



HAL
open science

Selection-mutation dynamics with asymmetrical reproduction kernels

Benoît Perthame, Martin Strugarek, Cécile Taing

► **To cite this version:**

Benoît Perthame, Martin Strugarek, Cécile Taing. Selection-mutation dynamics with asymmetrical reproduction kernels. 2021. hal-03423260v1

HAL Id: hal-03423260

<https://hal.science/hal-03423260v1>

Preprint submitted on 10 Nov 2021 (v1), last revised 7 Apr 2022 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Selection-mutation dynamics with asymmetrical reproduction kernels

Benoît Perthame^{*§}

Martin Strugarek^{*†§}

Cécile Taing^{‡§}

November 10, 2021

Abstract

We study a family of selection-mutation models of a sexual population structured by a phenotypical trait. The main feature of these models is the asymmetric trait heredity or fecundity between the parents : we assume that each individual inherits mostly its trait from the female or that the trait acts on the female fecundity but does not affect male. Following previous works inspired from principles of adaptive dynamics, we rescale time and assume that mutations have limited effects on the phenotype. Our goal is to study the asymptotic behavior of the population distribution. We derive non-extinction conditions and BV estimates on the total population. We also obtain Lipschitz estimates on the solutions of Hamilton-Jacobi equations that arise from the study of the population distribution concentration at fittest traits. Concentration results are obtained in some special cases by using a Lyapunov functional.

2010 *Mathematics Subject Classification.* 35F21, 35B40, 35Q92, 45K05

Keywords and phrases. Integro-differential equations; Asymptotic analysis; Adaptive dynamics; Population biology;

1 Introduction

We study mathematically a family of models of selection-mutation for sexual populations structured with a continuous phenotype, which we call "trait" and denote by $x \in \mathbb{R}$. We assume that all individuals compete for survival because they share the same resources. This assumption implies the boundedness of the total population.

Although our approach is formal and mathematical, the models under study arise in various biological problems, as cell alignment [14] or protein exchanges [2, 27]. Our specific motivation comes from insecticide resistance. This phenomenon has been observed among insects of interest for human health, in particular in species of mosquitoes that are vectors for dengue (in the *Aedes* genus) or malaria (in the *Anopheles* genus). For this specific problem of selection-mutation, the trait variable should contain, for instance, the expression level for the *kdr* gene (*knock-down resistance*, see [30]). The present study is part of a more general program on the analysis of models, and their control, in the context of evolutionary epidemiology (see [29, 37] and the references therein).

Because of this motivation, our models have a sexual reproduction kernel. This is not the case in similar selection-mutation models developed for bacteria or resistance to treatment in cancer (see, e.g., [33, 25]), where the reproduction is clonal. The major feature of equations for sexual reproduction is to yield nonlinear and nonlocal birth terms with a quadratic aspect, though 1-homogeneous. All models studied in the present paper are derived from the general form

$$\begin{cases} \epsilon \partial_t n_\epsilon(t, x) = \frac{1}{\rho_\epsilon(t)} \iint_{\mathbb{R}^2} K_\epsilon(x, y, z) n_\epsilon(t, y) n_\epsilon(t, z) dy dz - R(x, \rho_\epsilon(t)) n_\epsilon(t, x), \\ \rho_\epsilon(t) = \int_{\mathbb{R}} n_\epsilon(t, x) dx, \quad n_\epsilon(0, x) = n_\epsilon^0(x). \end{cases} \quad (1)$$

^{*}Sorbonne Université, CNRS, Université de Paris, Inria, Laboratoire Jacques-Louis Lions, F-75005 Paris, France.

[†]AgroParisTech, 16 rue Claude Bernard, 75231 Paris Cedex 05, France

[‡]Laboratoire de Mathématiques et Applications, Université de Poitiers, CNRS, F-86073 Poitiers, France.

[§]Emails: benoit.perthame@sorbonne-universite.fr, martin.strugarek@agriculture.gouv.fr

The variable t stands for time, $n_\epsilon(t, x) \in [0, +\infty)$ is the population number density at time t and trait x and $\rho_\epsilon(t)$ is the total population. The positive function R is the saturation term, which contains the death rate and the insecticide effect. Competition is taken into account through the dependency of R in its second argument.

In equation (1), we interpret y (the second argument for K_ϵ) as the female trait, and z (the third argument) as the male trait. Thus $x \mapsto K_\epsilon(x, y, z)$ is equal to the distribution of individuals that are born from any encounter between a female of trait y and a male of trait z , per unit of time. Of course, this model is valid only assuming that the sex ratio is constant in time and independent of the trait. We make this simplification in order to obtain a single equation rather than a system.

It is worth highlighting that we aim here at general properties and methods for dealing with the nonlinear and nonlocal birth term, rather than at a realistic model for the evolution of a specific trait (see [38, 39] for more realistic models). We hope that the techniques developed here will successfully apply to such specific contexts.

The relationships between sexual selection and speciation are not well understood. Models of sexual reproduction have already been discussed in different contexts. Studies of individual-based models of sexual population were performed to determine the necessary conditions to evolutionary branching in [16, 23, 40], with a structure in genetic types (see [4, 5] for a review of mathematical models of population genetics). In [11] for instance, the authors investigate a stochastic birth and death process model for sexually reproducing diploids with Lotka-Volterra type dynamics and single locus genetics. At the small mutation steps limit, they derive a differential equation in allele space, referred to as a form of the canonical equation of the adaptive dynamics. In [12], another stochastic birth and death process model is studied with sexual reproduction according to mating preferences and a space structure with patches. In this case, reproductive isolation between patches occurs, and the authors prove that the time needed for this isolation to occur is a function of the population size. In the framework of insecticide resistance, a deterministic system with three genotypes (two alleles at a single locus) was studied in [36], with a focus on the “reversal time” that is a measure of the persistence of resistance in a population after exposition to insecticide.

From a large population point of view, in [28] the authors considered sexual populations structured by a trait and a space variable in a non-homogeneous environment, and after performing an asymptotic limit and a simplification of the model, they derived an estimate of the invasion speed or extinction speed of the population. In [3], the authors study the same kind of models as in the present paper, where the traits of the newborns are distributed through a gaussian kernel centered on the mean of the parents’ traits and with a constant variance, as in [18], which is the so-called infinitesimal model. They prove the existence of principal eigenelements for the corresponding eigenproblem, using the Schauder fixed point theorem. This work has been extended in [6] with the study of the same stationary problem at the asymptotic of vanishing variance. In the same regime, the associated Cauchy problem has then been investigated in [31], showing that solutions can be approximated by Gaussian profiles with small variance.

The main results of this paper concern the behavior of ρ_ϵ and n_ϵ in the asymptotic of large time scale and mutations with limited effect on the phenotype. We consider two particular classes of reproduction kernels in equation (1) which share the common property of an asymmetric structure. Indeed, back to the insecticide resistance modeling, it has been observed that good resistance levels also result in a high fitness cost, and especially on the fecundity. We simply assume here that either fecundity is female-trait-dependent, or that new individuals inherit mostly their trait from the female. Since female mosquitoes have a longer lifespan than male ones, they will be more susceptible to be affected by insecticides and to become resistant. Also, females will perform several ovipositions during their lives, suggesting a higher impact of acquired resistance on female fecundity.

We consider a first class of models, with **asymmetric fecundity** (AF in short),

$$\epsilon \partial_t n_\epsilon(t, x) = \frac{1}{\rho_\epsilon(t)} \iint_{\mathbb{R}^2} B(y) \alpha_\epsilon(x, y, z) n_\epsilon(t, y) n_\epsilon(t, z) dy dz - R(x, \rho_\epsilon(t)) n_\epsilon(t, x), \quad (\text{AF})$$

where B is a positive function and represents the crossing fecundity, which is assumed to depend only on female’s trait, $\alpha_\epsilon(\cdot, y, z)$ is the probability distribution of the offspring from a y female and

a z male. Then the reproduction kernel reads

$$K_\epsilon(x, y, z) = B(y)\alpha_\epsilon(x, y, z), \quad \text{with } \int_{\mathbb{R}} \alpha_\epsilon(x, y, z) dx = 1 \text{ for all } y, z \in \mathbb{R}. \quad (2)$$

The second class of models features an **asymmetric trait heredity** (ATH in short), which reads

$$\epsilon \partial_t n_\epsilon(t, x) = \frac{1}{\rho_\epsilon(t)} \iint_{\mathbb{R}^2} K_0(x-z) G_\epsilon(x-y) n_\epsilon(t, y) n_\epsilon(t, z) dy dz - R(x, \rho_\epsilon(t)) n_\epsilon(t, x), \quad (\text{ATH})$$

where

$$K_\epsilon(x, y, z) = K_0(x-z) G_\epsilon(x-y), \quad (3)$$

with K_0 a positive function, and G_ϵ the rescaling of a positive function G by letting

$$G_\epsilon(x-z) = \frac{1}{\epsilon} G\left(\frac{x-z}{\epsilon}\right), \quad \text{with } \int_{\mathbb{R}} G(z) dz = 1.$$

We can write the ATH equation under the following form

$$\epsilon \partial_t n_\epsilon(t, x) = \frac{1}{\rho_\epsilon(t)} [K_0 * n_\epsilon(t, \cdot) G_\epsilon * n_\epsilon(t, \cdot)](x) - R(x, \rho_\epsilon(t)) n_\epsilon(t, x).$$

Our convergence proof uses two ingredients. Firstly, we identify a consistent limit object as $\epsilon \rightarrow 0$, which is a constrained Hamilton-Jacobi equation. Secondly, we obtain compactness estimates on the solutions at the ϵ -level in order to be able to extract converging subsequences and to use the stability property of viscosity solutions. The most intricate step is this second ingredient which we conclude thanks to a new Bounded Variation (BV in short) estimate for ρ_ϵ .

To better show the technical ideas and highlight the new arguments, we first study a model without mutations, which is a particular case of the two classes of models presented above. We also assume for this model that the saturation function R does not depend on the trait variable and is such that $R(x, \rho) \equiv \nu \rho$, with $\nu > 0$. The model with no mutations reads

$$\epsilon \partial_t n_\epsilon(t, x) = \left(\frac{1}{\rho_\epsilon(t)} K_0 * n_\epsilon(t, \cdot)(x) - \nu \rho_\epsilon(t) \right) n_\epsilon(t, x), \quad (\text{nM})$$

This equation can be written under the form of equation (AF) with

$$B \equiv \int_{\mathbb{R}} K_0(z) dz, \quad \text{and } \alpha_\epsilon(x, y, z) = \frac{1}{B} K_0(x-z) \delta_0(x-y),$$

and also under the form of (ATH) with

$$G_\epsilon = \delta_0.$$

We also consider a generalization of (nM) with

$$\epsilon \partial_t n_\epsilon(t, x) = \left(\frac{1}{\rho_\epsilon(t)} \int K_S(x, y) n_\epsilon(t, y) dy - (R_0(x) + R_1(\rho_\epsilon)) \right) n_\epsilon(t, x), \quad (\text{gnM})$$

for some symmetric kernel $K_S : \mathbb{R}^2 \rightarrow \mathbb{R}_+$, and obtain Lyapunov convergence results for (gnM).

The paper is organized as follows. In Section 2, we state our assumptions and results. We also establish some non-extinction conditions and bounds on the total population. In Section 3, we focus on the models without mutations (nM)-(gnM) in order to introduce the main arguments that will be used for the more general cases. In particular, we derive BV estimates for the total population, and prove a Lyapunov stability result for the population distribution. In Section 4, we address the derivation of BV estimates for the (ATH) and (AF) models when R only depends on the total population variable and we explain the difficulties encountered when R is generic. Also, we briefly discuss the settings of the Lyapunov method applied to these mutation models. Finally in Section 5, we deal with the Hamilton-Jacobi approach. To conclude we identify some difficulties raised by the application of our methods to the general case of (1) and other possible approaches.

2 Main results

2.1 Assumptions and statements

The function R stands for the death rate and the competition effects. We make the standard assumption that it increases with the total population:

$$\forall x, \rho, \quad \partial_\rho R(x, \rho) > 0. \quad (4)$$

Some more specific results are obtained when R has the very simple form

$$R(x, \rho) = \nu\rho, \quad \forall x \in \mathbb{R}, \text{ with } \nu > 0. \quad (5)$$

We also assume usually that the initial data satisfies

$$\epsilon(\dot{\rho}_\epsilon)_-(0) = \left(\int n_\epsilon^0(x) \frac{K_0 * n_\epsilon^0(x)}{\rho_\epsilon^0} dx - \nu(\rho_\epsilon^0)^2 \right)_- \text{ is uniformly bounded,} \quad (6)$$

where, for $a \in \mathbb{R}$, we use the notation $a_- = \max(-a, 0)$.

For models with no mutations (nM) and asymmetric trait heredity (ATH), we assume

$$K_0 \in \mathcal{C}_b(\mathbb{R}, \mathbb{R}_+) \text{ is a symmetric kernel,} \quad (7)$$

where $\mathcal{C}_b(\mathbb{R}, \mathbb{R}_+)$ is the space of continuous and bounded functions on \mathbb{R} with values in \mathbb{R}_+ .

For equation (nM), we have the following theorem which is proved in Section 3.

Theorem 1 (BV bound for model (nM)). *Let $T > 0$ and let n_ϵ be the solution to (nM) associated with initial data n_ϵ^0 . We assume (6) and (7).*

Then, ρ_ϵ is uniformly bounded in $BV(0, T)$. Namely, we obtain

$$\int_0^T |\dot{\rho}_\epsilon(t)| dt \leq \rho_M + 2(\dot{\rho}_\epsilon)_-(0) \frac{\epsilon}{\kappa_m''} (1 - e^{-\frac{\kappa_m'' T}{\epsilon}}),$$

with ρ_M and κ_m'' defined later on. This implies that, up to extraction of subsequences, there exist limits $\rho_\epsilon \rightarrow \rho$ in $L^1(0, T)$, and $n_\epsilon \rightarrow n \in L_t^\infty(0, T; \mathcal{M}_+(\mathbb{R}))$ in the sense of measures.

Moreover, we have

$$\int_0^T \int_{\mathbb{R}} n_\epsilon \left(\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu\rho_\epsilon \right)^2 dx dt = O(\epsilon). \quad (8)$$

For the model with asymmetric fecundity (AF), we need the following assumption on B and α :

$$\begin{aligned} \exists C > 0, \forall \epsilon > 0, \forall \phi \in \mathcal{M}_+^1(\mathbb{R}), \\ \iiint_{\mathbb{R}^3} \alpha_\epsilon(x, y, z) B(x) B(y) \phi(y) \phi(z) dx dy dz - \left(\int_{\mathbb{R}} B(y) \phi(y) dy \right)^2 \geq -C\epsilon. \end{aligned} \quad (9)$$

This assumption means that the fecundity variation from one generation to the next is controlled and in fact is non-decreasing as ϵ goes to 0. We obtain the following result whose proof is given in Section 4.1.

Corollary 1 (BV bound for (AF)). *Let $T > 0$ and let n_ϵ be the solution to (AF) associated with initial data n_ϵ^0 . Assume (5) and (9).*

Then, ρ_ϵ is uniformly bounded in $BV(0, T)$. Namely, we have

$$\int_0^T |\dot{\rho}_\epsilon(t)| dt \leq \rho_M + 2(\dot{\rho}_\epsilon)_-(0) \frac{\epsilon}{\nu\rho_m} (1 - e^{-\frac{\nu\rho_m T}{\epsilon}}) + 2\frac{C}{\nu\rho_m} \left(T + \frac{\epsilon}{\nu\rho_m} (e^{-\frac{\nu\rho_m T}{\epsilon}} - 1) \right),$$

with C , ρ_M and ρ_m defined later on. This implies that, up to extraction of subsequences, there exist limits $\rho_\epsilon \rightarrow \rho$ in $L^1(0, T)$, and $n_\epsilon \rightarrow n \in L_t^\infty(0, T; \mathcal{M}_+(\mathbb{R}))$ in the sense of measures.

For (ATH), we also need to assume that, for all $\phi \in W^{1,1}$, $G_\epsilon * \phi = \phi + O(\epsilon)$, in the sense

$$\frac{1}{\epsilon \|\phi\|_{Lip}} \|G_\epsilon * \phi - \phi\|_{L^1} \text{ is uniformly bounded in } \epsilon. \quad (10)$$

Additionally, we assume that K_0 belongs to $W^{1,1}$, and

$$\epsilon(\dot{\rho}_\epsilon)_-(0) = \left(\int \frac{K_0 * n_\epsilon^0}{\rho_\epsilon^0}(x) G_\epsilon * n_\epsilon^0(x) dx - \nu(\rho_\epsilon^0)^2 \right)_- \text{ is uniformly bounded,} \quad (11)$$

which replaces assumption (6). We obtain the following result whose proof is given in Section 4.1.

Corollary 2 (BV bound for (ATH)). *Let n_ϵ be the solution to (ATH) associated with initial data n_ϵ^0 . Assume (7), (10), (11) and the following ("non-extinction" in this case) condition*

$$\exists \eta_0 > 0, \quad \forall \epsilon > 0, \quad \eta_\epsilon := \inf_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \int K_0 * \phi \cdot G_\epsilon * \phi dx \geq \eta_0. \quad (12)$$

Then ρ_ϵ is uniformly bounded in $BV(0, T)$. Namely, we have

$$\int_0^T |\dot{\rho}_\epsilon(t)| dt \leq \rho_M + 2(\dot{\rho}_\epsilon(0))_- \frac{\epsilon}{C_1} (1 - e^{-C_1 T/\epsilon}) + 2 \frac{\epsilon C_2}{C_1^2} (e^{-C_1 T/\epsilon} - 1) + 2 \frac{C_2}{C_1} T.$$

Then, up to extraction there exist $\rho \in L_{loc}^1(0, \infty)$ and $n \in L_t^\infty(0, T; \mathcal{M}_+(\mathbb{R}))$ such that (ρ_ϵ) converges towards ρ in $L_{loc}^1(0, \infty)$, and (n_ϵ) towards n in the sense of measures, when ϵ vanishes.

Moreover, for all $T > 0$, we have

$$\int_0^T \int_{\mathbb{R}} (G_\epsilon * n_\epsilon) \left[\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu \rho_\epsilon \right]^2 dx dt = O(\epsilon).$$

For the generalized no mutation model (gnM), a Lyapunov structure is identified under the following assumptions on $K_S : \mathbb{R}^2 \rightarrow \mathbb{R}_+$, $R_0 : \mathbb{R} \rightarrow \mathbb{R}_+$ and $R_1 : \mathbb{R}_+ \rightarrow \mathbb{R}_+$:

$$K_S \in \mathcal{C}_b(\mathbb{R}^2, \mathbb{R}_+) \text{ is symmetric: } \forall x, y \in \mathbb{R}, K_S(x, y) = K_S(y, x), \quad (13)$$

$$\forall \xi \in \mathcal{M}_+(\mathbb{R}) \setminus \{0\}, \quad \iint_{\mathbb{R}^2} K_S(x, y) \xi(x) \xi(y) dx dy > 0, \quad (14)$$

$$\text{supp}(q^0) \text{ is compact or } R_0 \text{ is proper,} \quad (15)$$

$$R_1 \text{ is increasing and proper,} \quad (16)$$

$$\exists! x_M \in \text{supp}(q^0), \quad y \mapsto K_S(x_M, y) - R_0(y) \text{ reaches its maximum at } x_M. \quad (17)$$

In this framework, a Lyapunov stability result is obtained for the state δ_{x_M} .

Theorem 2. *Under assumptions (13)-(17), δ_{x_M} is asymptotically stable for (gnM).*

In the general case of a death rate depending on both traits and the total population, we can perform the Hopf-Cole transform

$$u_\epsilon(t, x) = \epsilon \ln n_\epsilon(t, x),$$

and apply a Hamilton-Jacobi approach. For the models under investigation, we obtain the following result that is the topic of Section 5.

Theorem 3 (Lipschitz estimates for u_ϵ). *Under some assumptions on the initial data u_ϵ^0 , for both models (AF) and (ATH), the corresponding u_ϵ are locally Lipschitz uniformly in ϵ .*

Moreover, we have a global upper bound on u_ϵ . Namely, there exists a constant C , such that

$$u_\epsilon(t, x) \leq \epsilon \ln \left(C + \frac{C(1+t)}{\epsilon} \right).$$

The specific assumptions required for the proof of this theorem in each case (AF or ATH) are specified in the corresponding section.

2.2 Boundedness of the total population and non-extinction

In preparation to prove these theorems, we begin with some controls of the total population, ρ_ϵ , which, in full generality satisfies

$$\epsilon \dot{\rho}_\epsilon(t) = \int_{\mathbb{R}} \left(\iint_{\mathbb{R}^2} K_\epsilon(x, y, z) \frac{n_\epsilon(t, z)}{\rho_\epsilon(t)} n_\epsilon(t, y) dy dz - R(x, \rho_\epsilon(t)) n_\epsilon(t, x) \right) dx.$$

To ensure that ρ_ϵ remains bounded along all trajectories, we complement (4) with

$$\begin{aligned} \exists R_m : \mathbb{R}_+ &\rightarrow \mathbb{R}_+, \text{ increasing, with } R_m(0) = 0, \\ R_m(+\infty) &= +\infty \quad \text{and} \quad \forall x, R(x, \rho) \geq R_m(\rho), \quad \rho_M := R_m^{-1}(K_M). \end{aligned} \quad (18)$$

We also assume that

$$K_M := \sup_{0 < \epsilon \leq 1} \sup_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \sup_y \iint_{\mathbb{R}^2} K_\epsilon(x, y, z) dx \phi(z) dz < +\infty. \quad (19)$$

The following boundedness result is straightforward:

Proposition 1 (Upper bound for ρ_ϵ). *Under assumptions (4), (18) and (19), all trajectories of (1) are forward- ρ_M -bounded from above in ρ_ϵ , by which we mean that $\dot{\rho}_\epsilon(t) < 0$ as long as $\rho_\epsilon(t) > \rho_M$.*

Conversely, we can study conditions that ensure non-extinction of the population: $\rho_\epsilon(t) \geq \rho_m > 0$. As a first example, let

$$\kappa_m(\rho) := \inf_{0 < \epsilon \leq 1} \inf_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \inf_y \iint_{\mathbb{R}^2} K_\epsilon(x, y, z) dx \phi(z) dz - R(y, \rho), \quad (20)$$

where $\mathcal{M}_+^1(\mathbb{R})$ is the set of probability measures on \mathbb{R} .

Proposition 2 (Lower bound for ρ_ϵ under assumption (20)). *Under assumption (4) and if there exists $\rho_m > 0$ such that $\kappa_m(\rho_m) = 0$, with κ_m defined in (20), then all trajectories of (1) are forward- ρ_m -bounded from below in ρ_ϵ , by which we mean that $\dot{\rho}_\epsilon(t) > 0$ as long as $\rho_\epsilon(t) < \rho_m$.*

However, $\kappa_m(0) > 0$ is not expected to be a necessary condition. It is an open and challenging question to determine more general conditions for non-extinction, and study the set of extinction trajectories in cases when these conditions are not met.

For instance, a second non-extinction result is

$$\kappa'_m(\rho) := \inf_{0 < \epsilon \leq 1} \inf_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \int_{\mathbb{R}} \left(\iint_{\mathbb{R}^2} K_\epsilon(x, y, z) dx \phi(z) dz - R(y, \rho) \right) \phi(y) dy. \quad (21)$$

Proposition 3 (Lower bound for ρ_ϵ with a condition on (21)). *Under assumption (4) and if there exists $\rho_m > 0$ such that $\kappa'_m(\rho_m) = 0$ then all trajectories of (1) are forward- ρ_m -bounded from below in ρ_ϵ .*

And likewise, let

$$\kappa''_m := \inf_{0 < \epsilon \leq 1} \inf_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \iiint_{\mathbb{R}^3} K_\epsilon(x, y, z) \phi(y) \phi(z) dx dy dz. \quad (22)$$

Then, assuming also

$$\begin{aligned} \exists R_M : \mathbb{R}_+ &\rightarrow \mathbb{R}_+, \text{ increasing, with } R_M(0) \geq 0, \\ R_M(+\infty) &= +\infty \quad \text{and} \quad \forall x, R(x, \rho) \leq R_M(\rho), \end{aligned} \quad (23)$$

we have $\dot{\rho} \geq (\kappa''_m - R_M(\rho))\rho$.

Proposition 4 (Lower bound for ρ_ϵ with a condition on (22)). *Assume (23) holds and $\kappa''_m > R_M(0)$ defined in (22). Then all trajectories of (1) are forward- ρ_m -bounded from below in ρ_ϵ , with $\rho_m = R_M^{-1}(\kappa''_m) > 0$.*

3 The model without mutations

In order to see clearly the kind of results to be expected, we first study in detail a very simple example, which is equation (nM). The form of the birth rate assumes that the trait is perfectly transmitted from the females to their progeny, and the cross-fecundity between a male of trait z and a female of trait x depends only on the distance between x and z through K_0 .

Assumptions (4) and (18) (for $R_m = \nu\rho$) obviously hold in case (nM). Assumption (19) holds with $K_M = \max_x K_0(x)$. However, $\kappa_m(\rho) = \inf K_0 - \rho$ so the non-extinction condition from Proposition 2 holds if and only if $\inf_x K_0(x) > 0$.

Even though $\inf_x K_0(x) = 0$, following [21] in the context of entropy-based stability, we may assume that K_0 is such that

$$\kappa_m'' = \inf_{\phi \in \mathcal{M}_+^1(\mathbb{R})} \int_{\mathbb{R}} (K_0 * \phi)(x) \phi(x) dx > 0,$$

and then, Proposition 4 holds.

3.1 Proof of Theorem 1

We prove the BV bound stated in Theorem 1. From equation (nM) we can compute

$$\epsilon \dot{\rho}_\epsilon(t) = \int_{\mathbb{R}} n_\epsilon(t, x) \frac{K_0 * n_\epsilon(t, \cdot)}{\rho_\epsilon(t)}(x) dx - \nu \rho_\epsilon^2.$$

Assuming (7) yields $\frac{d}{dt} \int_{\mathbb{R}} n K_0 * n = 2 \int_{\mathbb{R}} n K_0 * (\partial_t n)$. Hence

$$\epsilon \ddot{\rho}_\epsilon = -\nu \rho_\epsilon \dot{\rho}_\epsilon - \nu \rho_\epsilon \dot{\rho}_\epsilon - \frac{\dot{\rho}_\epsilon}{\rho_\epsilon^2} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon + \frac{1}{2\rho_\epsilon} \frac{d}{dt} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon + \frac{1}{\rho_\epsilon} \int_{\mathbb{R}} \partial_t n_\epsilon K_0 * n_\epsilon.$$

We rewrite this as

$$\begin{aligned} \epsilon \ddot{\rho}_\epsilon = -\nu \rho_\epsilon \dot{\rho}_\epsilon - \frac{\dot{\rho}_\epsilon}{2\rho_\epsilon^2} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon + \frac{1}{2} \frac{d}{dt} \left(\frac{1}{\rho_\epsilon} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon - \nu \rho_\epsilon^2 \right) \\ + \frac{1}{\epsilon} \int_{\mathbb{R}} \left(\frac{n_\epsilon (K_0 * n_\epsilon)^2}{\rho_\epsilon^2} - \nu n_\epsilon K_0 * n_\epsilon \right), \end{aligned}$$

and since $\epsilon \dot{\rho}_\epsilon = \frac{1}{\rho_\epsilon} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon - \nu \rho_\epsilon^2$, we get

$$\frac{\epsilon}{2} \ddot{\rho}_\epsilon = -\frac{\dot{\rho}_\epsilon}{2\rho_\epsilon^2} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon + \frac{1}{\epsilon} \int_{\mathbb{R}} n_\epsilon \left(\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu \rho_\epsilon \right)^2. \quad (24)$$

Several conclusions follow from (24). Firstly, $\ddot{\rho}_\epsilon \geq -\frac{\dot{\rho}_\epsilon}{\epsilon \rho_\epsilon^2} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon$, hence if $\dot{\rho}_\epsilon = 0$ then $\ddot{\rho}_\epsilon \geq 0$. In particular, ρ_ϵ has no strict local maximum. We can conclude that ρ_ϵ is either decreasing, increasing or decreasing-increasing, and since it is bounded, $\rho_\epsilon(t)$ must converge to some finite value ρ_ϵ^∞ as t goes to $+\infty$.

Secondly, let $b_\epsilon(t) := \frac{1}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} n_\epsilon(t, x) (K_0 * n_\epsilon(t, \cdot))(x) dx \geq \kappa_m'' > 0$. Then from (24),

$$\frac{d}{dt} (\dot{\rho}_\epsilon)_- \leq -\frac{\kappa_m''}{\epsilon} (\dot{\rho}_\epsilon)_-.$$

Hence $(\dot{\rho}_\epsilon)_-(t) \leq e^{-\frac{\kappa_m'' t}{\epsilon}} (\dot{\rho}_\epsilon)_-(0)$. We write

$$\begin{aligned} \int_0^T |\dot{\rho}_\epsilon(t)| dt &\leq \int_0^T \dot{\rho}_\epsilon(t) dt + 2 \int_0^T (\dot{\rho}_\epsilon)_-(t) dt \\ &\leq \rho_M + 2(\dot{\rho}_\epsilon)_-(0) \int_0^T e^{-\frac{\kappa_m'' t}{\epsilon}} dt \\ &\leq \rho_M + 2(\dot{\rho}_\epsilon)_-(0) \frac{\epsilon}{\kappa_m''} (1 - e^{-\frac{\kappa_m'' T}{\epsilon}}). \end{aligned}$$

Therefore, under the mild assumption (6), the family $(\rho_\epsilon)_\epsilon$ is uniformly bounded in $BV(\mathbb{R}_+)$.

We now establish equation (8). Going back to equation (24), and integrating this one over $[0, T]$ for $T > 0$, we obtain

$$\int_0^T \int_{\mathbb{R}} n_\epsilon \left(\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu \rho_\epsilon \right)^2 dx dt = \epsilon \int_0^T \frac{\dot{\rho}_\epsilon}{2\rho^2} \int_{\mathbb{R}} n_\epsilon K_0 * n_\epsilon dx dt + \frac{\epsilon^2}{2} (\dot{\rho}_\epsilon(T) - \dot{\rho}_\epsilon(0)). \quad (25)$$

Since ρ_ϵ is locally BV uniformly in ϵ and using (6) and (7), we deduce that

$$\int_0^T \int_{\mathbb{R}} n_\epsilon \left(\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu \rho_\epsilon \right)^2 dx dt = O(\epsilon),$$

which is equation (8).

3.2 Concentration in Dirac masses

Formally, at the limit $\epsilon \rightarrow 0$ the previous estimate yields

$$\int_{\mathbb{R}} n(t, x) \left(\frac{K_0 * n(t, \cdot)}{\rho(t)}(x) - \nu \rho(t) \right)^2 dx = 0. \quad (26)$$

It turns out that combinations of Dirac masses are admissible solutions to (26), $n = \sum_{i=1}^N \rho_i \delta_{x_i}$, $\rho_i > 0$ with $\sum_{i=1}^N \rho_i = \rho$, and

$$\sum_{i=1}^N \rho_i \left(\sum_{j=1}^N \frac{\rho_j}{\rho} K_0(x_i - x_j) - \nu \rho \right)^2 = 0,$$

then for all $i \in \{1, \dots, N\}$, we have

$$\sum_{j=1}^N \frac{\rho_j}{\rho} K_0(x_i - x_j) = \nu \rho. \quad (27)$$

We define the matrix \mathbf{K} , whose coefficient with indices (i, j) is equal to $K_0(x_i - x_j)$. \mathbf{K} is symmetric with positive coefficients and constant main diagonal equal to $K_0(0)$. If the family $(x_i)_{1 \leq i \leq N}$ is given, the problem amounts to finding a positive vector P such that $\mathbf{K}P = \mathbf{1}$. Then we obtain $\rho_i = \nu P_i \rho^2$ and $\rho = 1/(\nu \mathbf{1}^T P)$.

One readily checks that, if

$$\max_{i \neq j} K_0(x_i - x_j) < \frac{K_0(0)}{N-1},$$

then \mathbf{K} is invertible (in this case indeed, \mathbf{K} is strictly diagonally dominant). It is worth noting that if $N = 2$ and $\max K_0 = K_0(0)$, with the maximum of K_0 being reached only at 0, then this is always satisfied. However, in the generic case when $(x_i)_i$ is such that \mathbf{K} is invertible, it remains unclear whether $P := \mathbf{K}^{-1} \mathbf{1} > 0$ or not.

In spite of this, an alternative viewpoint using a Lyapunov functional helps describing the asymptotically stable solutions, as detailed below.

3.3 A Lyapunov concentration result: proof of Theorem 2

We consider the special form of equation (1) given by (gnM). Then, we define

$$q(t, x) := n_\epsilon(\epsilon t, x) / \rho_\epsilon(\epsilon t), \quad \text{and } q^0(x) := n^0(x) / \int_{\mathbb{R}} n^0 \in \mathcal{M}_+^1(\mathbb{R}),$$

for some initial data $n^0 \in \mathcal{M}_+(\mathbb{R})$. There is a closed form equation for q , namely

$$\begin{cases} \partial_t q(t, x) = q(t, x) \left(\int_{\mathbb{R}} K_S(x, y) q(t, y) dy - R_0(x) \right) \\ \quad - q(t, x) \int_{\mathbb{R}} q(t, x') \left(\int_{\mathbb{R}} K_S(x', y) q(t, y) dy - R_0(x') \right) dx', \\ q(0, x) = q^0(x). \end{cases} \quad (28)$$

Therefore we simply need to study the asymptotic behavior of q as $t \rightarrow +\infty$ to be able to describe that of n_ϵ as $\epsilon \rightarrow 0$.

Notice that Equation (28) has a replicator-type structure, as it can be written under the form

$$\partial_t q(t, x) = q(t, x) \left[\mathcal{G}(x, q(t, \cdot)) - \int_{\mathbb{R}} q(t, x) \mathcal{G}(x, q(t, \cdot)) dx \right],$$

where $\mathcal{G}(x, q(t, \cdot)) := \int_{\mathbb{R}} K_S(x, y) q(t, y) dy$ is the effective growth rate, or fitness, of $q(t, x)$ and the integral term $\int_{\mathbb{R}} q(t, x) \mathcal{G}(x, q(t, \cdot)) dx$ the average of this growth rate in the population. This structure means that the frequency of the x -carrying individuals in the population evolves with the deviation of its corresponding fitness from the mean fitness in the population.

Thanks to the structure of (28), we obtain the asymptotic stability of δ_{x_M} stated in Theorem 2, by using a Lyapunov's method for stability. The rest of this section is devoted to the proof of this result, which relies on a strict Lyapunov stability argument stated in [34, Theorem 4.4] and [35]. This type of convergence result has appeared in the economic literature devoted to game theory with continuous strategy space, which we denote here by \mathcal{P} (for "phenotype"). For instance it is stated in [10, Theorem 3.a] and follows from [9, Theorem 2].

First, we get a Lyapunov functional for (28) by defining

$$J(q) := \frac{1}{2} \iint_{\mathbb{R}^2} K_S(x, y) q(x) q(y) dx dy - \int_{\mathbb{R}} R_0(x) q(x) dx. \quad (29)$$

Indeed, along an orbit of (28) we have, thanks to (13),

$$\begin{aligned} \frac{d}{dt} J(q(t, \cdot)) &= \int_{\mathbb{R}} q(t, x) \left(\int_{\mathbb{R}} K_S(x, y) q(t, y) dy - R_0(x) \right)^2 dx \\ &\quad - \left(\int_{\mathbb{R}} q(t, x) \left(\int_{\mathbb{R}} K_S(x, y) q(t, y) dy - R_0(x) \right) dx \right)^2 \geq 0, \end{aligned}$$

with equality (by the Cauchy-Schwarz inequality) if and only if

$$\int_{\mathbb{R}} K_S(x, y) q(t, y) dy - R_0(x) \equiv C \in \mathbb{R} \text{ on } \text{supp}(q(t, \cdot)),$$

so that we have strict monotonicity except if $q(t, \cdot)$ is a rest point for the dynamics of (28). This Lyapunov functional can be seen as an embodiment of the "positive correlation" property from game dynamics (see [20]), and this feature has been exploited to get a gradient flow formulation of a non-local model with a diffusion term in [22], where the kernel acts for death induced by competition rather than for birth as is the case here.

In order to use the Lyapunov functional properly, we need $\{q(t, \cdot), t \geq 0\} \subset \mathcal{M}_+^1(\mathbb{R})$ to be relatively compact for a topology for which J is continuous and Fréchet-differentiable. This is the case if either q^0 is compactly supported in \mathbb{R} , or if K is bounded and R_0 is proper (by Prokhorov's theorem), for the weak- \star topology on $\mathcal{M}_+^1(\mathbb{R})$, hence the use of (15)

The study of the maximizer sets for J is greatly simplified by (14):

Lemma 1. *Under (14), the functional J is strictly convex on the convex set $\mathcal{M}_+^1(\mathbb{R})$.*

Therefore its local maximum points are extreme points of $\mathcal{M}_+^1(\mathbb{R})$, that is Dirac masses. The Dirac mass δ_x is a local maximizer of J only if $y \mapsto K_S(x, y) - R_0(y)$ reaches its maximum at x .

Proof. For $q_1, q_2 \in \mathcal{M}_+^1(\mathbb{R})$ and $\theta \in [0, 1]$ we compute

$$\begin{aligned} J(\theta q_1 + (1 - \theta) q_2) &= \iint_{\mathbb{R}^2} K_S(\theta^2 q_1 q_1 + (1 - \theta)^2 q_2 q_2 + 2\theta(1 - \theta) q_1 q_2) - \int_{\mathbb{R}} R_0(\theta q_1 + (1 - \theta) q_2) \\ &= \theta J(q_1) + (1 - \theta) J(q_2) - \theta(1 - \theta) \iint_{\mathbb{R}^2} K_S(x, y) (q_1 - q_2)(x) (q_1 - q_2)(y) dx dy. \end{aligned}$$

Therefore (14) (with $\xi = q_1 - q_2$) implies that J is strictly convex.

If J reaches a local maximum at $\xi \in \mathcal{M}_+^1(\mathbb{R})$ belonging to some interval (ξ_-, ξ_+) , that is $\xi = \theta \xi_- + (1 - \theta) \xi_+$ for some $\theta \in (0, 1)$ with $\xi_{\pm} \in \mathcal{M}_+^1(\mathbb{R})$, then for $\epsilon > 0$ small enough we have

$$J(\xi) < \frac{1}{2} (J(\xi + \epsilon(\xi_+ - \xi_-)) + J(\xi - \epsilon(\xi_+ - \xi_-))) \leq J(\xi),$$

where the left inequality holds by strict convexity and the right one by the local maximum condition. This is absurd, hence local maxima are only reached at extreme points.

The support of an extreme probability measure must be reduced to a singleton: otherwise, we can construct a segment on which the measure lies by exchanging mass between any two separable points of the support. Conversely, a Dirac mass is obviously extreme, as any segment to which it belongs would consist of probability measures with the same support, reduced to a singleton.

Then, the first-order optimality condition for J at δ_x reads: for all admissible perturbation h ,

$$\int_{\mathbb{R}} (K(x, y) - R_0(y))h(y)dy \leq 0,$$

and admissible perturbations have the general form $h = -\delta_x + h_0$, with $h_0 \in \mathcal{M}_+^1(\mathbb{R})$, whence the last point. □

Thanks to (17) we get that $\{\delta_{x_M}\}$ is a local maximizer set of J for which J is a strict Lyapunov function (and that there is no other local maximizer set of J). Then, it follows that $\{\delta_{x_M}\}$ is asymptotically stable.

4 Models with mutations

With the above methodology set, we can extend it to the more elaborate cases when we include mutations.

4.1 BV estimates on the total population

We begin with *BV* estimates on ρ_ϵ assuming that R is independent of the trait variable and features a linear dependency on ρ , as it is specified in assumption (5). Thereafter we address the difficulties encountered when R has a general form.

4.1.1 Linear dependency on the competition variable in the AF model

Although the asymptotic behavior of n_ϵ solution to (1) may be difficult to obtain in general, under some assumptions on K and R , the total population ρ_ϵ can be proved to have bounded variations.

Recall that, integrating equation (1), we have

$$\epsilon \dot{\rho}_\epsilon = \frac{1}{\rho_\epsilon} \iiint_{\mathbb{R}^3} K_\epsilon(x, y, z) n_\epsilon(t, y) n_\epsilon(t, z) dx dy dz - \int_{\mathbb{R}} R(x, \rho_\epsilon) n_\epsilon(t, x) dx.$$

The proofs of Corollaries 1 and 2 rely on estimates obtained through the equation satisfied by $\ddot{\rho}_\epsilon$. In general, we start from

$$\begin{aligned} \epsilon \ddot{\rho}_\epsilon &= - \frac{\dot{\rho}_\epsilon}{\rho_\epsilon^2} \iiint_{\mathbb{R}^3} K_\epsilon(x, y, z) n_\epsilon(t, y) n_\epsilon(t, z) dx dy dz \\ &+ \frac{1}{\rho_\epsilon} \iiint_{\mathbb{R}^3} K_\epsilon(x, y, z) (\partial_t n_\epsilon(t, y) n_\epsilon(t, z) + n_\epsilon(t, y) \partial_t n_\epsilon(t, z)) dx dy dz \\ &- \dot{\rho}_\epsilon \int_{\mathbb{R}} \partial_\rho R(x, \rho) n_\epsilon(t, x) dx \\ &- \frac{1}{\epsilon} \int_{\mathbb{R}} R(x, \rho_\epsilon) \left(\frac{1}{\rho_\epsilon} \iint_{\mathbb{R}^2} K_\epsilon(x, y, z) n_\epsilon(t, y) n_\epsilon(t, z) dy dz - R(x, \rho_\epsilon) n_\epsilon(t, x) \right) dx. \end{aligned} \tag{30}$$

Proof of Corollary 1. We treat the case of the model with asymmetric fecundity. Then, ρ_ϵ satisfies

$$\epsilon \dot{\rho}_\epsilon = \int_{\mathbb{R}} B(x) n_\epsilon(t, x) dx - \nu \rho_\epsilon^2,$$

and (30) reads

$$\begin{aligned}\epsilon\ddot{\rho} &= \int B(x)\partial_t n_\epsilon(t,x)dx - 2\nu\rho_\epsilon\dot{\rho}_\epsilon \\ &= -\nu\rho_\epsilon\dot{\rho}_\epsilon + \frac{\nu^2}{\epsilon}\rho_\epsilon^3 - \frac{\nu\rho_\epsilon}{\epsilon} \int B(x)n_\epsilon(t,x)dx \\ &\quad + \frac{1}{\epsilon\rho_\epsilon} \iiint \alpha_\epsilon(x,y,z)B(x)B(y)n_\epsilon(t,y)n_\epsilon(t,z)dx dy dz - \frac{\nu\rho_\epsilon}{\epsilon} \int B(x)n_\epsilon(t,x)dx.\end{aligned}$$

We rewrite the last equation as

$$\begin{aligned}\epsilon\frac{d}{dt}\dot{\rho}_\epsilon &= -\nu\rho_\epsilon\dot{\rho}_\epsilon + \overbrace{\frac{\rho_\epsilon}{\epsilon} \left(\frac{\int B(x)n_\epsilon(t,x)dx}{\rho_\epsilon} - \nu\rho_\epsilon \right)^2}^{\text{demographic stabilization}} \\ &\quad + \underbrace{\frac{1}{\epsilon\rho_\epsilon} \left(\iiint \alpha_\epsilon(x,y,z)B(x)B(y)n_\epsilon(t,y)n_\epsilon(t,z)dx dy dz - \left(\int B(x)n_\epsilon(t,x)dx \right)^2 \right)}_{\text{mixing-induced fecundity variation}}. \quad (31)\end{aligned}$$

In order to apply the same technique as for the simple case (nM) in Section 3.1, we need to assume that the mixing-induced fecundity variation term is bounded from below. Under assumption (9), we obtain from (31) and Proposition 1

$$\epsilon\frac{d}{dt}\dot{\rho}_\epsilon \geq -\nu\rho_\epsilon\dot{\rho}_\epsilon - C. \quad (32)$$

From Proposition 4, we deduce

$$\frac{d}{dt}(\dot{\rho}_\epsilon)_- \leq -\frac{\nu\rho_m}{\epsilon}(\dot{\rho}_\epsilon)_- + \frac{C}{\epsilon},$$

and thus

$$(\dot{\rho}_\epsilon)_-(t) \leq e^{-\frac{\nu\rho_m t}{\epsilon}}(\dot{\rho}_\epsilon)_-(0) + \frac{C}{\nu\rho_m}(1 - e^{-\frac{\nu\rho_m t}{\epsilon}}).$$

Then we use the same argument as in the case without mutations, which proves uniform boundedness of ρ_ϵ in $BV(0, T)$ for all $T > 0$. \square

We discuss here assumption (9). Firstly, when B is constant, this assumption is obviously satisfied. Secondly, by taking ϕ concentrated at a point x_M where B reaches its maximum, we obtain for some $C > 0$

$$\int_{\mathbb{R}} \alpha_\epsilon(x, x_M, x_M)B(x)dx \geq B(x_M) - C\epsilon, \quad \forall \epsilon > 0.$$

Recalling that $\int \alpha_\epsilon(x, y, z)dx = 1$ for all y, z , this implies that as ϵ vanishes, $\alpha_\epsilon(\cdot, x_M, x_M)$ is concentrated at points where B is equal to its maximum $B(x_M)$, which is a restrictive necessary condition for (9) to hold. Thirdly, we state a sufficient condition: if $\alpha_\epsilon(\cdot, y, z) \rightarrow \alpha_0(y, z) \in \mathcal{M}_+^1(\mathbb{R})$ with either

$$\forall y, z, \quad \int_{\mathbb{R}} \alpha_0(y, z)(x)B(x)dx \geq B(y),$$

or

$$\forall y, z, \quad \int_{\mathbb{R}} \alpha_0(y, z)(x)B(x)dx \geq B(z),$$

and if convergence is sufficiently fast, then (9) holds. In the first case this is a consequence of the Cauchy-Schwarz inequality, and in the second case we simply obtain that the left-hand side in (9) converges to 0 as ϵ vanishes. In particular, we may assume $\alpha_\epsilon(x, y, z) = \frac{1}{\epsilon}G\left(\frac{x-y}{\epsilon}\right)$ or $\frac{1}{\epsilon}G\left(\frac{x-z}{\epsilon}\right)$ for some appropriate kernel G . These situations are those we have in mind, although (9) in all generality may allow for some other cases.

All in all, (9) means that the trait inheritance pattern α_ϵ does not allow next generation's fecundity to get smaller than the one of the current generation as ϵ goes to 0. Unsurprisingly, this dissipative feature implies that the variations of ρ_ϵ can be controlled at the limit $\epsilon \rightarrow 0$, as stated in Corollary 1.

4.1.2 Linear dependency on the competition variable in the ATH model

We now address the model with asymmetric trait heredity, i.e., the ATH model (ATH).

In order to apply the same technique as for the model without mutations addressed in Section 3, we need the convergence assumption (10) on G_ϵ as ϵ goes to 0. More precisely, we assume that there exists $C \in \mathbb{R}_+^*$ such that

$$\begin{aligned} \forall \epsilon > 0, \forall \phi \in W^{1,1} \text{ with } \|\phi'\|_{L^1} \leq 1, \forall \psi \in L^\infty \text{ with } \|\psi\|_{L^\infty} \leq 1, \\ \left| \int_{\mathbb{R}} \psi(x)(G_\epsilon * \phi)(x) dx - \int_{\mathbb{R}} \psi(x)\phi(x) dx \right| \leq C\epsilon. \end{aligned} \quad (33)$$

This assumption on the convergence of G_ϵ as ϵ vanishes holds in the typical case where G_ϵ is Gaussian with variance ϵ^2 . Specifically, we write $G_\epsilon(x) = \frac{1}{(2\pi\epsilon^2)^{1/2}} e^{-x^2/2\epsilon^2}$. Then we compute

$$\begin{aligned} \left| \int_{\mathbb{R}} \psi(x)(G_\epsilon * \phi)(x) dx - \int_{\mathbb{R}} \psi(x)\phi(x) dx \right| &\leq \int_{\mathbb{R}} |\psi(x)| |G_\epsilon * \phi(x) - \phi(x)| dx \\ &\leq \iint_{\mathbb{R}^2} \frac{1}{(2\pi\epsilon^2)^{1/2}} e^{-\frac{(x-y)^2}{2\epsilon^2}} |\phi(y) - \phi(x)| dy dx. \end{aligned}$$

We apply the change of variables $\hat{y} = \epsilon^{-1}(y - x)$, then $d\hat{y} = \epsilon^{-1}dy$, and we obtain

$$\begin{aligned} \left| \int_{\mathbb{R}} \psi(x)(G_\epsilon * \phi)(x) dx - \int_{\mathbb{R}} \psi(x)\phi(x) dx \right| &\leq (2\pi)^{-1/2} \iint_{\mathbb{R}^2} e^{-\hat{y}^2/2} |\phi(x + \epsilon\hat{y}) - \phi(x)| d\hat{y} dx \\ &\leq \frac{2\|\phi'\|_{L^1}}{(2\pi)^{1/2}} \epsilon. \end{aligned}$$

Proof of Corollary 2. Departing from (ATH), the equation satisfied by ρ_ϵ reads

$$\epsilon \frac{d}{dt} \rho_\epsilon(t) = \int_{\mathbb{R}} \left(\frac{1}{\rho_\epsilon(t)} K * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) - \nu \rho_\epsilon(t) n_\epsilon(t, x) \right) dx.$$

Differentiating this equation, we obtain

$$\begin{aligned} \epsilon \ddot{\rho}_\epsilon(t) &= \frac{1}{\rho_\epsilon(t)} \int_{\mathbb{R}} \left[K_0 * \partial_t n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) + K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * \partial_t n_\epsilon(t, \cdot)(x) \right] dx \\ &\quad - \nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) - \nu \int_{\mathbb{R}} \partial_t n_\epsilon(t, x) \rho_\epsilon(t) dx \\ &\quad - \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} [K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x)] dx. \end{aligned}$$

By the same trick as in Section 3, assuming (7) induces

$$\begin{aligned} \epsilon \ddot{\rho}_\epsilon(t) &= \frac{1}{2\rho_\epsilon(t)} \frac{d}{dt} \left[\int_{\mathbb{R}} K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) dx \right] \\ &\quad + \frac{1}{\rho_\epsilon(t)} \int_{\mathbb{R}} [G_\epsilon * (K_0 * n_\epsilon(t, \cdot))(x) \partial_t n_\epsilon(t, x)] dx \\ &\quad - \nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) - \nu \int_{\mathbb{R}} \partial_t n_\epsilon(t, x) \rho_\epsilon(t) dx \\ &\quad - \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} [K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x)] dx. \end{aligned}$$

Then we compute

$$\begin{aligned} \epsilon \ddot{\rho}_\epsilon(t) &= -\nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) + \frac{1}{2\rho_\epsilon(t)} \frac{d}{dt} \left[\int_{\mathbb{R}} K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) dx \right] \\ &\quad + \frac{1}{\epsilon \rho_\epsilon(t)} \int_{\mathbb{R}} G_\epsilon * (K_0 * n_\epsilon(t, \cdot))(x) \left[\frac{1}{\rho_\epsilon(t)} K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) - \nu n_\epsilon(t, x) \rho_\epsilon(t) \right] dx \\ &\quad - \frac{\nu}{\epsilon} \rho_\epsilon(t) \int_{\mathbb{R}} \left[\frac{1}{\rho_\epsilon(t)} K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) - \nu n_\epsilon(t, x) \rho_\epsilon(t) \right] dx \\ &\quad - \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} [K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x)] dx, \end{aligned}$$

and get

$$\begin{aligned}
\epsilon \ddot{\rho}_\epsilon(t) &= -\nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) + \frac{1}{2} \frac{d}{dt} \left[\int_{\mathbb{R}} \frac{1}{\rho_\epsilon(t)} K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x) dx \right] \\
&\quad - \frac{1}{2} \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} [K_0 * n_\epsilon(t, \cdot)(x) G_\epsilon * n_\epsilon(t, \cdot)(x)] dx \\
&\quad + \frac{1}{\epsilon} \int_{\mathbb{R}} (G_\epsilon * n_\epsilon) \left[G_\epsilon * (K_0 * n_\epsilon) \frac{(K_0 * n_\epsilon)}{\rho_\epsilon^2} - 2\nu K_0 * n \right] dx \\
&\quad + \frac{1}{\epsilon} \nu^2 \rho_\epsilon^2 \int_{\mathbb{R}} G_\epsilon * n_\epsilon dx.
\end{aligned}$$

We rewrite this as

$$\begin{aligned}
\epsilon \ddot{\rho}_\epsilon(t) &= -\nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) - \frac{1}{2} \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} K_0 * n_\epsilon(t, \cdot) G_\epsilon * n_\epsilon(t, \cdot) \\
&\quad + \frac{1}{\epsilon} \int_{\mathbb{R}} (G_\epsilon * n_\epsilon) \left[\frac{(K_0 * n_\epsilon)}{\rho_\epsilon} - \nu \rho_\epsilon \right]^2 dx \\
&\quad + \frac{1}{\epsilon \rho_\epsilon^2(t)} \int_{\mathbb{R}} (K_0 * n_\epsilon) (G_\epsilon * n_\epsilon) \left(G_\epsilon * (K_0 * n_\epsilon) - K_0 * n_\epsilon \right) dx.
\end{aligned}$$

Now we use the convergence assumption (33) on G_ϵ . We simply need to check that $\phi(x) := \int K_0(x-y)n_\epsilon(t,y)dy$ is in $W^{1,1}$. This is obvious since $\phi' = K_0' * n_\epsilon$. Hence we have

$$\begin{aligned}
\frac{\epsilon}{2} \ddot{\rho}_\epsilon(t) &= -\nu \rho_\epsilon(t) \dot{\rho}_\epsilon(t) - \frac{1}{2} \frac{\dot{\rho}_\epsilon(t)}{\rho_\epsilon^2(t)} \int_{\mathbb{R}} K_0 * n_\epsilon(t, \cdot) G_\epsilon * n_\epsilon(t, \cdot) \\
&\quad + \frac{1}{\epsilon} \int_{\mathbb{R}} (G_\epsilon * n_\epsilon) \left[\frac{(K_0 * n_\epsilon)}{\rho_\epsilon} - \nu \rho_\epsilon \right]^2 dx + O(1).
\end{aligned} \tag{34}$$

Thanks to (12), we deduce the inequality

$$\frac{\epsilon}{2} \frac{d}{dt} (\dot{\rho}_\epsilon(t))_- \leq -\left(\frac{1}{2}\eta_0 + \nu \rho_\epsilon(t)\right) (\dot{\rho}_\epsilon(t))_- + O(1).$$

Then, we conclude that ρ_ϵ is bounded in $BV_{\text{loc}}(\mathbb{R}_+)$ uniformly in ϵ . Indeed, we obtain that for some constants $C_1, C_2 > 0$,

$$(\dot{\rho}_\epsilon(t))_- \leq e^{-C_1 t/\epsilon} \left((\dot{\rho}_\epsilon(0))_- + \frac{C_2}{\epsilon} \int_0^t e^{C_1 t'/\epsilon} dt' \right),$$

hence

$$(\dot{\rho}_\epsilon(t))_- \leq (\dot{\rho}_\epsilon(0))_- e^{-C_1 t/\epsilon} + \frac{C_2}{C_1} (1 - e^{-C_1 t/\epsilon}).$$

As in the proof of Theorem 1, we deduce that for all $T > 0$, $(\rho_\epsilon)_\epsilon$ is uniformly in ϵ bounded in $BV([0, T])$ with assumption (11) on the initial data. Going back to (34), we derive the estimate, for $T > 0$,

$$\int_0^T \int_{\mathbb{R}} (G_\epsilon * n_\epsilon) \left[\frac{K_0 * n_\epsilon}{\rho_\epsilon} - \nu \rho_\epsilon \right]^2 dx dt = O(\epsilon),$$

as in the proof of Theorem 1. □

4.1.3 Extensions and open questions for the general case

Firstly, we address the case of a general saturation term for the AF model, featuring the competition effect and the trait-dependency:

$$R \in \mathcal{C}^1(\mathbb{R}^d \times \mathbb{R}_+; \mathbb{R}_+), \quad K(x, y, z) = B(y) \alpha_\epsilon(x, y, z), \quad \forall y, z, \quad \int_{\mathbb{R}} \alpha_\epsilon(x, y, z) dx = 1.$$

Thus in this case, ρ_ϵ satisfies

$$\epsilon \dot{\rho}_\epsilon = \int_{\mathbb{R}} (B(x) - R(x, \rho_\epsilon)) n_\epsilon(t, x) dx$$

Then, deriving this equation, we find

$$\begin{aligned}\epsilon \frac{d}{dt} \dot{\rho}_\epsilon &= \int_{\mathbb{R}} (B(x) - R(x, \rho_\epsilon)) \partial_t n_\epsilon(t, x) dx - \dot{\rho}_\epsilon \int_{\mathbb{R}} \partial_\rho R(x, \rho_\epsilon) n_\epsilon(t, x) dx \\ &= -\dot{\rho}_\epsilon \int_{\mathbb{R}} \partial_\rho R(x, \rho_\epsilon) n_\epsilon(t, x) dx + \frac{1}{\epsilon} \int_{\mathbb{R}} n_\epsilon(t, x) (B(x) - R(x, \rho_\epsilon))^2 \\ &\quad + \frac{1}{\epsilon} \int_{\mathbb{R}} (B(x) - R(x, \rho_\epsilon)) \left(\frac{1}{\rho_\epsilon} \iint_{\mathbb{R}^2} \alpha_\epsilon(x, y, z) B(y) n_\epsilon(t, y) n_\epsilon(t, z) dy dz - B(x) n_\epsilon(t, x) \right) dx\end{aligned}$$

The last term can be seen as the integral of the net fitness $B - R(\cdot, \rho_\epsilon)$ weighted by a fecundity deviation $\Delta_{n_\epsilon(t, \cdot)} B$, with $\int \Delta_{n_\epsilon(t, \cdot)} B(x) dx = 0$.

To apply the same argument as before, we need to assume

$$\begin{aligned}\exists C > 0, \forall \epsilon > 0, \forall y, z, \forall \phi \in L^1_+ \text{ with } \|\phi\|_{L^1} = 1, \\ \left\| \iint_{\mathbb{R}^2} \alpha_\epsilon(\cdot, y, z) B(y) \phi(y) \phi(z) dy dz - B(\cdot) \phi(\cdot) \right\|_{L^1} \leq C\epsilon,\end{aligned}\tag{35}$$

and also

$$\forall \rho \leq \rho_M, C_f(\rho) := \|B(\cdot) - R(\cdot, \rho)\|_\infty < \infty, \quad \overline{C_f} = \sup_{0 \leq \rho \leq \rho_M} C_f(\rho).\tag{36}$$

Under assumptions (35) and (36), this additional term is treated as in the case (5), replacing the negative constant on the right-hand side of (32) by $-\rho_M \overline{C_f}$, which gives

$$\epsilon \frac{d}{dt} \dot{\rho}_\epsilon(t) \geq -\dot{\rho}_\epsilon \int_{\mathbb{R}} \partial_\rho R(x, \rho_\epsilon) n_\epsilon(t, x) dx - \rho_M \overline{C_f}.$$

Therefore, similarly to the proof of Corollary 1 we obtain

Corollary 3. *Assume (35) and (36). Then, for all $T > 0$, $(\rho_\epsilon)_\epsilon$ is uniformly in ϵ bounded in $BV([0, T])$.*

Secondly, we address the case of a general death term for the ATH model:

$$R \in \mathcal{C}^1(\mathbb{R}^d \times \mathbb{R}_+; \mathbb{R}_+), \quad K_\epsilon(x, y, z) = G_\epsilon(x - z) K_0(x - y).$$

In order to see clearly where the difficulty lies, we replace $G_\epsilon(x - z)$ by $\delta_{x=z}$ (letting $\epsilon \rightarrow 0$ in this term only). For simplicity, we define

$$\zeta(t, x) := \frac{K_0 * n_\epsilon(t, \cdot)(x)}{\rho_\epsilon(t)}, \quad Q(t) := \int_{\mathbb{R}} \partial_\rho R(x, \rho_\epsilon(t)) n_\epsilon(t, x) dx.$$

After computations similar to the previous ones, we find

$$\frac{1}{2} \epsilon \frac{d}{dt} \dot{\rho}_\epsilon = -\frac{\dot{\rho}_\epsilon}{2\rho_\epsilon} \int_{\mathbb{R}} n_\epsilon \zeta + \frac{1}{\epsilon} \int_{\mathbb{R}} n_\epsilon \left[\zeta^2 - R\zeta + \frac{R+Q}{2} (R - \zeta) \right],\tag{37}$$

and the term in $\frac{1}{\epsilon}$ rewrites

$$\int_{\mathbb{R}} n \left(\zeta - \frac{R+Q}{2} \right) (\zeta - R).$$

Meanwhile, one can check that

$$\epsilon \dot{\rho}_\epsilon = \int_{\mathbb{R}} n_\epsilon (\zeta - R).$$

When $\dot{\rho}_\epsilon \leq 0$ we would like to prove that the term in $\frac{1}{\epsilon}$ in (37) is non-negative. We could be less restrictive and simply require $\dot{\rho}_\epsilon \geq 0$. This reads (with $q_\epsilon(t, x) = n_\epsilon(t, x)/\rho_\epsilon(t)$):

$$\int_{\mathbb{R}} q_\epsilon(t, x) \left(\zeta(t, x) - R(x, \rho_\epsilon(t)) \right) \left(\zeta(t, x) - \frac{R(x, \rho_\epsilon(t)) + Q(t)}{2} - \int_{\mathbb{R}} q_\epsilon(t, y) \zeta(t, y) dy \right) dx \geq 0$$

if

$$\int_{\mathbb{R}} q_\epsilon(t, x) (\zeta(t, x) - R(x, \rho_\epsilon(t))) dx \leq 0.$$

We do not treat the general case but a straightforward computation gives

Lemma 2. *If $R(x, \rho) = R_1(\rho)$ and $\rho R'_1(\rho) \geq R_1(\rho)$, then $\dot{\rho}_\epsilon \leq 0$ implies $\dot{\rho}_\epsilon \geq -\frac{\dot{\rho}_\epsilon}{2\rho_\epsilon} \int n \zeta$. Then in particular for all $T > 0$, $(\rho_\epsilon)_\epsilon$ is uniformly in ϵ bounded in $BV([0, T])$.*

For instance, this is the case if $R_1(\rho) = \nu \rho^\gamma$ for some $\gamma \geq 1$.

4.2 Discussion on the Lyapunov approach

We may also discuss the Lyapunov approach applied to reproduction terms including mutations. As in Section 3.3, we define $q_\epsilon(t, x) := n_\epsilon(\epsilon t, x)/\rho_\epsilon(\epsilon t)$. For equation (1), assuming $R(x, \rho) = R_0(x) + R_1(\rho)$, we find

$$\left\{ \begin{array}{l} \partial_t q_\epsilon(t, x) = \iint_{\mathbb{R}^2} K_\epsilon(x, y, z) q_\epsilon(t, y) q_\epsilon(t, z) dy dz - R_0(x) q_\epsilon(t, x) \\ \quad - q_\epsilon(t, x) \left(\iiint_{\mathbb{R}^3} K_\epsilon(x', y, z) q_\epsilon(t, y) q_\epsilon(t, z) dx' dy dz - \int_{\mathbb{R}} R_0(x') q_\epsilon(t, x') dx' \right), \\ q_\epsilon(0, x) = q_\epsilon^0(x). \end{array} \right. \quad (38)$$

A natural candidate Lyapunov functional is given by

$$J^\epsilon(q) := \frac{1}{2} \iiint_{\mathbb{R}^3} K_\epsilon^S(x, y, z) q(y) q(z) dx dy dz - \int_{\mathbb{R}} R_0(x) q(x) dx,$$

$$K_\epsilon^S(x, y, z) := \frac{K_\epsilon(x, z, y) + K_\epsilon(x, y, z)}{2}.$$

Then, we can compute along an orbit of (38)

$$\begin{aligned} \frac{d}{dt} J^\epsilon(q_\epsilon(t, \cdot)) &= \int_{\mathbb{R}} \partial_t q_\epsilon(t, y) \left(\iint_{\mathbb{R}^2} K_\epsilon^S(x, y, z) q_\epsilon(t, z) dz dx - R_0(y) \right) dy \\ &= \int \cdots \int_{\mathbb{R}^5} K_\epsilon^S(x, y, z) K_\epsilon^S(y, y', z') q_\epsilon(t, y') q_\epsilon(t, z') q_\epsilon(t, z) dz' dy' dz dy dx \\ &\quad - \iiint_{\mathbb{R}^3} K_\epsilon^S(x, y, z) (R_0(x) + R_0(y)) q_\epsilon(t, y) q_\epsilon(t, z) dx dy dz + \int_{\mathbb{R}} q_\epsilon(t, x) R_0^2(x) dx \\ &\quad - \left(\iiint_{\mathbb{R}^3} K_\epsilon^S(x, y, z) q_\epsilon(t, y) q_\epsilon(t, z) dx dy dz - \int_{\mathbb{R}} q_\epsilon(t, y) R_0(y) dy \right)^2. \end{aligned}$$

In the special case $R_0 \equiv 0$, to get a non-decreasing J^ϵ along orbits, we need to assume

$$\forall \xi \in \mathcal{M}_+^1(\mathbb{R}), \quad \int \cdots \int_{\mathbb{R}^5} K_\epsilon^S(x, y, z) K_\epsilon^S(y, y', z') \xi(y') \xi(z') \xi(z) dz' dy' dz dy dx \geq \left(\iiint_{\mathbb{R}^3} K_\epsilon^S(x, y, z) \xi(y) \xi(z) dx dy dz \right)^2, \quad (39)$$

which could be interpreted as an increase of fecundity from parents to offspring, with equality only if the dynamic is at rest, that is

$$\iint_{\mathbb{R}^2} K_\epsilon^S(\cdot, y, z) \xi(y) \xi(z) dy dz \text{ is constant on } \text{supp}(\xi).$$

In other words, to obtain a Lyapunov functional requires a perfect analogue of the Cauchy-Schwarz inequality.

When $R_0 \neq 0$, this Lyapunov functional also applies for (AF) with constant B , that is under the assumption

$$\exists B > 0, \forall y, z, \quad \int_{\mathbb{R}} K_\epsilon(x, y, z) dx = B.$$

Then, we write $K_\epsilon = B\alpha_\epsilon$ and get $J^\epsilon(q) = \frac{B}{2} - \int_{\mathbb{R}} q(y) R_0(y) dy$ so that

$$\begin{aligned} \frac{d}{dt} J^\epsilon(q_\epsilon(t, \cdot)) &= \int_{\mathbb{R}} q_\epsilon(t, y) R_0^2(y) dy - \left(\int_{\mathbb{R}} q_\epsilon(t, y) R_0(y) dy \right)^2 \\ &\quad + B \left(\int_{\mathbb{R}} q_\epsilon(t, y) R_0(y) dy - \iiint_{\mathbb{R}^3} R_0(x) \alpha_\epsilon(x, y, z) q_\epsilon(t, y) q_\epsilon(t, z) dx dy dz \right). \end{aligned}$$

To get that J^ϵ is non-decreasing along orbits, one possible additional assumption is therefore

$$\forall \xi \in \mathcal{M}_+^1(\mathbb{R}), \quad \int_{\mathbb{R}} R_0(y) \xi(y) dy \geq \iiint_{\mathbb{R}^3} R_0(x) \alpha_\epsilon(x, y, z) \xi(y) \xi(z) dx dy dz, \quad (40)$$

which could be interpreted as a decrease of the death rate from parents to offspring.

These two conditions could be combined for more generality. However, more realistic assumptions such as (9), (35) or (33) do not imply that J^ϵ itself is a non-decreasing Lyapunov function, but rather that along an orbit of (38),

$$\frac{d}{dt} J^\epsilon(q_\epsilon(t, \cdot)) = j^0(q_\epsilon(t, \cdot)) + \epsilon j_\epsilon^1(q_\epsilon(t, \cdot)),$$

where j_ϵ^1 is uniformly bounded, and $j^0(q) \geq 0$ with equality if and only if q is a rest point of the limit dynamics. In other words, we get Lyapunov stability *asymptotically* as $\epsilon \rightarrow 0$. The possible outcomes of this approach are still to be investigated.

5 The Hamilton-Jacobi equation

In the context of evolutionary dynamics, the Hamilton-Jacobi approach has been introduced in [17] and then developed in [32, 26] to study the concentration effect for phenotypically structured PDEs. This consists in determining the possible Dirac distributions through the zeros of u_ϵ defined from the Hopf-Cole transform

$$u_\epsilon(t, x) = \epsilon \ln n_\epsilon(t, x).$$

In the mentioned works, the convergence of u_ϵ as ϵ goes to 0 is rigorously established and the limit u satisfies a constrained Hamilton-Jacobi equation, using the theory of viscosity solutions (see [13, 1] for an introduction). The constraint on the solution u reads

$$\max_{x \in \mathbb{R}} u(t, x) = 0, \quad \forall t > 0,$$

and comes from the control in L^1 of the total population. Then, some properties on the concentration points can be derived from the study of this constrained Hamilton-Jacobi equation and the solution u . In some particular cases, it is proved that the population density remains monomorphic, that is composed of a single Dirac mass, and then a form of canonical equation is derived, giving the dynamics of the dominant trait.

In the present work, this Hamilton-Jacobi structure arises in the different situations that were previously studied. We show in this section different results obtained on the regularity of u_ϵ . Then, we deal with the limiting equations as ϵ goes to 0, and discuss the potential concentration points.

The convergence of u_ϵ to a solution of the limiting constrained Hamilton-Jacobi equation, at least in the sense of viscosity, remains to be rigorously proved. The main obstacles to the proof we encounter are the time-dependency of the coefficients and their lack of regularity.

5.1 Derivation of the constrained H-J equations

Asymmetric fecundity: we use the particular form

$$K_\epsilon(x, y, z) = B(y) \frac{1}{\epsilon} \alpha\left(\frac{x-z}{\epsilon}, y\right) \text{ with } \int_{\mathbb{R}} \alpha(z', y) dz' = 1 \text{ for all } y,$$

and we define

$$b_\epsilon(t, x) := R(x, \rho_\epsilon(t)), \quad q_\epsilon(t, y) = \frac{n_\epsilon(t, y)}{\rho_\epsilon(t)}. \quad (41)$$

In this case, the equation on u_ϵ reads

$$\partial_t u_\epsilon(t, x) = \int_{\mathbb{R}} B(y) q_\epsilon(t, y) \int_{\mathbb{R}} \alpha(z, y) e^{\frac{u_\epsilon(t, x - \epsilon z) - u_\epsilon(t, x)}{\epsilon}} dz dy - b_\epsilon(t, x), \quad (42)$$

and we compute the formal limiting equation

$$\begin{aligned} \partial_t u(t, x) &= \int_{\mathbb{R}} B(y) q(t, y) \int_{\mathbb{R}} \alpha(z, y) e^{-\partial_x u(t, x) \cdot z} dz dy - b(t, x) \\ &= \int_{\mathbb{R}} B(y) q(t, y) \mathcal{L}[\alpha(\cdot, y)](\partial_x u(t, x)) dy - b(t, x), \end{aligned} \quad (43)$$

with $\mathcal{L}[\alpha(\cdot, y)]$ the Laplace transform of $\alpha(\cdot, y)$ for all y :

$$\mathcal{L}[\alpha](p) := \int_{\mathbb{R}} \alpha(z) e^{-p \cdot z} dz,$$

for α a probability density function.

Asymmetric trait heredity: The interest of this problem comes from the time- and trait-dependent coefficients of the Hamiltonian. We use the generic form

$$K_\epsilon(x, y, z) = G_\epsilon(x - z) K_1(x, y).$$

After the change of variable $z' = \frac{x-z}{\epsilon}$, the equation on u_ϵ reads

$$\partial_t u_\epsilon(t, x) = \frac{1}{\rho_\epsilon(t)} \int_{\mathbb{R}} K_1(x, y) n_\epsilon(t, y) dy \cdot \int_{\mathbb{R}} G(z') e^{\frac{u_\epsilon(t, x - \epsilon z') - u_\epsilon(t, x)}{\epsilon}} dz' - b_\epsilon(t, x). \quad (44)$$

For clarity, we define

$$a_\epsilon(t, x) := \int_{\mathbb{R}} K_1(x, y) q_\epsilon(t, y) dy. \quad (45)$$

At the limit $\epsilon \rightarrow 0$, we obtain the formal limiting equation

$$\begin{aligned} \partial_t u(t, x) &= a(t, x) \int_{\mathbb{R}} G(z) e^{-\partial_x u(t, x) \cdot z} dz - b(t, x) \\ &= a(t, x) \mathcal{L}[G](\partial_x u(t, x)) - b(t, x), \end{aligned} \quad (46)$$

with a and b the formal limits of a_ϵ and b_ϵ defined in (45) and (41), and $\mathcal{L}[G]$ the Laplace transform of G . From now on, we choose G such that its Laplace transform is well defined on \mathbb{R} .

In the case G is the gaussian density, the equation on u_ϵ reads

$$\partial_t u_\epsilon(t, x) = a_\epsilon(t, x) \int_{\mathbb{R}} \frac{1}{\sqrt{2\pi}} e^{-\frac{|z|^2}{2}} e^{\frac{u_\epsilon(t, x - \epsilon z) - u_\epsilon(t, x)}{\epsilon}} dz - b_\epsilon(t, x). \quad (47)$$

Then, passing formally to the limit $\epsilon \rightarrow 0$, we arrive at

$$\begin{aligned} \partial_t u(t, x) &= a(t, x) \int_{\mathbb{R}} \frac{1}{\sqrt{2\pi}} e^{-\frac{|z|^2}{2}} e^{-\partial_x u(t, x) \cdot z} dz - b(t, x) \\ &= a(t, x) e^{\frac{(\partial_x u(t, x))^2}{2}} - b(t, x). \end{aligned}$$

The statements of Theorem 3 concern, for both models, the convergence of u_ϵ as ϵ vanishes, and the existence of a uniform upper bound on u_ϵ that converges to 0. To prove the first point, we derive a priori estimates on u_ϵ , and then on its derivatives, in order to use compactness arguments. The second point relies on these derived estimates.

The uniqueness of the solution to the limit equation has not been proved in our context (see [7] for the most general result so far), thus we only derive convergence up to extraction of subsequences. Moreover, the stability result is not complete, since we do not have convergence results on the coefficients of the corresponding equations.

The complete proof of Theorem 3 is deferred to Appendix A, since it uses quite standard and technical arguments. We mostly focus on Equation (47), but the methods are identical for the generic ATH case. The proof of the theorem in the AF case is similar and we also give the formal ideas where it is necessary.

Assumptions for Theorem 3: We assume on the function R

$$\exists C_0 > 0, \forall \rho_m \leq \rho \leq \rho_M, \forall x \in \mathbb{R}, \quad R(x, \rho) \leq C_0(1 + |x|), \quad (48)$$

$$\exists L_b > 0, \forall \rho_m \leq \rho \leq \rho_M, \forall x \in \mathbb{R}, \quad |\partial_x R(x, \rho)| \leq L_b. \quad (49)$$

We choose the positive function K_1 bounded

$$\exists \bar{K} > 0, \forall x, y \in \mathbb{R}, \quad K_1(x, y) \leq \bar{K}, \quad (50)$$

and such that,

$$\exists \lambda > 0, \exists C_\lambda > 0, \forall \epsilon > 0, t \geq 0, x \in \mathbb{R}, \quad e^{\frac{|\partial_x a_\epsilon(t, x)|}{\lambda a_\epsilon(t, x)}} \lambda a_\epsilon(t, x) \leq C_\lambda. \quad (51)$$

This assumption is satisfied for example when K_1 is bounded and there exists a constant L_K such that

$$|\partial_x K_1(x, y)| \leq L_K |K_1(x, y)|, \quad \forall x, y \in \mathbb{R},$$

or, when K_1 induces a gaussian type distribution for a_ϵ , that is,

$$a_\epsilon(t, x) \sim C e^{-\frac{(x-m)^2}{\sigma^2}}.$$

We also assume on the initial condition

$$u_\epsilon^0(x) \leq -A|x| + C, \quad \|\partial_x u_\epsilon^0\| \leq L_0. \quad (52)$$

For the model with asymmetric fecundity, we assume that B and α are positive and bounded.

5.2 Limiting equations and polymorphism

In the context of viscosity solutions, cf. [13, 1], we may establish the formal limit of the constrained Hamilton-Jacobi equations to study the potential concentration points.

5.2.1 Limiting Hamilton-Jacobi equations

By Lipschitz regularity, as it is classically proved with the Hamilton-Jacobi approach to adaptive dynamics, the limit function u satisfies the constraint

$$\max_{x \in \mathbb{R}} u(t, x) = 0, \quad \forall t > 0.$$

Then, when u is differentiable at maximum points, we deduce that $\partial_t u$ equals 0 and, going back to (43) and (46), we obtain, for \bar{n} the formal limit of n_ϵ ,

$$\text{supp } \bar{n} \subset \{(t, x) \in (0, \infty) \times \mathbb{R} | B(x) - b(t, x) = 0\}, \quad \text{in case (AF)},$$

$$\text{supp } \bar{n} \subset \{(t, x) \in (0, \infty) \times \mathbb{R} | a(t, x) - b(t, x) = 0\}, \quad \text{in case (ATH)}.$$

It would be then interesting to determine the conditions required to have these null sets reduced to an isolated point. If, for all $t > 0$, we identify a unique point $\bar{x}(t)$ satisfying

$$B(\bar{x}(t)) - b(t, \bar{x}(t)) = B(\bar{x}(t)) - R(\bar{x}(t), \bar{\rho}(t)) = 0, \quad \text{in case (AF)},$$

$$a(t, \bar{x}(t)) - R(\bar{x}(t), \bar{\rho}(t)) = 0, \quad \text{in case (ATH)},$$

then the population is monomorphic, that composed of a single Dirac mass located on $\bar{x}(t)$. Provided some regularity properties on u_ϵ , we could derive a canonical equation for both (AF) and (ATH).

5.2.2 An example where the population has to be monomorphic

Going back to (nM), we define $\bar{n} \in \mathcal{M}_+(\mathbb{R})$ as an Evolutionary Stable Distribution (ESD) in the sense of [15, 21] by

$$K_0 * \bar{n} = \nu \bar{\rho}^2 \text{ on } \text{supp}(\bar{n}), \quad (53)$$

$$K_0 * \bar{n} \leq \nu \bar{\rho}^2 \text{ on } \mathbb{R}, \quad (54)$$

where $\bar{\rho} = \int \bar{n}$. The interest of the ESD concept is huge: it is readily established that a stationary solution to (nM) is asymptotically stable if and only if it satisfies (53) and (54).

If we assume that K_0 is radial-decreasing, then we prove that extreme points in $\text{supp}(\bar{n})$ (if it is bounded) cannot support a positive Dirac mass, by using (54). In particular, among all

combinations of Dirac masses, only the single-point measure $\bar{n}_{\bar{x}}(x) := K_0(0)/\nu\delta_{x=\bar{x}}$ is an ESD. Indeed, assume that \bar{n} is composed of $k \geq 2$ Dirac masses located on $(x_i)_{1 \leq i \leq k}$, then defining

$$\bar{K}(x) := K_0 * \bar{n}(x) = \sum_{i=1}^k \rho_i K_0(x - x_i),$$

we deduce from (53) and (54) that \bar{K} is maximal on the support of \bar{n} , that is the points x_i . With no loss of generality, we assume that the sequence (x_i) is ordered and $x_1 = \min_i x_i$. Then, differentiating \bar{K} , we obtain

$$\bar{K}'(x_1) = \sum_{i \geq 1} \rho_i K_0'(x_1 - x_i) > 0,$$

which contradicts the optimality of \bar{K} on the support of \bar{n} . Hence the population, at the asymptotic limit, cannot be polymorphic.

6 Conclusion and perspectives

We investigated adaptive dynamics for population dynamics model including sexual reproduction, when the trait is mainly inherited from the mother. We determined non-extinction conditions and a control on the total population. In the particular case of a saturation term R depending only on the competition, we derived BV estimates on the total population. In general, estimating the variations of ρ_ϵ when R depends on both trait variable and competition seems difficult, and a Lyapunov functional approach yields complementary results under some structure conditions. An open problem is to find another method allowing for more appropriate assumptions in order to get stability results.

Concerning the sequences $u_\epsilon = \epsilon \ln n_\epsilon$ associated to each model, we obtained local Lipschitz estimates uniform in ϵ . To deduce the convergence of u_ϵ to the solution of the limiting Hamilton-Jacobi equation with constraint, we still need time compactness on the coefficients of (42) and (44). As a special case of both, for the Hamilton-Jacobi equation associated to the model without mutations (gnM), if we provide some convergence result on $\int K(x, y) * n_\epsilon(t, y) / \rho_\epsilon(t)$ and on ρ_ϵ , then, up to extraction of a subsequence, the limit function u has an explicit formulation and its maximum points can be described. In general, Hamilton-Jacobi equations with time- and space-dependent coefficients are difficult to deal with when there is a lack of regularity. The authors in [24] developed a theory of stochastic viscosity solutions to tackle nonlinear stochastic PDEs. In particular, they prove existence, regularity and uniqueness results for the viscosity solution when the time-dependent coefficient of the Hamiltonian can be written as the derivative of a trajectory. This theory does not apply to our models since the coefficients in front of the gradient-dependent term are not under the form of a time derivative.

Another question is the determination of a convenient framework to observe Dirac concentrations. The convergence of the population distribution to a sum of Dirac masses illustrates the selection of well-adapted or dominant phenotypical traits. In [26, 8], the Hamilton-Jacobi approach enables to characterize the dynamics of the dominant traits under specific assumptions of regularity. In our framework, the required hypotheses to prove Dirac concentrations are to be clarified.

Using the Wasserstein distance has been recently developed in [27, 14, 19] to derive asymptotics of population distributions for similar equations. It is proved that specific cases of the sexual reproduction operator, possibly in an infinitesimal model, induce a control, possibly a contraction, for the Wasserstein distance on the phenotypical trait space. It could be interesting to further explore this method in full generality.

Acknowledgements

The authors are very thankful to Pierre-Alexandre Bliman for proposing the biological motivations and the directions that led to this work. B.P. has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No 740623).

A Proof of Theorem 3

A.1 A priori bounds

We begin with the estimates for the ATH case, and especially with a gaussian trait female heredity distribution.

Lemma 3. *Let u_ϵ be solution to equation (42) or (47). Then, there exist constants $C_1 > 0$ and $C_2 > 0$, such that for all $t > 0, x \in \mathbb{R}$ and $\epsilon > 0$ we have*

$$-C_1(1+t)(1+|x|) \leq u_\epsilon(t, x) \leq -A|x| + C_2(1+t).$$

We prove this lemma in the case of a gaussian trait female heredity distribution, but the argument exactly applies to equation (44) in the generic ATH case.

Proof. We first prove the lower bound

$$u_\epsilon(t, x) \geq -C_1(1+t)(1+|x|).$$

Indeed, because $a_\epsilon \geq 0$ and $\mathcal{L}(G) \geq 0$, we deduce from (48) that

$$\partial_t u_\epsilon \geq -b_\epsilon(t, x) \geq -C_0(1+|x|).$$

From (52) we obtain

$$u_\epsilon(t, x) \geq \inf_\epsilon u_\epsilon^0(0) - \inf_\epsilon \|\partial_x u_\epsilon^0\| - C_0 t(1+|x|).$$

Hence the lower bound.

We also derive the inequality

$$u_\epsilon(t, x) \leq -A|x| + C_2(1+t),$$

where $C_2 = \bar{K} \frac{1}{\sqrt{2\pi}} \int e^{-|z|^2/2} e^{A|z|} dz$. Indeed, defining $v(t, x) := -A|x| + C_2(1+t)$, we compute

$$\partial_t v(t, x) - a_\epsilon(t, x) \int \frac{1}{\sqrt{2\pi}} e^{-|z|^2/2} e^{\frac{v(t, x - \epsilon z) - v(t, x)}{\epsilon}} dz \geq C_2 - \bar{K} \frac{1}{\sqrt{2\pi}} \int e^{-|z|^2/2} e^{A|z|} dz \geq 0.$$

Thus, v is a super-solution of (47), and since $u^0(x) \leq v(0, x)$ we deduce that $u_\epsilon(t, x) \leq v(t, x)$ by a comparison principle argument. \square

We obtain the same kind of bounds for the asymmetric fecundity case, with the constant $C_2 := \sup_y B(y) \int \alpha(z, y) e^{A|z|} dz$.

A.2 Regularity in space

We prove the following

Lemma 4. *Let u_ϵ be the solution to the equation (47). For $\lambda > 0$ given by (51) and for all $t > 0, x \in \mathbb{R}$, we have*

$$|\partial_x u_\epsilon(t, x)| \leq \|\partial_x u_\epsilon^0\|_{L^\infty} + (C_\lambda + L_b)t + \lambda \left(\sup_\epsilon \|u_\epsilon^0\|_{L^\infty} + C_1(1+t)(1+|x|) \right).$$

This implies that u_ϵ is Lipschitz in space, uniformly in ϵ and locally in time.

Proof. We use the notations

$$p_\epsilon(t, x) = \partial_x u_\epsilon(t, x), \quad p(t, x) = \partial_x u(t, x).$$

Differentiating (47), p_ϵ satisfies

$$\begin{aligned} \partial_t p_\epsilon(t, x) &= \partial_x a_\epsilon(t, x) \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{\frac{u_\epsilon(t, x - \epsilon z) - u_\epsilon(t, x)}{\epsilon}} dz \\ &\quad + a_\epsilon(t, x) \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{\frac{u_\epsilon(t, x - \epsilon z) - u_\epsilon(t, x)}{\epsilon}} \left(\frac{p_\epsilon(t, x - \epsilon z) - p_\epsilon(t, x)}{\epsilon} \right) dz - \partial_x b_\epsilon(t, x). \end{aligned}$$

Let $\lambda > 0$. We define

$$w_\epsilon^\lambda(t, x) = p_\epsilon(t, x) + \lambda u_\epsilon(t, x), \quad D_\epsilon(t, x, z) = \frac{u_\epsilon(t, x - \epsilon z) - u_\epsilon(t, x)}{\epsilon}.$$

Then, w_ϵ^λ satisfies

$$\begin{aligned} \partial_t w_\epsilon^\lambda &= a_\epsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\epsilon(t, x, z)} \left(\frac{w_\epsilon^\lambda(t, x - \epsilon z) - w_\epsilon^\lambda(t, x)}{\epsilon} \right) dz \\ &\quad - \lambda \left[a_\epsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\epsilon(t, x, z)} (D_\epsilon(t, x, z) - 1) \right] dy \\ &\quad + \partial_x a_\epsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\epsilon(t, x, z)} dz - (\partial_x b_\epsilon + \lambda b_\epsilon). \end{aligned}$$

Then, using (49), we have

$$\begin{aligned} \partial_t w_\epsilon^\lambda - L_b - a_\epsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\epsilon} \left(\frac{w_\epsilon^\lambda(t, x - \epsilon z) - w_\epsilon^\lambda(t, x)}{\epsilon} \right) dz \\ \leq \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\epsilon} [\partial_x a_\epsilon + \lambda a_\epsilon - \lambda a_\epsilon D_\epsilon] dz. \end{aligned}$$

Defining $f(D) := e^D (\partial_x a_\epsilon + \lambda a_\epsilon - \lambda a_\epsilon D)$, the maximum of f on \mathbb{R} is reached at $D^* := \frac{\partial_x a_\epsilon}{\lambda a_\epsilon}$ and equals

$$e^{\frac{\partial_x a_\epsilon}{\lambda a_\epsilon}} \lambda a_\epsilon \leq C_\lambda,$$

from (51). Then we have the upper bound

$$w_\epsilon^\lambda(t, x) \leq \max_{\mathbb{R}} w_\epsilon^\lambda(0, x) + Ct, \quad C = C_\lambda + L_b,$$

which implies the upper bound on p_ϵ

$$p_\epsilon(t, x) \leq \|\partial_x u_\epsilon^0\|_{L^\infty} + Ct + \lambda \left(\sup_{\epsilon} \|u_\epsilon^0\|_{L^\infty} + C_1(1+t)(1+|x|) \right).$$

We have the same estimate for $-p_\epsilon$. □

For the AF model, we have the following estimate on the derivative in space of u_ϵ :

Lemma 5. *Let u_ϵ be the solution of equation (42). Then, for all $t > 0, x \in \mathbb{R}$ and $\epsilon > 0$, we have*

$$|\partial_x u_\epsilon(t, x)| \leq \|\partial_x u_\epsilon^0\|_{L^\infty} + L_b t.$$

This implies that u_ϵ is Lipschitz in space, uniformly in ϵ and locally in time.

We address the limit equation

$$\partial_t p(t, x) = (-\partial_x p(t, x)) \int B(y) q(t, y) \int z \alpha(z, y) e^{-p(t, x) \cdot z} dz dy - \partial_x b(t, x), \quad (55)$$

and give formal arguments, since the proof for the ϵ -level problem is similar to the one of the ATH case. We compute that $w(t) := \|\partial_x u_\epsilon^0\|_{L^\infty} + L_b t$ is a super-solution of (55). Since $p(0, x) \leq w(0)$ for all $x \in \mathbb{R}$, we deduce that, from the comparison principle, u_ϵ is Lipschitz in space, uniformly in ϵ and locally in time.

A.3 Regularity in time

In the ATH case, since we proved that u_ϵ is uniformly Lipschitz in space locally in time, we can deduce that $\partial_t u_\epsilon$ is locally uniformly bounded.

Lemma 6. *Let u_ϵ be the solution to equation (44) and let $T > 0$ and $r > 0$ be fixed. Assume (49) and (50). Then, there exists $C(T, r) > 0$ such that, for all $t \in [0, T], x \in B(0, r)$, we have*

$$|\partial_t u_\epsilon| \leq C(T, r) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))}.$$

This implies that u_ϵ is Lipschitz in time, uniformly in ϵ .

Proof. Let $T > 0$ and $R > r > 0$ be fixed with R large enough. We choose some constants L_1 and L_2 such that

$$\begin{aligned} u_\epsilon(t, x) &< -L_1, \quad \forall (t, x) \in [0, T] \times \mathbb{R} \setminus B(0, R), \\ |p_\epsilon| &< L_2, \quad \forall (t, x) \in [0, T] \times B(0, R). \end{aligned}$$

Then, we obtain for $t \in [0, T]$, $x \in B(0, r)$,

$$\begin{aligned} |\partial_t u_\epsilon| &\leq \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))} \\ &+ \frac{1}{\rho_\epsilon(t)} \int K(x, z) n_\epsilon(t, z) dz \cdot \left(\int_{|x-\epsilon y| < R} e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\epsilon y| > R} e^{-|y|^2} e^{\frac{u_\epsilon(t, x-\epsilon y) - u_\epsilon(t, x)}{\epsilon}} dy \right). \end{aligned}$$

Thus, for ϵ small enough, and assuming that

$$\begin{aligned} u_\epsilon(t, x) &> -L_1, \quad \forall t \in [0, T], \forall x \in B(0, r), \\ u_\epsilon(t, x) &< -L_1, \quad \forall t \in [0, T], \forall x \in \mathbb{R} \setminus B(0, R), \end{aligned}$$

we have

$$\begin{aligned} |\partial_t u_\epsilon| &\leq \bar{K} \left(\int_{|x-\epsilon y| < R} e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\epsilon y| > R} e^{-|y|^2} e^{\frac{-L_1 - u_\epsilon(t, x)}{\epsilon}} dy \right) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))} \\ &\leq \bar{K} \left(\int e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\epsilon y| > R} e^{-|y|^2} dy \right) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))} \\ &\leq \bar{K} \left(\int e^{-|y|^2} e^{L_2 y} dy + \sqrt{\pi} \right) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))}. \end{aligned}$$

Hence the local uniform bound on $\partial_t u_\epsilon$. □

The proof is similar for the AF case.

Lemma 7. *Let u_ϵ be the solution to equation (42) and let $T > 0$ and $r > 0$ be fixed. Then, there exists $C(T, r) > 0$ such that, for all $t \in [0, T]$, $x \in B(0, r)$, we have*

$$|\partial_t u_\epsilon| \leq C(T, r) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot, \rho)\|_{L^\infty(B(0, r))}.$$

This implies that u_ϵ is Lipschitz in time, uniformly in ϵ .

A.4 A more precise upper bound

The following argument concerns both cases and gives a sharper upper bound on u_ϵ .

Lemma 8. *Let u_ϵ be the solution to equation (42) or (44). Then, for all $x, y \in \mathbb{R}$, we have*

$$u_\epsilon(t, x) \leq \epsilon \ln \left(\rho_M m_{x, \frac{C(1+t)}{\epsilon}} \right),$$

where $m_{x, A} > 0$ is the minimum on \mathbb{R} of $g_{x, A} : y \mapsto A \frac{1 + \max(|x|, |y|)}{1 - e^{-|y-x|A(1 + \max(|x|, |y|))}}$.

In addition, if $A > 0$ we have $A < m_{x, A} \leq A + 3/2$. Thus, we obtain the global upper bound

$$u_\epsilon(t, x) \leq \epsilon \ln \left(\rho_M (3/2 + C(1+t)/\epsilon) \right) \xrightarrow{\epsilon \rightarrow 0} 0.$$

Proof. For all $z \in (x, y)$, by the mean value theorem there exists $\theta_\epsilon(t, x, z)$ between x and y such that

$$u_\epsilon(t, z) = u_\epsilon(t, x) + (z - x) \partial_x u_\epsilon(t, \theta_\epsilon(t, x, z)).$$

In addition, by the previous point there exists C (independent of t, x and ϵ) such that for all t, x , $|\partial_x u_\epsilon(t, x)| \leq C(1+t)(1+|x|)$. Hence

$$u_\epsilon(t, z) \geq u_\epsilon(t, x) - (z - x)C(1+t)(1 + \max(|x|, |y|)).$$

Since we have, for $x < y$,

$$\int_x^y e^{\frac{u_\epsilon(t,z)}{\epsilon}} dz \leq \rho_M,$$

we deduce that

$$\epsilon e^{\frac{u_\epsilon(t,x)}{\epsilon}} \frac{1 - e^{-(y-x) \frac{C(1+t)(1+\max(|x|,|y|))}{\epsilon}}}{C(1+t)(1+\max(|x|,|y|))} \leq \rho_M, \quad \forall y.$$

Then, we compute

$$u_\epsilon(t,x) \leq \epsilon \ln \left(\frac{\rho_M C(1+t)(1+\max(|x|,|y|))}{\epsilon(1 - e^{-(y-x) \frac{C(1+t)(1+\max(|x|,|y|))}{\epsilon}})} \right),$$

and this holds for all $y > x$. We can also choose $y < x$ and get in more generality

$$u_\epsilon(t,x) \leq \epsilon \ln \left(\frac{\rho_M C(1+t)(1+\max(|x|,|y|))}{\epsilon(1 - e^{-|y-x| \frac{C(1+t)(1+\max(|x|,|y|))}{\epsilon}}} \right) = \epsilon \ln \left(\rho_M g_{x, \frac{C(1+t)}{\epsilon}}(y) \right).$$

Observe that $g_{x,A}$ is positive and goes to $+\infty$ at $y = \pm\infty$ and at $y = x$. Minimizing in y , we find that

$$u_\epsilon(t,x) \leq \epsilon \ln \left(\rho_M m_{x, \frac{C(1+t)}{\epsilon}} \right).$$

To conclude we first remark that if $A > 0$ and $x, y \in \mathbb{R}$, then we have

$$\frac{1 + \max(|x|, |y|)}{1 - e^{-|y-x|A(1+\max(|x|,|y|))}} > 1,$$

so $g_{x,A}(y) > A$ for all $y \in \mathbb{R}$ and thus $m_{x,A} > A$. Then, with $A > 0$ we also have

$$g_{1/A,A}(-1/A) = \frac{A+1}{1 - e^{-2(1+A)}} \leq A + 3/2,$$

which implies $m_{x,A} \leq A + 3/2$. Thus, we obtain the global upper bound

$$u_\epsilon(t,x) \leq \epsilon \ln \left(\rho_M(3/2 + C(1+t)/\epsilon) \right) \xrightarrow{\epsilon \rightarrow 0} 0.$$

□

The proof of Theorem 3 is achieved.

References

- [1] Guy Barles. *Solutions de viscosité des équations de Hamilton-Jacobi*, volume 17 of *Mathématiques & Applications (Berlin)*. Springer-Verlag, Paris, 1994.
- [2] Sylvain Billiard, Pierre Collet, Régis Ferrière, Sylvie Méléard, and Viet Chi Tran. Stochastic dynamics for adaptation and evolution of microorganisms. In *European Congress of Mathematics*, pages 525–550. Eur. Math. Soc., Zürich, 2018.
- [3] T. Bourgeron, V. Calvez, J. Garnier, and T. Lepoutre. Existence of recombination-selection equilibria for sexual populations. *ArXiv e-prints*, March 2017.
- [4] Michael George Bulmer. *The mathematical theory of quantitative genetics*. The Clarendon Press, Oxford University Press, New York, 1980. Oxford Science Publications.
- [5] R. Bürger. *The mathematical theory of selection, recombination, and mutation*. Wiley Series in Mathematical and Computational Biology. John Wiley & Sons, Ltd., Chichester, 2000.
- [6] Vincent Calvez, Jimmy Garnier, and Florian Patout. Asymptotic analysis of a quantitative genetics model with nonlinear integral operator. *J. Éc. Polytech. Math.*, 6:537–579, 2019.
- [7] Vincent Calvez and King-Yeung Lam. Uniqueness of the viscosity solution of a constrained Hamilton-Jacobi equation. *Calc. Var. Partial Differential Equations*, 59(5):Paper No. 163, 22, 2020.

- [8] Nicolas Champagnat and Pierre-Emmanuel Jabin. The evolutionary limit for models of populations interacting competitively via several resources. *J. Differential Equations*, 251(1):176–195, 2011.
- [9] M.W. Cheung. Pairwise comparison dynamics for games with continuous strategy space. *J. Econ. Theory*, 153:344–375, 2014.
- [10] M.W. Cheung. Imitative dynamics for games with continuous strategy space. *Games and Economic Behavior*, 99:206–223, 2016.
- [11] Pierre Collet, Sylvie Méléard, and Johan A. J. Metz. A rigorous model study of the adaptive dynamics of Mendelian diploids. *J. Math. Biol.*, 67(3):569–607, 2013.
- [12] Camille Coron, Manon Costa, H el ene Leman, and Charline Smadi. A stochastic model for speciation by mating preferences. *J. Math. Biol.*, 76(6):1421–1463, May 2018.
- [13] Michael G. Crandall, Hitoshi Ishii, and Pierre-Louis Lions. User’s guide to viscosity solutions of second order partial differential equations. *Bull. Amer. Math. Soc. (N.S.)*, 27(1):1–67, 1992.
- [14] Pierre Degond, Amic Frouvelle, and Ga el Raoul. Local stability of perfect alignment for a spatially homogeneous kinetic model. *J. Stat. Phys.*, 157(1):84–112, 2014.
- [15] L. Desvillettes, P. E. Jabin, S. Mischler, and G. Raoul. On selection dynamics for continuous structured populations. *Communications in Mathematical Sciences*, 6(3):729–747, 2008.
- [16] U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400:354–357, 1999.
- [17] O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation: an illuminating example and a Hamilton-Jacobi approach. *Theor. Popul. Biol.*, 67(4):257–271, 2005.
- [18] Michael Doebeli, Hendrik J Blok, Olof Leimar, and Ulf Dieckmann. Multimodal pattern formation in phenotype distributions of sexual populations. *Proc. R. Soc. B*, 274(1608):347–357, 2007.
- [19] Nicolas Fournier and Beno t Perthame. A non-expanding transport distance for some structured equations. working paper or preprint, February 2021.
- [20] J Hofbauer and K. Sigmund. Evolutionary game dynamics. *Bulletin of the American Mathematical Society*, 40:479–519, 2003.
- [21] P. E. Jabin and G. Raoul. On Selection dynamics for competitive interactions. *Journal of Mathematical Biology*, 63(3):493–517, 2011.
- [22] Pierre-Emmanuel Jabin and Hailiang Liu. On a non-local selection-mutation model with a gradient flow structure. *Nonlinearity*, 30(11):4220–4238, 2017.
- [23] E. Kisdi and S. A. H Geritz. Adaptive Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment. *Evolution*, 53(4):993–1008, 1999.
- [24] Pierre-Louis Lions and Panagiotis E. Souganidis. Fully nonlinear stochastic partial differential equations: non-smooth equations and applications. *C. R. Acad. Sci. Paris S er. I Math.*, 327(8):735–741, 1998.
- [25] Alexander Lorz, Tommaso Lorenzi, Jean Clairambault, Alexandre Escargueil, and Beno t Perthame. Modeling the effects of space structure and combination therapies on phenotypic heterogeneity and drug resistance in solid tumors. *Bull. Math. Biol.*, 77(1):1–22, 2015.
- [26] Alexander Lorz, Sepideh Mirrahimi, and Beno t Perthame. Dirac mass dynamics in multidimensional nonlocal parabolic equations. *Comm. Partial Differential Equations*, 36(6):1071–1098, 2011.

- [27] P. Magal and G. Raoul. Dynamics of a kinetic model describing protein exchanges in a cell population. *ArXiv e-prints*, November 2015.
- [28] S. Mirrahimi and G. Raoul. Dynamics of sexual populations structured by a space variable and a phenotypical trait. *Theoretical Population Biology*, 84:87–103, 2013.
- [29] G. Nadin, M. Strugarek, and N. Vauchelet. Hindrances to bistable front propagation, application to *Wolbachia*. *Journal of Mathematical Biology*, 76(6):1489–1533, 2018.
- [30] N. Pasteur and M. Raymond. Insecticide resistance genes in mosquitoes: their mutations, migration, and selection in field populations. *J. Hered.*, 87(6):444–449, 1996.
- [31] Florian Patout. The cauchy problem for the infinitesimal model in the regime of small variance. *ArXiv e-prints*, 2020.
- [32] Benoît Perthame and Guy Barles. Dirac concentrations in Lotka-Volterra parabolic PDEs. *Indiana Univ. Math. J.*, 57(7):3275–3301, 2008.
- [33] Gaël Raoul. Long time evolution of populations under selection and vanishing mutations. *Acta Appl. Math.*, 114(1-2):1–14, 2011.
- [34] W.H. Sandholm. Potential games with continuous player sets. *J. Econ. Theory*, 97:81–103, 2001.
- [35] W.H. Sandholm. *Population Games and Evolutionary Dynamics*. MIT Press, Cambridge, 2010.
- [36] Helio Schechtman and Max O. Souza. Costly Inheritance and the Persistence of Insecticide Resistance in *Aedes aegypti* Populations. *PLOS ONE*, 10(5):1–22, 05 2015.
- [37] M. Strugarek, N. Vauchelet, and J. P. Zubelli. Quantifying the survival uncertainty of *Wolbachia*-infected mosquitoes in a spatial model. *Mathematical Biosciences and Engineering*, 15(4):961–991, 2018.
- [38] J. Tufto. Quantitative genetic models for the balance between migration and stabilizing selection. *Genet. Res.*, 76(3):285–293, 2000.
- [39] M. Turelli and N. H. Barton. Genetic and Statistical Analyses of Strong Selection on Polygenic Traits: What, Me Normal? *Genetics*, 138(3):913–941, 1994.
- [40] G. G. van Doorn and U. Dieckmann. The Long-Term Evolution of Multilocus Traits under Frequency-Dependent Disruptive Selection. *Evolution*, 60(11):2226–2238, 2006.