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Abstract

The evolution of dispersal is a classical question in evolutionary ecology, which has been widely studied with several mathematical models. The main question is to define the fittest dispersal rate for a population in a bounded domain, and, more recently, for traveling waves in the full space.

In the present study, we reformulate the problem in the context of adaptive evolution. We consider a population structured by space and a genetic trait acting directly on the dispersal (diffusion) rate under the effect of rare mutations on the genetic trait. We show that, as in simpler models, in the limit of vanishing mutations, the population concentrates on a single trait associated to the lowest dispersal rate. We also explain how to compute the evolution speed towards this evolutionary stable distribution.

The mathematical interest stems from the asymptotic analysis which requires a completely different treatment of the different variables. For the space variable, the ellipticity leads to the use the maximum principle and Sobolev-type regularity results. For the trait variable, the concentration to a Dirac mass requires a different treatment. This is based on the WKB method and viscosity solutions leading to an effective Hamiltonian (effective fitness of the population) and a constrained Hamilton-Jacobi equation.

Key words: Dispersion evolution; Nonlocal pde; Constrained Hamilton-Jacobi equation; Effective fitness;
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1 Evolution of dispersion

sec:ed

The model. We consider here the rare mutation limit of the steady state version of a simple model of evolution of dispersal in a population. The main modeling assumptions are: (i) all individuals wear a genotype characterized by a parameter θ, which induces a dispersal rate $D(\theta)$, (ii) a Fisher-type Lotka-Volterra growth/death rate with a space dependent carrying capacity K and limitation by the total population whatever the trait is, and (iii) rare mutations acting on the genetic variable and modeled by a diffusion with covariance $\sqrt{2}\varepsilon$; we refer to [6] for a derivation of this type of equations from individual based stochastic models.

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More precisely, we study the asymptotic behavior, as $\varepsilon \to 0$, of the density $n_\varepsilon = n_\varepsilon(x,\theta) : \Omega \times \mathbb{R} \to (0,\infty)$, with $\Omega \subset \mathbb{R}^d$ a smooth domain, of the nonlocal and nonlinear problem

$$\begin{cases} -D(\theta)\Delta_x n_\varepsilon - \varepsilon^2 \Delta_\theta n_\varepsilon = n_\varepsilon\big(K(x) - \rho_\varepsilon(x)\big) \quad \text{in} \quad \Omega \times \mathbb{R}, \\ \rho_\varepsilon(x) = \displaystyle\int_0^1 n_\varepsilon(x,\theta)d\theta, \end{cases} \tag{1}$$

`equation`

with Neumann boundary condition on $\partial\Omega$ and $1-$ periodicity in θ, that is, if ν is the external normal vector to Ω,

$$\frac{\partial}{\partial \nu} n_\varepsilon = 0 \quad \text{on } \partial\Omega \times \mathbb{R} \text{ and } n_\varepsilon \text{ is } \ 1-\text{periodic in } \theta. \tag{2}$$

`bc`

As far as the carrying capacity K and the dispersion rate D are concerned, we assume

$$K \in C^1(\bar{\Omega}), \qquad \text{there exists } K_m > 0 \text{ such that } K(x) \geq K_m > 0, \qquad K \text{ is not constant.} \tag{3}$$

`asK`

and

$$\begin{cases} D \in C^1\big(\mathbb{R}; (0,\infty)\big) \ \text{ is 1-periodic and} \\ \text{there exists a unique local minimizer } \theta_m \in [0,1) \text{ such that } D \geq D(\theta_m) := D_m > 0; \end{cases} \tag{4}$$

`asD`

we note (4) is used to assert that the effective Hamiltonian also has a minimum at θ_m.
Finally, for technical reasons, we also assume that

$$\Omega \text{ is convex.} \tag{5}$$

`convex`

It follows from, for example, [1, 8], that, given (3) and (4), the problem (1) and (2) admits a strictly positive solution $n_\varepsilon : \Omega \times \mathbb{R} \to (0,\infty)$.

Formal derivation of the mathematical result. We proceed now formally to explain what happens in the limit $\varepsilon \to 0$ and, hence, motivate the statement of the results. As it is often the case with problems where it is expected to see concentration in the limit, we make the exponential change of variables

$$n_\varepsilon = \exp\big(u_\varepsilon/\varepsilon\big), \tag{6}$$

`exp`

which leads to

$$-\frac{D(\theta)}{\varepsilon}\Delta_x u_\varepsilon - \frac{D(\theta)}{\varepsilon^2}|\nabla_x u_\varepsilon|^2 - \varepsilon\Delta_\theta u_\varepsilon - |\nabla_\theta u_\varepsilon|^2 = K(x) - \rho_\varepsilon(x) \quad \text{in} \quad \Omega \times \mathbb{R}, \tag{7}$$

`eqhje1`

with

$$u_\varepsilon \ 1-\text{periodic in } \theta \quad \text{and} \quad \frac{\partial}{\partial \nu} u_\varepsilon = 0 \quad \text{on } \partial\Omega \times \mathbb{R}. \tag{8}$$

`expbc`

It is clear from (7) that, if the u_ε's have, as $\varepsilon \to 0$, a limit u, it must be independent of x, and, hence, it is natural to expect the expansion

$$u_\varepsilon(x,\theta) = u(\theta) + \varepsilon \ln \mathcal{N}(x,\theta) + O(\varepsilon). \tag{9}$$

`ansatz`

Assuming that, as $\varepsilon \to 0$, the ρ_ε's converge to some ρ, a formal computation suggests that $\mathcal{N}$ is the positive eigenfunction of

$$\begin{cases} -D(\theta)\Delta_x \mathcal{N} = \mathcal{N}\ \big(K - \rho\big) + \mathcal{N}\ H\big(\theta, \rho(\cdot)\big) \text{ in } \Omega, \\ \frac{\partial}{\partial \nu}\mathcal{N} = 0 \text{ on } \partial\Omega, \end{cases} \tag{10}$$

`ef`

with eigenvalue $H\big(\theta, \rho(\cdot)\big)$, and that u solves the constrained Hamilton-Jacobi equation

$$\begin{cases} -|\nabla_\theta u|^2 = -H\big(\theta, \rho(\cdot)\big) \;\text{ in }\; \mathbb{R}, \\ \max_{\theta\in\mathbb{R}} u(\theta) = 0, \\ u \text{ is } 1- \text{ periodic.} \end{cases} \tag{11}$$

chj

The constraint on the max u becomes evident from the facts that, as it turns out, the ρ_ε's are bounded uniformly in ε and the equality

$$\rho_\varepsilon(x) = \int_0^1 n_\varepsilon(x,\theta)d\theta = \int_0^1 \exp\big(u_\varepsilon(x,\theta)/\varepsilon\big)d\theta, \tag{12}$$

which also suggests that, as $\varepsilon \to 0$, the n_ε's behave like a Dirac mass with weight ρ.

The mathematical result. To state the result we recall that δ denotes the Dirac mass at 0 and we introduce the nonlinear Fisher-type stationary problem

$$\begin{cases} -D_m\Delta_x N_m = N_m\,(K - N_m) \text{ on } \Omega \\ \frac{\partial}{\partial\nu}N_m = 0 \;\text{ on } \partial\Omega, \end{cases} \tag{13}$$

eq:Nm

which, in view of (3) and (4), admits a positive solution $N_m > 0$ (see, for example, [1, 8].)
We have:

Theorem 1.1 *Assume* (3), (4), *and* (5). *Then, as $\varepsilon \to 0$ and in the sense of distributions,*

$$n_\varepsilon \to N_m(x)\delta(\theta - \theta_m) \quad \textit{and} \quad \rho_\varepsilon \to N_m.$$

Moreover, as $\varepsilon \to 0$ and uniformly in x and θ, $\varepsilon \ln n_\varepsilon \to u$, where u is the unique $1-$periodic solution
th1 *to* (11), *with $\rho = N_m$, such that* $\max u = u(\theta_m) = 0$.

Biological interpretation and motivation. The conclusions of Theorem 1.1 can be thought as a justification of the fact that the population selects the "slowest" individuals in accordance with several previous observations on the evolution of dispersal. In this respect, the eigenvalue $-H\big(\theta, \rho(\cdot)\big)$ defines the fitness of individuals depending upon their trait. This fact can be stated using the canonical equation (30), which is formally derived in Section 6. In the words of adaptive dynamics, our result characterizes the unique Evolutionary Stable Distribution (or Strategy), [9, 16].

That mutants with lower dispersal rates can invade a population, that is property (18), is known from the first mathematical studies [14, 11]. Our approach here is more intrinsic since we consider structured populations competing for resources. Surprisingly when set in the full space where the problem is characterized in terms of traveling waves, the opposite effect is observed, that is mutants with higher dispersal rates are selected giving rise to accelerating waves, [3, 4, 24, 2]. For two competing populations, the combined effect of dispersal and a drift is studied in [13]. The analysis of dispersal evolution also gave rise to the notion of ideal free distribution [5, 7].

The question of dispersal evolution is a classical and important topic in evolutionary biology. The reader can consult [23] for a survey of the many related issues, to [20] for the case with patches and demographic stochasticity, to [15] for the case of trajectories with jumps (nonlocal operators) and to

[3] for other biological references about accelerating fronts. A formalism using Fokker-Planck equation is used in [22].

Another motivation for the study of the model in this note is to represent selection of the fittest individuals without a proliferative advantage. In this context the formalism we use here, with a population structured by a trait, has been studied widely when there is only proliferative advantage; see [10, 21, 16, 18]. Other formalisms to study evolution can be found in [9, 6] and the references therein. The extension to cases when the trait is combined another structuring variable is more recent, [3, 4, 24, 19, 7].

Organization of the paper. The paper is devoted to the proof of Theorem 1.1. In Section 2 we derive some uniform in ε estimates for the ρ_ε's that are then used in Section 3 where we derive the effective Hamiltonian, that is the eigenvalue problem of (10). In Section 4 we derive the constrained Hamilton-Jacobi equation to conclude the proof of Theorem 1.1 and Theorem 4.1. In Section 6, we provide some perspectives about the problem and some numerical examples, and, finally, in Section 5 we prove the two technical lemmata that were used in Section 4.

2 Estimates on ρ_ε

sec:est_rho

We state and prove here some, uniform in ε, estimates for the ρ_ε's, which are fundamental for the analysis in the rest of the paper; here $|\Omega|$ is the measure of Ω and $C(A)$ denotes a constant that depends on A.

lm:takis2 **Lemma 2.1** *Assume* (3) *and* (4). *There exist positive independent of ε constants $C_1 = C_1(K, D, \Omega)$, $C_2 = C_2(K, D, \Omega)$ and $C_3 = C_3(|\Omega|, \min K)$ such that*

$$\begin{cases} (i) \quad 0 \le \rho_\varepsilon \le C_1, \\ (ii) \quad \sup_{\varepsilon\in(0,1)} \|\rho_\varepsilon\|_{W^{2,p}(\Omega)} \le C_2 \ \ \text{for all } p \in [1,\infty), \text{ and} \\ (iii) \quad \int_\Omega \rho_\varepsilon(x)dx \ge C_3, \end{cases} \tag{14}$$

lm:est_rh

and, along subsequences $\varepsilon \to 0$, the ρ_ε's converge uniformly in $\overline{\Omega}$ to $\rho \in C(\overline{\Omega})$.

Proof. We first observe that ρ_ε trivially satisfies the Neumann condition

$$\frac{\partial}{\partial \nu}\rho_\varepsilon = 0 \ \text{ on } \partial\Omega. \tag{15}$$

takis1

After dividing (1) by $D(\theta)$, integrating in θ and using the periodicity in θ, we find

$$-\Delta_x \rho_\varepsilon - \varepsilon^2 \int_0^1 n_\varepsilon(x,\theta)\Delta_\theta \frac{1}{D} d\theta = \int_0^1 \frac{1}{D} n_\varepsilon d\theta \, (K - \rho_\varepsilon),$$

and, hence, for some constant C, which only depends on D and K, we have

$$-\Delta_x \rho_\varepsilon + \frac{1}{\|D\|_\infty}\rho_\varepsilon^2 \le C\rho_\varepsilon.$$

Then (14)(i) follows from the strong maximum principle, while the $W^{2,p}$-estimates are a consequence of the classical elliptic regularity theory.

The lower bound (14)(iii) comes from integrating (1) in x and θ. Indeed, in view of the assumed periodicity, we find

$$\max K \int_\Omega \rho_\varepsilon(x)dx \geq \int_\Omega \rho_\varepsilon(x)K(x)dx = \int_\Omega \rho_\varepsilon(x)^2 dx \geq \frac{1}{|\Omega|}\Big(\int_\Omega \rho_\varepsilon(x)dx\Big)^2.$$

The last claim is an immediate consequence of the a priori estimates and the usual Sobolev imbedding theorems.

□

3 The effective Hamiltonian

sec:H

For $\theta \in [0,1]$ and $\rho \in L^\infty\big(\Omega;[0,\infty)\big)$ we consider the eigenfunction $\mathcal{N} = \mathcal{N}\big(\cdot;\theta,\rho(\cdot)\big) \in H^1(\Omega)$ and the eigenvalue $H = H\big(\theta,\rho(\cdot)\big)$ of

$$\begin{cases} -D(\theta)\Delta_x \mathcal{N} = \mathcal{N}\ (K-\rho) + \mathcal{N}\ H \quad \text{in } \Omega, \\ \frac{\partial}{\partial \nu}\mathcal{N} = 0 \text{ on } \partial\Omega \qquad \text{and} \quad \int_\Omega \mathcal{N}\big(x;\theta,\rho(\cdot)\big)^2 dx = 1. \end{cases} \tag{16}$$ effective

Note that in view of (3) and the regularity of Ω, the existence of the pair $\Big(\mathcal{N}\big(\cdot;\theta,\rho(\cdot)\big), H\big(\theta,\rho(\cdot)\big)\Big)$ follows from, for example, [1, 8].

The next lemma provides some important estimates and information about $H\big(\theta,\rho(\cdot)\big)$. In the statement we use the notation $K_M := \max_{\overline{\Omega}} K$.

Lemma 3.1 *Assume* (3) *and* (4). *Then*

$$(i)\ -K_M \leq H\big(\theta,\rho(\cdot)\big) \ \ \textit{and} \ \ (ii)\ H\big(\theta,\rho(\cdot)\big) \leq \frac{1}{|\Omega|}\int_\Omega \rho(x)dx, \tag{17}$$ H:est1

the maps $\theta \to H\big(\theta,\rho(\cdot)\big)$ and $\theta \to D(\theta)$ have the same momotonicity properties for all ρ, (18) H:est3

lm:H *and, in particular, θ_m is the unique minimum of $H(\theta,\rho)$ in $[0,1]$ for all ρ.*

Proof. Multiplying the equation by $\mathcal{N}$ and integrating in x gives

$$0 \leq D(\theta)\int_\Omega |\nabla \mathcal{N}|^2 = \int_\Omega \mathcal{N}^2[K-\rho+H]dx \leq \int_\Omega \mathcal{N}^2 dx\ [K_M + H],$$

and, thus, (17)(i) holds.

The upper bound (17)(ii) follows from the positivity of K, since, after dividing the equation by $\mathcal{N}$ and integrating by parts, we find

$$-\int_\Omega \frac{\big|\nabla_x \mathcal{N}\big|^2}{\mathcal{N}^2}dx = \int_\Omega [K-\rho+H]\,dx \leq 0.$$

For (18), we differentiate in θ the equation in (16) to find

$$-D'(\theta)\Delta_x \mathcal{N} - D(\theta)\Delta_x \mathcal{N}_\theta = \mathcal{N}_\theta\ \big(K(x)-\rho(x)+H\big) + \mathcal{N}\ H_\theta, \tag{19}$$ takis

where $\mathcal{N}_\theta$ and H_θ denote derivatives with respect to θ, we multiply by $\mathcal{N}$ and integrate by parts using the boundary condition to get

$$D'(\theta)\int_\Omega \left|\nabla_x \mathcal{N}\right|^2 + D(\theta)\int \nabla_x\mathcal{N}.\nabla_x\mathcal{N}_\theta = \int \mathcal{N}\mathcal{N}_\theta[K-\rho] + H_\theta\big(\theta;\rho(\cdot)\big). \qquad (20)$$

takis2

Next we use the fact that the L^2-normalization of $\mathcal{N}$ yields $\int_\Omega \mathcal{N}_\theta \mathcal{N} dx = 0$ and after multiplying the equation in (16) by $\mathcal{N}_\theta$, integrating by parts and subtracting the result from (20) we find

$$D'(\theta)\int_\Omega \left|\nabla_x \mathcal{N}\right|^2 = H_\theta\big(\theta;\rho(\cdot)\big).$$

Since we have assumed in (3) that K is not constant, $\nabla_x\mathcal{N}$ does not vanish and the result follows.

To conclude, we observe that (4) and (18) yield that H as the same monotonicity, in θ, as D and, thus, has a unique local minimum at θ_m.

□

4 The constrained Hamilton-Jacobi equation

sec:chj

We prove here the generalized Gaussian-type convergence asserted in Theorem 1.1, derive the constrained Hamilton-Jacobi equation (11) and state some more properties. For the benefit of the reader we restate these assertions as a separate theorem below.

Theorem 4.1 *The family u_ε is uniformly in ε Lipschitz continuous and converges, uniformly in x and θ, to u, which is independent of x and satisfies, in the viscosity sense, the constrained Hamilton-Jacobi equation* (11)*. Moreover,*

$$\min_\theta H\big(\theta,\rho(\cdot)\big) = 0 = H\big(\theta_m,\rho(\cdot)\big) = H_\theta\big(\theta_m,\rho(\cdot)\big). \qquad (21)$$

eq:ESS

th:u

Since $-H$ represents the fitness, it turns out that (21) characterizes $\delta(\theta-\theta_m)$ as the Evolutionary Stable Distribution (or θ_m as the Evolutionary Stable Strategy). See [9, 16].

The proof is a consequence of the next two lemmata which are proved later in the paper.

Lemma 4.2 (Bounds on u_ε) *There exists an independent of ε constant C such that*

$$\int_\Omega \max_\theta u_\varepsilon(x,\theta)dx \le C\varepsilon. \qquad (22)$$

eq:u_uppe

lm:ubdd

Lemma 4.3 (Lipschitz estimates) *There exist an independent of ε constant C such that*

$$\frac{1}{\varepsilon^2}|\nabla_x u_\varepsilon|^2 + |\nabla_\theta u_\varepsilon|^2 \le C \text{ and } \max_{x\in\Omega, 0\le\theta\le 1} u_\varepsilon(x,\theta) \le C\varepsilon.$$

Moreover, the u_ε's converge, along a subsequence $\varepsilon\to 0$ and uniformly x and θ, to a Lipschitz and 1-periodic function $u:\mathbb{R}\to\mathbb{R}$ such that $\max_{0\le\theta\le 1} u(\theta) = 0$.

lm:ulip

We continue with the proofs of Theorem 4.1 and Theorem 1.1.

Proof of Theorem 4.1. The fact that any limit u of the u_ε's satisfies (11) is a standard application of the so-called perturbed test function method (see [12]) and we do not repeat the argument.

It follows from (11) that $H\big(\theta,\rho(\cdot)\big) \geq 0$, while, at any maximum point $\bar\theta$ of u, we must have $H\big(\bar\theta,\rho(\cdot)\big) \leq 0$, and, hence, $H\big(\bar\theta,\rho(\cdot)\big) = 0$, and, in view of Lemma 3.1,

$$\min_\theta H\big(\theta,\rho(\cdot)\big) = 0 = H\big(\theta_m,\rho(\cdot)\big).$$

As a result the only possible maximum point of any solution of (11) must be at at θ_m, which implies that the equation has a unique solution.

Also the knowledge of θ_m determines uniquely the limit $\rho(x) = \bar N_m(x)$ (see below), from equation (13), and, thus, the full family $(\rho_\varepsilon, u_\varepsilon)$ converges.

□

Proof of Theorem 1.1. The statement in terms of n_ε is an immediate consequence of Theorem 4.1. Because u_ε achieves a unique maximum at θ_m, from the Laplace formula for n_ε written as (6), we conlude that the $n_\varepsilon(x,\theta)$'s converge weakly in the sense of measures to $\rho(x)\delta(\theta-\theta_m)$, with $\rho(x)$ the limit of ρ_ε (see Section 2).
Next, integrating equation (1) in θ we conclude that

$$-\Delta \int_0^1 D(\theta) n_\varepsilon d\theta = \rho_\varepsilon(x)\big(K(x)-\rho_\varepsilon(x)\big).$$

Passing to the limit $\varepsilon \to 0$, and taking into account that n is a Dirac mass at θ_m, we find that $\rho = N_m$ because they both satisfy the equation (13).

□

5 The proofs

sec:proofs

We begin with the proof of Lemma 4.2

Proof of Lemma 4.2. Integrating (7), we find

$$\frac{1}{\varepsilon^2}\int\int |\nabla_x u_\varepsilon|^2 dx d\theta + \int\int |\nabla_\theta u_\varepsilon|^2 dx d\theta \leq C. \tag{23}$$ hj:h1est

The claim for the maximum bound follows from the $L^\infty-$estimate on ρ_ε.

For each $x \in \Omega$, let $M_\varepsilon(x) := \max_\theta u_\varepsilon(x,\theta)$ and choose $\theta_\varepsilon(x)$ such that $M_\varepsilon(x) = u_\varepsilon(x,\theta_\varepsilon(x))$. Then it follows from (14)(i) that

$$e^{M_\varepsilon(x)/\varepsilon}\int_0^1 e^{\big(u_\varepsilon(x,\theta)-u_\varepsilon(x,\theta_\varepsilon)\big)/\varepsilon} d\theta = \rho_\varepsilon(x) \leq C. \tag{24}$$ hjc:estu

Inserting in (24) the estimate

$$u_\varepsilon(x,\theta) - u_\varepsilon(x,\theta_\varepsilon(x)) = \int_\theta^{\theta_\varepsilon(x)} \partial_\theta u_\varepsilon(x,\theta')d\theta' \geq -1 - \int_0^1 |\partial_\theta u_\varepsilon(x,\theta')|^2 d\theta',$$

we get

$$e^{M_\varepsilon(x)/\varepsilon}\, e^{-\dfrac{1}{\varepsilon}[1+\displaystyle\int_0^1 |\partial_\theta u_\varepsilon(x,\theta')|^2 d\theta']} \leq C,$$

and, hence,

$$\frac{M_\varepsilon(x)}{\varepsilon} - \frac{1}{\varepsilon}[1+\int_0^1 |\partial_\theta u_\varepsilon(x,\theta')|^2 d\theta'] \leq \ln C.$$

Using (23), we obtain

$$\int_\Omega M_\varepsilon(x)dx \leq C\varepsilon,$$

and this concludes the proof.

□

Next we discuss the proof of Lemma 4.3.

Proof of Lemma 4.3. We first assume the Lipschitz bound and prove the rest of the claims.

Let $\mathcal{M}_\varepsilon := \max_{x\in\overline{\Omega}} M_\varepsilon(x)$, with $M_\varepsilon(x)$ as in the proof of the previous lemma. It is immediate from (22) and the fact that $|\nabla_x u_\varepsilon|^2 \leq \varepsilon C$ that, for some $C>0$,

$$\mathcal{M}_\varepsilon \leq \varepsilon C.$$

Next we show that $\liminf_{\varepsilon\to0}\mathcal{M}_\varepsilon \geq 0$, which, in turn, yields that $\lim_{\varepsilon\to0}\mathcal{M}_\varepsilon = 0$.

Let $y_\varepsilon \in \overline{\Omega}$ be such that $\mathcal{M}_\varepsilon := M_\varepsilon(y_\varepsilon = u_\varepsilon\big(y_\varepsilon, \theta_\varepsilon(y_\varepsilon)\big)$ and write

$$\rho_\varepsilon(x) = e^{\mathcal{M}_\varepsilon/\varepsilon}\int_0^1 e^{\big(u_\varepsilon(x,\theta)-u_\varepsilon(y_\varepsilon,\theta_\varepsilon)\big)/\varepsilon} d\theta.$$

Combining the lower bound on ρ_ε in Lemma 20 and the (Lipschitz) estimate $|\nabla_x u_\varepsilon|^2 \leq \varepsilon C$, we get

$$C_3 \leq \int_\Omega \rho_\varepsilon(x)) \leq |\Omega| e^{\mathcal{M}_\varepsilon/\varepsilon} e^C \int_0^1 e^{\big(u_\varepsilon(y_\varepsilon,\theta)-u_\varepsilon(y_\varepsilon,\theta_\varepsilon)\big)/\varepsilon} d\theta \leq e^{\mathcal{M}_\varepsilon/\varepsilon} e^C |\Omega|,$$

and, thus, $\mathcal{M}_\varepsilon \geq -C\varepsilon$.

Now we turn to the proof of the Lipschitz bounds, which is an appropriate modification of the classical Bernstein estimates to take into account the different scales. We note and prove Lemma 4.3. Note that the convexity assumption on Ω is used solely in this proof.

We begin by writing the equations satisfied by $|D_x u_\varepsilon|^2$ and $|\partial_\theta u_\varepsilon|^2$ which we obtain by differentiating (7) in x and θ and multipying by $D_x u_\varepsilon$ and $\partial_\theta u_\varepsilon$. We have:

$$\begin{aligned} -\tfrac{D(\theta)}{\varepsilon}\Delta_x |D_x u_\varepsilon|^2 - \quad & \varepsilon\Delta_\theta |D_x u_\varepsilon|^2 + 2\tfrac{D(\theta)}{\varepsilon}|D^2_{xx}u_\varepsilon|^2 + 2\varepsilon|D^2_{x\theta}u_\varepsilon|^2 \\ & -2\tfrac{D(\theta)}{\varepsilon^2} D_x u_\varepsilon . D_x |D_x u_\varepsilon|^2 - 2\partial_\theta u_\varepsilon . \partial_\theta |D_x u_\varepsilon|^2 = 2D_x(K-\rho_\varepsilon).Du_\varepsilon, \end{aligned} \tag{25}$$ ge:ux

and

$$\begin{aligned} -\tfrac{D(\theta)}{\varepsilon} \quad & \Delta_x |\partial_\theta u_\varepsilon|^2 - \varepsilon\Delta_\theta |\partial_\theta u_\varepsilon|^2 + 2\tfrac{D(\theta)}{\varepsilon}|D^2_{x\theta}u_\varepsilon|^2 + 2\varepsilon|D^2_{\theta\theta}u_\varepsilon|^2 \\ & -2\tfrac{D(\theta)}{\varepsilon^2} D_x u_\varepsilon . D_x |\partial_\theta u_\varepsilon|^2 - 2\partial_\theta u_\varepsilon . \partial_\theta |\partial_\theta u_\varepsilon|^2 = 2\tfrac{D'(\theta)}{\varepsilon}\Delta_x u_\varepsilon \partial_\theta u_\varepsilon + 4\tfrac{D'(\theta)}{\varepsilon^2}|D_x u_\varepsilon|^2 \partial_\theta u_\varepsilon. \end{aligned} \tag{26}$$ ge:utheta

Let $w = \frac{|D_x u_\varepsilon|^2}{\varepsilon^2} + |\partial_\theta u_\varepsilon|^2$ and compute

$$
\begin{aligned}
- \quad & \tfrac{D(\theta)}{\varepsilon}\Delta_x w - \varepsilon \Delta_\theta w + 2\tfrac{D(\theta)}{\varepsilon^3}|D^2_{xx}u_\varepsilon|^2 + \tfrac{1+D(\theta)}{\varepsilon}|D^2_{x\theta}u_\varepsilon|^2 + 2\varepsilon|D^2_{\theta\theta}u_\varepsilon|^2 \\
& -2\tfrac{D(\theta)}{\varepsilon^2}D_x u_\varepsilon . D_x w - 2\partial_\theta u_\varepsilon . \partial_\theta w = \tfrac{2}{\varepsilon^2}D_x(K-\rho_\varepsilon).Du_\varepsilon + 2\tfrac{D'(\theta)}{\varepsilon}\Delta_x u_\varepsilon \partial_\theta u_\varepsilon + 4\tfrac{D'(\theta)}{\varepsilon^2}|D_x u_\varepsilon|^2 \partial_\theta u_\varepsilon .
\end{aligned}
$$

Assume that $(\bar{x}, \bar{\theta})$ is a maximum point of w. Because of the convexity assumption, we have $\frac{\partial}{\partial \nu} w < 0$ on the boundary (see [17]) and thus $x_\varepsilon \notin \partial\Omega \times [0,1]$.
Therefore, at this point $(\bar{x}, \bar{\theta})$, we have

$$
\begin{aligned}
\tfrac{D}{\varepsilon^3}|D^2_{xx}u_\varepsilon|^2 + \varepsilon|D^2_{\theta\theta}u_\varepsilon|^2 &\le \tfrac{1}{\varepsilon^2}D_x(K-\rho_\varepsilon).Du_\varepsilon + \tfrac{D'}{\varepsilon}\Delta_x u_\varepsilon \partial_\theta u_\varepsilon + 2\tfrac{D'}{\varepsilon^2}|D_x u_\varepsilon|^2 \partial_\theta u_\varepsilon \\
&\le \tfrac{1}{\varepsilon^2}D_x(K-\rho_\varepsilon).Du_\varepsilon + \delta\tfrac{D}{\varepsilon^3}(\Delta_x u_\varepsilon)^2 + \tfrac{\varepsilon}{\delta}(\partial_\theta u_\varepsilon)^2 + 2\tfrac{D'}{\varepsilon^2}|D_x u_\varepsilon|^2 \partial_\theta u_\varepsilon
\end{aligned}
$$

and we choose δ small enough so that we can absorb the term $\delta\frac{D}{\varepsilon^3}(\Delta_x u_\varepsilon)^2$ in the left hand side.
Since there is a constant $C_4(d, D)$ such that

$$
\frac{1}{\varepsilon}\left[\frac{D}{\varepsilon}\Delta_x u_\varepsilon + \varepsilon \Delta_\theta u_\varepsilon\right]^2 \le C_1 \frac{D}{\varepsilon^3}|D^2_{xx}u_\varepsilon|^2 + C_1 \varepsilon |D^2_{\theta\theta}u_\varepsilon|^2,
$$

we conclude (using the equation) that, for some $C_5(d, D, \delta) > 0$,

$$
\frac{1}{\varepsilon}\left[D\frac{|D_x u_\varepsilon|^2}{\varepsilon^2} + |\partial_\theta u_\varepsilon|^2 + K - \rho_\varepsilon\right]^2 \le C_2\left[\frac{1}{\varepsilon^2}D_x(K-\rho_\varepsilon).Du_\varepsilon + \varepsilon(\partial_\theta u_\varepsilon)^2 + \frac{2}{\varepsilon^2}|D_x u_\varepsilon|^2 \partial_\theta u_\varepsilon\right].
$$

It follows that there exists some positive constant C such that

$$
\begin{aligned}
w^2 \quad &\le C\left[1 + \tfrac{1}{\varepsilon}|Du_\varepsilon| + \varepsilon^2(\partial_\theta u_\varepsilon)^2 + \tfrac{2}{\varepsilon}|D_x u_\varepsilon|^2|\partial_\theta u_\varepsilon|\right] \\
&\le C\left[1 + \sqrt{w} + \varepsilon^2 w + \varepsilon w^{3/2}\right].
\end{aligned}
$$

From this we conclude that w is bounded and the Lipschitz continuity statement is proved.

□

6 Perspectives

::conclusion

The dynamics of evolution of dispersal also motivates to study the time dependent problem

$$
\begin{cases}
\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,\theta,t) - \theta \Delta_x n_\varepsilon = n_\varepsilon\big(K(x) - \rho_\varepsilon(x,t)\big) \text{ in } \Omega \times \mathbb{R} \times (0,\infty), \\
\rho_\varepsilon(x,t) = \int_0^1 n_\varepsilon(x,\theta,t)d\theta,
\end{cases} \tag{27}
$$

eq:parabo

with the Neuman boundary conditions on $\partial\Omega$ and $1-$periodicicty in θ. For this problem, we expect that

$$
n_\varepsilon(x,\theta,t) \underset{\varepsilon\to 0}{\longrightarrow} \mathcal{N}(x,t)\delta(\theta - \bar{\theta}(t)).
$$

The weight $\mathcal{N}(x,t)$ is, at least formally, defined by

$$
\begin{cases}
-\bar{\theta}(t)\Delta_x \mathcal{N} = \mathcal{N}\big(K - \mathcal{N}\big) \text{ in } \Omega, \\
\frac{\partial}{\partial \nu}\mathcal{N}(x,t) = 0 \ \text{ on } \partial\Omega,
\end{cases} \tag{28}
$$

eq:No

and the value $\bar{\theta}(t)$ is now obtained through the constrained Hamilton-Jacobi equation

$$\begin{cases} \partial_t u(\theta,t) - |\nabla_\theta u|^2 = -H\big(\theta, \mathcal{N}(\cdot,t)\big) \text{ in } \mathbb{R} \\ \max_\theta u(\theta,t) = 0 = u(\bar{\theta}(t),t). \end{cases} \tag{29}$$ eq:u

We recall that, still formally, we can derive a canonical equation for the fittest trait $\bar{\theta}(t)$ which takes the form [10, 18]

$$\frac{d}{dt}\bar{\theta}(t) = -\big(-D^2_\theta u(\bar{\theta}(t),t)\big)^{-1}.\nabla H_\theta\big(\theta, \mathcal{N}(\cdot,t)\big). \tag{30}$$ canonical

The main difficulties compared to the stationary case are to derive a priori estimates for $\rho_\varepsilon(x,t)$ analogous to those in Lemma 14 and to obtain gradient estimates on u_ε. Since Lipschitz regularity for u is optimal, and only differentiability can be proved at the maximum point [21], giving a meaning to (30) is also a challenge.

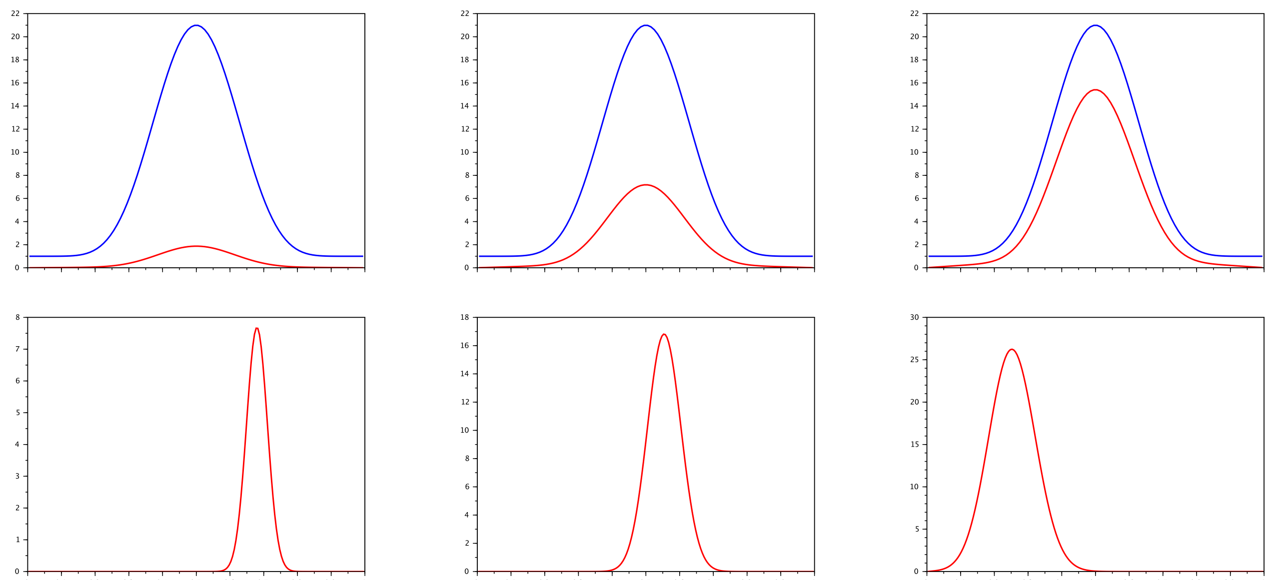

Figure 1: Snapshots of the evolution of the dispersal for three different times. Top figures depict the space repartition $\rho(x)$ (fixed blue curve = K, increasing red = ρ). Bottom figures depict the trait distribution $\int_0^1 n(x,\theta,t)dx$. fig1

Numerical simulations are presented in Figure 1 which illustrates the convergence of the fittest trait to the smaller values of the trait. For this simulation we have chosen $\Omega = (0,1)$ and the data

$$D(\theta) = 1.5\ \theta, \qquad K(x) = 1 + 20\big(1 - 4(x - .5)^2\big)^8,$$

and we have used the Dirichlet boundary conditions, both in x and θ, for the convenience of numerics.

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