Time fluctuations in a population model of adaptive dynamics

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Abstract

We study the dynamics of phenotypically structured populations in environments with fluctuations. In particular, using novel arguments from the theories of Hamilton-Jacobi equations with constraints and homogenization, we obtain results about the evolution of populations in environments with time oscillations, the development of concentrations in the form of Dirac masses, the location of the dominant traits and their evolution in time. Such questions have already been studied in time homogeneous environments. More precisely we consider the dynamics of a phenotypically structured population in a changing environment under mutations and competition for a single resource. The mathematical model is a non-local parabolic equation with a periodic in time reaction term. We study the asymptotic behavior of the solutions in the limit of small diffusion and fast reaction. Under concavity assumptions on the reaction term, we prove that the solution converges to a Dirac mass whose evolution in time is driven by a Hamilton-Jacobi equation with constraint and an effective growth/death rate which is derived as a homogenization limit. We also prove that, after long-time, the population concentrates on a trait where the maximum of an effective growth rate is attained. Finally we provide an example showing that the time oscillations may lead to a strict increase of the asymptotic population size.

Key-words: Reaction-diffusion equations, Asymptotic analysis, Hamilton-Jacobi equation, Adaptive dynamics, Population biology, Homogenization.

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1 Introduction

Phenotypically structured populations can be modeled using non-local Lotka-Volterra equations, which have the property that, in the small mutations limit, the solutions concentrate on one or several evolving in time Dirac masses. A recently developed mathematical approach, which uses Hamilton-Jacobi equations with constraint, allows us to understand the behavior of the solutions in constant environments [5, 12, 1, 10].

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Since stochastic and periodic modulations are important for the modeling [9, 14, 15, 8, 16], a natural and relevant question is whether it is possible to further develop the theory to models with time fluctuating environments.

In this note we consider an environment which varies periodically in time in order, for instance, to take into account the effect of seasonal variations in the dynamics, and we study the asymptotic properties of the initial value problem

$$\begin{cases} \varepsilon\, n_{\varepsilon,t} = n_\varepsilon\, R\big(x, \tfrac{t}{\varepsilon}, I_\varepsilon(t)\big) + \varepsilon^2 \Delta n_\varepsilon \quad \text{in} \quad \mathbb{R}^N \times (0,\infty), \\ n_\varepsilon(\cdot, 0) = n_{0,\varepsilon} \quad \text{in} \quad \mathbb{R}^N, \\ I_\varepsilon(t) := \int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x,t)dx, \end{cases} \tag{1}$$

where

$$R : \mathbb{R}^N \times \mathbb{R} \times [0,\infty) \to \mathbb{R} \quad \text{is smooth and 1-periodic in its second argument.} \tag{2}$$

The population is structured by phenotypical traits $x \in \mathbb{R}^N$ with density $n_\varepsilon(x,t)$ at time t. It is assumed that there exists a single type of resource which is consumed by each individual trait x at a rate $\psi(x)$; $I_\varepsilon(t)$ is then the total consumption of the population. The mutations and the growth rate are represented respectively by the Laplacian term and R. The novelty is the periodic in time dependence of the growth rate R. The small coefficient ε is used to consider only rare mutations and to rescale time in order to study a time scale much larger than the generation one.

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

$$\max_{0 \le s \le 1,\ x \in \mathbb{R}^N} R(x, s, I_M) = 0 \quad \text{and} \quad \mathcal{X} := \{x \in \mathbb{R}^N,\ \int_0^1 R(x,s,0)ds > 0\} \neq \emptyset. \tag{3}$$

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

$$-2K_1 \le D_x^2 R(x,s,I) \le -2K_2, \qquad -K_3 - K_1|x|^2 \le R(x,s,I) \le K_4 - K_2|x|^2, \tag{4}$$

$$-K_5 \le D_I R(x,s,I) \le -K_6, \tag{5}$$

$$D_x^3 R \in L^\infty\big(\mathbb{R}^N \times (0,1) \times [0,A]\big) \quad \text{and} \quad |D_{x,I}^2 R| \le K_7. \tag{6}$$

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

$$0 < \psi_m \le \psi \le \psi_M \quad \text{and} \quad \|\psi\|_{C^2} \le K_8. \tag{7}$$

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

$$n_{0,\varepsilon} = e^{u_\varepsilon^0/\varepsilon} \ \text{ and, as } \varepsilon \to 0, \tag{8}$$

$$n_\varepsilon(\cdot,0) \underset{\varepsilon\to 0}{\longrightarrow} \varrho^0\delta(\cdot - x^0) \quad \text{weakly in the sense of measures.} \tag{9}$$

In addition there exist constants $L_i > 0, i = 1, \ldots, 4$, and a smooth $u^0 : \mathbb{R}^N \to \mathbb{R}$ such that, for all $x \in \mathbb{R}^N$,

$$-2L_1 I \le D_x^2 u_\varepsilon^0 \le -2L_2 I, \quad -L_3 - L_1|x|^2 \le u_\varepsilon^0(x) \le L_4 - L_2|x|^2, \quad \max_{x\in\mathbb{R}^N} u^0(x) = 0 = u^0(x^0) \tag{10}$$

and, as $\varepsilon \to 0$,

$$u_\varepsilon^0 \longrightarrow u^0 \quad \text{locally uniformly in } \mathbb{R}^N. \tag{11}$$

Finally, in order to ensure the same control on D^2u as for D^2u^0, it is necessary to impose the following compatibility relation on the parameters in the initial data and in the growth rate R:

$$4L_2^2 \le K_2 \le K_1 \le 4L_1^2. \tag{12}$$

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

Lemma 1.1. *Assume (3), (5) and (7). For all $x \in \mathcal{X}$, there exists a unique 1-periodic positive solution $\mathcal{I}(x,s) : [0,1] \to (0, I_M)$ to*

$$\begin{cases} \frac{d}{ds}\mathcal{I}(x,s) = \mathcal{I}(x,s)\ R\big(x,s,\mathcal{I}(x,s)\big), \\ \mathcal{I}(x,0) = \mathcal{I}(x,1). \end{cases} \tag{13}$$

Moreover, as $\mathcal{X} \ni x \to x_0 \in \partial\mathcal{X}$,

$$\max_{0\le s\le 1} \mathcal{I}(x,s) \to 0. \tag{14}$$

In view of (14), for $x \in \partial\mathcal{X}$, we define, by continuity, $\mathcal{I}(x,s) = 0$. The function $\mathcal{I}(x,s)$ helps us to identify the weak limit of $I_\varepsilon(t)$ (see Lemma 2.1). It also helps to derive, using a homogenization process, an effective growth rate $\mathcal{R}$ which will replace R (see Theorem 1.2) and is defined, for all $x \in R^N$ and $y \in \overline{\mathcal{X}}$ (here $\overline{\mathcal{X}}$ stands for the closure of $\mathcal{X}$), by

$$\mathcal{R}(x,y) := \int_0^1 R(x,s,\mathcal{I}(y,s))ds. \tag{15}$$

Notice that, integrating (15) above in s and using the periodicity, we always have, for $x \in \overline{\mathcal{X}}$,

$$\mathcal{R}(x,x) \equiv 0. \tag{16}$$

Moreover, if $y \in \partial\mathcal{X}$, then $\mathcal{R}(x,y) = \int_0^1 R(x,s,0)ds$. Finally, it is immediate from (4) and (15), that $\mathcal{R}(x,y)$ is strictly concave in the first variable.

Our first result is about the behavior of the n_ε's as $\varepsilon \to 0$. It asserts the existence of a fittest trait $\overline{x}(t)$ and a total population size $\overline{\rho}(t)$ at time t and provides a "canonical equation" for the evolution in time of $\overline{x}$ in terms of the "effective fitness" $\mathcal{R}(x,y)$. In the sequel, $D_1\mathcal{R}$ denotes the derivative of $\mathcal{R}$ with respect to the first argument.

Theorem 1.2 (Limit as $\varepsilon \to 0$)**.** *Assume (2)–(12). There exist a fittest trait* $\overline{x} \in \mathrm{C}^1([0,\infty);\mathcal{X})$ *and a total population size* $\overline{\rho} \in \mathrm{C}^1([0,\infty);(0,\infty))$ *such that, along subsequences* $\varepsilon \to 0$,

$$n_\varepsilon(\cdot,t) \longrightarrow \overline{\varrho}(t)\delta(\cdot - \overline{x}(t)) \quad \text{weakly in the sense of measures,}$$

$$I_\varepsilon \longrightarrow \overline{I} := \overline{\varrho}\psi(\overline{x}) \quad \text{in } L^\infty(0,\infty) \text{ weak-}\star,$$

and

$$R(x, \frac{t}{\varepsilon}, I_\varepsilon(t)) \longrightarrow \mathcal{R}(x, \overline{x}(t)) \quad \text{weakly in the sense of measures in } t \text{ and strongly in } x.$$

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

$$\dot{\overline{x}}(t) = \left(-D_x^2 u(\overline{x}(t),t)\right)^{-1} \cdot D_1\mathcal{R}(\overline{x}(t),\overline{x}(t)). \tag{17}$$

We note that, in the language of adaptive dynamics, $\mathcal{R}(y,x)$ can be interpreted as the effective fitness of a mutant y in a resident population with a dominant trait x, while $D_1\mathcal{R}$ is usually called the selection gradient, since it represents the capability of invasion. The extra term $\left(-D_x^2 u(\overline{x}(t),t)\right)^{-1}$ is an indicator of the diversity around the dominant trait in the resident population.

The second issue is the identification of the long time limit of the fittest trait $\overline{x}$. We prove that, in the limit $t \to \infty$, the population converges to a, so called, Evolutionary Stable Distribution (ESD) corresponding to a distribution of population which is stable under introduction of small mutations (see [11, 6, 7] for a more detailed definition). See also [4, 13] for recent studies of the local and global stability of stationary solutions of integro-differential population models in constant environments.

Theorem 1.3 (Limit as $t \to \infty$)**.** *In addition to (2)–(12) assume that either* $N = 1$ *or, if* $N > 1$, R *is given, for some smooth* $b, d, B, D : \mathbb{R}^N \to (0,\infty)$ *by*

$$R(x,s,I) = b(x)B(s,I) - d(x)D(s,I). \tag{18}$$

Then, as $t \to \infty$, *the population reaches an Evolutionary Stable Distribution* $\overline{\varrho}_\infty\delta(\cdot - \overline{x}_\infty)$, *i.e.,* $\overline{\varrho}(t) \longrightarrow \overline{\varrho}_\infty$ *and* $\overline{x}(t) \longrightarrow \overline{x}_\infty$, *where* $\overline{\varrho}_\infty > 0$ *and* $\overline{x}_\infty$ *are characterized by (*$\mathcal{I}$ *is defined in (13))*

$$\mathcal{R}(\overline{x}_\infty,\overline{x}_\infty) = 0 = \max_{x\in\mathbb{R}^N} \mathcal{R}(x,\overline{x}_\infty) \quad \text{and} \quad \overline{\varrho}_\infty = \frac{1}{\psi(\overline{x}_\infty)}\int_0^1 \mathcal{I}(\overline{x}_\infty,s)ds. \tag{19}$$

The proof of the above result for a growth rate R given by (18) is based on a Lyapunov functional defined by

$$L(t) := \frac{b(\overline{x}(t))}{d(\overline{x}(t))}.$$

Notice that we do not claim the uniqueness of the Evolutionary Stable Distribution. Indeed there may exist several $(\rho_\infty, \overline{x}_\infty)$ satisfying (19). Here we only prove that there exists $(\rho_\infty, \overline{x}_\infty)$ satisfying (19) such that, as $t \to \infty$, the population converges to $\varrho_\infty\delta(\cdot - \overline{x}_\infty)$.

The difference between our conclusions and the results for time homogeneous environments in [10] is that, in the canonical equation (17), the growth rate R is replaced by an effective growth rate $\mathcal{R}$ which is derived after a homogenization process. Moreover, we are only able to prove that the I_ε's converge in L^∞ weak-$*$ and not a.e., which is the case for constant environments in [10]. This adds a difficulty in Theorem 1.3 and it is the reason why we are not able to describe, without additional assumptions, the long-time limit behavior of the fittest trait $\overline{x}$ for general growth rate R when $N > 1$. This remains an open question.

In Section 3.3, we give an example of $\mathcal{R}$ not satisfying the assumptions of Theorem 1.3 for which $\overline{x}(t)$ exhibits a periodic behavior. This example fits the structure (22) below with general concavity properties on $\mathcal{R}$ but it is not necessarily derived from a homogenization limit.

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

$$u_\varepsilon = \varepsilon \ln n_\varepsilon, \tag{20}$$

which yields the following Hamilton-Jacobi equation for u_ε :

$$\begin{cases} u_{\varepsilon,t} = R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big) + |D_x u_\varepsilon|^2 + \varepsilon \Delta u_\varepsilon & \text{in } \mathbb{R}^N \times (0,\infty), \\ u_\varepsilon(\cdot, 0) = u_\varepsilon^0, & \text{in } \mathbb{R}^N. \end{cases} \tag{21}$$

The next theorem describes the behavior of the u_ε's, as $\varepsilon \to 0$ (recall that $\mathcal{R}$ is defined in Section 2).

Theorem 1.4. *Assume (2)–(12). Along subsequences $\varepsilon \to 0$, $u_\varepsilon \to u$ locally uniformly in $\mathbb{R}^N \times [0,\infty)$, where $u \in \mathrm{C}(\mathbb{R}^N \times [0,\infty))$ is a solution of*

$$\begin{cases} u_t = \mathcal{R}(x, \overline{x}(t)) + |D_x u|^2 & \text{in } \mathbb{R}^N \times (0,\infty), \\ \max\limits_{x \in \mathbb{R}^N} u(x,t) = 0 = u(\overline{x}(t), t) & \text{in } (0,\infty), \\ u(\cdot, 0) = u^0 & \text{in } \mathbb{R}^N. \end{cases} \tag{22}$$

Note that the convergence of the u_ε's in Theorem 1.4 and, thus, the convergence of the n_ε's in Theorem 1.2 are established only along subsequences. To prove convergence for all ε, we need that (22) has a unique solution. This is, however, not known even for non oscillatory environments except for some particular form of growth rate R (see [2, 12]).

When the environment is time homogeneous, it is possible to derive such Hamilton-Jacobi equations without any concavity assumption on R and u^0 (see [12, 1]). However, here we need assumptions (4), (10) and (12) to ensure a priori that n_ε goes to a single Dirac mass at the point $\overline{x}(t)$. This information is needed in order to write (22). We also point out that, for $x \in \mathbb{R}$, R is monotonic with respect to x and without the concavity assumption, it is possible to show that the n_ε's still converge to a single Dirac mass. This suggests that it may be possible to relax the concavity assumptions in this latter case or in similar situations where such information is known a priori. Here, however, we concentrate on the difficulty coming from the time fluctuations and do not try to state a more general result.

In Section 4 we consider a non-concave rate of the form

$$R(x, s, I) = b(x)B(s, I) - D(s, I),$$

and show that the effective growth rate $\mathcal{R}$ can be computed independently of $\overline{x}(t)$ and has the form

$$\mathcal{R}(x, F) = \int_0^1 \mathcal{I}(F, s) ds \left(\frac{b(x)}{F} - 1 \right),$$

with

$$F(t) := \lim_{\varepsilon \to 0} \frac{\int \psi(x)\, b(x)\, n_\varepsilon(x, t)\, dx}{I_\varepsilon(t)},$$

in the Hamilton-Jacobi limit. Note that, if the $(n_\varepsilon)_\varepsilon$'s converge to a single Dirac mass $\rho(t)\delta(x - \overline{x}(t)$, then we can compute $F(t) = b(\overline{x}(t))$. This example is even more interesting, since it is possible to compute explicitly the effective growth rate $\mathcal{R}$, while, in general, not much is known about the structure of $\mathcal{R}$.

In Section 5, we study the particular case

$$R(x, I) = b(x) - D_1(s)D_2(I).$$

We compute the population size at the evolutionary stable state of the oscillatory model and compare it to the one of a non oscillatory averaged environment. We observe that the time oscillations lead to a strict increase in the population size. This example emphasizes the importance of including the time oscillations in population models.

The paper is organized as follows. In Section 2 we study the asymptotic behavior of the solution under rare mutations (limit $\varepsilon \to 0$) and we provide the proofs of Theorems 1.2 and 1.4. In Section 3 we consider the long time behavior of the dynamics (limit $t \to \infty$) and we give the proof of Theorem 1.3. In Section 4 we study a particular form of growth rate R, for which the results can be proved without any concavity assumptions on R and the effective growth rate $\mathcal{R}$ has a natural structure. Finally in Section 5 we present an example of an oscillatory environment which yields an asymptotic effective population density that is strictly larger than the averaged one.

2 The behavior as $\varepsilon \to 0$ and the proofs of Theorems 1.2 and 1.4

We present the proofs of Theorems 1.2 and 1.4 which are closely related. Since the argument is long, we next summarize briefly the several steps. First we obtain some a priori bounds on u_ε and I_ε. Then we identify the equation for the fittest trait $\overline{x}$. The limit of the I_ε's is studied in Lemma 1.1. The last three steps are the identification (and properties) of the effective growth rate $\mathcal{R}$, the effective Hamilton-Jacobi equation and the canonical equation.

Proofs of Theorems 1.2 and 1.4 . Step 1: a priori bounds. Multiplying (1) by $\psi(x)$, integrating with respect to x, it and arguing as in [10], we find, that for all $t \geq 0$,

$$0 < I_\varepsilon(t) \leq I_M + O(\varepsilon). \tag{23}$$

Next we differentiate (21) twice with respect to x and use (4), (10), (12) and the maximum principle to get, for some C_1, $C_2>0$, $\varepsilon\le 1$ and all $(x,t)\in\mathbb{R}^N\times[0,\infty)$,

$$-2L_1\le D_x^2u_\varepsilon\le -2L_2 \quad\text{and}\quad -L_3-L_1|x|^2-C_1t\le u_\varepsilon(x,t)\le L_4-L_2|x|^2+C_2t. \tag{24}$$

Note that to obtain the second inequality, we do not need to differentiate with respect to x, but use directly the maximum principle for (21) and the fact that the lower and upper bounds are respectively sub- and super-solutions. For a detailed proof of (24) see Appendix A.

It follows from the uniform bounds on u_ε and $D^2_{xx}u_\varepsilon$ that D_xu_ε is locally uniformly bounded and, hence, we obtain, from (21), that, for all balls B_R centered at the origin and of radius R, there exists $C_3=C_3(R)>0$ such that

$$\|u_{\varepsilon,t}(x,t)\|_{L^\infty(B_R\times(0,\infty))}\le C_3. \tag{25}$$

Finally the regularity properties of the "viscous" Hamilton-Jacobi equations and (6) yield that, for all $T>0$, there exists $C_4=C_4(R,T)>0$ such that

$$\|D_x^3u_\varepsilon\|_{L^\infty(B_R\times[0,T])}\le C_4. \tag{26}$$

Hence, after differentiating (21) in x, the previous estimates yield a $C_5=C_5(R,T)>0$ such that

$$\|D^2_{t,x}u_\varepsilon\|_{L^\infty(B_R\times[0,T])}\le C_5. \tag{27}$$

All the above bounds allow us to pass to the limit, along subsequences $\varepsilon\to 0$, and to obtain $u:\mathbb{R}^N\times[0,\infty)\to\mathbb{R}$ such that, as $\varepsilon\to0$,

$$u_\varepsilon\longrightarrow u \;\text{ in }\; C_{\rm loc}(\mathbb{R}^N\times[0,\infty)) \quad\text{and, for all } T>0 \text{ and } (x,t)\in\mathbb{R}^N\times[0,T],$$
$$-2L_1\le D_x^2u(x,t)\le -2L_2 \quad\text{and}\quad u, D^2_{t,x}u, D^3_xu\in L^\infty(\mathbb{R}^N\times[0,T]).$$

For more details on the above arguments see [10].

Step 2. The fittest trait. In view of the strict concavity of u_ε, for each $\varepsilon>0$, there exists a unique $\overline{x}_\varepsilon(t)$ such that

$$u_\varepsilon(\overline{x}_\varepsilon(t),t)=\max_{x\in\mathbb{R}^N}u_\varepsilon(x,t) \quad\text{and}\quad D_xu_\varepsilon(\overline{x}_\varepsilon(t),t)=0.$$

Differentiating the latter equality with respect to t and using (21) we find

$$\dot{\overline{x}}_\varepsilon(t)\cdot D_x^2u_\varepsilon(\overline{x}_\varepsilon(t),t)=-D_xu_{\varepsilon,t}(\overline{x}_\varepsilon(t),t)$$
$$=-D_xR\big(\overline{x}_\varepsilon(t),\frac{t}{\varepsilon},I_\varepsilon(t)\big)-2D_x^2u_\varepsilon(\overline{x}_\varepsilon(t),t)\cdot D_xu_\varepsilon(\overline{x}_\varepsilon(t),t)-\varepsilon\Delta D_xu_\varepsilon(\overline{x}_\varepsilon(t),t)$$
$$=-D_xR\big(\overline{x}_\varepsilon(t),\frac{t}{\varepsilon},I_\varepsilon(t)\big)-\varepsilon\Delta D_xu_\varepsilon(\overline{x}_\varepsilon(t),t).$$

Since $D_x^2u_\varepsilon(\overline{x}_\varepsilon(t),t)$ is invertible and $\|D_x^3u\|_{L^\infty(B_R\times[0,T])}\le C_4$, it follows that $\dot{\overline{x}}_\varepsilon(t)$ is bounded in $(0,T)$, and, hence, along subsequences $\varepsilon\to0$, $\overline{x}_\varepsilon\to\overline{x}$ in $C_{\rm loc}((0,\infty))$, for some $\overline{x}\in C^{0,1}((0,\infty))$ such that

$$\begin{cases} u(\overline{x}(t),t)=\max_{x\in\mathbb{R}^N}u(x,t), \qquad D_xu(\overline{x}(t),t)=0,\\ \text{and}\\ \dot{\overline{x}}(t)=\big(-D_x^2u(\overline{x}(t),t)\big)^{-1}\cdot D_x\Big\langle R\big(\overline{x}(t),\frac{t}{\varepsilon},I_\varepsilon(t)\big)\Big\rangle, \end{cases} \tag{28}$$

where the bracket denotes the weak limit of $R\big(\overline{x}(t), \frac{t}{\varepsilon}, I_\varepsilon(t)\big)$ which exists, since R is locally bounded.

Step 3. The weak limit of I_ε. To identify the weak limit of the I_ε's, we consider the first exit time $T^* > 0$ of $\overline{x}$ from $\mathcal{X}$, i.e., the smallest time $T^* > 0$ such that $\overline{x}(t) \in \mathcal{X}$ for all $0 \le t < T^*$ and $\overline{x}(T^*) \in \partial\mathcal{X}$ if $T^* < \infty$. Note that T^* is well defined since $\overline{x}(0) = x^0 \in \mathcal{X}$. The last step of the ongoing proof is to show that $T^* = \infty$.

The weak limit of the I_ε's for $t \in (0, T^*)$ follows from Lemma 1.1 and the lemma below. Their proofs are given after the end of the ongoing one.

Lemma 2.1. *Assume (3), (5) and (7). Let T_ε^* be the smallest time $T_\varepsilon^* > 0$ such that $\overline{x}_\varepsilon(t) \in \mathcal{X}$ for all $0 \le t < T_\varepsilon^*$ and $\overline{x}(T_\varepsilon^*) \in \partial\mathcal{X}$ if $T_\varepsilon^* < \infty$. Then, for all $0 < t < T_\varepsilon^*$,*

$$\Big|\ln I_\varepsilon(t) - \ln \mathcal{I}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon})\Big| \le \Big|\ln I_\varepsilon(0) - \ln \mathcal{I}(\overline{x}_\varepsilon(0), 0)\Big| e^{-\frac{K_6 t}{\varepsilon}} + C\sqrt{\varepsilon},$$

where C only depends on the constants K_i. Moreover, as $\varepsilon \to 0$, $T_\varepsilon^* \to T^*$. Consequently, if $\overline{x}(t) \in \mathcal{X}$ for $0 \le t < T^*$ and $\overline{x}(T^*) \in \partial\mathcal{X}$, then, as $\varepsilon \to 0$ and $t \to T^*$, $I_\varepsilon(t) \longrightarrow 0$.

It follows that, as $\varepsilon \to 0$,

$$I_\varepsilon(\cdot) \rightharpoonup \overline{I}(\cdot) = \int_0^1 \mathcal{I}(\overline{x}(\cdot), s) ds > 0 \qquad \text{in } L^\infty((0, T^*)) \text{ weak-}\star. \tag{29}$$

Once $\overline{I}$ is known, it is possible to compute the weight $\overline{\varrho}$ of the Dirac mass. Indeed, we show in the next steps that, as $\varepsilon \to 0$,

$$I_\varepsilon(\cdot) = \int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x, \cdot) dx \rightharpoonup \overline{I}(\cdot) = \overline{\varrho}(\cdot)\psi(\overline{x}(\cdot)) \quad \text{in } L^\infty((0, T^*)) \text{ weak-}\star.$$

Step 4. The effective growth rate. We can now explain the average used to determine the effective growth rate. Again (5) and Lemma 2.1 yield that, as $\varepsilon \to 0$,

$$\int_0^{T^*} \Big|R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big) - R\big(x, \frac{t}{\varepsilon}, \mathcal{I}(\overline{x}(t), \frac{t}{\varepsilon})\big)\Big| dt \le K_5 \int_0^{T^*} \big|I_\varepsilon(t) - \mathcal{I}(\overline{x}(t), \frac{t}{\varepsilon})\big| dt \longrightarrow 0.$$

Therefore the weak limit in (28) is computed as the weak limit (in time) of $R\big(x, \frac{t}{\varepsilon}, \mathcal{I}(\overline{x}(t), \frac{t}{\varepsilon})\big)$. It follows that, for $0 \le t \le T^*$,

$$\Big\langle R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big)\Big\rangle = \mathcal{R}(x, \overline{x}(t)), \tag{30}$$

where $\mathcal{R}$ is defined by (15).

Step 5. The limiting Hamilton-Jacobi equation. It is now possible to pass to the limit $\varepsilon \to 0$ in (21) for $(x, t) \in \mathbb{R}^N \times [0, T^*)$. To this end, observe that

$$\varphi_\varepsilon(x, t) := u_\varepsilon(x, t) - \int_0^t R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau$$

solves

$$\varphi_{\varepsilon,t} - \varepsilon\Delta\varphi_\varepsilon = \varepsilon \int_0^t \Delta R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau + |D_x\varphi_\varepsilon + \int_0^t D_x R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau|^2.$$

Since the u_ε's converges locally uniformly from Step 1 and $R\left(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\right)$ converges weakly in t and strongly in x to $\mathcal{R}\left(x, \overline{x}(t)\right)$ from Step 2, we find that, as $\varepsilon \to 0$,

$$\varphi_\varepsilon(x,t) \longrightarrow \varphi(x,t) = u(x,t) - \int_0^t \mathcal{R}\left(x, \overline{x}(\tau)\right) d\tau \quad \text{in } \ C_{\text{loc}}(\mathbb{R}^N \times (0,T^*)).$$

Moreover, in view of (4), (6) and Lemma 1.1, for any $T \in (0,T^*)$ and $R > 0$, there exists $C = C(R,T) > 0$ such that, for $(x,t) \in B_R \times [0,T]$

$$\left| \int_0^t \Delta R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau \right| \leq C,$$

and, as $\varepsilon \to 0$,

$$\int_0^t |D_x R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau - D_x R\left(x, \frac{\tau}{\varepsilon}, \mathcal{I}(\overline{x}(\tau), \frac{\tau}{\varepsilon})\right) |d\tau \leq K_7 \int_0^T \left|I_\varepsilon(t) - \mathcal{I}(\overline{x}(t), \frac{t}{\varepsilon})\right| dt \longrightarrow 0.$$

Thus, as $\varepsilon \to 0$ and for all $(x,t) \in B_R \times [0,T]$,

$$\int_0^t D_x R\left(x, \frac{\tau}{\varepsilon}, I_\varepsilon(\tau)\right) d\tau \longrightarrow \int_0^t D_1\mathcal{R}\left(x, \overline{x}(\tau)\right) d\tau.$$

It follows from the stability of viscosity solutions that φ is a viscosity solution to

$$\varphi_t = \left|D_x\varphi + \int_0^t D_1\mathcal{R}\left(x, \overline{x}(\tau)\right) d\tau\right|^2 \text{ in } \ \mathbb{R}^N \times (0,T^*),$$

which, written in terms of u, reads

$$u_t = \mathcal{R}\big(x, \overline{x}(t)\big) + |D_x u|^2 \text{ in } \ \mathbb{R}^N \times (0,T^*).$$

The constraint $\max_{x\in\mathbb{R}^N} u(x,t) = 0$ follows from (20) and (23) (see [12, 1]). We then conclude following [12] that, for all $t \in (0,T^*)$,

$$n_\varepsilon(\cdot,t) \longrightarrow \overline{\varrho}(t)\delta(\cdot - \overline{x}(t)) \quad \text{weakly in the sense of measures.}$$

Step 6. The canonical equation. The canonical equation (17) now follows from (28) and (30).

Step 7. The global time $T^* = \infty$. Assume $T^* < \infty$. Then $\overline{x}(T^*) \in \partial\mathcal{X}$. It follows from the canonical equation (17) that, for all $t \in (0,T^*)$,

$$\begin{aligned} \tfrac{d}{dt} \textstyle\int_0^1 R(\overline{x}(t), s, 0) ds \ &= \dot{\overline{x}}(t) \textstyle\int_0^1 D_x R(\overline{x}(t), s, 0) ds \\ &= D_1\mathcal{R}\big(\overline{x}(t), \overline{x}(t)\big)\big(-D^2 u(\overline{x}(t), t)\big)^{-1} \textstyle\int_0^1 D_x R(\overline{x}(t), s, 0) ds, \end{aligned}$$

while, when $t = T^*$, Lemma 2.1 yields that $D_1\mathcal{R}\big(\overline{x}(t), \overline{x}(t)\big) = \int_0^1 D_x R(\overline{x}(t), s, 0) ds$. Hence

$$\frac{d}{dt} \int_0^1 R(\overline{x}(T^*), s, 0) ds > 0,$$

which is a contradicition because, by the definition of the open set $\mathcal{X}$, $\int_0^1 R(\overline{x}(t), s, 0) ds > 0$ for $t \in [0,T^*)$ and $\int_0^1 R(\overline{x}(T^*), s, 0) ds = 0$. □

Proof of Lemma 1.1. First we prove that, for a fixed $x \in \mathcal{X}$, there exists a solution $\mathcal{I}$ of (13). To this end observe that $\mathcal{J} := \ln \mathcal{I}$ solves

$$\begin{cases} \frac{d}{ds}\mathcal{J}(x,s) = R\big(x,s,\exp(\mathcal{J}(x,s)\big) \text{ in } \; s \in [0,1], \\ \mathcal{J}(x,0) = \alpha. \end{cases} \tag{31}$$

It turns out that it is possible to choose $\alpha \leq \ln I_M$ so that $\mathcal{J}(x,0) = \mathcal{J}(x,1)$. Indeed, the definition of I_M in (3) yields that, if $\alpha = \ln I_M$, then $\mathcal{J}(x,1) < \alpha$. On the other hand, for α very small we claim that $\mathcal{J}(x,1) > \alpha$, which is enough to conclude, since $\mathcal{J}(x,s)$ been a continuous increasing function of α, it has a fixed point α^*. Choosing $\alpha = \alpha^*$ yields a periodic solution.

To prove the claim, we set $\mu = \int_0^1 R(x,s,0)ds > 0$ since $x \in \mathcal{X}$. Because R is locally bounded, there exists a constant $C > 0$, which is independent of α, such that $\mathcal{J}(x,s) \leq \alpha + C$ and, for α small enough,

$$\mathcal{J}(x,1) = \mathcal{J}(x,0) + \int_0^1 R(x,s,\exp(\mathcal{J}(x,s)\big)ds \geq \mathcal{J}(x,0) + \int_0^1 R(x,s,0\big)ds + O(e^\alpha) \geq \mathcal{J}(x,0) + \frac{\mu}{2}.$$

This proves the claim and the existence of a periodic solution.

The uniqueness follows from a contraction argument. Indeed let $\mathcal{J}_1$ and $\mathcal{J}_2$ be two periodic solutions to (31). Then

$$\frac{d}{ds}(\mathcal{J}_1 - \mathcal{J}_2) = R\big(x,s,\exp(\mathcal{J}_1(x,s)\big) - R\big(x,s,\exp(\mathcal{J}_2(x,s)\big).$$

Multiplying the above equation by sgn $(\mathcal{J}_1 - \mathcal{J}_2)$ and using the monotonicity in I according to (5), we find

$$\frac{d}{ds}\big|\mathcal{J}_1 - \mathcal{J}_2\big| \leq -C\big|\mathcal{J}_1 - \mathcal{J}_2\big|,$$

and, after integration,

$$C \int_0^1 \big|\mathcal{J}_1(s) - \mathcal{J}_2(s)\big|ds \leq -|\mathcal{J}_1(1) - \mathcal{J}_2(1)| + |\mathcal{J}_1(0) - \mathcal{J}_2(0)| = 0,$$

and, hence, $\mathcal{J}_1 = \mathcal{J}_2$.

Finally we prove (14). It follows from (31) that, for $x \in \mathcal{X}$,

$$0 = \int_0^1 R(x,s,e^{\mathcal{J}(x,s)})ds \leq \int_0^1 R(x,s,0)ds - K_6 e^{\min_{0\leq s\leq 1}\mathcal{J}(x,s)}.$$

If $x \to x_0 \in \partial\mathcal{X}$, then $\int_0^1 R(x,s,0)ds \to 0$ and, since the variations of $\mathcal{J}(x,s)$ are bounded, because R is locally bounded, the result follows. □

Proof of Lemma 2.1. We identify the weak limit of I_ε and prove (29). We begin with the observation that in the "gaussian"- type concentration, $x - \overline{x}_\varepsilon(t)$ scales as $\sqrt{\varepsilon}$.

Indeed multiplying (1) by ψ and integrating with respect to x we find (recall that with $J_\varepsilon := \ln I_\varepsilon$),

$$\varepsilon \frac{d}{dt} J_\varepsilon(t) = \frac{\int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x,t) \; R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big)dx}{\int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x,t)dx} + \varepsilon^2 \frac{\int_{\mathbb{R}^N} \Delta\psi(x) \; n_\varepsilon(x,t)dx}{\int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x,t)}.$$

Note that in order to justify the integration by parts above, we first replace ψ by $\psi_L = \chi_L\psi$ where χ_L is a compactly supported smooth function such that $\chi_L \equiv 1$ in $\mathrm{B}(0,\mathrm{L})$ and $\chi_L \equiv 0$ in $\mathbb{R}^N \backslash \mathrm{B}(0,2\mathrm{L})$. Then we integrate by parts and finally let $L \to +\infty$.
Returning to the above equation we find

$$\varepsilon \frac{d}{dt} J_\varepsilon(t) = \frac{\int_{\mathbb{R}^N} \psi(x) e^{\frac{u_\varepsilon(x,t) - u_\varepsilon(\overline{x}_\varepsilon(t),t)}{\varepsilon}} R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big) dx}{\int_{\mathbb{R}^N} \psi(x) e^{\frac{u_\varepsilon(x,t) - u_\varepsilon(\overline{x}_\varepsilon(t),t)}{\varepsilon}} dx} + O(\varepsilon^2)$$

$$= \frac{\int_{\mathbb{R}^N} \psi(x) e^{\frac{u_\varepsilon(x,t) - u_\varepsilon(\overline{x}_\varepsilon(t),t)}{\varepsilon}} \big[R\big(x, \frac{t}{\varepsilon}, I_\varepsilon(t)\big) - R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, I_\varepsilon(t)\big)\big] dx}{\int_{\mathbb{R}^N} \psi(x) e^{\frac{u_\varepsilon(x,t) - u_\varepsilon(\overline{x}_\varepsilon(t),t)}{\varepsilon}} dx} + R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, I_\varepsilon(t)\big) + O(\varepsilon^2).$$

Using Laplace's method for approximation of integrals, (24) and (26), we find that the first term is of order $\sqrt{\varepsilon}$ and, hence,

$$\varepsilon \frac{d}{dt} J_\varepsilon(t) = R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, I_\varepsilon(t)\big) + O(\sqrt{\varepsilon}).$$

Next we compute

$$\varepsilon \frac{d}{dt}[\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}) - J_\varepsilon(t)] = R\Big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, \exp\big(\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon})\big)\Big) - R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, \exp(J_\varepsilon(t))\big)$$
$$+ O(\sqrt{\varepsilon}) + \varepsilon\, D_x\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon})\, \dot{\overline{x}}_\varepsilon(t).$$

Multiplying the above equality by $\mathrm{sgn}(\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}) - J_\varepsilon(t))$, using our previous estimates and employing the monotonicity property in (5), we get

$$\varepsilon \frac{d}{dt}\big|\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}) - J_\varepsilon(t)\big| = -\big|R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, \exp(\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}))\big) - R\big(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}, \exp(J_\varepsilon(t))\big)\big| + O(\sqrt{\varepsilon})$$

$$\leq -K_6\big|\mathcal{J}(\overline{x}_\varepsilon(t), \frac{t}{\varepsilon}) - J_\varepsilon(t)\big| + O(\sqrt{\varepsilon}).$$

The first claim of Lemma 2.1 is now immediate. Moreover, since $\overline{x}_\varepsilon(t) \to \overline{x}(t)$, locally uniformly as $\varepsilon \to 0$, we obtain that, as $\varepsilon \to 0$,

$$T_\varepsilon^* \to T^*.$$

The last claim is a consequence of the previous steps and Lemma 1.1. □

3 The long time behavior

3.1 Convergence as $t \to \infty$ when $N = 1$ (The proof of Theorem 1.3 (i))

Throughout this subsection we assume that $N = 1$. The goal is to prove the existence of some $\overline{x}_\infty \in \mathbb{R}^N$ such that, as $t \to \infty$, $\overline{x}(t) \to \overline{x}_\infty$ and

$$\mathcal{R}(\overline{x}_\infty, \overline{x}_\infty) = 0 = \max_{x \in R} \mathcal{R}(x, \overline{x}_\infty). \tag{32}$$

To this end, we consider the map $A : \mathbb{R} \longrightarrow \mathbb{R}$ defined by $A(x) = y$, where y is the unique maximum point of $\mathcal{R}(\cdot, x)$. We obviously have

$$D_x\mathcal{R}(A(x), x) = 0.$$

We consider the following three cases depending on the comparison between $\overline{x}(\cdot)$ and $A(\overline{x}(\cdot))$. If $\overline{x}(t) < A(\overline{x}(t))$, then $D_x\mathcal{R}(\overline{x}(t), \overline{x}(t)) > 0$ and, if $\overline{x}(t) > A(\overline{x}(t))$, then $D_x\mathcal{R}(\overline{x}(t), \overline{x}(t)) < 0$. It then follows using (17) and the concavity of u that, if $\overline{x}(t) < A(\overline{x}(t))$ (resp. $\overline{x}(t) > A(\overline{x}(t))$), then $\dot{\overline{x}}(t) > 0$ (resp. $\dot{\overline{x}}(t) < 0$). If $\overline{x}(t) = A(\overline{x}(t))$, then $D_x\mathcal{R}(\overline{x}(t), \overline{x}(t)) = 0$ and hence again (17) yields $\dot{\overline{x}}(t) = 0$. We also notice that, if $A(\overline{x}(0)) = \overline{x}(0) = x_\infty$, then from the above argument we have that for all $t \geq 0$, $\overline{x}(t) = x_\infty$, with x_∞ satisfying (32).

Now we assume that $A(\overline{x}(0)) > \overline{x}(0)$ (the case $A(\overline{x}(0)) < \overline{x}(0)$ can be treated similarly) and set

$$t_0 := \inf \{t \in \mathbb{R} \, : \, A(\overline{x}(t)) \, \leq \, \overline{x}(t)\}.$$

If $t_0 < \infty$, then $A(\overline{x}(t_0)) = \overline{x}(t_0)$ and, hence, for all $t \geq t_0$, $\overline{x}(t) = \overline{x}(t_0) = x_\infty$. If $t_0 = \infty$, then $\dot{\overline{x}}(t) > 0$ for all $t \geq 0$, and thus, since the set $B = \{\overline{x}(t) \, : t \, \in [0, \infty)\}$ is compact (see below), there exists $\overline{x}_0 \in \mathbb{R}$ such that

$$\lim_{t \to \infty} \overline{x}(t) = \overline{x}_0.$$

The compactness of B follows from the observation that, in view of (15), (4) and (5),

$$\mathcal{R}(x, \overline{x}(t)) \leq K_4 - K_2 |x|^2,$$

and, since $\mathcal{R}(\overline{x}(t), \overline{x}(t)) = 0$,

$$|\overline{x}(t)| \leq (K_4/K_2)^{1/2}. \tag{33}$$

We now claim that $\overline{x}_0$ satisfies (32). Indeed, if there exists $z \in \mathbb{R}^N$ such that $\mathcal{R}(z, \overline{x}_0) > 0$, then using (22), we have $\lim_{t \to \infty} u(z, t) = +\infty$, a contradiction to the constraint $\max_{x \in \mathbb{R}} u(x, t) = 0$.

3.2 Convergence for a particular case with $N > 1$ (The proof of Theorem 1.3 (ii))

We prove Theorem 1.3 in the multi-d case with a growth rate R as in (18). In this case we find

$$b(\overline{x}(t)) \langle B(s, I(t) \rangle - d(\overline{x}(t)) \langle D(s, I(t) \rangle = 0, \tag{34}$$

and thus

$$\begin{aligned} \big(- D_x^2 u(\overline{x}(t), t) \big) \dot{\overline{x}}(t) &= b'(\overline{x}(t)) \langle B(s, I(t) \rangle - d'(\overline{x}(t)) \langle D(s, I(t) \rangle \\ &= \left[\frac{b'(\overline{x}(t))}{b(\overline{x}(t))} - \frac{d'(\overline{x}(t))}{d(\overline{x}(t))} \right] d(\overline{x}(t)) \langle D(s, I(t) \rangle. \end{aligned}$$

Therefore, after taking inner product with $\dot{\overline{x}}(t)$, dividing by $d(\overline{x}(t)) \langle D(s, I(t) \rangle$ and using the strict concavity of u, we obtain

$$|\dot{\overline{x}}(t)|^2 \leq C \frac{d}{dt} \ln \left(\frac{b(\overline{x}(t))}{d(\overline{x}(t))} \right).$$

This proves that $t \mapsto L(t) = b(\overline{x}(t))/d(\overline{x}(t))$ is a Lyapunov functional which is increasing and thus converges, as $t \to \infty$, to some constant l. For this we need to show that $\{\overline{x}(t) : t \in [0, \infty)\}$ is bounded, a fact which follows exactly as in the proof of (33). Finally, in view of (34), we also have

$$\lim_{t \to \infty} \frac{\langle D(s, I(t) \rangle}{\langle B(s, I(t) \rangle} = l.$$

We prove next that

$$l = \max_x \frac{b(x)}{d(x)}.$$

Arguing by contradiction we assume that $l < \max_x(b(x)/d(x))$. Then there must exist $\widetilde{x} \in \mathbb{R}^N$ such that $l < (b(\widetilde{x})/d(\widetilde{x}))$, in which case

$$0 < \liminf_{t\to\infty} b(\widetilde{x})\langle B(s, I(t)\rangle - d(\widetilde{x})\langle D(s, I(t)\rangle.$$

Finally, since u solves

$$\partial_t u = |D_x u|^2 + b(x)\langle B(s, I(t)\rangle - d(x)\langle D(s, I(t)\rangle,$$

we find

$$\lim_{t\to\infty} u(\widetilde{x}, t) = \infty,$$

a contradiction to the constraint $\max_{x\in\mathbb{R}^N} u(x,t) = 0$.

3.3 A counterexample in the multi-dimension case

In this subsection we present an example showing that, when $N > 1$, the $\overline{x}$'s may not converge, as $t \to \infty$, at least for the Hamilton-Jacobi problem (22). Indeed we find a strictly concave with respect to the first variable $\mathcal{R} : \mathbb{R}^N \times \mathbb{R}^N \to \mathbb{R}$, an 1-periodic map $t \to \overline{x}(t)$ and a function $u : \mathbb{R}^N \times [0,\infty] \to \mathbb{R}$ which satisfies

$$\begin{cases} \partial_t u - |D_x u|^2 = \mathcal{R}\left(x, \overline{x}(t)\right) \quad \text{in} \quad R^N \times (0,\infty), \\ \max_{x\in\mathbb{R}^N} u(x,t) = u\left(\overline{x}(t), t\right) = 0, \\ u(\cdot, 0) = u_0 \ \text{ in } \ \mathbb{R}^N. \end{cases}$$

We choose $G : \mathbb{R}^N \to \mathbb{R}^N$ so that the ode $\dot{x} = G(x)$ has a periodic solution; note that such function exists only for $N > 1$. A simple example for $N = 2$ is $G(x_1, x_2) = (-x_2, x_1)$, which admits $(x_1(t), x_2(t)) = (r\cos t, r\sin t)$ as periodic solutions.

Let $F : \mathbb{R}^N \to \mathbb{R}$ be an arbitrary smooth function and define $\mathcal{R} : \mathbb{R}^N \times \mathbb{R}^N \to \mathbb{R}$ by

$$\mathcal{R}(x,y) = -\left(DF(y)G(y) + 4F(y)^2\right)|x-y|^2 + 2F(y)G(y)(x-y). \tag{35}$$

It is immediate that $\mathcal{R}$ is a concave function with respect to x and satisfies $\mathcal{R}(x,x) = 0$. It is also easily verified that

$$u(x,t) = -F(\overline{x}(t))|x - \overline{x}(t)|^2 \qquad \text{with} \quad \dot{\overline{x}}(t) = G(\overline{x}(t)) \text{ and } \overline{x}(0) = x_0,$$

is a viscosity solution of (3.3) for $\mathcal{R}$ as in (35) and $u_0(x) = -F(x_0)|x - x_0|^2$. Moreover the canonical equation (28) is written as

$$\dot{\overline{x}}(t) = \left(-D_x^2 u(\overline{x}(t), t)\right)^{-1} D_x\mathcal{R}(\overline{x}(t), \overline{x}(t)) = (2F(\overline{x}(t))^{-1}\left(2F(\overline{x}(t))G(\overline{x}(t))\right) = G(\overline{x}(t)).$$

Finally we choose $x_0 \in \mathbb{R}^N$ such that $t \mapsto \overline{x}(t)$ with $x(t_0) = x_0$ is 1-periodic. Then the limit $\lim_{t\to\infty} \overline{x}(t)$ does not exist.

Note that the counterexample presented above is for the Hamilton-Jacobi problem (22). We do not know if such periodic oscillation can arise in the $\varepsilon \to 0$ limit of the viscous Hamilton-Jacobi equation (21). When the growth rate independent of time, a result similar to Theorem 1.3 was proved in [10] for general R. In that problem, the key point leading to the convergence, as $t \to \infty$, of the $\overline{x}(t)$'s is that $\overline{I}(t)$, which is the strong limit of the I_ε's as $\varepsilon \to 0$, is increasing in time. In the case at hand, we can only prove that the I_ε's converge weakly to $\overline{I}$. We know nothing about the monotonicity of $\overline{I}$. We remark that numerical computations suggest (see Figure 1) that monotonicity holds, if at all, in the average.

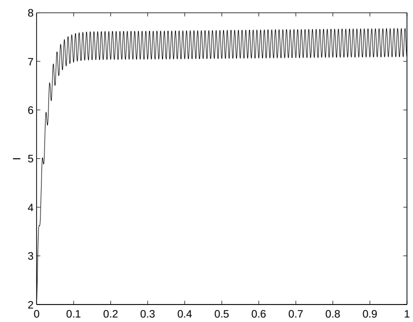

Figure 1: Dynamics of the total population $I_\varepsilon(t)$ for $R(x,s,I) = (2+\sin(2\pi s))\frac{2-x^2}{I+.5} - .5$, $\psi(x) = 1$ and $\varepsilon = 0.01$. The I_ε's oscillate with period of order ε around a monotone curve $\overline{I}$.

4 A particular case with a natural structure for $\mathcal{R}$

The concavity assumption (4) is very strong. Here we study, using a different method based on BV estimates, a class of growth rates R which do not satisfy (4). Throughout this section, for several arguments, we follow [1] which studies a similar problem but without time oscillations.

We consider growth rates of the form

$$R(x,s,I) = b(x)B(s,I) - D(s,I), \tag{36}$$

with

$$B, D : \mathbb{R} \times [0,\infty) \to R \quad \text{1-periodic with respect to the first argument} \tag{37}$$

and we assume that, for all $(s,I) \in \mathbb{R} \times \left[\frac{\widetilde{I}_m}{2}, 2\widetilde{I}_M\right]$ and $x \in \mathbb{R}^N$,

$$0 < B(s,I),\ 0 < D(s,I) \quad \text{and} \quad 0 < b_m \le b(x) \le b_M, \tag{38}$$

where $\widetilde{I}_M > \widetilde{I}_m > 0$ are such that

$$\max_{0\le s\le 1,\, x\in\mathbb{R}^N} R(x,s,\widetilde{I}_M) = 0 \quad \text{and} \quad \min_{0\le s\le 1,\, x\in\mathbb{R}^N} R(x,s,\widetilde{I}_m) = 0, \tag{39}$$

and there exist constants $a_1 > 0$ and $a_2 > 0$ such that, for all $(s,I) \in \mathbb{R} \times [0,\infty)$,

$$D_I\, B(s,I) < -a_1 \ \text{ and } a_2 < D_I\, D(s,I). \tag{40}$$

As far as $n_\varepsilon(\cdot,0)$ is concerned, we replace (9)–(11) by

$$\begin{gathered} \widetilde{I}_m \le \int \psi(x) n_\varepsilon(x,0)dx \le \widetilde{I}_M, \text{ and} \\ n_\varepsilon(x,0) \le \exp\left(\frac{-A|x|+B}{\varepsilon}\right) \quad \text{for some } A, B > 0 \text{ and all } x \in \mathbb{R}^N. \end{gathered} \tag{41}$$

Eventhough (36) seems close to (18), no concavity assumption is made and the analysis of Section 3 does not apply here.

Theorem 4.1. *Assume (7) and (40)–(41). Along subsequences $\varepsilon \to 0$, the u_ε's converge locally uniformly to $u \in \mathrm{C}(\mathbb{R}^{\mathrm{N}} \times \mathbb{R})$ satisfying the constrained Hamilton-Jacobi equation*

$$\begin{cases} u_t = \mathcal{R}(x, F(t)) + |D_x u|^2 \quad in \;\; \mathbb{R}^N \times (0,\infty), \\ \max\limits_{x\in\mathbb{R}^N} u(x,t) = 0, \\ u(\cdot,0) = u^0 \quad in \;\; \mathbb{R}^N, \end{cases} \tag{42}$$

with

$$\mathcal{R}(x,F) = \int_0^1 \mathcal{I}(F,s)ds \left(\frac{b(x)}{F} - 1\right) \quad and \quad F(t) = \lim_{\varepsilon\to 0} \frac{\int \psi(x)\, b(x)\, n_\varepsilon(x,t)\, dx}{I_\varepsilon(t)},$$

and $\mathcal{I}$ defined in (48) below. In particular, along subsequences $\varepsilon \to 0$ and in the sense of measures, $n_\varepsilon \rightharpoonup n$ with supp $n \subset \{(x,t) \,:\, u(x,t) = 0\} \subset \{(x,t) \,:\, \mathcal{R}(x, F(t)) = 0\}$.

As in Theorem 1.3, we can deduce the long time convergence to the Evolutionary Stable Distribution. To this end we assume that

$$\text{there exists a unique } x_* \in \mathbb{R}^N \text{ such that } b(x_*) = \max_{x\in\mathbb{R}^N} \; b(x). \tag{43}$$

Theorem 4.2. *Assume (7), (40)–(41) and (43) Then, as $t \to \infty$, the population reaches the Evolutionary Stable Distribution $\rho_*\delta(\cdot - x_*)$, i.e.,*

$$n(\cdot,t) \underset{t\to\infty}{\longrightarrow} \rho_*\delta(\cdot - x_*) \quad in\ the\ sense\ of\ measures, \tag{44}$$

with

$$\rho_* = \frac{1}{\psi(x_*)} \int_0^1 \mathcal{I}\left(b(x_*), s\right) ds.$$

Proof of Theorem 4.1. It follows easily from (39), (41) and the arguments in [1] that

$$\widetilde{I}_m + O(\varepsilon) \le I_\varepsilon(t) \le \widetilde{I}_M + O(\varepsilon). \tag{45}$$

Define next

$$F_\varepsilon(t) := \frac{\int b(x)\, \psi(x)\, n_\varepsilon(x,t)\, dx}{I_\varepsilon(t)},$$

and note that

$$b_m \le F_\varepsilon(t) \le b_M. \tag{46}$$

We next prove that $F_\varepsilon \in \mathrm{BV}_{\mathrm{loc}}(0,\infty)$ uniformly in ε. Indeed, using (7), (38) and (45), we find

$$\begin{aligned} \tfrac{d}{dt} F_\varepsilon(t) &= I_\varepsilon^{-2} \left(I_\varepsilon \int n_{\varepsilon,t}\, b\, \psi\, dx - \int n_{\varepsilon,t}\, \psi\, dx \; \int n_\varepsilon\, b\, \psi\, dx \right) \\ &= I_\varepsilon^{-2} (I_\varepsilon \int \left(\varepsilon \Delta n_\varepsilon + \varepsilon^{-1} n_\varepsilon \left(b\, B(\tfrac{t}{\varepsilon}, I_\varepsilon) - D(\tfrac{t}{\varepsilon}, I_\varepsilon) \right) \right) \, b\, \psi\, dx \\ &- \int n_\varepsilon\, b\, \psi\, dx \int \left(\varepsilon \Delta n_\varepsilon + \varepsilon^{-1} n_\varepsilon \left(b\, B(\tfrac{t}{\varepsilon}, I_\varepsilon) - D(\tfrac{t}{\varepsilon}, I_\varepsilon) \right) \psi\, dx \right) \\ &= O(\varepsilon) + (\varepsilon I_\varepsilon^2)^{-1} B(\tfrac{t}{\varepsilon}, I_\varepsilon) \left(\int n_\varepsilon\, \psi\, dx \cdot \int n_\varepsilon\, b^2\, \psi\, dx - (\int n_\varepsilon\, b\, \psi\, dx)^2 \right) \ge O(\varepsilon). \end{aligned} \tag{47}$$

Then (46) and (47) yield that, for each $T > 0$, there exists $C = C(T) > 0$ such that

$$\int_0^T |\frac{d}{dt} F_\varepsilon| dt \le C.$$

It follows that, along subsequences $\varepsilon \to 0$, the F_ε's converge a.e. and in L^1 to some F.
To conclude we need a result similar to the one of Lemma 1.1

Lemma 4.3. *Assume (7) and (40)–(41). For all $t \in \mathbb{R}$, there exists a unique, 1-periodic solution $\mathcal{I}(t, \cdot) \in C^1(\mathbb{R} \to [\widetilde{I}_m, \widetilde{I}_M]$ to*

$$\begin{cases} \frac{d}{ds}\mathcal{I}(F(t), s) = \mathcal{I}(F(t), s) \ \big(F(t) B\left(s, \mathcal{I}(F(t), s)\right) - D\left(s, \mathcal{I}(F(t), s)\right)\big), \\ \mathcal{I}(F(t), 0) = \mathcal{I}(F(t), 1). \end{cases} \tag{48}$$

Moreover, for all $T > 0$ and as $\varepsilon \to 0$, $\quad \int_0^T |I_\varepsilon(t) - \mathcal{I}(F(t), \frac{t}{\varepsilon})| dt \to 0.$

The first claim is proved as in Lemma 1.1. We postpone the proof of the second assertion to the end of this section.

Using (7), (40)–(41) and following [1], we show that the u_ε's are bounded and locally Lipschitz continuous uniformly in ε and, hence, converge along subsequences $\varepsilon \to 0$ to a solution u of

$$u_t = |D_x u|^2 + \int_0^1 B(s, \mathcal{I}(F(t), s)) ds b(x) - \int_0^1 D\left(s, \mathcal{I}(F(t), s)\right) ds.$$

Since $\mathcal{I}(F, \cdot)$ is a periodic solution to (48), we have

$$\int_0^1 B(s, \mathcal{I}(F(t), s) ds \ F(t) - \int_0^1 D(s, \mathcal{I}(F(t), s)) ds = 0.$$

It follows that

$$u_t = |D_x u|^2 + \mathcal{R}(x, F(t))$$

with

$$\mathcal{R}(x, F(t)) = \int_0^1 D(s, \mathcal{I}(F(t), s)) ds \ (\frac{b(x)}{F(t)} - 1).$$

The last claim of Theorem 4.1 can be proved using (20), (42) and following [12]. □

We conclude with

Proof of Theorem 4.2. It follows from (47) that F is an increasing function. Hence, in view of (46), there exists F_* such that, as $t \to \infty$, $F(t) \longrightarrow F_*$. Moreover

$$F_* = \max_{x \in \mathbb{R}^N} \ b(x) = b(x_*). \tag{49}$$

Indeed, if not, then $\mathcal{R}(x_*, F_*) > 0$ and, hence, from (42), $\lim_{t\to\infty} u(x_*, t) = \infty$, a contradiction to the constraint $\max_{x \in \mathbb{R}^N} \ u(x, t) = 0$.
Finally (44) follows from (49) and the observation that

$$supp\, n(x, t) \subset \{(x, t) \, : \, \mathcal{R}(x, t) = 0\} = \{(x, t) \, : \, b(x) = F(t)\}.$$

□

Proof of the second claim of Lemma 4.3. Eventhough we follow the same ideas as in Lemma 1.1, to prove the second claim, we need to modify the arguments, since, without the concavity assumption (4), u_ε may have several maxima.

We use again the log transformations $J_\varepsilon = \log I_\varepsilon$ and $\mathcal{J} = \log \mathcal{I}$. Multiplying (1) by $\psi(x)$ and integrating with respect to x leads to

$$\varepsilon \frac{d}{dt} I_\varepsilon(t) = B(\frac{t}{\varepsilon}, I_\varepsilon(t)) \int_{\mathbb{R}^N} \psi(x) n_\varepsilon(x,t)\, b(x) dx - I_\varepsilon(t) D(\frac{t}{\varepsilon}, I_\varepsilon(t)) + \varepsilon^2 \int_{\mathbb{R}^N} \Delta\psi(x)\, n_\varepsilon(x,t) dx.$$

It follows from (48) that

$$\begin{aligned} \varepsilon \tfrac{d}{dt}\left(J_\varepsilon(t) - \mathcal{J}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right) &= F_\varepsilon(t) B\left(\tfrac{t}{\varepsilon}, I_\varepsilon(t)\right) - F(t) B\left(\tfrac{t}{\varepsilon}, \mathcal{I}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right) \\ &\quad - D\left(\tfrac{t}{\varepsilon}, I_\varepsilon(t)\right) + D\left(\tfrac{t}{\varepsilon}, \mathcal{I}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right) + O(\varepsilon^2). \end{aligned}$$

Multiplying the above equality by $\mathrm{sgn}(\mathrm{J}_\varepsilon(\mathrm{t}) - \mathcal{J}(\mathrm{F}_\varepsilon(\mathrm{t}), \frac{\mathrm{t}}{\varepsilon}))$ and employing (40), we obtain

$$\begin{aligned} \varepsilon \tfrac{d}{dt}\left|J_\varepsilon(t) - \mathcal{J}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right| &= -\left|F_\varepsilon(t) B\left(\tfrac{t}{\varepsilon}, I_\varepsilon(t)\right) - F_\varepsilon(t) B\left(\tfrac{t}{\varepsilon}, \mathcal{I}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right)\right| \\ &\quad - \left|D\left(\tfrac{t}{\varepsilon}, I_\varepsilon(t)\right) - D\left(\tfrac{t}{\varepsilon}, \mathcal{I}\left(F_\varepsilon(t), \tfrac{t}{\varepsilon}\right)\right)\right| + O(\varepsilon^2). \end{aligned}$$

Integrating in time over $[0,T]$, for some fixed $T > 0$, and using the convergence of the F_ε's we find that, as $\varepsilon \to 0$,

$$\int_0^T |F(t)B(\frac{t}{\varepsilon}, I_\varepsilon(t)) - F(t)B(\frac{t}{\varepsilon}, \mathcal{I}(F(t), \frac{t}{\varepsilon}))| + |D(\frac{t}{\varepsilon}, I_\varepsilon(t)) - D(\frac{t}{\varepsilon}, \mathcal{I}(F(t), \frac{t}{\varepsilon}))| dt \longrightarrow 0.$$

The second claim of Lemma 4.3 follows in view of (40). $\square$

5 A qualitative effect: fluctuations may increase the population size

We conclude with an example that shows that the time-oscillations may lead to a strict increase of the population size at the evolutionary stable state, a conclusion which also holds in the context of physiologically structured populations [3].

To this end, we consider, along the lines of Section 4, the rate function

$$R(x, I) = b(x) - D_1(s) D_2(I) \tag{50}$$

with b and $D(s,I) = D_1(s)D_2(I)$ satisfying (37)–(40) and (43) and, for simplicity, we take $\psi \equiv 1$ in (1). The goal is to compare the size of the ESD in Theorem 4.2 to the one obtained from the model with the "averaged rate"

$$R_{\mathrm{av}}(x, I) = b(x) - D_{1,\mathrm{av}} D_2(I) \quad \text{with } D_{1,\mathrm{av}} = \int_0^1 D_1(s) ds.$$

Later, we write f_{av} for the average of the 1-periodic map $f : \mathbb{R} \to \mathbb{R}$, i.e., $f_{\mathrm{av}} = \int_0^1 f(s) ds$.

Let $\mathcal{I}$ be the 1-periodic solution of (48) with $F(t) \equiv b(x_\star)$ according to (49). With the above simplifications, the magnitude $\rho_\star$ of the Evolutionary Stable Distribution obtained in (4.2) is

$$\rho_\star = \int_0^1 \mathcal{I}(s)ds.$$

Since we can multiply equation (48) by any function of $\mathcal{I}(s)$, elementary maipulations lead to the identities

$$b(x_\star) = \int_0^1 D_1(s)D_2(\mathcal{I}(s))ds \quad \text{and} \quad \int_0^1 D_2(\mathcal{I}(s))ds\; b(x_\star) = \int_0^1 D_1(s)D_2^2(\mathcal{I}(s))ds. \tag{51}$$

A straightforward application of the Cauchy-Schwarz inequality in (51) yields

$$b(x_\star)^2 \le D_{1,\mathrm{av}}\; D_2(\mathcal{I})_{\mathrm{av}} b(x_\star)$$

and thus

$$b(x_\star) \le D_{1,\mathrm{av}} \int_0^1 D_2(\mathcal{I}(s))ds. \tag{52}$$

Consider next the "averaged" version of (1), i.e., the equation

$$\begin{cases} \varepsilon n_{\varepsilon,\mathrm{av},t} = n_{\varepsilon,\mathrm{av}}\; R_{\mathrm{av}}(x, I_{\varepsilon,\mathrm{av}}(t)) + \varepsilon^2 \Delta n_{\varepsilon,\mathrm{av}} \quad \text{in} \quad \mathbb{R}^N \times (0,\infty), \\ I_{\varepsilon,\mathrm{av}}(t) = \int_{\mathbb{R}^N} n_{\varepsilon,\mathrm{av}}(x,t)dx. \end{cases} \tag{53}$$

It follows from the earlier results [10] that the magnitude ρ_{av} of the Evolutionary Stable Distribution corresponding to (53) satisfies the identity

$$b(x_\star) = D_{1,\mathrm{av}} D_2(\rho_{\mathrm{av}}), \tag{54}$$

and, therefore, unless D_1 is constant, in which case (52) must be an equality, we conclude

$$D_2(\rho_{\mathrm{av}}) < \int_0^1 D_2(\mathcal{I}(s)ds. \tag{55}$$

If, in addition to above hypotheses, we also assume that

$$I \to D_2(I) \quad \text{is concave,} \tag{56}$$

then (55) yields

$$\rho_{\mathrm{av}} < \rho_\star,$$

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

A The proof of (24)

In this section, for the convenience of the reader we recall the proof of (24) given in [10].

A.1 Quadratic estimates on u_ε

We prove that, for C_2 a large enough constant, $\overline{u}_\varepsilon(x,t) := L_4 - L_2|x|^2 + C_2 t$ is a supersolution of (21). To this end we compute, using (4) and (12),

$$\partial_t \overline{u}_\varepsilon - |D\overline{u}_\varepsilon|^2 - R(x, \frac{t}{\varepsilon}, I_\varepsilon) - \varepsilon \Delta \overline{u}_\varepsilon \geq C_2 - 4L_2^2|x|^2 - K_4 + K_2|x|^2 - 2d\varepsilon L_2 \geq 0,$$

for C_2 large enough. It then follows from the comparison principle and (10) that

$$u_\varepsilon(x,t) \leq L_4 - L_2|x|^2 + C_2 t.$$

Next for the lower bound, we define $\underline{u}_\varepsilon(x,t) := -L_3 - L_1|x|^2 - C_1 t$ and prove that $\underline{u}_\varepsilon(x,t)$ is a subsolution of (21) for C_1 large enough. We again compute, using (4) and (12),

$$\partial_t \underline{u}_\varepsilon - |D\underline{u}_\varepsilon|^2 - R(x, \frac{t}{\varepsilon}, I_\varepsilon) - \varepsilon \Delta \underline{u}_\varepsilon \leq -C_1 - 4L_1^2|x|^2 + K_3 + K_1|x|^2 - 2d\varepsilon L_1 \leq 0,$$

for C_1 large enough. It then follows from the comparison principle and (10) that

$$u_\varepsilon(x,t) \geq -L_3 - L_1|x|^2 - C_1 t.$$

A.2 Bounds on $D^2 u_\varepsilon$

For a unit vector ξ, we use the notation $u_\xi := D_\xi u_\varepsilon$ and $u_{\xi\xi} := D^2_{\xi\xi} u_\varepsilon$ to obtain

$$u_{\xi t} = R_\xi(x, \frac{t}{\varepsilon}, I) + 2Du \cdot Du_\xi + \varepsilon \Delta u_\xi,$$
$$u_{\xi\xi t} = R_{\xi\xi}(x, \frac{t}{\varepsilon}, I) + 2Du_\xi \cdot Du_\xi + 2Du \cdot Du_{\xi\xi} + \varepsilon \Delta u_{\xi\xi}.$$

We first give a lower bound on $D^2 u_\varepsilon$. To this end, we define $\underline{w}(t,x) := \min_\xi u_{\xi\xi}(t,x)$ and using $|Du_\xi| \geq |u_{\xi\xi}|$ and (4) we obtain

$$\partial_t \underline{w} \geq -2K_1 + 2\underline{w}^2 + 2Du \cdot D\underline{w} + \varepsilon \Delta \underline{w}.$$

By a comparison principle and assumptions (10) and (12), we obtain

$$\underline{w} \geq -2L_1. \tag{57}$$

At every point $(x,t) \in \mathbb{R}^N \times \mathbb{R}^+$, we can choose an orthonormal basis such that $D^2 u_\varepsilon(x,t)$ is diagonal because it is a symmetric matrix. Therefore it follows from (57) that

$$D^2 u_\varepsilon(x,t) \geq -2L_1 I, \qquad \text{for all } (x,t) \in \mathbb{R}^N \times \mathbb{R}^+.$$

We can also estimate the mixed second derivatives in terms of $u_{\xi\xi}$. In particular, for each element ξ of the latter basis, we have $Du_\xi = u_{\xi\xi}\xi$ and $|Du_\xi| = |u_{\xi\xi}|$. This enables us to show concavity in the next step.

To prove the upper bound we define again $\overline{w}(t,x) := \max_\xi u_{\xi\xi}(t,x)$ and using $|Du_\xi| = |u_{\xi\xi}|$ and (4) we obtain

$$\partial_t \overline{w} \leq -2K_2 + 2\overline{w}^2 + 2Du \cdot D\overline{w} + \varepsilon \Delta \overline{w}.$$

By a comparison principle and assumptions (10) and (12), we obtain

$$\overline{w} \leq -2L_2, \tag{58}$$

and hence

$$D^2 u_\varepsilon(x,t) \leq -2L_2 I, \qquad \text{for all } (x,t) \in \mathbb{R}^N \times \mathbb{R}^+.$$

References

[1] 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.

[2] G. Barles and B. Perthame. Concentrations and constrained Hamilton-Jacobi equations arising in adaptive dynamics. *Contemp. Math.*, 439:57–68, 2007.

[3] J. Clairambault, S. Gaubert, and B. Perthame. Comparison of the perron and floquet eigenvalues in monotone differential systems and age structured equations. *C. R. Acad. Sc. Paris*, 345((10):549–555, 2007.

[4] L. Desvillettes, P.-E. Jabin, S. Mischler, and G. Raoul. On mutation-selection dynamics for continuous structured populations. *Commun. Math. Sci.*, 6(3):729–747, 2008.

[5] O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation: an illuminating example and a Hamilton-Jacobi approach. *Th. Pop. Biol.*, 67(4):257–271, 2005.

[6] I. Eshel. Evolutionary and continuous stability. *Journal of Theoretical Biology*, 103(1):99–111, 1983.

[7] P.-E. Jabin and G. Raoul. On selection dynamics for competitive interactions. *J. Math. Biol.*, 63(3):493–517, 2011.

[8] E. Kussel, R. Kishony, N. Q. Balaban, and S. Leibler. Bacterial persistence: a model of survival in changing environments. *Genetics*, 169:1807–1814, 2005.

[9] R. Lande. Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30:314–334, 1976.

[10] A. Lorz, S. Mirrahimi, and B. Perthame. Dirac mass dynamics in multidimensional nonlocal parabolic equations. *Comm. Partial Differential Equations*, 36(6):1071–1098, 2011.

[11] J. Maynard Smith and G. R. Price. The logic of animal conflict. *Nature*, 246:15–18, 1973.

[12] B. Perthame and G. Barles. Dirac concentrations in Lotka-Volterra parabolic PDEs. *Indiana Univ. Math. J.*, 57(7):3275–3301, 2008.

[13] G. Raoul. Long time evolution of populations under selection and vanishing mutations. *Acta Applicandae Mathematica*, 114:1–14, 2011.

[14] S. Rosenblat. Population models in a periodically fluctuating environment. *Journal of Mathematical Biology*, 9:23–36, 1980.

[15] A. Sasaki and S. Ellner. The evolutionarily stable phenotype distribution in a random environment. *Evolution*, 49(2):337–350, 1995.

[16] H. Svardal, C. Rueffler, and J. Hermisson. Comparing environmental and genetic variance as adaptive response to fluctuating selection. *Evolution*, 65:2492–2513, 2011.