context of front propagation theory for reaction-diffusion equations (see [4, 9, 19]). For example in the case of the simple Fisher-KPP equation, the dynamics of the front are described by the level set of a solution of a Hamilton-Jacobi equation. In this framework, it is naturally appropriate to use the theory of viscosity solutions to derive the convergence of the sequence u_ϵ (see [2, 3, 20] for an introduction to this notion). In this paper we also prove a uniqueness result in the viscosity sense that is not standard because the Hamiltonian under investigation have exponential growth.

The paper is organized as follows. We first state the general assumptions in section 2. Section 3 is devoted to the formulation and the proof of the convergence results in the case without mutation. In section 4, we discuss the case with mutations and tackle the formal limit of the stationary problem. Finally we present some numerics in section 5.

2 Assumptions

Since the analysis requires several technical assumptions on the coefficients and the initial data, we present them first.

Regularity of the coefficients. We assume that $x \mapsto b(x, y) > 0$ and $x \mapsto d(x, y) > 0$ are uniformly continuous, that $x \mapsto A(x, y)$ is C^1 and such that, for all $y \in \mathbb{R}^n$,

$$\lim_{x \rightarrow +\infty} d(x, y) = +\infty, \quad (5)$$

$$0 < \underline{r} \leq b(x, y) - d(x, y) \leq \bar{r}, \quad (6)$$

$$0 < A_0 \leq A(x, y) \leq A_\infty, \quad \text{for two positive constants } A_0 \text{ and } A_\infty. \quad (7)$$

Conditions on the initial data. We suppose that the total density is initially bounded

$$0 < \underline{\rho}^0 \leq \rho_\epsilon^0 \leq \bar{\rho}^0, \quad (8)$$

with $\underline{\rho}_0$ and $\bar{\rho}_0$ two constants. Besides we assume the population to be well prepared for concentration, that is we can write

$$m_\epsilon^0(x, y) = p_\epsilon^0(x, y) e^{\frac{u_\epsilon^0(y)}{\epsilon}},$$

where u_ϵ^0 is uniformly Lipschitz continuous and

$$\left\{ \begin{array}{l} \exists k_0 > 0, \forall \epsilon > 0, \forall (y, y') \in \mathbb{R}^{2n}, |u_\epsilon^0(y) - u_\epsilon^0(y')| \leq k_0 |y - y'|, \\ u_\epsilon^0(y) \rightarrow u^0(y) \leq 0 \text{ uniformly in } y, \\ \exists! \bar{y}^0 \in \mathbb{R}^n, \max_{y \in \mathbb{R}^n} u^0(y) = u^0(\bar{y}^0) = 0, \\ e^{\frac{u_\epsilon^0}{\epsilon}} \xrightarrow{\epsilon \rightarrow 0} \delta_{\bar{y}^0}. \end{array} \right. \quad (9)$$

Finally, we assume that, for all $y \in \mathbb{R}^d$, there are positive constants $\underline{\gamma}(y)$ and $\bar{\gamma}(y)$ such that, for all $\epsilon > 0, x \in \mathbb{R}_+$

$$\underline{\gamma}(y)Q(x, y) \leq p_\epsilon^0(x, y) \leq \bar{\gamma}(y)Q(x, y), \quad (10)$$

$$\int_{\mathbb{R}_+} |p_\epsilon^0(x, y) - \gamma^0(y)Q(x, y)| \Phi(x, y) dx \xrightarrow{\epsilon \rightarrow 0} 0, \quad \text{uniformly in } y, \quad (11)$$

where Q, Φ are eigenlements associated with the eigenproblem (3)-(4) which properties are analyzed in section 3.1.

Some notations: We define, for $x \in \mathbb{R}_+, y \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$, the functions

$$f(x, y, \lambda) = \frac{b(x, y)}{A(x, y)} \exp\left(-\int_0^x \frac{d(x', y) - \lambda}{A(x', y)} dx'\right), \quad F(y, \lambda) = \int_{\mathbb{R}_+} f(x, y, \lambda) dx. \quad (12)$$

3 Case without mutations

We present our new approach to understand how solutions of (2) behave when ϵ vanishes. To show that a concentration in the y variable may occur, we first consider the principal eigenvalue Λ of (3), and define u_ϵ as the solution of the equation

$$\begin{cases} \partial_t u_\epsilon(t, y) = -\Lambda(y) - \rho_\epsilon(t), & t > 0, y \in \mathbb{R}^n, \\ u_\epsilon(0, y) = u_\epsilon^0, & y \in \mathbb{R}^n. \end{cases} \quad (13)$$

We first show that u_ϵ converges locally uniformly. Then, by defining p_ϵ such that

$$m_\epsilon(t, x, y) = p_\epsilon(t, x, y) e^{\frac{u_\epsilon(t, y)}{\epsilon}}, \quad (14)$$

we show that p_ϵ converges when $\epsilon \rightarrow 0$ respectively to a function p in some way that we will specify. This section is devoted to the proof of the following theorem, which states the concentration of the population density on the fittest traits.

Theorem 3.1. Assume (5)-(11). Let m_ϵ be the solution of (2), u_ϵ the solution of (13) and p_ϵ defined by the factorization (14). Then, the following assertions hold true:

- (i) ρ_ϵ converges to a function ρ when ϵ vanishes in $L^\infty(0, \infty)$ weak- \star .
- (ii) u_ϵ converges locally uniformly when ϵ vanishes to a continuous function u solution of

$$\begin{cases} \partial_t u(t, y) = -\Lambda(y) - \rho(t), & t > 0, y \in \mathbb{R}^n, \\ u(0, y) = u^0(y), & y \in \mathbb{R}^n, \\ \sup_{y \in \mathbb{R}^n} u(t, y) = 0, & \forall t > 0. \end{cases}$$

- (iii) p_ϵ converges to a multiple of the normalized eigenfunction Q for a weighted L^1 norm.
- (iv) Hence, m_ϵ converges weakly as ϵ vanishes to a measure μ which support is included in $\{(t, y) \in \mathbb{R}_+^* \times \mathbb{R}^n | u(t, y) = 0\}$.
- (v) Furthermore, assuming u^0 and $-\Lambda$ are strictly concave

$$m_\epsilon(t, x, y) \xrightarrow{\epsilon \rightarrow 0} \rho(t) \frac{Q(x, y)}{\|Q(\cdot, y)\|_{L^1}} \delta_{y=\bar{y}(t)},$$

where $\bar{y}(t) \in \mathbb{R}^n$ satisfies a canonical differential equation.

3.1 The eigenproblem

We first study the eigenproblem (3) and the associated dual problem (4). The operator in (3), which is time independent, is obtained by formally taking $\epsilon = 0$ in system (2) and by removing the formal limiting term $\rho(t)$. We point out that this approach relies on the observation that $\rho_\epsilon(t)$ operates linearly on m_ϵ , therefore its effect on the eigenvalue Λ is no more than a shift. The following theorem states existence and uniqueness for these eigenlements as well as some properties.

Theorem 3.2. We assume (5) and (7). For a given $y \in \mathbb{R}^n$, there exists a unique triplet $(\Lambda(y), Q(x, y), \Phi(x, y))$ solution of (3)-(4). Moreover, the function $x \mapsto Q(x, y)$ is bounded and belongs to $L^1((0, +\infty))$, the function $y \mapsto \Lambda(y)$ is \mathcal{C}^1 and we have

$$\partial_\lambda F > 0, \quad F(y, \Lambda(y)) = 1, \quad \nabla_y \Lambda(y) = -\frac{\nabla_y F(y, \Lambda(y))}{\partial_\lambda F(y, \Lambda(y))}. \quad (15)$$

The complete proof, which only uses classical arguments, is postponed to Appendix B. We give here a formal idea of the method. The eigenfunction Q satisfies a linear differential equation that allows us to derive

$$Q(x, y) = \frac{1}{A(x, y)} \exp\left(-\int_0^x \frac{d(x', y) - \Lambda(y)}{A(x', y)} dx'\right).$$

From this formulation, we deduce that the eigenvalue $\Lambda(y)$ must satisfy $F(y, \Lambda(y)) = 1$, for all $y \in \mathbb{R}^d$, where F is defined in (12). Since $\partial_\lambda F > 0$, the above equality determines a unique Λ , and therefore a unique Q . Similarly, we derive an explicit formula for Φ .

Note that Q represents the age distribution at equilibrium for a fixed y , thus it seems natural that it exponentially decreases. The eigenvalue Λ defines what we call the "effective fitness". It drives the adaptive dynamics of the population, as discussed in what follows.

3.2 Concentration

3.2.1 Saturation of the population density

The nonlocal term ρ_ϵ in (2) can be interpreted as the pressure exerted by the total population on the survival of individuals with trait y . It leads the total population to be bounded. This saturation property is stated in the following proposition, which proof, using very classical arguments, is postponed to Appendix A.

Proposition 3.3. *We assume (6)-(8), then,*

$$\forall t \geq 0, \quad \rho_m \leq \rho_\epsilon(t) \leq \rho_M,$$

where $\rho_m := \min(\underline{r}, \underline{\rho}^0)$ and $\rho_M := \max(\bar{r}, \bar{\rho}^0)$. Hence, after extraction of a subsequence, ρ_ϵ converges weakly- \star to a function ρ in $L^\infty(0, +\infty)$.

Thereafter, in order to remove the restriction to a subsequence, we need a uniqueness statement to prove the assertion (i) of Theorem 3.1. This is done in section 3.2.2.

We now introduce u_ϵ solution to (13), and then we define $p_\epsilon(t, x, y)$ by the factorization (14). In this way, we show a convergence result for p_ϵ as stated in the following theorem, which proof is given at the end of the section.

Theorem 3.4. We assume (5)-(11). With the constants defined in (10)-(11),

- (i) we have $\underline{\gamma}(y)Q(x, y) \leq p_\epsilon(t, x, y) \leq \bar{\gamma}(y)Q(x, y)$ for all $t \geq 0$,
- (ii) moreover, the profile p_ϵ converges to the eigenfunction Q for a weighted L^2 norm. Namely, for γ^0 defined in assumption (11) we have, uniformly in (t, y)

$$\int_{\mathbb{R}^+} \left| \frac{p_\epsilon}{Q}(t, x, y) - \gamma^0(y) \right| Q(x, y) \Phi(x, y) dx \rightarrow 0 \quad \text{when } \epsilon \rightarrow 0.$$

3.2.2 Convergence of u_ϵ

Integrating (13), we obtain the explicit formula

$$u_\epsilon(t, y) = u_\epsilon^0(y) - t\Lambda(y) - \int_0^t \rho_\epsilon(s) ds. \quad (16)$$

Hence, after extraction of a subsequence, $u_\epsilon(t, y)$ converges locally uniformly to a function $u(t, y)$ which is given by

$$u(t, y) = u^0(y) - t\Lambda(y) - \int_0^t \rho(s) ds. \quad (17)$$

Next, we claim that

$$\sup_{y \in \mathbb{R}^n} u(t, y) = 0, \quad \forall t \geq 0. \quad (18)$$

Indeed, we recall $m_\epsilon(t, x, y) = p_\epsilon(t, x, y)e^{\frac{u_\epsilon(t, y)}{\epsilon}}$ and $p_\epsilon(t, x, y)$ converges in virtue of Theorem 3.4 (that we prove independently). If there existed a point y_0 for some t such that $u(t, y_0) > 0$, $\rho_\epsilon(t)$ would diverge, which is a contradiction with Proposition 3.3. In a similar way, $\sup_y u(t, \cdot) < 0$ would imply $\rho_\epsilon(t) \rightarrow 0$, which also contradicts Proposition 3.3. Hence (18) must hold.

Thus, up to extraction of a subsequence, m_ϵ weakly converges to a measure which support is included in the set $\{(t, y) \in [0, +\infty) \times \mathbb{R}^n \mid u(t, y) = 0\}$. Outside of this set, we know that the population density vanishes locally uniformly as $\epsilon \rightarrow 0$.

Finally we prove the convergence of the whole sequence u_ϵ . From (17) and (18) we obtain

$$\int_0^t \rho(s) ds = \sup_{y \in \mathbb{R}^n} [u^0(y) - t\Lambda(y)], \quad \forall t \geq 0. \quad (19)$$

The uniqueness of the limit function ρ is therefore ensured, which implies that the full sequence ρ_ϵ converges to ρ . Then, the convergence of the full family u_ϵ follows from (16). Hence the statements (iii) and (iv) of Theorem 3.1, provided (ii).

3.3 Convergence of p_ϵ

This section is devoted to the proof of Theorem 3.4, which completes (ii) of Theorem 3.1. The main ingredients of the proof are as follows: in a first step we show that $\frac{p_\epsilon}{Q}$ is bounded so we can extract a weak- \star limit for the L^∞ norm. Then we use an entropy in order to identify this limit, and to show that the convergence occurs in a weighted L^2 space. Our approach follows closely [28, 32].

First step: bounds on $\frac{p_\epsilon}{Q}$. From (2) and (13)-(14), we infer that p_ϵ satisfies

$$\begin{cases} \epsilon \partial_t p_\epsilon(t, x, y) + \partial_x [A(x, y)p_\epsilon(t, x, y)] + [d(x, y) - \Lambda(y)] p_\epsilon(t, x, y) = 0, \\ A(x = 0, y)p_\epsilon(t, x = 0, y) = \int b(x', y)p_\epsilon(t, x', y) dx'. \end{cases}$$

Moreover Q satisfies the same linear equation. Assumption (10) and the comparison principle for transport equations show the first statement of Theorem 3.4.

Second step: Entropy inequality. In the sequel, we consider

$$v_\epsilon(t, x, y) := \frac{p_\epsilon(t, x, y)}{Q(x, y)} - \gamma^0(y).$$

We also define, for any function $f(t, x, y)$, the average

$$\langle f \rangle(t, y) := \int_{\mathbb{R}_+} f(t, x, y) b(x, y) Q(x, y) dx,$$

and we notice that a direct computation shows

$$\begin{cases} \epsilon \partial_t v_\epsilon(t, x, y) + A(x, y) \partial_x v_\epsilon(t, x, y) = 0, \\ v_\epsilon(t, x = 0, y) = \langle v_\epsilon \rangle(t, y). \end{cases}$$

Thus we have, in a weak sense

$$\epsilon \partial_t |v_\epsilon(t, x, y)| + A(x, y) \partial_x |v_\epsilon(t, x, y)| = 0.$$

We now introduce the generalized relative entropy $E_\epsilon(t, y) = \int_{\mathbb{R}_+} |v_\epsilon(t, x, y)| Q(x, y) \Phi(x, y) dx$ and compute

$$\begin{aligned} \epsilon \partial_t E_\epsilon(t, y) &= \int_{\mathbb{R}_+} \epsilon |\partial_t v_\epsilon(t, x, y)| Q(x, y) \Phi(x, y) dx \\ &= - \int_{\mathbb{R}_+} A(x, y) |\partial_x v_\epsilon(t, x, y)| Q(x, y) \Phi(x, y) dx \\ &= - [v_\epsilon |AQ\Phi]_{x=0}^\infty + \int_{\mathbb{R}_+} |v_\epsilon| \partial_x (AQ\Phi) dx \\ &= \Phi(0, y) |\langle v_\epsilon \rangle|(t, y) - \Phi(0, y) \int_{\mathbb{R}_+} bQ |v_\epsilon| dx. \end{aligned}$$

Hence, using the Cauchy-Schwarz inequality,

$$\epsilon \partial_t E_\epsilon(t, y) = -\Phi(0, y) (|\langle v_\epsilon \rangle| - |\langle v_\epsilon \rangle|) \leq 0.$$

Therefore $0 \leq E_\epsilon(t, y) \leq E_\epsilon(0, y)$, and we conclude for (ii) using (11).

Remark 3.5. As v_ϵ is bounded, the convergence stated in (ii) occurs in all weighted L^p norms. Namely, for all $p \geq 1$

$$\int_{\mathbb{R}_+} \left| \frac{p_\epsilon}{Q}(t, x, y) - \gamma^0(y) \right|^p Q \Phi dx \longrightarrow 0, \quad \text{when } \epsilon \rightarrow 0.$$

3.4 Properties of concentration points

Since we can explicitly integrate (13) to obtain (17), we are able to identify the points where the population concentrates, which are the points where u vanishes.

Proposition 3.6. *Let $t \in (0, \infty)$ and $\bar{y}(t) \in \mathbb{R}^n$ such that $u(t, \bar{y}(t)) = 0$. As $\bar{y}(t)$ is a maximum point of $u(t, \cdot)$, it satisfies*

$$\nabla u^0(\bar{y}(t)) = t \nabla \Lambda(\bar{y}(t)), \quad (20)$$

and we have

$$u^0(\bar{y}(t)) = \int_0^t \rho(t') dt' - t\rho(t). \quad (21)$$

Proof. From equation (17) we derive

$$u^0(\bar{y}(t)) = t\Lambda(\bar{y}(t)) + \int_0^t \rho(t') dt'. \quad (22)$$

Besides, $\bar{y}(t)$ is a maximum point of $u(t, \cdot)$, therefore $\nabla_y u(t, \bar{y}(t)) = 0$ which shows (20). Moreover $\partial_t u(t, \bar{y}(t)) = 0$, and using (13) we obtain

$$\Lambda(\bar{y}(t)) = -\rho(t). \quad (23)$$

Thus, combining (22) and (23), we obtain equation (21) \square

At this stage, the concentration of the population density on a single trait $\bar{y}(t)$ cannot be concluded yet because the above relation defines a hypersurface. There are two frameworks in which one can show that the population is monomorphic, that is the population converges in measure toward a Dirac mass located on a unique point $\bar{y}(t)$ at each time $t \geq 0$. The first framework assumes that y is one dimensional, and $y \mapsto \Lambda(y)$ is strictly monotonic. The second assumes, for $y \in \mathbb{R}^d$, that $u_\epsilon^0(\cdot)$ and $-\Lambda(\cdot)$ are strictly concave uniformly in ϵ . The interested reader can refer to [8] and [25] for a complete analysis of these two cases.

In the framework of uniform strict concavity, we obtain the additional result of uniform regularity on u_ϵ and u , which enables to rigorously derive a form of canonical equation in the language of adaptive dynamics. This canonical equation gives the dynamics of the selected trait, that is the evolution of the concentration point in an evolutionary time scale.

Theorem 3.7. Assume u^0 and $-\Lambda$ are strictly concave. Then $u(t, \cdot)$ is strictly concave and there exists $T > 0$ such that for all $t \in (0, T)$, $u(t, \cdot)$ reaches its maximum 0 on a unique point $\bar{y}(t)$. Moreover $t \mapsto \bar{y}(t) \in \mathcal{C}^1(0, T)$ and its dynamics is described by the equation

$$\dot{\bar{y}}(t) = (\nabla_y^2 u(t, \bar{y}(t)))^{-1} \cdot \nabla_y \Lambda(\bar{y}(t)), \quad \bar{y}(0) = \bar{y}^0. \quad (24)$$

If, in addition, $y \mapsto \Lambda(y)$ is coercive, then the above result holds globally in time.

Proof. We are interested in the solutions $\bar{y}(t) \in \mathbb{R}^n$ of

$$\nabla_y u(t, \bar{y}(t)) = 0. \quad (25)$$

Note that u is strictly concave, because u^0 and $-\Lambda$ are. Therefore, such a $\bar{y}(t)$ must satisfy $u(t, \bar{y}(t)) = \max_y u(t, y) = 0$.

From (9) we know that at initial time there exists a unique solution \bar{y}^0 of (25). Besides, as u is strictly concave, $\nabla_y^2 u$ is invertible. Hence, thanks to the implicit functions theorem, there exists $T > 0$ such that for all $t \in (0, T)$, there exists a unique $\bar{y}(t) \in \mathbb{R}^n$ satisfying (25). Moreover, $t \mapsto \bar{y}(t)$ is a \mathcal{C}^1 function, and then differentiating (25) with respect to t , we obtain, using (17)

$$0 = \frac{d}{dt} [\nabla_y u(t, \bar{y}(t))] = -\nabla_y \Lambda(\bar{y}(t)) + \dot{\bar{y}}(t) \nabla_y^2 u(t, \bar{y}(t)),$$

and (24) follows.

Finally, note that we have

$$\frac{d}{dt} [\Lambda(\bar{y}(t))] = \nabla_y \Lambda(\bar{y}(t)) \cdot (\nabla_y^2 u(t, \bar{y}(t)))^{-1} \cdot \nabla_y \Lambda(\bar{y}(t)) \leq 0.$$

Therefore, if $y \mapsto \Lambda(y)$ is coercive, $\bar{y}(t)$ remains in a compact set of \mathbb{R}^n , and thus the result holds globally in time. \square

From this result we infer the statement (v) of Theorem 3.1. We also give the following additional results. The first one is derived directly from (15).

Corollary 3.8. *Under the same hypothesis as in Theorem 3.7, the critical points for evolutionary dynamics satisfy $\nabla_y F(y^*, \Lambda(y^*)) = 0$.*

Corollary 3.9. *Under the same hypothesis as in Theorem 3.7, we have $t \mapsto \rho(t) \in \mathcal{C}^1(0, T)$ and $\dot{\rho}(t) \geq 0$ for all $t \in (0, T)$.*

Proof. From (19), (23) and the regularity of $\bar{y}(t)$, we infer that $t \mapsto \rho(t)$ is \mathcal{C}^1 for $t \in (0, T)$. We have

$$0 = \frac{d}{dt} [\partial_t u(t, \bar{y}(t))] = -\nabla_y \Lambda(\bar{y}(t)) \dot{\bar{y}}(t) - \dot{\rho}(t),$$

thus

$$\dot{\rho}(t) = -\nabla_y \Lambda(\bar{y}(t)) \cdot (\nabla_y^2 u(t, \bar{y}(t)))^{-1} \nabla_y \Lambda(\bar{y}(t)),$$

and $\dot{\rho}(t) \geq 0$ since $\nabla_y^2 u$ is negative in $(t, \bar{y}(t))$. \square

4 Case with mutations

We turn to the model (1) including mutations. We use the same approach as in the previous section, that is we write $m_\epsilon(t, x, y) = p_\epsilon(t, x, y) e^{\frac{u_\epsilon(t, y)}{\epsilon}}$ and insert this form in (1). We obtain

$$\begin{cases} \epsilon \partial_t p_\epsilon(t, x, y) + \partial_x [A(x, y) p_\epsilon(t, x, y)] + d(x, y) p_\epsilon(t, x, y) = -(\rho_\epsilon(t) + \partial_t u_\epsilon(t, y)) p_\epsilon(t, x, y), \\ A(x=0, y) p_\epsilon(t, x=0, y) = \frac{1}{\epsilon^n} \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} M\left(\frac{y'-y}{\epsilon}\right) b(x', y') p_\epsilon(t, x', y') e^{\frac{u_\epsilon(t, y') - u_\epsilon(t, y)}{\epsilon}} dx' dy', \\ \rho_\epsilon(t) = \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} m_\epsilon(t, x, y) dx dy, \\ p_\epsilon(t=0, x, y) = p_\epsilon^0(x, y) > 0. \end{cases} \quad (26)$$

With the change of variable $z = \frac{y'-y}{\epsilon}$, the renewal term is written as

$$A(x=0) p_\epsilon(t, x=0, y) = \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} M(z) e^{\frac{u_\epsilon(t, y+\epsilon z) - u_\epsilon(t, y)}{\epsilon}} b(x', y+\epsilon z) p_\epsilon(t, x', y+\epsilon z) dx' dz. \quad (27)$$

By taking formally the limit $\epsilon \rightarrow 0$, we get

$$A(x=0) p(t, x=0, y) = \int_{\mathbb{R}^n} M(z) e^{\nabla u(t, y) \cdot z} dz \int_{\mathbb{R}_+} b(x', y) p(t, x', y) dx'.$$

Denoting

$$\eta(t, y) := \int_{\mathbb{R}^n} M(z) e^{\nabla_y u(t, y) \cdot z} dz,$$

the formal limit of (26) is written as

$$\begin{cases} \partial_x [A(x, y)p(t, x, y)] + d(x, y)p(t, x, y) = -(\rho(t) + \partial_t u(t, y))p(t, x, y), \\ A(x = 0)p(t, x = 0, y) = \eta(t, y) \int_{\mathbb{R}_+} b(x', y)p(t, x', y)dx', \\ \rho(t) = \int_{\mathbb{R}_+} \int_{\mathbb{R}^n} m(t, x, y)dx dy, \\ p(t = 0, x, y) = p^0(x, y) > 0, \quad u(t = 0, y) = u^0(y). \end{cases}$$

With this form, one can consider the following eigenproblem: for fixed $(y, \eta) \in \mathbb{R}^n \times (0, +\infty)$, find $(\Lambda(y, \eta), Q(x, y, \eta))$, solution of

$$\begin{cases} \partial_x [A(x, y)Q(x, y, \eta)] + d(x, y)Q(x, y, \eta) = \Lambda(y, \eta)Q(x, y, \eta), \\ A(x = 0, y)Q(x = 0, y, \eta) = \eta \int_{\mathbb{R}_+} b(x', y)Q(x', y, \eta)dx', \\ Q(x, y, \eta) > 0, \quad \int_{\mathbb{R}_+} b(x, y)Q(x, y, \eta)dx = 1. \end{cases} \quad (28)$$

Using this eigenproblem, we firstly compute the formal limit u of the sequence u_ϵ , and show that it satisfies the following Hamilton-Jacobi equation

$$\begin{cases} \partial_t u(t, y) = -\Lambda \left(y, \int M(z) e^{\nabla u(t, y) \cdot z} dz \right) - \rho(t), \quad t \geq 0, y \in \mathbb{R}^n, \\ u(0, y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases} \quad (29)$$

In this way, we formally recover the limit profile p using (28) with $\eta = \eta(t, y)$. Back to the question of adaptative dynamics, $\Lambda(y, \eta(t, y))$ defines the effective fitness of the population with trait y .

In what follows, we study this limit problem and construct a solution u . Actually the convergence of p_ϵ towards the solution Q of the eigenproblem is an unsolved question. Indeed because of the particular form of the boundary condition (27), we derive a stationary problem which depends on ϵ and thus we do not know how to study the asymptotic of p_ϵ as $\epsilon \rightarrow 0$. However, we construct a sequence u_ϵ from an approximation problem of (29) that is well defined and we prove it converges to the solution of (29) in the viscosity sense.

To begin with, we state the saturation of the population density, and the existence and uniqueness of the eigenelements of (28).

4.1 Saturation and stationary problem

As in the case without mutations in the previous section, it still holds that the total population is bounded.

Proposition 4.1. *We assume (6)-(8). Then there exist two constants $\rho_m, \rho_M > 0$ such that*

$$\forall t \geq 0, \quad 0 < \rho_m \leq \rho_\epsilon(t) \leq \rho_M.$$

Hence, after extracting a subsequence, ρ_ϵ converges to a function ρ in weak- $L^\infty(0, +\infty)$.*

We now establish the existence and uniqueness of the eigenelements in (28). Hence we introduce the associated dual problem: find $\Phi(x, y, \eta)$ solution of

$$\begin{cases} A(x, y)\partial_x \Phi(x, y, \eta) + [\Lambda(y, \eta) - d(x, y)] \Phi(x, y, \eta) = -\eta b(x, y)\Phi(0, y, \eta), \\ \int Q(x, y, \eta)\Phi(x, y, \eta)dx = 1. \end{cases} \quad (30)$$

We also recall the definition (12) for the function F . The proof of the following theorem is given in Appendix B.

Theorem 4.2. We assume (5)-(7). For given $y \in \mathbb{R}^n$ and $\eta \in \mathbb{R}_+$, there exists a unique triplet $(\Lambda(y, \eta), Q(x, y, \eta), \Phi(x, y, \eta))$ solution of (28) and (30). The map $x \mapsto Q(x, y, \eta)$ is bounded and integrable, $y \mapsto \Lambda(y, \eta)$ is \mathcal{C}^1 and we have

$$\partial_\lambda F > 0, \quad F(y, \Lambda(y, \eta)) = \frac{1}{\eta}, \quad (31)$$

$$\nabla_y \Lambda(y, \eta) = -\frac{\nabla F(y, \Lambda(y, \eta))}{\partial_\lambda F(y, \Lambda(y, \eta))}, \quad \partial_\eta \Lambda(y, \eta) = -\frac{1}{\eta^2 \partial_\lambda F(y, \Lambda(y, \eta))} < 0. \quad (32)$$

In the sequel we consider the effective Hamiltonian (fitness)

$$H(y, p) := -\Lambda(y, \eta(p)), \quad \eta(p) := \int M(z) e^{p \cdot z} dz > 0. \quad (33)$$

Before constructing a solution to the associated Hamilton-Jacobi equation in the next section, we state the following result, which is proved in Appendix C.

Proposition 4.3. *The mapping $p \mapsto H(y, p)$ is convex, for all $y \in \mathbb{R}^n$.*

4.2 The Hamilton-Jacobi equation

Here we consider the Hamilton-Jacobi equation (29) that we may write from (33) as

$$\begin{cases} \partial_t u(t, y) = H(y, \nabla_y u) - \rho(t), \\ u(0, y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases}$$

Our goal is to build a solution to this equation. Therefore, we introduce u_ϵ solution of an approximate problem motivated by the form in (26), which reads

$$\begin{cases} \partial_t u_\epsilon(t, y) = -\Lambda\left(y, \int M(z) e^{\frac{u_\epsilon(t, y+\epsilon z) - u_\epsilon(t, y)}{\epsilon}} dz\right) - \rho_\epsilon(t), \\ u_\epsilon(0, y) = u_\epsilon^0(y), \quad y \in \mathbb{R}^n. \end{cases} \quad (34)$$

To simplify the Hamiltonian in equation (34), we set $U_\epsilon(t, y) := u_\epsilon(t, y) + \int_0^t \rho_\epsilon(t') dt$, which satisfies

$$\partial_t U_\epsilon(t, y) = -\Lambda\left(y, \int M(z) e^{\frac{U_\epsilon(t, y+\epsilon z) - U_\epsilon(t, y)}{\epsilon}} dz\right). \quad (35)$$

For clarity, we set

$$\eta_\epsilon(t, y) = \int M(z) e^{\frac{U_\epsilon(t, y+\epsilon z) - U_\epsilon(t, y)}{\epsilon}} dz.$$

We state the following theorem, which is the main result of this section. The set of assumptions (\mathcal{H}) is presented below.

Theorem 4.4. Assuming (\mathcal{H}) there exists a unique solution U_ϵ to (35). Furthermore, U_ϵ converges locally uniformly to a function U which is a viscosity solution of the equation

$$\partial_t U(t, y) = H(y, \nabla_y U) = -\Lambda\left(y, \int M(z) e^{\nabla_y U \cdot z} dz\right). \quad (36)$$

In other words, we prove a stability result in the language of the viscosity solutions theory (see [3]) in a situation where the Hamiltonian depends on ∇U with an exponential growth, which is the major difficulty here. The plan of the proof is as follows. Firstly we consider the truncated equation associated to (35), for which classical results give existence and uniqueness of a global solution. Then we provide a uniform a priori estimate on the time derivative of the solution. It allows us to remove the truncation and to infer a global solution U_ϵ of (35). This proves the first step.

Secondly, we consider the semi-relaxed limits $\bar{U} := \limsup U_\epsilon$ and $\underline{U} := \liminf U_\epsilon$, and prove that they are respectively subsolution and supersolution of (36) in the viscosity sense. Then, an assumption of coercivity of $\eta \mapsto \Lambda(y, \eta)$ in (38), allows us to state that \underline{U} is Lipschitzian. Finally, using a nonclassical uniqueness result on the Hamiltonian H , we prove that $\bar{U} = \underline{U}$, and conclude that U_ϵ converges locally uniformly to a viscosity solution of (36).

Assumptions (\mathcal{H}). We assume (9). In addition, for any compact interval I , we assume there exist two constants $L_0, L_1 > 0$, (depending on I) such that

$$\forall y \in \mathbb{R}^n, \forall \eta \in I, \quad \begin{cases} |\Lambda(y, \eta)| \leq L_0, \\ |\partial_\eta \Lambda(y, \eta)| \leq L_1. \end{cases} \quad (37)$$

We also assume

$$|\Lambda(y, \eta)| \rightarrow +\infty \text{ when } \eta \rightarrow +\infty \text{ or } \eta \rightarrow 0, \text{ uniformly in } y \in \mathbb{R}^n. \quad (38)$$

Finally, the following assumption is required for our uniqueness result, stated in Theorem 4.13. For all compact set $K_p \subset \mathbb{R}^n$, we assume there exist $C > 0, \gamma_1 \in [0, 4), \gamma_2 \in [0, 6)$ such that

$$\forall y \in \mathbb{R}^n, \forall p \in K_p, \quad \begin{cases} |\nabla_y H(y, p)| \leq C(1 + |y|^{\gamma_1}), \\ |\nabla_p H(y, p)| \leq C(1 + |y|^{\gamma_2}). \end{cases} \quad (39)$$

4.3 Global existence and a priori estimate

This section is devoted to the proof of the following, which is the first step towards Theorem 4.4.

Theorem 4.5. Assume (37). Then, for all $\epsilon > 0$, there exists a unique global solution U_ϵ to the equation (35), such that $|\partial_t U_\epsilon(t, y)| \leq C_V$ for a constant $C_V > 0$, uniformly in $\epsilon > 0, t > 0, y \in \mathbb{R}^n$.

4.3.1 The truncated problem

We first consider a truncated problem associated to (35). For a fixed $R > 0$, we define the function $\phi_R : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ which is smooth, increasing and satisfies

$$\phi_R(r) = \begin{cases} r & \text{for } r \in [-\frac{R}{2}, \frac{R}{2}], \\ R & \text{for } r \geq R, \\ -R & \text{for } r \leq -R, \end{cases} \quad (40)$$

$$0 \leq \phi'_R \leq 1, \quad |\phi''_R| \text{ uniformly bounded.}$$

Let $\epsilon > 0$ be fixed. We consider the Cauchy problem

$$\begin{cases} \partial_t U_\epsilon^R(t, y) = \phi_R \left(-\Lambda \left(y, \int M(z) e^{\frac{U_\epsilon^R(t, y+\epsilon z) - U_\epsilon^R(t, y)}{\epsilon}} dz \right) \right), \\ U_\epsilon^R(0, \cdot) = u_\epsilon^0. \end{cases} \quad (41)$$

We state the following result

Lemma 4.6. *Assuming (37), there exists a unique solution of (41), defined globally in time.*

The proof is based on the Cauchy-Lipschitz Theorem and uses only classical arguments. It is left to the reader.

4.3.2 Estimate on the time derivative

The particular form of (41) allows us to infer uniform a priori estimates on $\partial_t U_\epsilon^R$. It is stated in the following result.

Proposition 4.7. *For all $R > 0, \epsilon > 0$, we have*

$$\|\partial_t U_\epsilon^R\|_\infty \leq \|\partial_t u_\epsilon^0\|_\infty := \|\Lambda(y, \eta_\epsilon(0, y))\|_\infty.$$

As a consequence, there exists a positive constant C_V , independant of R and ϵ such that

$$\forall \epsilon > 0, \forall R > 0, \forall t \geq 0, \forall y \in \mathbb{R}^n, \quad |\partial_t U_\epsilon^R(t, y)| \leq C_V.$$

The complete proof is postponed to Appendix D. However we give the formal idea here. As R is fixed, we simply write U_ϵ instead of U_ϵ^R . We set $V_\epsilon(t, y) := \partial_t U_\epsilon(t, y)$. Differentiating (36) with respect to t , we obtain

$$\partial_t V_\epsilon(t, y) = \int K_\epsilon(t, y, z) \left(\frac{V_\epsilon(t, y + \epsilon z) - V_\epsilon(t, y)}{\epsilon} \right) dz,$$

where $K_\epsilon(t, y, z) := (-\partial_\eta \Lambda(y, \eta_\epsilon(t, y))) \times M(z) e^{\frac{U_\epsilon(t, y+\epsilon z) - U_\epsilon(t, y)}{\epsilon}}$. Note that $K_\epsilon \geq 0$ from (32). Then, if for some $t > 0$, $V_\epsilon(t, \cdot)$ reaches its maximum at $\bar{y} \in \mathbb{R}^n$, we obtain the inequality

$$\partial_t V_\epsilon(t, \bar{y}) = \int K_\epsilon(t, \bar{y}, z) \left(\frac{V_\epsilon(t, \bar{y} + \epsilon z) - V_\epsilon(t, \bar{y})}{\epsilon} \right) dz \leq 0.$$

Formally, it shows that the maximum value of V_ϵ is decreasing with time, that is $\sup_y V_\epsilon(t, y) \leq \sup_y V_\epsilon(0, y) = \sup_y \partial_t u_\epsilon^0$. With the same method we show $\inf_y \partial_t U_\epsilon \geq \inf_y \partial_t u_\epsilon^0$, which completes the first step of the proof. Then, using (37) and that u_ϵ^0 is Lipschitzian from (9), we infer an estimate on $\partial_t U_\epsilon$, uniform in $R > 0$ and $\epsilon > 0$.

4.3.3 Removing the truncation

From Proposition 4.7, $V_\epsilon^R(t, y) = \phi_R(-\Lambda(y, \eta_\epsilon(t, y)))$ is bounded uniformly in R . As $\phi_R \equiv \text{Id}$ on $[-\frac{R}{2}, \frac{R}{2}]$, then for large enough R , the truncated and the non-truncated problems are equivalent. Hence $U_\epsilon := U_\epsilon^R$ is the unique solution of (35) with $\|\partial_t U_\epsilon\|_\infty \leq C_V$, for large enough R . The proof of Theorem 4.5 is thereby complete.

4.4 The semi-relaxed limits

We assume (37). Thanks to Theorem 4.5, there exists a constant $C > 0$ such that

$$|U_\epsilon(t, y)| \leq |u_\epsilon^0(y)| + C_V t \leq C(1+t) + k_0|y|, \quad \forall t > 0, \forall y \in \mathbb{R}^n, \quad (42)$$

uniformly in $\epsilon > 0$. This allows us to consider the following semi-relaxed limits (see [6, 22])

$$\bar{U}(t, y) = \limsup_{\substack{x \rightarrow y \\ s \rightarrow t \\ \epsilon \rightarrow 0}} U_\epsilon(s, x), \quad \underline{U}(t, y) = \liminf_{\substack{x \rightarrow y \\ s \rightarrow t \\ \epsilon \rightarrow 0}} U_\epsilon(s, x).$$

Note that accordingly \underline{U} and \bar{U} satisfy the inequality (42). In this section, we prove

Theorem 4.8. Assuming (37), (38) and (39), we have $\bar{U} = \underline{U}$.

This result implies that U_ϵ converges locally uniformly to a solution U of equation (36), which completes the proof of Theorem 4.4.

4.4.1 Subsolution and supersolution

The following proposition is adapted from very classical stability results for viscosity solutions of Hamilton-Jacobi equations (see [3]). Note that it slightly differs from the usual case because of the nonlocal term $\eta_\epsilon(t, y)$.

Proposition 4.9. *The semi-continuous functions \bar{U} and \underline{U} are respectively subsolution and supersolution of (36) in the viscosity sense in $(0, \infty) \times \mathbb{R}^n$. Also, for all $T > 0$, the viscosity inequalities stand for $t \in (0, T]$.*

Proof of Proposition 4.9. In order to show that \bar{U} is a viscosity subsolution of (36), let us consider a test function φ and a point (t_0, y_0) such that $\bar{U} - \varphi$ reaches a global maximum at (t_0, y_0) . It is classical that up to extraction of a subsequence $\epsilon \rightarrow 0$, there exists (t_ϵ, x_ϵ) such that

$$\begin{cases} (t_\epsilon, y_\epsilon) \xrightarrow{\epsilon \rightarrow 0} (t_0, y_0), \\ \max_{t, y} U_\epsilon - \varphi = (U_\epsilon - \varphi)(t_\epsilon, y_\epsilon). \end{cases}$$

Besides, note that for all $z \in \mathbb{R}^n$, $\varphi(t_\epsilon, y_\epsilon + \epsilon z) - U_\epsilon(t_\epsilon, y_\epsilon + \epsilon z) \geq \varphi(t_\epsilon, y_\epsilon) - U_\epsilon(t_\epsilon, y_\epsilon)$, thus we have

$$\frac{\varphi(t_\epsilon, y_\epsilon + \epsilon z) - \varphi(t_\epsilon, y_\epsilon)}{\epsilon} \geq \frac{U_\epsilon(t_\epsilon, y_\epsilon + \epsilon z) - U_\epsilon(t_\epsilon, y_\epsilon)}{\epsilon}.$$

Since $\partial_\eta \Lambda < 0$ from (32), equation (35) gives

$$\partial_t \varphi(t_\epsilon, y_\epsilon) = -\Lambda \left(y_\epsilon, \int M(z) e^{\frac{U_\epsilon(t_\epsilon, y_\epsilon + \epsilon z) - U_\epsilon(t_\epsilon, y_\epsilon)}{\epsilon}} dz \right) \leq -\Lambda \left(y_\epsilon, \int M(z) e^{\frac{\varphi(t_\epsilon, y_\epsilon + \epsilon z) - \varphi(t_\epsilon, y_\epsilon)}{\epsilon}} dz \right).$$

As ϵ goes to 0,

$$\partial_t \varphi(t_0, y_0) \leq -\Lambda \left(y_0, \int M(z) e^{\nabla_y \varphi(t_0, y_0) \cdot z} dz \right) = H(y_0, \nabla_y \varphi(t_0, y_0)).$$

Since \bar{U} is upper semi-continuous, it is a viscosity subsolution of (36). With the same method, we prove that \underline{U} is a viscosity supersolution. It completes the first part of the proof. The second part of the statement is a well known result, and a proof can be found in [3]. \square

4.4.2 A posteriori Lipschitz estimate on \underline{U}

The announced Lipschitz continuity of \underline{U} is stated in the following result.

Proposition 4.10. *Assume (37)-(38). Then the lower semi-continuous function \underline{U} is K_2 -Lipschitzian with $K_2 = \max(k_0, \bar{K})$ and \bar{K} defined below.*

We first prove these two preliminary lemmas. We point out that (38) plays a crucial role in the proof.

Lemma 4.11. *Assume (37)-(38) and let be $T > 0$. Then there exist some positive constants $\eta, \bar{\eta}, L_1$ such that, uniformly in ϵ , $\forall (t, y) \in (0, +\infty) \times \mathbb{R}^n$,*

$$\underline{\eta} \leq \eta_\epsilon(t, y) \leq \bar{\eta}, \quad (43)$$

$$|\partial_\eta \Lambda(y, \eta_\epsilon(t, y))| \leq L_1. \quad (44)$$

Proof. From Theorem 4.5, we know $\partial_t U_\epsilon(t, y) = -\Lambda(y, \eta_\epsilon(t, y))$ is bounded for $(t, y) \in (0, +\infty) \times \mathbb{R}^n$, uniformly in $\epsilon > 0$. From (38), we deduce that $\eta_\epsilon(t, y)$ is bounded, which shows (43). Then we derive (44) directly from assumption (37). \square

Lemma 4.12. *In the viscosity sense, $\nabla_y \underline{U}$ is bounded, i.e. there exists a constant $K_1 > 0$ such that if ψ is a smooth function and $\underline{U} - \psi$ reaches its minimum in a point (t_0, y_0) , then*

$$|\nabla_y \psi(t_0, y_0)| \leq K_1.$$

Proof. Let ψ be a smooth function such that $\underline{U} - \psi$ reaches its minimum at a point (t_0, y_0) . Similarly to the proof of Proposition 4.9, up to extraction of a subsequence, there exists a sequence of minimum points (t_ϵ, y_ϵ) of $U_\epsilon - \psi$ which converges to (t_0, y_0) . As \underline{U} is a supersolution, we obtain

$$-\Lambda\left(y_\epsilon, \int M(z) e^{\frac{\psi(t_\epsilon, y_\epsilon + \epsilon z) - \psi(t_\epsilon, y_\epsilon)}{\epsilon}} dz\right) \leq \partial_t \psi(t_\epsilon, y_\epsilon) = \partial_t U_\epsilon(t_\epsilon, y_\epsilon) = -\Lambda(y_\epsilon, \eta_\epsilon(t_\epsilon, y_\epsilon)).$$

From $\partial_\eta \Lambda < 0$, as ϵ goes to 0 and using (43) we derive

$$\int M(z) e^{\nabla_y \psi(t_0, y_0) \cdot z} dz \leq \bar{\eta}.$$

Since $M(z) > 0$, the proof is complete. \square

Proof of Proposition 4.10. We want to prove that

$$\forall t \in [0, T], \forall (y, y') \in (\mathbb{R}^n)^2, \quad \underline{U}(t, y) - \underline{U}(t, y') \leq K_2 |y - y'|,$$

where $K_2 := \max(K_1, k_0)$. By contradiction, we assume

$$\exists K > K_2, \exists t_0 \in [0, T], \exists (y_0, y'_0) \in (\mathbb{R}^n)^2, \quad \underline{U}(t_0, y_0) - \underline{U}(t_0, y'_0) - K |y_0 - y'_0| > 0. \quad (45)$$

The difficulty here is that the viscosity sense is in (t, y) and not only in y . Let us define the test function $\psi(t, y) := \underline{U}(t, y'_0) + K |y - y'_0|$. As $k_0 < K$, from (42) we derive that $\underline{U}(t, y) - \psi(t, y) \rightarrow -\infty$ when $|y| \rightarrow \infty$, uniformly in $t \in [0, T]$. Because this function is lower semicontinuous, it reaches its minimum at a point $(\bar{t}, \bar{y}) \in [0, T] \times \mathbb{R}^n$. Thanks to (45), we know that $\bar{y} \neq y_0$, and thus ψ is smooth in a neighborhood of \bar{y} . Moreover, as u^0 is k_0 -Lipschitzian, we have $\bar{t} > 0$. Using Lemma 4.12, we obtain $\nabla_y \psi(\bar{t}, \bar{y}) = K \leq K_1$, which is a contradiction. \square

4.5 Uniqueness result using (H2)

We show the following theorem.

Theorem 4.13. Assume (37)-(39). Then, we have

$$\bar{U} \equiv \underline{U}.$$

This implies that U_ϵ converges locally uniformly to a function U solution of (36) in the viscosity sense. Therefore, it completes the proof of Theorem 4.4.

In fact, we show that a Lipschitz continuous supersolution remains above a subsolution provided it is the case at initial time. We point out that this uniqueness result is not standard since our assumption (39) allows the Hamiltonian to have superlinear growth. The fact that \underline{U} is Lipschitz continuous, as stated in Proposition 4.10, is used as a key ingredient.

Proof. We fix $T > 0$. By contradiction, we assume

$$\sigma := \sup_{\substack{y \in \mathbb{R}^n \\ t \in [0, T]}} (\bar{U}(t, y) - \underline{U}(t, y)) > 0.$$

From (42), there exists a constant $C > 0$ such that

$$\forall t > 0, \forall y \in \mathbb{R}^n, \quad |\underline{U}(t, y)| + |\bar{U}(t, y)| \leq C + k_0|y|, \quad (46)$$

The same estimate also holds for \underline{U} . We use the classical method of doubling the variables in the framework of viscosity solutions (see [13, 14]). We also use correction terms to ensure that $\bar{U} - \underline{U} - \varphi$ reaches its maximum in a localized compact set for a test function φ . Namely, let us fix $\alpha > 0$, $\delta \in [0, 1]$ and set for all $t \in [0, T]$, $t' \in [0, T]$, $y \in \mathbb{R}^n$, $y' \in \mathbb{R}^n$,

$$V_\delta(t, y, t', y') := [\bar{U}(t, y) - \alpha t - \delta|y|^2] - [\underline{U}(t', y') + \alpha t' + \delta|y'|^2] - \frac{|y - y'|^2}{\delta^2} - \frac{|t - t'|^2}{\delta^2}.$$

Thanks to (46), V_δ reaches its maximum M_δ at a point $(t_\delta, y_\delta, t'_\delta, y'_\delta)$. In what follows we use the following lemma (for which the Lipschitz continuity of \underline{U} is crucial).

Lemma 4.14. *When δ vanishes, the estimates hold*

1. $\delta|y_\delta|, \delta|y'_\delta| = O(\sqrt{\delta})$,
2. $|t_\delta - t'_\delta|, |y_\delta - y'_\delta| = O(\delta^2)$,
3. $t_\delta, t'_\delta > 0$ for δ small enough.

The proof of this lemma is postponed to the end of this section.

We now use that \bar{U} and \underline{U} are subsolution and supersolution in the viscosity sense. We define the test function

$$\varphi_{\alpha, \delta}(t, y) := \alpha t + \delta|y|^2 + [\underline{U}(t'_\delta, y'_\delta) + \alpha t'_\delta + \delta|y'_\delta|^2] + \frac{|y - y'_\delta|^2}{\delta^2} + \frac{|t - t'_\delta|^2}{\delta^2},$$

which is smooth and is such that $\bar{U} - \varphi_{\alpha, \delta}$ reaches its global maximum at the point (t_δ, y_δ) . Since \bar{U} is a subsolution of (36) and $t_\delta \in (0, T]$, the viscosity inequality holds

$$\partial_t \varphi_{\alpha, \delta}(t_\delta, y_\delta) = \alpha + \frac{2}{\delta^2}(t_\delta - t'_\delta) \leq H \left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta) \right).$$

In the same way, since \underline{U} is a supersolution, we derive

$$-\alpha + \frac{2}{\delta^2}(t_\delta - t'_\delta) \geq H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right).$$

Subtracting this last inequality from the previous one and using Lemma 4.14, we obtain

$$\begin{aligned} 2\alpha &\leq H\left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) \\ &\leq \left[H\left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) \right] \\ &\quad + \left[H\left(y_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) \right] \\ &\leq C(1 + |y_\delta|^{\gamma_2}) \times 2\delta|y_\delta - y'_\delta| + C(1 + |y_\delta|^{\gamma_1} + |y'_\delta|^{\gamma_1}) \times |y_\delta - y'_\delta| \\ &= O(\delta^{3-\frac{\gamma_2}{2}}) + O(\delta^{2-\frac{\gamma_1}{2}}). \end{aligned}$$

From assumption (39) we have $2\alpha = o(1)$, and as δ goes to 0, we find $\alpha \leq 0$, which is a contradiction. Therefore $\sigma = 0$ and we have $\bar{U} = \underline{U}$. The proof of Theorem 4.13 is thereby complete. \square

To complete this section, we prove Lemma 4.14 which is essentially technical. Note that the Lipschitz continuity of \underline{U} is a key ingredient, since usual estimates cannot give any better result than $|y_\delta - y'_\delta| = O(\delta)$.

Proof of Lemma 4.14. From $M_\delta \geq V_\delta(t_\delta, y_\delta, t_\delta, y_\delta)$ and because \underline{U} is K_2 -Lipschitzian from Proposition 4.10, we have

$$\begin{aligned} \alpha(t_\delta + t'_\delta) + \delta(|y_\delta|^2 + |y'_\delta|^2) + \frac{|y_\delta - y'_\delta|^2}{\delta^2} + \frac{|t_\delta - t'_\delta|^2}{\delta^2} &\leq \bar{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) - \bar{U}(t_\delta, y_\delta) + \underline{U}(t_\delta, y_\delta) \\ &\leq K_2|y_\delta - y'_\delta|. \end{aligned}$$

Consequently, we obtain $\frac{|y_\delta - y'_\delta|^2}{\delta^2} \leq K_2|y_\delta - y'_\delta|$ and thus the second assertion. Then from $\delta(|y_\delta|^2 + |y'_\delta|^2) \leq K_2|y_\delta - y'_\delta|$, we infer the first assertion.

Set $M := \max_{(t,y) \in [0,T] \times \mathbb{R}^n} V_\delta(t, y, t, y)$ and choose δ and α small enough to ensure $M \geq \frac{\sigma}{2}$. We write

$$\begin{aligned} \frac{\sigma}{2} \leq M &\leq M_\delta \leq \bar{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) \\ &\leq [\bar{U}(t_\delta, y_\delta) - u^0(y_\delta)] + [u^0(y_\delta) - u^0(y'_\delta)] + [u^0(y'_\delta) - \underline{U}(t'_\delta, y'_\delta)] \\ &\leq C_V(t_\delta + t'_\delta) + k_0|y_\delta - y'_\delta|. \end{aligned}$$

From that and $|y_\delta - y'_\delta| \rightarrow 0$ as δ goes to 0, we can choose δ small enough so that $C_V(t_\delta + t'_\delta) \geq \frac{\sigma}{4} > 0$. Along with $|t_\delta - t'_\delta| \rightarrow 0$, this last inequality implies $t_\delta, t'_\delta > 0$ for δ small enough, which ends the proof. \square

4.6 Additional result: a priori estimate on the gradient

In regards of Proposition 4.7, one can derive an a priori estimate on $\nabla_y U_\epsilon$ by further assuming that for any compact interval I , there exists a constant $L_2 > 0$ such that

$$\forall y \in \mathbb{R}^n, \forall \eta \in I, \quad |\nabla_y \Lambda(y, \eta)| \leq L_2. \quad (47)$$

It is stated in the following proposition.

Proposition 4.15. *Assume (37) and (47). There exists a constant L_2 such that for all $\epsilon > 0, i \in \{1, \dots, n\}, t > 0, y \in \mathbb{R}^n$, we have*

$$\|\partial_{y_i} U_\epsilon^R\|_\infty \leq \|\partial_{y_i} u_\epsilon^0\|_\infty + L_2 t.$$

As a consequence, for all $T > 0$, $U_\epsilon(t, y)$ is Lipschitz continuous in the y variable, uniformly in $\epsilon > 0$ and $t \in [0, T]$.

This proposition gives an alternative to the approach we have developed here. Indeed, by making the further assumption (47) we show that all the derivatives of U_ϵ are uniformly bounded. Thus we can use Ascoli's theorem and extract a converging subsequence, avoiding the introduction of the semi-relaxed limits $\limsup U_\epsilon$ and $\liminf U_\epsilon$.

The rigorous proof of this proposition is given in Appendix E and follows closely the proof of Proposition 4.7. However we have to deal here with a "source term" $\partial_{y_i} \Lambda(y, \eta_\epsilon(t, y))$ that we can bound by a constant L_2 thanks to (47) along with (43). More precisely, fixing $i \in \{1, \dots, n\}$ and defining

$$W_\epsilon(t, y) = \partial_{y_i} U_\epsilon(t, y),$$

we have

$$\partial_t W_\epsilon(t, y) = -\partial_{y_i} \Lambda(y, \eta_\epsilon) + \int K_\epsilon(t, y, z) \left[\frac{W_\epsilon(t, y + \epsilon z) - W_\epsilon(t, y)}{\epsilon} \right] dz,$$

with $K_\epsilon \geq 0$, and we proceed as in the proof of Proposition 4.7 to conclude that

$$W_\epsilon(t, y) \leq \sup_{y \in \mathbb{R}^n} \partial_{y_i} u_\epsilon^0(y) + L_2 t.$$

We deduce the reverse inequality similarly and, since $\sup_{y \in \mathbb{R}^n} |\partial_{y_i} u_\epsilon^0(y)|$ is bounded uniformly in ϵ , we obtain that U_ϵ is Lipschitz continuous in the y variable uniformly in $\epsilon > 0$ and $t \in [0, T]$.

5 Numerical simulations

In order to complete the theory, we present numerical results in the case without mutations studied in Section 3. We perform a simulation of equation (2) with $\epsilon = 5 \cdot 10^{-3}$. The numerical results allow to visualize u_ϵ and then the concentration dynamics of the population density. We choose the variable pair (x, y) to be in the set $[0, 1] \times [0, 4]$ which we discretize with the steps $\Delta x = \frac{1}{M}$ and $\Delta y = \frac{1}{N}$ with $M = 90, N = 40$. The time step Δt is chosen to be $5 \cdot 10^{-5}$ according to the CFL condition. We denote by $m_{i,j}^k$ the numerical solution at grid point $x_i = i\Delta x, y_j = j\Delta y$ and time $t_k = k\Delta t$. The equation (2) is solved by an implicit-explicit finite-difference method with the following scheme: for $i = 1, \dots, N$ and $j = 1, \dots, M$,

$$m_{i,j}^{k+1} = m_{i,j}^k - \frac{\Delta t}{\epsilon} \frac{A(x_i, y_j)m_{i,j}^k - A(x_{i-1}, y_j)m_{i-1,j}^k}{\Delta x} - \frac{\Delta t}{\epsilon} (\rho^k m_{i,j}^k - d(x_i, y_j)m_{i,j}^{k+1}), \quad (48)$$

and the boundary term is discretized as

$$A(0, y_j)m_{0,j}^{k+1} = \sum_{i=1}^M b(x_i, y_j)m_{i,j}^k,$$

which is necessary for computing when $i = 0$ in (48).

The numerics is performed using Matlab with parameters as follows. We choose the initial number of individuals to be 1000 and the final time $T = 1.5$. We choose the following functions A, b and d as follows

$$A(x, y) = 1, \quad b(x, y) = 10 \cdot \frac{y}{1 + x^2}, \quad d(x, y) = 2 \cdot \frac{y^3}{1 + x/6},$$

and the initial data

$$m^0(x, y) = p^0(x, y)e^{\frac{u^0(y)}{\epsilon}},$$

with

$$p^0(x, y) = \exp(-0.8x), \quad u^0(y) = -\frac{(y - 0.5)^2}{2}.$$

We choose to create a trade-off between the birth and death rates with regards to the y variable, by assuming that $y \mapsto b(x, y)$ and $y \mapsto d(x, y)$ are increasing, which means that a greater natality also induces a greater mortality. This assumption allows to determine an Evolutionary Stable Distribution or ESD from the language of adaptive dynamics, which gives the repartition of the fittest traits (see [10, 16, 23]). We do not know this ESD from the beginning, however it is important to select, according to assumptions (5)-(6), a death rate with a stronger increase for large x than the growth rate with regards to the trait variable in order to avoid that the dominant traits go to infinity.

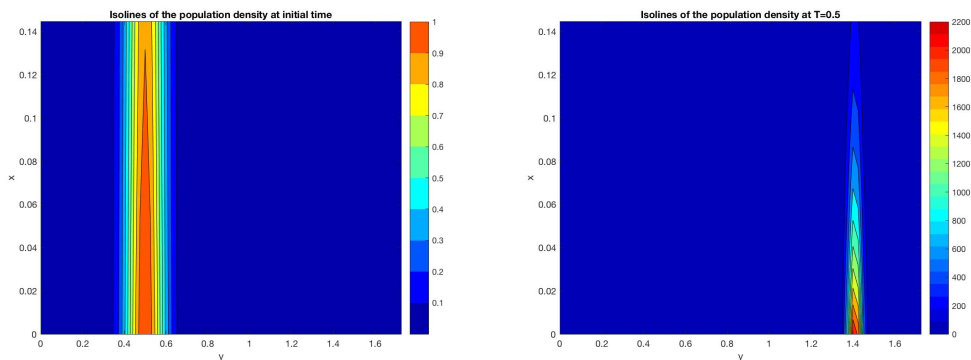


Figure 1: Isolines in (x, y) of the population distribution

The Figure 1 shows the population distribution with regards to y (abscissa) and x (ordinates) at two different times. The population has moved and concentrated to a location which is different from its initial one. One can observe this continuous evolution of the population distribution in Figure 2 where we show the distribution of individuals with age $x = 0$ at different times and identify an ESD.

The ESD can also be identified thanks to the principal eigenvalue. We show in Figure 3 the eigenvalue $\Lambda(y)$ solved by the Newton method using (15). From equation (24) one can notice that the equilibrium points have to satisfy $\nabla_y \Lambda(y) = 0$ and moreover that the dynamics of the concentration is directed towards the minimum points of $\Lambda(y)$, as predicted by our analysis.

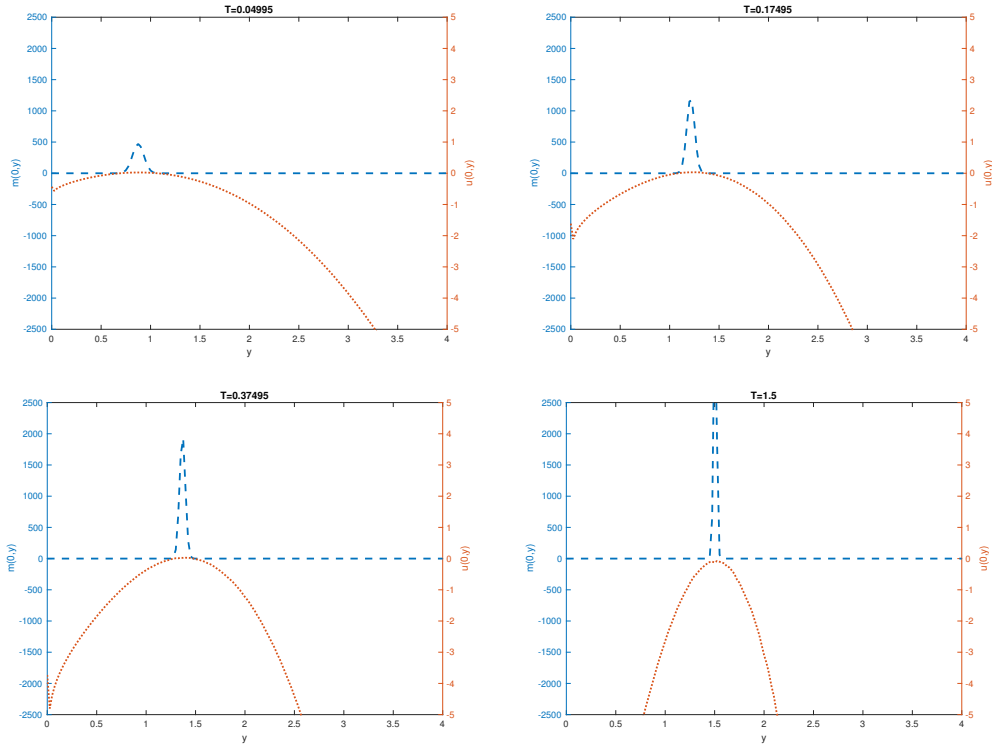


Figure 2: Concentration dynamics: snapshots of the population distribution in y at four different times with respect to the trait variable. Blue dashed line = m_ϵ , red dotted line = u_ϵ .

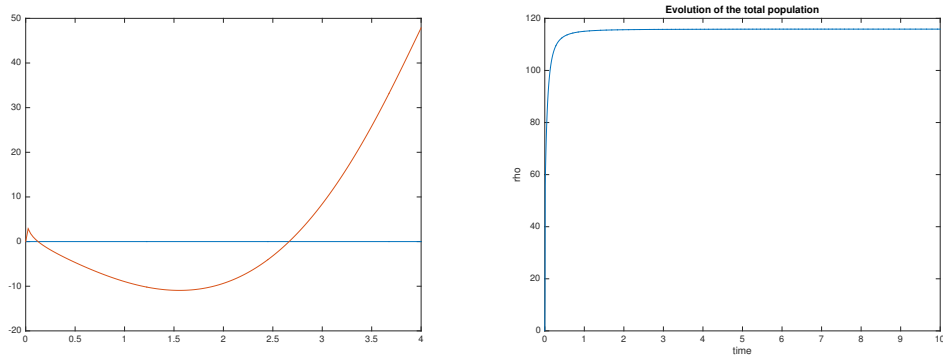


Figure 3: Left: Principal eigenvalue $\Lambda(y)$. Right: Evolution of ρ over time

6 Conclusion

The approach we develop here, based on the transformation $m_\epsilon = p_\epsilon e^{\frac{u_\epsilon}{\epsilon}}$, seems convenient for the study concentration phenomena. In the case without mutations, we get precise results on the concentration points as well as on the asymptotical age profile of the population. In particular

we have developed a method where the asymptotic analysis is not performed on u_ϵ but on p_ϵ , using relative entropy methods. Because of technical difficulties, we are not able yet to infer the same conclusion for the case with mutations. However the result seems to hold, at least for short time, more precisely before the Hamilton-Jacobi singularities occur in (36). Indeed, denoting $Q_\epsilon(t, x, y) = Q(x, y, \eta_\epsilon(t, y))$ we have that $v_\epsilon = \frac{p_\epsilon}{Q_\epsilon}$ satisfies a transport equation with a source term which reads

$$\epsilon \partial_t v_\epsilon(t, x, y) + A(x, y) \partial_x v_\epsilon(t, x, y) = \epsilon \frac{\partial_\eta Q(x, y, \eta_\epsilon(t, y))}{Q(x, y, \eta_\epsilon(t, y))} \partial_t \eta_\epsilon(t, y) v_\epsilon(t, x, y).$$

If $\partial_t \eta_\epsilon$ is bounded uniformly, we can show that v_ϵ is also bounded uniformly, which implies a weak concentration of the population on the set $\{(t, y) / u(t, y) = 0\}$. A rigorous proof of this result along with an entropy method to prove strong convergence of p_ϵ will be proposed in a forthcoming paper.

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A Saturation of the population density

We prove Proposition 3.3. Integrating (1) and using (6), we obtain

$$\begin{aligned} \epsilon \frac{d}{dt} \rho_\epsilon(t) &= - \iint \partial_x [A(x, y) m_\epsilon(t, x, y)] dx dy - \iint d(x, y) m_\epsilon(t, x, y) dx dy - \rho_\epsilon(t) \iint m_\epsilon dx dy \\ &= \iint \left(\frac{1}{\epsilon^n} \int M\left(\frac{y' - y}{\epsilon}\right) dy \right) b(x, y') m_\epsilon(t, x, y') dx dy' - \iint d(x, y) m_\epsilon(t, x, y) dx dy - \rho_\epsilon^2(t) \\ &\leq \bar{r} \rho_\epsilon(t) - \rho_\epsilon^2(t). \end{aligned}$$

Therefore, using (8) we conclude

$$0 \leq \rho_\epsilon(t) \leq \max(\bar{r}, \rho_\epsilon^0).$$

The other inequality can be proved the same way.

B Proof of Theorem 4.2 and Theorem 3.2

We only prove Theorem 4.2, as Theorem 3.2 is a particular case with $\eta = 1$. Equation (28) is equivalent to write

$$Q(x, y, \eta) = Q(0, y, \eta) \exp\left(- \int_0^x \frac{\partial_x A(x', y) + d(x', y) - \Lambda(y, \eta)}{A(x', y)} dx'\right),$$

and thanks to the condition at $x = 0$,

$$Q(x, y, \eta) = \eta \frac{1}{A(x, y)} \exp\left(- \int_0^x \frac{d(x', y) - \Lambda(y, \eta)}{A(x', y)} dx'\right). \quad (49)$$

Multiplying by $b(x, y)$ and integrating with regard to the x variable, we obtain

$$\frac{1}{\eta} = F(y, \Lambda(y, \eta)). \quad (50)$$

A direct calculation shows $\partial_\lambda F > 0$, thus (50) ensures uniqueness for Λ and then for Q .

Moreover, as $F(y, +\infty) = +\infty$ and $F(y, -\infty) = 0$, there exists such a $\Lambda(y, \eta)$. Besides, defining Q as in (49) implies that Q is in $L^1 \cap L^\infty$, thanks to (5), thus it proves existence. Finally, using the implicit function theorem in (50) we deduce that $\Lambda(y, \eta)$ is C^1 and (32) holds true.

For the dual equation (30), a simple calculation shows that the solution Φ must be given by

$$\Phi(x, y, \eta) = \Phi(0, y, \eta) e^{-\int_0^x \frac{\Lambda(y, \eta) - d(x', y)}{A(x', y)} dx'} \left(1 - \eta \int_0^x \frac{b(x', y)}{A(x', y)} e^{\int_0^{x'} \frac{\Lambda(y, \eta) - d(x'', y)}{A(x'', y)} dx''} dx' \right),$$

where $\Phi(0, y, \eta) > 0$ is determined by the normalization $\int Q(x, y, \eta) \Phi(x, y, \eta) dx = 1$.

C Proof of Proposition 4.3

We first state the following lemma, which proof is given below.

Lemma C.1. *We have*

$$\eta(p) [\partial_\lambda F(y, \Lambda(y, \eta(p)))]^2 \leq \partial_\lambda^2 F(y, \Lambda(y, \eta(p))), \quad (51)$$

and

$$[\partial_{p_i} \eta(p)]^2 \leq \eta(p) \partial_{p_i}^2 \eta(p). \quad (52)$$

By differentiating twice (31) with respect to p_i , we obtain

$$\partial_\lambda F(y, \Lambda(y, \eta(p))) D_{p_i} \Lambda(y, \eta(p)) = -\frac{\partial_{p_i} \eta(p)}{\eta(p)^2}, \quad (53)$$

$$\partial_\lambda F \cdot D_{p_i}^2 \Lambda(y, \eta(p)) + \partial_\lambda^2 F \cdot [D_{p_i} \Lambda(y, \eta(p))]^2 = -\frac{\partial_{p_i}^2 \eta(p)}{\eta(p)^2} + 2 \frac{\partial_{p_i} \eta(p)}{\eta(p)^3}.$$

Then using (51), (52) and (53), we derive

$$\begin{aligned} \partial_\lambda F \cdot D_{p_i}^2 \Lambda(y, p) &= -\partial_\lambda^2 F \left[\frac{\partial_{p_i} \eta(p)}{\eta(p)^2 \partial_\lambda F} \right]^2 - \frac{\partial_{p_i}^2 \eta(p)}{\eta(p)^2} + 2 \frac{[\partial_{p_i} \eta(p)]^2}{\eta(p)^3} \\ &\leq -\frac{[\partial_{p_i} \eta(p)]^2}{\eta(p)^3} - \frac{\partial_{p_i}^2 \eta(p)}{\eta(p)^2} + 2 \frac{[\partial_{p_i} \eta(p)]^2}{\eta(p)^3} \\ &= -\frac{1}{\eta(p)^3} \left(\eta(p) \partial_{p_i}^2 \eta(p) - [\partial_{p_i} \eta(p)]^2 \right) \leq 0., \end{aligned}$$

hence the announced convexity result on $p \mapsto H(y, p)$.

Proof of Lemma C.1. We define and compute using (12)

$$g(x, y) := \int_0^x \frac{1}{A(x', y)} dx', \quad \partial_\lambda F(y, \lambda) = \int_0^\infty g(x, y) f(x, y, \lambda) dx,$$

With these notations we may write

$$\partial_\lambda^2 F(y, \lambda) = \int_0^\infty g(x, y)^2 f(x, y, \lambda) dx.$$

Using the Cauchy-Schwarz inequality we obtain

$$[\partial_\lambda F(y, \Lambda(y, \eta(p)))]^2 \leq \partial_\lambda^2 F(y, \Lambda(y, \eta(p))) \times F(y, \Lambda(y, \eta(p))),$$

and then thanks to (31) the first inequality follows. The second inequality is a simple consequence of the Cauchy-Schwarz inequality on $\eta(p) = \int_{\mathbb{R}^n} M(z) e^{p \cdot z} dz$. \square

D Proof of Proposition 4.7

Our goal is to show

$$\partial_t U_\epsilon^R(t, y) \leq \sup_{y \in \mathbb{R}^d} \partial_t U_\epsilon^{R,0} := \sup_{y \in \mathbb{R}^n} \partial_t u_\epsilon^0(0, y), \quad \forall R > 0, \forall y \in \mathbb{R}^n, \forall t > 0. \quad (54)$$

The reverse inequality can be obtained similarly. Note that from (37) we have that

$$\partial_t U_\epsilon^{0,R} = -\Lambda \left(y, \int M(z) e^{\frac{u_\epsilon^0(y+\epsilon z) - u_\epsilon^0(y)}{\epsilon}} dz \right) \text{ is bounded uniformly in } \epsilon,$$

thus (54) allows us to conclude that $\partial_t U_\epsilon^R$ is bounded uniformly in R and ϵ .

We prove (54) by contradiction. We assume that there exists $(T, y_0) \in (0, +\infty) \times \mathbb{R}^n$ such that

$$\partial_t U_\epsilon^R(T, y_0) - \sup \partial_t U_\epsilon^{R,0} > 0. \quad (55)$$

For conciseness, we define $V_\epsilon^R(t, y) := \partial_t U_\epsilon^R(t, y)$. For $\beta > 0$, $\alpha > 0$ small and for $t \in [0, T]$, $y \in \mathbb{R}^n$, we also introduce

$$\varphi_{\alpha,\beta}(t, y) := V_\epsilon^R(t, y) - \alpha t - \beta |y - y_0|.$$

We choose α small enough to ensure $\varphi_{\alpha,\beta}(T, y_0) > \varphi_{\alpha,\beta}(0, y_0) = \partial_t U_\epsilon^{R,0}(y_0)$, which is possible thanks to assumption (55). From (40) we have $|V_\epsilon^R(t, y)| \leq R$, therefore $\varphi_{\alpha,\beta}$ decreases to $-\infty$ as $|y| \rightarrow \infty$ and reaches its maximum on $[0, T] \times \mathbb{R}^n$ at a point (\bar{t}, \bar{y}) . We have

$$\varphi_{\alpha,\beta}(\bar{t}, \bar{y} + \epsilon z) \leq \varphi_{\alpha,\beta}(\bar{t}, \bar{y}), \quad \forall z \in \mathbb{R}^n,$$

and thus

$$\frac{V_\epsilon^R(\bar{t}, \bar{y} + \epsilon z) - V_\epsilon^R(\bar{t}, \bar{y})}{\epsilon} \leq \beta \frac{|\bar{y} + \epsilon z| - |\bar{y}|}{\epsilon} \leq \beta |z|, \quad \forall z \in \mathbb{R}^n. \quad (56)$$

Moreover, as u_ϵ^0 is k_0 -Lipschitz continuous from (9), then we obtain for all $t > 0$, $(y, y') \in \mathbb{R}^{2n}$,

$$\begin{aligned} |U_\epsilon^R(t, y) - U_\epsilon^R(t, y')| &\leq |U_\epsilon^R(t, y) - U_\epsilon^{R,0}(y)| + |U_\epsilon^{R,0}(y) - U_\epsilon^{R,0}(y')| + |U_\epsilon^{R,0}(y') - U_\epsilon^R(t, y')| \\ &\leq 2RT + k_0 |y - y'|. \end{aligned} \quad (57)$$

Next, we set

$$\begin{aligned}\eta_\epsilon^R(t, y) &:= \int M(z) e^{\frac{U_\epsilon^R(t, y+\epsilon z) - U_\epsilon^R(t, y)}{\epsilon}} dz, \\ \eta_\pm &:= \int M(z) e^{\pm(\frac{2RT}{\epsilon} + k_0|z|)} dz,\end{aligned}$$

and notice that $0 < \eta_- \leq \eta_\epsilon^R(t, y) \leq \eta_+$.

We have chosen α such that $\varphi_{\alpha, \beta}(0, y_0) < \varphi_{\alpha, \beta}(T, y_0)$, then we know that $\bar{t} > 0$. Hence $\partial_t \varphi_{\alpha, \beta}(\bar{t}, \bar{y}) \geq 0$, that is $\partial_t V_\epsilon^R(\bar{t}, \bar{y}) \geq \alpha$ (if $\bar{t} = T$ then $\partial_t V_\epsilon^R(\bar{t}, \bar{y})$ stands for the left-derivative). Differentiating (41), we have

$$\partial_t V_\epsilon^R(t, y) = \phi'_R(-\Lambda(y, \eta_\epsilon^R)) \times (-\partial_\eta \Lambda(y, \eta_\epsilon^R)) \times \Gamma_\epsilon^R(t, y), \quad (58)$$

where $\Gamma_\epsilon^R(t, y) := \int M(z) e^{\frac{U_\epsilon^R(t, y+\epsilon z) - U_\epsilon^R(t, y)}{\epsilon}} \left(\frac{V_\epsilon^R(t, y+\epsilon z) - V_\epsilon^R(t, y)}{\epsilon} \right) dz$.

Writing (58) at (\bar{t}, \bar{y}) , using (32) and (56)-(57) we have

$$\begin{aligned}\alpha &\leq \partial_t V_\epsilon^R(\bar{t}, \bar{y}) = \phi'_R(-\Lambda(y, \eta_\epsilon^R(\bar{t}, \bar{y}))) \times (-\partial_\eta \Lambda(y, \eta_\epsilon^R(\bar{t}, \bar{y}))) \times \Gamma_\epsilon^R(\bar{t}, \bar{y}) \\ &\leq \sup_{r \in \mathbb{R}} \phi'_R(r) \times \sup_{\substack{\eta \in (\eta_-, \eta_+) \\ y \in \mathbb{R}^n}} [-\partial_\eta \Lambda(y, \eta)] \times \left(\int M(z) e^{\frac{U_\epsilon^R(\bar{t}, \bar{y}+\epsilon z) - U_\epsilon^R(\bar{t}, \bar{y})}{\epsilon}} |z| dz \right) \times \beta \\ &\leq \sup_{r \in \mathbb{R}} \phi'_R(r) \times \sup_{\substack{\eta \in (\eta_-, \eta_+) \\ y \in \mathbb{R}^n}} [-\partial_\eta \Lambda(y, \eta)] \times \left(\int M(z) e^{\frac{2RT}{\epsilon} + k_0|z|} |z| dz \right) \times \beta.\end{aligned}$$

Hence $\alpha \leq \bar{C}\beta$, where \bar{C} is a constant that does not depend on β . Then as β goes to 0, we obtain $\alpha \leq 0$, which is absurd. The proof is thereby achieved.

E Proof of Lemma 4.15

We fix $i \in \{1, \dots, n\}$, and for all $t \in [0, T]$, $\forall y \in \mathbb{R}^n$, we set

$$W_\epsilon(t, y) := \partial_{y_i} U_\epsilon.$$

Differentiating (35), we obtain

$$\begin{aligned}\partial_t w_\epsilon(t, y) &= -\partial_{y_i} \Lambda(y, \eta_\epsilon) - \partial_\eta \Lambda(y, \eta_\epsilon) \left(\int M(z) e^{\frac{U_\epsilon(t, y+\epsilon z) - U_\epsilon(t, y)}{\epsilon}} \left[\frac{W_\epsilon(t, y+\epsilon z) - W_\epsilon(t, y)}{\epsilon} \right] dz \right) \\ &:= \mathcal{F}(t, y, W_\epsilon(t, \cdot)).\end{aligned}$$

For $R > 0$, we define a truncated problem, and its solution W_ϵ^R satisfying

$$W_\epsilon^R(t, y) = \phi_R \left(\partial_{y_i} u_\epsilon^0(y) + \int_0^t \mathcal{F}(s, y, W_\epsilon^R(s, \cdot)) ds \right), \quad (59)$$

where \mathcal{F} is defined above. One may infer that we have existence and uniqueness of a global solution of (59) by a direct application of the Cauchy-Lipschitz theorem. Hence such a solution W_ϵ^R exists.

We set $\bar{W}_\epsilon^R := W_\epsilon^R - tL_2$, where L_2 is defined in assumption (47) along with (43). We want to show

$$\forall t \in [0, T], \forall y \in \mathbb{R}^n, \quad \bar{W}_\epsilon^R(t, y) \leq \max \partial_{y_i} u_\epsilon^0. \quad (60)$$

Since we proceed as in the proof of Proposition 4.7, we do not give all the details of the proof but only the main points. By contradiction, we assume (60) does not hold, so there exists $y_0 \in \mathbb{R}^n, t_0 \in [0, T]$ such that

$$\bar{W}_\epsilon^R(t_0, y_0) - \sup \partial_{y_i} u_\epsilon^0 > 0. \quad (61)$$

For $\beta > 0, \alpha > 0$ small enough, $t \in [0, T], y \in \mathbb{R}^n$ we introduce

$$\varphi_{\alpha, \beta}(t, y) := \bar{W}_\epsilon^R(t, y) - \alpha t - \beta |y - y_0|.$$

As \bar{W}_ϵ^R is bounded, $\varphi_{\alpha, \beta}$ reaches its maximum on $[0, T] \times \mathbb{R}^n$ at a point (\bar{t}, \bar{y}) . We have

$$\forall z \in \mathbb{R}^n, \quad \varphi_{\alpha, \beta}(\bar{t}, \bar{y} + \epsilon z) \leq \varphi_{\alpha, \beta}(\bar{t}, \bar{y}).$$

Then, we obtain the inequality

$$\forall z \in \mathbb{R}^n, \quad \frac{\bar{W}_\epsilon^R(\bar{t}, \bar{y} + \epsilon z) - \bar{W}_\epsilon^R(\bar{t}, \bar{y})}{\epsilon} \leq \beta \frac{|\bar{y} + z - y_0| - |\bar{y} - y_0|}{\epsilon} \leq \beta |z|.$$

We choose α small enough so that $\varphi_{\alpha, \beta}(t_0, y_0) > \varphi_{\alpha, \beta}(0, y_0) = \partial_{y_i} u_\epsilon^0(y_0)$, which is possible thanks to (61). It implies $\bar{t} > 0$. Hence $\partial_t \varphi_{\alpha, \beta}(\bar{t}, \bar{y}) \geq 0$, i.e. $\partial_t \bar{W}^R(\bar{t}, \bar{y}) \geq \alpha$. Differentiating (59) at point (\bar{t}, \bar{y}) , we write

$$\begin{aligned} \alpha &\leq \partial_t \bar{W}_\epsilon^R(\bar{t}, \bar{y}) \\ &\leq -\sup \phi'_R \times \partial_{y_i} \Lambda(y, \eta_\epsilon(t, y)) - L_2 \\ &\quad + \sup \phi'_R \times (-\partial_\eta \Lambda(y, \eta)) \int M(z) e^{\frac{U_\epsilon(\bar{t}, \bar{y} + \epsilon z) - U(\bar{t}, \bar{y})}{\epsilon}} \left[\frac{W_\epsilon^R(\bar{t}, \bar{y} + \epsilon z) - W_\epsilon^R(\bar{t}, \bar{y})}{\epsilon} \right] dz \\ &\leq L_1 \left(\int M(z) e^{\frac{U_\epsilon(\bar{t}, \bar{y} + \epsilon z) - U(\bar{t}, \bar{y})}{\epsilon}} |z| dz \right) \times \beta \\ &\leq L_1 \left(\int M(z) e^{\frac{2C_V T}{\epsilon} + k_0 |z|} |z| dz \right) \times \beta. \end{aligned}$$

Then, passing to the limit $\beta \rightarrow 0$ we obtain $\alpha \leq 0$, which is absurd. Thus we have

$$\bar{W}_\epsilon^R \leq \sup |\partial_{y_i} u_\epsilon^0|.$$

We proceed similarly to obtain the reverse inequality. Then we derive, for all $R > 0, \epsilon > 0, t \in [0, T], y \in \mathbb{R}^n$

$$|W_\epsilon^R(t, y)| \leq \sup |\partial_{y_i} u_\epsilon^0| + TL_2.$$

Finally, as we performed previously in section 4.3.3, as the bound on W_ϵ^R is uniform in R , we can remove the truncation. Therefore $W_\epsilon^R = W_\epsilon$ for R large enough and

$$|\partial_{y_i} U_\epsilon(t, y)| \leq \sup |\partial_{y_i} u_\epsilon^0| + TL_2.$$

In addition, as u_ϵ^0 is assumed to be uniformly k_0 -Lipschitzian from (9), we can infer a bound on $|\nabla_y U_\epsilon(t, y)|$ which is uniform in $\epsilon > 0, t \in [0, T], y \in \mathbb{R}^n$.

References

- [1] M. Adimy, F. Crauste, and S. Ruan. A mathematical study of the hematopoiesis process with applications to chronic myelogenous leukemia. *SIAM J. Appl. Math.*, 65(4):1328–1352 (electronic), 2005.
- [2] M. Bardi and I. Capuzzo-Dolcetta. *Optimal control and viscosity solutions of Hamilton-Jacobi-Bellman equations*. Birkhäuser Boston, 1997.
- [3] G. Barles. *Solutions de viscosité des équations de Hamilton-Jacobi*. Springer-Verlag Berlin Heidelberg, 1994.
- [4] G. Barles, L. C. Evans, and P. E. Souganidis. Wavefront propagation for reaction diffusion systems of PDE. *Duke Math. J.*, 61(3):835–858, pages 835-858, 1990.
- [5] G. Barles, S. Mirrahimi, and B. Perthame. Concentration in Lotka-Volterra parabolic or integral equations: a general convergence result. *Methods Appl. Anal.*, 16(3):321–340, 2009.
- [6] G. Barles and B. Perthame. Exit time problems in optimal control and vanishing viscosity method. *SIAM J. Control Optim.*, 26(5):1133–1148, 1988.
- [7] G. Barles and B. Perthame. Concentrations and constrained Hamilton-Jacobi equations arising in adaptive dynamics. *Contemporary Mathematics*, 439:57, 2007.
- [8] G. Barles and B. Perthame. Dirac concentrations in Lotka-Volterra parabolic PDEs. *Indiana Univ. Math J.*, 57 (7):3275–3301, 2008.
- [9] G. Barles and P. E. Souganidis. Front propagation for reaction-diffusion equations arising in combustion theory. *Asymptot. Anal.*, 14(3):277–292, 1997.
- [10] Wenli Cai, Pierre-Emmanuel Jabin, and Hailiang Liu. Time-asymptotic convergence rates towards the discrete evolutionary stable distribution. *Math. Models Methods Appl. Sci.*, 25(8):1589–1616, 2015.
- [11] V. Calvez, P. Gabriel, and Á. Mateos González. Limiting Hamilton-Jacobi equation for the large scale asymptotics of a subdiffusion jump-renewal equation. *arXiv:1609.06933*, September 2016.
- [12] N. Champagnat and P.-E. Jabin. The evolutionary limit for models of populations interacting competitively via several resources. *Journal of Differential Equations*, 251(1):176–195, 2011.
- [13] M. G. Crandall, L. C. Evans, and P.-L. Lions. Some properties of viscosity solutions of Hamilton-Jacobi equations. *Trans. Amer. Math. Soc.*, 282(2):487–502, 1984.
- [14] M. G. Crandall, H. Ishii, and P.-L. Lions. User’s guide to viscosity solutions of second order partial differential equations. *Bulletin of the American Mathematical Society*, 27(1):1–67, 1992.
- [15] L. Desvillettes, P.-E. Jabin, S. Mischler, and G. Raoul. On mutation selection dynamics. *Commun. Math. Sci.*, 6(3):729–747, 2008.
- [16] O. Diekmann. A beginner’s guide to adaptive dynamics. *Banach Center publications*, 63:47–86, 2004.

- [17] O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation: an illuminating example and a Hamilton-Jacobi approach. *Theoretical Population Biology*, 67(4):257–271, 2005.
- [18] M. Doumic and P. Gabriel. Eigenelements of a general aggregation-fragmentation model. *Math. Models Methods Appl. Sci.*, 20(5):757–783, 2010.
- [19] L. C. Evans and P. E. Souganidis. A PDE approach to geometric optics for certain semilinear parabolic equations. *Indiana Univ. Math J.*, 38(1):141–172, 1989.
- [20] W. H. Fleming and H. M. Soner. *Controlled Markov Processes and Viscosity Solutions*. Applications of Mathematics 25. Springer, 1993.
- [21] M. Gyllenberg and G. F. Webb. A nonlinear structured population model of tumor growth with quiescence. *J. Math. Biol.*, 28(6):671–694, 1990.
- [22] Hitoshi Ishii. Hamilton-Jacobi equations with discontinuous Hamiltonians on arbitrary open sets. *Bull. Fac. Sci. Engrg. Chuo Univ.*, 28:33–77, 1985.
- [23] Pierre-Emmanuel Jabin and Gaël Raoul. On selection dynamics for competitive interactions. *J. Math. Biol.*, 63(3):493–517, 2011.
- [24] Pierre-Emmanuel Jabin and Raymond Strother Schram. Selection-Mutation dynamics with spatial dependence. *Submitted*, 2016.
- [25] A. Lorz, S. Mirrahimi, and B. Perthame. Dirac mass dynamics in multidimensional nonlocal parabolic equations. *Communications in Partial Differential Equations*, 36(6):1071–1098, 2011.
- [26] J. A. J. Metz and O. Diekmann. *The dynamics of physiologically structured populations*, volume 68 of *Lecture Notes in Biomathematics*. Springer-Verlag, Berlin, 1986.
- [27] Philippe Michel. Existence of a solution to the cell division eigenproblem. *Math. Models Methods Appl. Sci.*, 16(7, suppl.):1125–1153, 2006.
- [28] Philippe Michel, Stéphane Mischler, and Benoît Perthame. General relative entropy inequality: an illustration on growth models. *J. Math. Pures Appl. (9)*, 84(9):1235–1260, 2005.
- [29] S. Mirrahimi. Adaptation and migration of a population between patches. *Discrete and Continuous Dynamical System - B (DCDS-B)*, 18.3:753–768, 2013.
- [30] S. Mirrahimi and B. Perthame. Asymptotic analysis of a selection model with space. *Journal de Mathématiques Pures et Appliquées*, 104(6):1108–1118, 2015.
- [31] Stéphane Mischler, Benoît Perthame, and Lenya Ryzhik. Stability in a nonlinear population maturation model. *Math. Models Methods Appl. Sci.*, 12(12):1751–1772, 2002.
- [32] B. Perthame. *Transport equations in biology*. Frontiers in Mathematics. Birkhäuser Verlag, Basel, 2007.
- [33] Perthame, B. and Souganidis, P. E. Rare Mutations Limit of a Steady State Dispersal Evolution Model. *Math. Model. Nat. Phenom.*, 11(4):154–166, 2016.