Travelling waves for the cane toads equation with bounded traits.

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Abstract

In this paper, we study propagation in a nonlocal reaction-diffusion-mutation model describing the invasion of cane toads in Australia [30]. The population of toads is structured by a space variable and a phenotypical trait and the space-diffusivity depends on the trait. We use a Schauder topological degree argument for the construction of some travelling wave solutions of the model. The speed c^* of the wave is obtained after solving a suitable spectral problem in the trait variable. An eigenvector arising from this eigenvalue problem gives the flavor of the profile at the edge of the front. The major difficulty is to obtain uniform L^∞ bounds despite the combination of non local terms and an heterogeneous diffusivity.

Key-Words: Structured populations, Reaction-diffusion equations, Travelling waves, Spectral problem
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1 Introduction.

In this paper, we focus on propagation phenomena in a model for the invasion of cane toads in Australia, proposed in [5]. It is a structured population model with two structural variables, the space $x \in \mathbb{R}^n$ and the motility $\theta \in \Theta$ of the toads. The mobility of the toads is the ability to move spontaneously and actively. Here $\Theta := (\theta_{\min}, \theta_{\max})$, with $\theta_{\min} > 0$ denotes the bounded set of traits. One modeling assumption is that the space diffusivity depends only on θ. The mutations are simply modeled by a diffusion process with constant diffusivity α in the variable θ. Each toad is in local competition with all other individuals (independently of their trait) for resources. The free growth rate is r. The resulting reaction term is of monostable type. Denoting $n(t, x, \theta)$ the density of toads having trait $\theta \in \Theta$ in position $x \in \mathbb{R}^n$ at time $t \in \mathbb{R}^+$, the model writes:

$$\begin{cases} \partial_t n - \theta \Delta_x n - \alpha \partial_{\theta\theta} n = rn(1-\rho)\,, & (t, x, \theta) \in \mathbb{R}^+ \times \mathbb{R}^n \times \Theta, \\ \partial_\theta n(t, x, \theta_{\min}) = \partial_\theta n(t, x, \theta_{\max}) = 0\,, & (t, x) \in \mathbb{R}^+ \times \mathbb{R}^n. \end{cases} \tag{1.1}$$ eq:main

with

$$\forall (t, x) \in \mathbb{R}^+ \times \mathbb{R}^n, \qquad \rho(t, x) = \int_\Theta n(t, x, \theta)\, d\theta.$$

The Neumann boundary conditions ensure the conservation of individuals through the mutation process.

The invasion of cane toads has interested several field biologists. The data collected [33, 30] show that the speed of invasion has always been increasing during the eighty first years of propagation and that younger individuals at the edge of the invasion front have shown significant changes in their morphology compared to older populations. This example of ecological problem among others (see the expansion of bush crickets in Britain [35]) illustrates the necessity of having models able to describe space-trait interactions. Several works have addressed the issue of front invasion in ecology, where the trait is related to dispersal ability [18, 15]. It has been postulated that selection of more motile individuals can occur, even if they have no advantage regarding their reproductive rate, due to spatial sorting [25, 31, 33, 34].

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Recently, some models for populations structured simultaneously by phenotypical traits and a space variable have emerged. A similar model to (1.1) in a discrete trait setting has been studied by Dockery *et al.* in [19]. Interestingly, they prove that in a bounded space domain and with a rate of growth $r(x)$ heterogeneous in space, the only nontrivial Evolutionarily Stable State (ESS) is a population dominated by the slowest diffusing phenotype. This conclusion is precisely the opposite of what is expected at the edge of an invading front. In [2], the authors study propagation in a model close to (1.1), where the trait affects the growth rate r but not the dispersal ability. This latter assumption is made to take into account that the most favorable phenotypical trait may depend on space. The model reads

$$\partial_t n - \Delta_{x,\theta} n = \left(r\left(\theta - Bx\cdot e\right) - \int_{\mathbb{R}} k\left(\theta - Bx\cdot e, \theta' - Bx\cdot e\right) n(t,x,\theta')d\theta' \right) n(t,x,\theta),$$

and the authors prove the existence of travelling wave solutions. A version with local competition in trait of this equation has also been studied in [6]. As compared to [2, 6], the main difficulty here is to obtain a uniform $L^\infty(\mathbb{R}\times\Theta)$ bound on the density n solution of (1.1). It is worth recalling that this propagation phenomena in reaction diffusion equations, through the theory of travelling waves, has been widely studied since the pioneering work of Aronson and Weinberger [4] on the Fisher-KPP equation [21, 26]. We refer to [27, 28, 7] and the references therein for recent works concerning travelling waves for generalized Fisher-KPP equations in various heterogeneous media, and to [16, 17, 32] for works studying front propagation in models where the non locality appears in the dispersion operator.

Studying propagation phenomena in nonlocal equations can be pretty involved since some qualitative features like Turing instability may occur at the back of the front, see [8, 23], due to lack of comparison principles. Nevertheless, it is sometimes still possible to construct travelling fronts with rather abstract arguments. In this article, we aim to give a complete proof of some formal results that were previously announced in [9]. Namely construct some travelling waves solutions of (1.1) with the expected qualitative features at the edge of the front. Let us now give the definition of spatial travelling waves we seek for (1.1).

defonde **Definition 1.** *We say that a function $n(t,x,\theta)$ is a travelling wave solution of speed $c\in\mathbb{R}^+$ in direction $e\in\mathbb{S}^n$ if it writes*

$$\forall (t,x,\theta)\in\mathbb{R}^+\times\mathbb{R}^n\times\Theta, \qquad n(t,x,\theta) := \mu\left(\xi := x\cdot e - ct, \theta\right),$$

where the profile $\mu\in\mathcal{C}^2_b(\mathbb{R}\times\Theta)$ is nonnegative, satisfies

$$\liminf_{\xi\to-\infty} \mu(\xi,\cdot) > 0, \qquad \lim_{\xi\to+\infty}\mu(\xi,\cdot) = 0,$$

pointwise and solves

$$\begin{cases} -c\partial_\xi\mu = \theta\partial_{\xi\xi}\mu + \alpha\partial_{\theta\theta}\mu + r\mu(1-\nu), & (\xi,\theta)\in\mathbb{R}\times\Theta, \\ \partial_\theta\mu(\xi,\theta_{min}) = \partial_\theta\mu(\xi,\theta_{max}) = 0, & \xi\in\mathbb{R}. \end{cases} \tag{1.2}$$ eqkinwave

where ν is the macroscopic density associated to μ, that is $\nu(\xi) = \int_\Theta \mu(\xi,\theta)\,d\theta$.

To state the main existence result we first need to explain which heuristic considerations yield to the derivation of possible speeds for fronts. As for the standard Fisher-KPP equations, we expect that the fronts we build in this work are so-called *pulled fronts*: they are driven by the dynamics of small populations at the edge of the front. In this case, the speed of the front can be obtained through the linearized equation of (1.2) around $\mu << 1$. The resulting equation (which is now a local elliptic equation) writes

$$\begin{cases} -c\partial_\xi\widetilde{\mu} = \theta\partial_{\xi\xi}\widetilde{\mu} + \alpha\partial_{\theta\theta}\widetilde{\mu} + r\widetilde{\mu}, & (\xi,\theta)\in\mathbb{R}\times\Theta, \\ \partial_\theta\widetilde{\mu}(\xi,\theta_{\min}) = \partial_\theta\widetilde{\mu}(\xi,\theta_{\max}) = 0, & \xi\in\mathbb{R}. \end{cases} \tag{1.3}$$ eq:linmain

Particular solutions of (1.3) are a combination of an exponential decay in space and a monotonic profile in trait:

$$\forall(\xi,\theta)\in\mathbb{R}\times\Theta, \qquad \widetilde{\mu}(\xi,\theta) = Q_\lambda(\theta)e^{-\lambda\xi},$$

where $\lambda > 0$ represents the spatial decreasing rate and Q_λ the trait profile. The pair $(c(\lambda), Q_\lambda)$ solves the following *spectral problem*:

$$\begin{cases} \alpha Q_\lambda(\theta)'' + \left(-\lambda c(\lambda) + \theta\lambda^2 + r\right) Q_\lambda(\theta) = 0\,, \qquad \theta \in \Theta, \\ \partial_\theta Q_\lambda\left(\theta_{\min}\right) = \partial_\theta Q_\lambda\left(\theta_{\max}\right) = 0, \\ Q_\lambda(\theta) > 0,\ \int_\Theta Q_\lambda(\theta)\, d\theta = 1\,. \end{cases} \tag{1.4}$$

eq:eigenpb

We refer to Section 2, Proposition 5 for a proof showing that (1.4) has a unique solution $(c(\lambda), Q_\lambda)$ for all $\lambda > 0$. We also prove there that we can define the minimal speed c^* and its associated decreasing rate through the following formula:

$$c^* := c(\lambda^*) = \min_{\lambda > 0} c(\lambda). \tag{1.5}$$

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Remark 2. *We emphasize that this structure of spectral problem giving information about propagation in models of "kinetic" type is quite robust. We refer to [2, 6, 12, 13] for works where this kind of dispersion relations also give the speed of propagation of possible travelling wave solutions, and to [10, 11, 14] for recent works where the same kind of spectral problem appears to find the limiting Hamiltonian in the WKB expansion of hyperbolic limits.*

We are now ready to state the main Theorem of this paper:

wave **Theorem 3.** *Let $\Theta := (\theta_{min}, \theta_{max})\,, \theta_{min} > 0, \theta_{min} < +\infty$ and c^* be the minimal speed defined after* (1.5)*. Then, there exists a travelling wave solution of* (1.1) *of speed c^* in the sense of Definition 1 .*

This Theorem, together with the heuristic argument, has been announced in [9].

Remark 4. *As in [2, 4], we expect that waves going with faster speeds $c > c^*$ do exist and are constructible by a technique of sub- and super solutions. Nevertheless, since it does not make much difference with [2], we do not address this issue here.*

The paper is organized as follows. In Section 2, we study the spectral problem (1.4) and provide some qualitative properties. In Section 3, we elaborate a topological degree argument to solve (1.2) in a bounded slab. Finally in Section 4, we construct the profile going with speed c^* which proves the existence of Theorem 3.

2 The spectral problem.

tools

We discuss the spectral problem naturally associated to (1.1) that we have stated in (1.4). We state and prove some useful properties of Q_λ and some relations between c^* and λ^*.

propspec **Proposition 5** (**Qualitative properties of the spectral problem).** *For all $\lambda > 0$, the spectral problem* (1.4) *has a unique solution $(c(\lambda), Q_\lambda)$. Moreover, the function $\lambda \mapsto c(\lambda)$ has a minimum, that we denote by c^* and that we call the minimal speed. We denote by $\lambda^* > 0$ an associated decreasing rate and $Q_{\lambda^*} := Q^*$ the corresponding profile. Then we have the following properties:*

(i) For all $\lambda > 0$, the profile Q_λ is increasing w.r.t θ. There exists θ_0 such that Q_λ is convex on $[\theta_{min}, \theta_0]$ and concave on $[\theta_0, \theta_{max}]$. Moreover, θ_0 satisfies $-\lambda c(\lambda) + \lambda^2\theta_0 + r = 0$

(ii) We define $\langle\theta_\lambda\rangle := \int_\Theta \theta Q_\lambda(\theta) d\theta$, the mean trait associated to the decay rate λ. We also define $\langle\theta^*\rangle := \langle\theta_{\lambda^*}\rangle$. One has

$$\forall \lambda > 0, \qquad -\lambda c(\lambda) + \lambda^2 \left\langle \theta_\lambda \right\rangle + r = 0, \qquad \left\langle \theta_\lambda \right\rangle > \frac{\theta_{max} + \theta_{min}}{2}. \tag{2.6}$$

rel1

(iii) About the special features of the minimal speed, we have

$$c^* > 2\sqrt{r\langle\theta^*\rangle}, \tag{2.7}$$

rel6

$$c^* \geq \lambda^* \left(\theta_{max} + \theta_{min}\right). \tag{2.8}$$

rel4

Remark 6. *Even if it does not play much role in the analysis, let us notice that from the same equation defining θ_0 and $\langle\theta_\lambda\rangle$, one can deduce that Q_λ changes its convexity at the mean trait.*

Proof of Proposition 5. We first prove the existence and uniqueness of $(c(\lambda), Q_\lambda)$ for all positive λ. Let $\beta > 0$ and K be the positive cone of nonnegative functions in $\mathcal{C}^{1,\beta}(\Theta)$. We define L on $\mathcal{C}^{1,\beta}(\Theta)$ as below

$$L(u) = -\alpha u''(\theta) - (\theta - \theta_{\max})\,\lambda^2 u(\theta).$$

The resolvent of L endowed with the Neumann boundary condition is compact from the regularizing effect of the Laplace term. Moreover, the strong maximum principle and the boundedness of Θ gives that it is strongly positive. Using the Krein-Rutman theorem we obtain that there exists a nonnegative eigenvalue $\frac{1}{\gamma(\lambda)}$, corresponding to a positive eigenfunction Q_λ. This eigenvalue is simple and none of the other eigenvalues corresponds to a positive eigenfunction. As a consequence, $\lambda c(\lambda) := r + \lambda^2\theta_{\max} - \gamma(\lambda)$ solves the problem.

We come to the proof of (i). Since $Q_\lambda \in \mathcal{C}^2(\Theta)$ and satisfies Neumann boundary conditions, there exists θ_0 such that $Q_\lambda''(\theta_0) = 0$. Since $-\lambda c(\lambda) + \lambda^2\theta + r$ is increasing with θ, the sign of Q_λ'' and thus the convexity of Q_λ follows. We deduce:

$$\lambda^2\theta_{min} + r \le \lambda c(\lambda) \le \lambda^2\theta_{max} + r.$$

This yields

$$c(\lambda) \underset{\lambda\to 0}{\sim} \frac{r}{\lambda}, \qquad \lambda c(\lambda) = \mathcal{O}_{\lambda\to+\infty}(\lambda^2).$$

These latter relations and the continuity of $\lambda \mapsto c(\lambda)$ give the existence of a positive minimal speed c^* and a smallest positive minimizer λ^*.

We now prove (ii). We obtain the first relation of (2.6) after integrating (1.4) over Θ and recalling the Neumann boundary conditions. To get the second one, we divide the spectral problem by Q_λ and then integrate over Θ:

$$\langle\theta_\lambda\rangle = \frac{\theta_{max} + \theta_{min}}{2} + \frac{\alpha}{\lambda^2|\Theta|}\int_\Theta \left|\frac{Q_\lambda'}{Q_\lambda}\right|^2 d\theta > \frac{\theta_{max} + \theta_{min}}{2}. \tag{2.9}$$

rel2

We finish with (iii). For this purpose, we define $W_\lambda = (Q_\lambda)^2$. It satisfies Neumann boundary conditions on $\partial\Theta$ and

$$\forall\theta \in \Theta, \qquad \alpha W'' + 2\left(-\lambda c(\lambda) + \lambda^2\theta + r\right) W = \alpha\left(\frac{W'}{2\sqrt{W}}\right)^2 \ge 0.$$

We thus deduce that

$$\lambda^2 \int_\Theta \theta W d\theta + (-\lambda c(\lambda) + r)\int_\Theta W d\theta > 0,$$

from which we deduce

$$\frac{\int_\Theta \theta\,(Q^*)^2\,d\theta}{\int_\Theta (Q^*)^2\,d\theta} > \langle\theta^*\rangle\,. \tag{2.10}$$

rel5

Differentiating (1.4) with respect to λ, we obtain

$$(-\lambda c'(\lambda) - c(\lambda) + 2\theta\lambda)\,Q_\lambda + \left(-\lambda c(\lambda) + \theta\lambda^2 + r\right)\frac{\partial Q_\lambda}{\partial\lambda} + \alpha\partial_{\theta\theta}\left(\frac{\partial Q_\lambda}{\partial\lambda}\right) = 0.$$

We do not have any information about $\frac{\partial Q_\lambda}{\partial\lambda}$. Nevertheless, one can overcome this issue by testing directly against Q_λ. We obtain, for $\lambda = \lambda^*$:

$$-c^*\int_\Theta (Q^*)^2\,d\theta + 2\lambda^*\int_\Theta \theta\,(Q^*)^2\,d\theta = 0,$$

since $c'(\lambda^*) = 0$. As a consequence

$$c^* = 2\lambda^*\frac{\int_\Theta \theta\,(Q^*)^2\,d\theta}{\int_\Theta (Q^*)^2\,d\theta}. \tag{2.11}$$

rel3

Combining (2.11) with $-\lambda^* c^* + (\lambda^*)^2 \langle \theta^* \rangle + r = 0$, one obtains

$$\frac{(c^*)^2}{4r} = \frac{1}{2}\left(\frac{\int_\Theta \theta\,(Q^*)^2\,d\theta}{\int_\Theta (Q^*)^2\,d\theta}\right)^2 \left(\frac{\int_\Theta \theta\,(Q^*)^2\,d\theta}{\int_\Theta (Q^*)^2\,d\theta} - \frac{\langle \theta^* \rangle}{2}\right)^{-1}. \tag{2.12}$$

which gives (2.7) since $\frac{1}{2}\left(\frac{\int_\Theta \theta (Q^*)^2 d\theta}{\int_\Theta (Q^*)^2 d\theta}\right)^2 \left(\frac{\int_\Theta \theta (Q^*)^2 d\theta}{\int_\Theta (Q^*)^2 d\theta} - \frac{\langle \theta^* \rangle}{2}\right)^{-1} \geq \langle \theta^* \rangle$ always holds true and (2.10) rules out equality.

Finally, using (2.6) and (2.11), one has

$$c^* > 2\lambda^* \langle \theta^* \rangle \geq 2\lambda^* \frac{\theta_{max} + \theta_{min}}{2} = \lambda^* \left(\theta_{max} + \theta_{min}\right).$$

□

3 Solving the problem in a bounded slab.

Slab

In this Section, we solve an approximated problem in a bounded slab $(-a, a) \times \Theta$ as a first step to solve (1.2).

Definition 7. *For all $\tau \geq 0$, we define*

$$\forall \theta \in \Theta, \qquad g_\tau(\theta) = \theta_{min} + \tau\left(\theta - \theta_{min}\right).$$

Now, for all $a > 0$, the slab problem $P_{\tau,a}$ is defined as follows on $[-a, a] \times \Theta$:

$$[P_{\tau,a}]\begin{cases} -c\partial_\xi \mu^a - g_\tau(\theta)\partial_{\xi\xi}\mu^a - \alpha\partial_{\theta\theta}\mu^a = r\mu^a(1-\nu^a)\,, \qquad \mu^a \geq 0, \quad (\xi,\theta) \in (-a,a)\times\Theta, \\ \partial_\theta \mu^a(\xi, \theta_{\min}) = \partial_\theta \mu^a(\xi, \theta_{\max}) = 0\,, \quad \xi \in (-a,a), \\ \mu^a(-a,\theta) = |\Theta|^{-1}\,, \quad \mu^a(a,\theta) = 0\,, \quad \theta \in \Theta. \end{cases} \tag{3.13}$$

eq:slab

with $\nu^a := \int_\Theta \mu^a(\cdot,\theta)d\theta$ and the supplementary renormalization condition $\nu^a(0) = \varepsilon$. For legibility, we set $P_{1,a} := P_a$.

In this problem, the speed c is an unknown as well as μ^a. Moreover, without the supplementary renormalization condition $\nu^a(0) = \varepsilon$, the problem is underdetermined. Indeed, this additional condition is needed to ensure compactness of the family (c^a, μ^a) when a goes to $+\infty$, since the limit problem (1.2) is translation invariant. The boundary condition in $-a$ is chosen this way since we heuristically expect that the population is uniform in trait at the back of the front as observed in the ecological problem, see [30]. However, although we fix this boundary condition in the slab, let us recall again that in general the behavior at the back of the front for the limit problem is not easy to figure out due to possible Turing instabilities. The non-local character of the source term does not provide any full comparison principle for $P_{\tau,a}$. We will prove the existence of a non-negative solution of (3.13), but we don't claim that all the solutions of this slab problem are non-negative. We follow [2, 8] and shall use the Leray-Schauder theory. For this purpose, some uniform *a priori* estimates (with respect to τ, a) on the solutions of the slab problem are required. The main difference with [2, 8] is that it is more delicate to obtain these uniform L^∞ estimates since it is not possible to write neither a useful equation nor an inequation on ν due to the term $\theta\partial_{\xi\xi}\mu$ (as it is the case in kinetic equations). Our strategy is the following. We first prove in Lemma 9 that the speed is uniformly bounded from above. Then, Lemmas 10 and 11 focus on the case $c = 0$ and prove that there cannot exist any solution to the slab problem in this case, provided that the normalization ε is well chosen. Finally, when the speed is given and uniformly bounded, we can derive a uniform *a priori* estimate on the solutions of the slab problem (3.13). Thanks to these *a priori* estimates, we apply a Leray-Schauder topological degree argument with the parameter τ in Proposition 14. This strategy is reliable as the problem corresponding to $\tau = 0$ is easier to solve since it is more or less a standard Fisher-KPP equation. All along Section 3, we omit the superscript a in μ^a and ν^a.

3.1 A Harnack inequality up to the boundary.

We shall apply several times the following useful Harnack inequality for (1.2), which is true up to the boundary in the direction θ. This is possible thanks to the Neumann boundary conditions in this direction.

Harnack **Proposition 8.** *Suppose that μ is a positive solution of (1.2) such that the total density ν is locally bounded. Then for all $0 < b < +\infty$, there exists a constant $C(b) < +\infty$ such that the following Harnack inequality holds:*

$$\forall (\xi, \theta, \theta') \in (-b, b) \times \Theta \times \Theta, \qquad \mu(\xi, \theta) \leq C(b) \mu(\xi, \theta').$$

Proof of Proposition 8. One has to figure out how to obtain the validity of the Harnack inequality up to the boundary in Θ. Indeed, it holds on sub-compacts sets thanks to the standard elliptic regularity, given that the density ν is bounded. To obtain the full Harnack estimate, we consider the equation (1.2) after a reflection with respect to $\theta = \theta_{min}$ and $\theta = \theta_{max}$ and for positive values of θ. One obtains the following equation in the weak sense

$$\forall (\xi, \theta) \in \mathbb{R} \times \left(\mathbb{R}^{+*} \cap (\mathbb{R} \backslash \{\theta_{min} + \Theta\mathbb{Z}\}) \right), \qquad -c\partial_\xi \mu(\xi, \theta) - g(\theta) \partial_{\xi\xi} \mu(\xi, \theta) - \alpha \partial_{\theta\theta} \mu(\xi, \theta) = r\mu(\xi, \theta)(1 - \nu(t, \xi)) \,.$$

The crucial point is that this equation is also satisfied on the boundaries $\theta = \mathbb{R}^+ \cap \{\theta_{min} + \Theta\mathbb{Z}\}$ thanks to the Neumann boundary conditions. Indeed, no Dirac mass in $\theta = \mathbb{R}^+ \cap \{\theta_{min} + \Theta\mathbb{Z}\}$ arises while computing the second derivative $\partial_{\theta\theta}$ in the symmetrized equation.

□

3.2 An upper bound for c.

upboundc **Lemma 9.** *For any normalization parameter $\varepsilon > 0$, there exists a sufficiently large $a_0(\varepsilon)$ such that any pair (c, μ) solution of the slab problem $P_{\tau,a}$ with $a \geq a_0(\varepsilon)$ (and $\mu \geq 0$) satisfies $c \leq c_\tau^* \leq c^*$, where c_τ^* is defined after solving (3.15) below.*

Proof of Lemma 9. We just adapt an argument from [2, 8]. It consists in finding a relevant subsolution for a related problem. As $\mu \geq 0$, one has

$$\forall (\xi, \theta) \in (-a, a) \times \Theta, \qquad -c\partial_\xi \mu \leq g_\tau(\theta) \partial_{\xi\xi} \mu + \alpha \partial_{\theta\theta} \mu + r\mu. \tag{3.14}$$ eq:n

As (1.4), the following pertubated spectral problem has a unique solution associated with a minimal speed c_τ^*:

$$\begin{cases} \alpha Q_\tau^*(\theta)'' + \left(-\lambda_\tau^* c_\tau^* + g_\tau(\theta) \left(\lambda_\tau^*\right)^2 + r \right) Q_\tau^*(\theta) = 0 \,, \qquad \theta \in \Theta, \\ \left(Q_\tau^*\right)' (\theta_{\min}) = \left(Q_\tau^*\right)' (\theta_{\max}) = 0, \\ Q_\tau^*(\theta) > 0, \; \int_\Theta Q_\tau^*(\theta) \, d\theta = 1 \,. \end{cases} \tag{3.15}$$ eq:spectau

Let us assume by contradiction that $c > c_\tau^*$, then the family of functions $\psi_A(\xi, \theta) := Ae^{-\lambda_\tau^* \xi} Q_\tau^*(\theta)$ verifies

$$\forall (\xi, \theta) \in (-a, a) \times \Theta, \qquad g_\tau(\theta) \partial_{\xi\xi} \psi_A + \alpha \partial_{\theta\theta} \psi_A + r\psi_A = \lambda_\tau^* c_\tau^* \psi_A < -c\partial_\xi \psi_A, \tag{3.16}$$ eq:psi

As the eigenvector Q^* is positive, and $\mu \in L^\infty(-a, a)$, one has $\mu \leq \psi_A$ for A sufficiently large. As a consequence, one can define

$$A_0 = \inf \{ A \mid \forall (\xi, \theta) \in (-a, a) \times \Theta, \; \psi_A(\xi, \theta) > \mu(\xi, \theta) \} \,.$$

Necessarily, $A_0 > 0$ and there exists a point $(\xi_0, \theta_0) \in [-a, a] \times [\theta_{\min}, \theta_{\max}]$ where ψ_{A_0} touches μ:

$$\mu(\xi_0, \theta_0) = \psi_{A_0}(\xi_0, \theta_0).$$

This point minimizes $\psi_{A_0} - n$ and cannot be in $(-a, a) \times \Theta$. Indeed, combining (3.14) and (3.16), one has in the interior,

$$\forall (\xi, \theta) \in (-a, a) \times \Theta, \qquad c\partial_\xi \left(\psi_{A_0} - \mu \right) + g_\tau(\theta) \partial_{\xi\xi} \left(\psi_{A_0} - \mu \right) + \alpha \partial_{\theta\theta} \left(\psi_{A_0} - \mu \right) + r \left(\psi_{A_0} - \mu \right) < 0.$$

But, if (ξ_0, θ_0) is in the interior, this latter inequality cannot hold since

$$g_\tau(\theta)\partial_{\xi\xi}\left(\psi_{A_0} - \mu\right) + \alpha\partial_{\theta\theta}\left(\psi_{A_0} - \mu\right) \geq 0.$$

Next we eliminate the boundaries. First, (ξ_0, θ_0) cannot lie in the right boundary $\{x = a\} \times \Theta$ since $\psi_{A_0} > 0$ and $\mu = 0$ there. Moreover, thanks to the Neumann boundary conditions satisfied by both ψ_{A_0} and μ, (ξ_0, θ_0) cannot be in $[-a, a] \times \{\theta_{\min}, \theta_{\max}\}$, thanks to Hopf's Lemma. We now exclude the left boundary by adjusting the normalization. If $\xi_0 = -a$, then $\psi_{A_0}(\xi_0, \theta_0) = |\Theta|^{-1}$ and $A_0 = \frac{e^{-\lambda_\tau^* a}}{|\Theta| Q_\tau^*(\theta_0)}$. Then $\nu(0) \leq \frac{e^{-\lambda_\tau^* a}}{|\Theta| Q_\tau^*(\theta_0)}$ which is smaller than ε for a sufficiently large a. We thus conclude that $c \leq c_\tau^*$. We shall now prove that for all $\tau \in [0, 1]$, one has $c_\tau^* \leq c^*$. Differentiating (3.15) with respect to τ and testing against Q_τ^*, one obtains, similarly as in Proof of Proposition 5 (iii),

$$\int_\Theta \left[\frac{d\lambda}{d\tau}\left(2\lambda_\tau^* g_\tau(\theta) - c_\tau^*\right) + \left(\lambda_\tau^*\right)^2 g_\tau'(\theta) - \lambda_\tau^* \frac{dc_\tau^*}{d\tau}\right] \left(Q_\tau^*\right)^2 d\theta = 0.$$

But now recalling (2.11), which writes as follows in the τ-case:

$$c_\tau^* = 2\lambda_\tau^* \frac{\int_\Theta g_\tau(\theta) \left(Q_\tau^*\right)^2 d\theta}{\int_\Theta \left(Q_\tau^*\right)^2 d\theta}, \qquad (3.17)$$

rel3'

one obtains

$$\frac{dc_\tau^*}{d\tau} = \lambda_\tau^* \frac{\int_\Theta g_\tau'(\theta) \left(Q_\tau^*\right)^2 d\theta}{\int_\Theta \left(Q_\tau^*\right)^2 d\theta}.$$

We deduce that c_τ^* is increasing with respect to τ, so that $c_\tau^* \leq c_1^* = c^*$.

□

3.3 The special case $c = 0$.

We now focus on the special case $c = 0$. We first show (Lemma 10) that the density μ is uniformly bounded (with respect to $a > 0$). From this estimate, we deduce in Lemma 11 that there exists a constant ε_0 depending only on the fixed parameters of the problem such that necessarily $\nu(0) \geq \varepsilon_0$. Thus, provided that ε is set sufficiently small, our analysis will conclude that the slab problem does not admit a solution of the form $(c, \mu) = (0, \mu)$ for $\varepsilon < \varepsilon_0$. We emphasize that the key *a priori* estimate, *i.e.* $\nu \in L^\infty\left((-a, a) \times \Theta\right)$, is easier to obtain in the case $c = 0$ than in the case $c \neq 0$ (compare Lemmas 10 and 12).

3.3.1 A priori estimate for μ when $c = 0$.

lem:nc=0

Lemma 10. (A priori estimates, $c = 0$).
Assume $c = 0$, $b > 0$ and $\tau \in [0, 1]$. There exists a constant $C(b)$ such that every solution $(c = 0, \mu)$ of (3.13) *satisfies*

$$\forall (\xi, \theta) \in [-b, b] \times \Theta, \quad \mu(\xi, \theta) \leq \frac{C(b)}{\Theta} \frac{\theta_{max}}{\theta_{min}}.$$

Proof of Lemma 10. When $c = 0$, the slab problem (3.13) reduces to

$$[P_{\tau,b}] \begin{cases} -g_\tau(\theta)\partial_{\xi\xi}\mu - \alpha\partial_{\theta\theta}\mu = r\mu(1 - \nu), & (\xi, \theta) \in (-b, b) \times \Theta, \\ \partial_\theta \mu(\xi, \theta_{\min}) = \partial_\theta \mu(\xi, \theta_{\max}) = 0, & \xi \in (-b, b), \\ \mu(-b, \theta) = |\Theta|^{-1}, \quad \mu(b, \theta) = 0, & \theta \in \Theta. \end{cases}$$

Integration with respect to the trait variable θ yields

$$\begin{cases} -\partial_{\xi\xi}\left(\int_\Theta g_\tau(\theta)\mu(x, \theta) d\theta\right) = r\nu(\xi)(1 - \nu(\xi)), & \xi \in \mathbb{R}, \\ \nu(-b) = 1, \quad \nu(b) = 0. \end{cases}$$

Take a point ξ_0 where $\int_\Theta g_\tau(\theta)\mu(\xi,\theta)d\theta$ attains a maximum. At this point, one has necessarily $\nu(\xi_0) \leq 1$. The following sequence of inequalities holds true for all $\xi \in (-b,b)$:

$$\theta_{\min}\nu(\xi) = g_\tau(\theta_{min})\nu(\xi) = g_\tau(\theta_{min}) \int_\Theta \mu(\xi,\theta)d\theta \leq \int_\Theta g_\tau(\theta)\mu(\xi,\theta)d\theta$$
$$\leq \int_\Theta g_\tau(\theta)\mu(\xi_0,\theta)d\theta \leq g_\tau(\theta_{max})\nu(\xi_0) \leq g_\tau(\theta_{max}),$$

and give

$$\forall \xi \in (-b,b), \quad \nu(\xi) \leq \frac{g_\tau(\theta_{max})}{\theta_{min}} \leq \frac{\theta_{max}}{\theta_{min}}.$$

Now, the Harnack inequality of Proposition 8 gives

$$\forall (\xi,\theta) \in (-b,b)\times\Theta, \qquad n(\xi,\theta) \leq \frac{C(b)}{|\Theta|}\nu(\xi) \leq \frac{C(b)}{|\Theta|}\frac{\theta_{max}}{\theta_{min}}.$$

□

3.3.2 Non-existence of solutions of the slab problem when $c = 0$.

bottom **Lemma 11. (Lower bound for $\nu(0)$ when $c = 0$).** *There exists $\varepsilon_0 > 0$ such that if a is large enough, then for all $\tau \in [0,1]$, any (non-negative) solution of the slab problem $(c = 0, \mu)$ satisfies $\nu(0) > \varepsilon_0$.*

Proof of Lemma 11. We adapt an argument from [2]. It is a bit simpler here since the trait space is bounded. For $b > 0$, consider the following spectral problem in both variables (ξ,θ):

$$\begin{cases} g_\tau(\theta)\partial_{\xi\xi}\varphi_b + \alpha\partial_{\theta\theta}\varphi_b + r\varphi_b = \psi_b\varphi_b\,, \quad (\xi,\theta) \in (-b,b)\times\Theta, \\ \partial_\theta\varphi_b(\xi,\theta_{\min}) = \partial_\theta\varphi_b(\xi,\theta_{\max}) = 0\,, \quad \xi \in (-b,b)\,, \\ \varphi_b(-b,\theta) = 0\,, \quad \varphi_b(b,\theta) = 0\,, \quad \theta \in \Theta. \end{cases} \tag{3.18}$$ eq:evpb

Again, by Krein-Rutman theory, ψ_b is the only eigenvalue such that there exists a positive eigenvector φ_b. One can rescale the problem in the space direction setting $\xi = b\zeta$:

$$\begin{cases} \dfrac{g_\tau(\theta)}{b^2}\partial_{\zeta\zeta}\varphi_b + \alpha\partial_{\theta\theta}\varphi_b + r\varphi_b = \psi_b\varphi_b\,, \quad (\zeta,\theta) \in (-1,1)\times\Theta\,, \\ \partial_\theta\varphi_b(\zeta,\theta_{\min}) = \partial_\theta\varphi_b(\zeta,\theta_{\max}) = 0\,, \quad \zeta \in (-1,1)\,, \\ \varphi_b(-1,\theta) = 0\,, \quad \varphi_b(1,\theta) = 0\,, \quad \theta \in \Theta. \end{cases}$$

One can prove that $\lim_{b\to+\infty}\psi_b = r$. We give a sketch of proof for the sake of completeness. We introduce the problem

$$\begin{cases} \alpha V_b'' + \left(-\frac{\pi^2}{4}\dfrac{g_\tau(\theta)}{b^2} - \psi_b + r\right)V_b = 0\,, \quad V_b > 0, \qquad \theta \in \Theta, \\ V_b'(\theta_{\min}) = V_b'(\theta_{\max}) = 0\,. \end{cases}$$

The eigenvector (up to a multiplicative constant) φ_b is then given by

$$\forall (\zeta,\theta) \in (-1,1)\times\Theta, \qquad \varphi_b = \sin\left(\frac{\pi}{2}(\zeta+1)\right)V_b(\theta).$$

Moreover, one has

$$\frac{d\psi_b}{db} = \frac{\pi^2}{2b^3}\frac{\int_\Theta g_\tau(\theta)V_b^2 d\theta}{\int_\Theta V_b^2 d\theta}$$

so that $\lim_{b\to+\infty}\psi_b$ exists and solves

$$\begin{cases} \alpha V'' + (-\lim_{b\to+\infty}\psi_b + r)\,V = 0\,, \quad V > 0, \qquad \theta \in \Theta\,, \\ V'(\theta_{\min}) = V'(\theta_{\max}) = 0\,, \end{cases}$$

and it yields necessarily that V is constant and $\lim_{b\to+\infty} \psi_b = r$. As a consequence, we fix b sufficiently large to have $\psi_b > \frac{r}{2}$.

Thanks to the Harnack inequality (of Proposition 8), there exists a constant $C(b)$ which does not depend on $a > b$ such that

$$\forall \theta \in \Theta, \qquad C(b)\mu(0,\theta) \geq C(b) \inf_{(-b,b)\times\Theta} \mu(\xi,\theta) \geq \|\mu\|_{L^\infty((-b,b)\times\Theta)}.$$

To compare (3.13) to (3.18), one has, for all $(\xi,\theta) \in [-b,b]\times\Theta$,

$$g_\tau(\theta)\partial_{\xi\xi}\mu + \partial_{\theta\theta}\mu + r\mu = r\mu\nu \leq r\mu|\Theta|\|\mu\|_{L^\infty((-b,b)\times\Theta)} \leq rC\nu(0)\mu(\xi,\theta).$$

We deduce from this computation that as soon as $\nu(0) \leq \frac{1}{2C(b)}$, one has

$$\forall (\xi,\theta) \in [-b,b]\times\Theta, \quad rC\nu(0)\mu(\xi,\theta) < \psi_b\mu(\xi,\theta),$$

and this means that μ is a subsolution of (3.18). We can now use the same arguments as for the proof of Lemma 9. We define

$$A_0 = \max\left\{A \mid \forall(\xi,\theta) \in [-b,b]\times\Theta,\ A\varphi_b(\xi,\theta) < \mu(\xi,\theta)\right\},$$

so that $u_{A_0} := \mu - A_0\varphi_b$ has a zero minimum in (ξ_0,θ_0) and satisfies

$$\begin{cases} -g_\tau(\theta)\partial_{\xi\xi}u_{A_0} - \alpha\partial_{\theta\theta}u_{A_0} - ru_{A_0} > -\psi_b u_{A_0}\,, & (\xi,\theta) \in (-b,b)\times\Theta\,, \\ \partial_\theta u_{A_0}(\xi,\theta_{\min}) = \partial_\theta u_{A_0}(\xi,\theta_{\max}) = 0\,, \quad \xi \in (-b,b)\,, \\ u_{A_0}(-b,\theta) > 0\,, \quad u_{A_0}(b,\theta) > 0\,, \quad \theta \in \Theta. \end{cases}$$

For the same reasons as in Lemma 9 this cannot hold, so that necessarily $\nu(0) > \varepsilon_0 := \frac{1}{2C(b)}$.

□

3.4 Uniform bound over the steady states, for $c \in [0,c^*]$.

The previous Subsection is central in our analysis. Indeed, it gives a bounded set of speeds where to apply the Leray-Schauder topological degree argument, namely we can restrict ourselves to speeds $c \in [0,c^*]$. Based on this observation, we are now able to derive a uniform L^∞ estimate (with respect to a and τ) for solutions μ of (3.13). This is done in Lemma 12 below.

lem:nc **Lemma 12. (A priori estimates, $c \in [0,c^*]$).**
Assume $c \in [0,c^*]$, $\tau \in [0,1]$ and $a \geq 1$. Then there exists a constant C_0, depending only on the biological parameters $\theta_{\min}$, $|\Theta|$, r and α, such that any solution (c,μ) (with $\mu \geq 0$) of the slab problem $P_{a,\tau}$ satisfies

$$\|\mu\|_{L^\infty((-a,a)\times\Theta)} \leq C_0\,.$$

Proof of Lemma 12. We divide the proof into two steps. In the first step, we prove successively that μ and $\partial_\theta\mu$ are bounded uniformly in $H^1((-a,a)\times\Theta)$. In the second step, we use a suitable trace inequality to deduce a uniform $L^\infty((-a,a)\times\Theta)$ estimate on μ. We define $K_0(a) = \max_{[-a,a]\times\Theta}\mu$. We want to prove that $K_0(a)$ is in fact bounded uniformly in a.

The argument is inspired from [8]. The principle of the proof goes as follows: The maximum principle applied to (3.13) implies that $\nu(\xi_0) \leq 1$ if (ξ_0,θ_0) is a maximum point for μ. This does not imply that $\max\mu \leq 1$. However, we can control $\mu(\xi_0,\theta_0)$ by the non local term $\nu(\xi_0)$ provided some regularity of μ in the direction θ. In order to get this additional regularity we use the particular structure of the equation (the nonlocal term does not depend on θ and is non negative).

Step 0: Preliminary observations.

Denote by (ξ_0, θ_0) a point where the maximum of μ is reached. If the maximum is attained on the $\xi-$boundary $\xi_0 = \pm a$ then $K_0(a) \leq |\Theta|^{-1}$ by definition. If it is attained on the $\theta-$boundary $\theta_0 \in \{\theta_{\min}, \theta_{\max}\}$, then the tangential derivative $\partial_\xi \mu$ necessarily vanishes, and the first derivative $\partial_\theta \mu$ vanishes thanks to the boundary condition. Hence $\partial_{\theta\theta}\mu(\xi_0, \theta_0) \leq 0$ and $\partial_{\xi\xi}\mu(\xi_0, \theta_0) \leq 0$. The same holds true if (ξ_0, θ_0) is an interior point. Evaluating equation (3.13) at (ξ_0, θ_0) implies

$$K_0(a)(1 - \nu(\xi_0)) \geq 0\,,$$

and therefore $\nu_0(\xi_0) \leq 1$.

Step 1: Energy estimates on μ.

We derive local energy estimates. We introduce a smooth cut-off function $\chi : \mathbb{R} \to [0, 1]$ such that

$$\begin{cases} \chi = 1 & \text{on} \qquad J_1 = \left(\xi_0 - \frac{1}{2}, \xi_0 + \frac{1}{2}\right), \\ \chi = 0 & \text{outside} \qquad J_2 = [\xi_0 - 1, \xi_0 + 1]\,. \end{cases}$$

Notice that the support of the cut-off function does not necessarily avoid the $\xi-$boundary. We also introduce the following linear corrector

$$\forall \xi \in [-a, a], \qquad m(\xi) = \frac{1}{|\Theta|}\frac{a - \xi}{2a},$$

which is defined such that $m(-a) = |\Theta|^{-1}$, $m(a) = 0$, and $0 \leq m \leq |\Theta|^{-1}$ on $(-a, a)$. Testing against $(\mu - m)\chi$ over $[-a, a] \times \Theta$, we get

$$\begin{aligned} - c\int_{(-a,a)\times\Theta} (\mu - m)\chi\partial_\xi\mu \, d\xi d\theta - \int_{(-a,a)\times\Theta} g_\tau(\theta)\partial_{\xi\xi}(\mu - m)(\mu - m)\chi \, d\xi d\theta \\ - \int_{(-a,a)\times\Theta} \alpha\partial_{\theta\theta}\mu(\mu - m)\chi \, d\xi d\theta = \int_{(-a,a)\times\Theta} r\mu(1 - \nu)(\mu - m)\chi \, d\xi d\theta. \end{aligned}$$

We now transform each term of the l.h.s. by integration by parts. We emphasize that the linear correction m ensures that all the boundary terms vanish. We get

$$\begin{aligned} &\int_{(-a,a)\times\Theta} g_\tau(\theta) \left|\partial_\xi(\mu - m)\right|^2 \chi \, d\xi d\theta + \int_{(-a,a)\times\Theta} \alpha \left|\partial_\theta\mu\right|^2 \chi \, d\xi d\theta \\ &\qquad \leq \frac{1}{2}\int_{(-a,a)\times\Theta} g_\tau(\theta)(\mu - m)^2\chi'' \, d\xi d\theta + c\frac{|\Theta|^{-1}}{2a}\int_{(-a,a)\times\Theta} \chi(\mu - m) d\xi d\theta \\ &\qquad\quad - c\int_{(-a,a)\times\Theta} \frac{1}{2}(\mu - m)^2\chi' d\xi d\theta + \int_{(-a,a)\times\Theta} r\mu^2\chi \, d\xi d\theta + \int_{(-a,a)\times\Theta} r\mu\nu m\chi \, d\xi d\theta. \end{aligned}$$

We use that $\mu \leq K_0(a)$, $\nu(\xi) \leq |\Theta| K_0(a)$, $g_\tau(\theta) \geq \theta_{\min}$ and $|c| \leq c^*$ to get

$$\begin{aligned} &\theta_{\min}\int_{J_1\times\Theta} \left|\partial_\xi\mu - m'\right|^2 \, d\xi d\theta + \int_{J_1\times\Theta} \alpha \left|\partial_\theta\mu\right|^2 \, d\xi d\theta \\ &\qquad \leq c^*\frac{|\Theta|^{-1}}{2a} K_0 |J_2 \times \Theta| - c\int_{[-a,a]\times\Theta} \frac{1}{2}(\mu - m)^2\chi' d\xi d\theta \\ &\qquad\quad + \frac{1}{2}\int_{(-a,a)\times\Theta} g_\tau(\theta)(\mu - m)^2\chi'' \, d\xi d\theta + \int_{J_2\times\Theta} rK_0^2 \, d\xi d\theta + \int_{J_2\times\Theta} rK_0^2 \, d\xi d\theta\,, \end{aligned}$$

Then we use the pointwise inequality $|\partial_\xi\mu - m_\xi|^2 \geq \partial_\xi\mu^2/2 - m_\xi^2$ in the first integral of the l.h.s.:

$$\begin{aligned} &\frac{\theta_{\min}}{2}\int_{J_1} \left|\partial_\xi\mu\right|^2 \, d\xi d\theta + \int_{J_1} \alpha \left|\partial_\theta\mu\right|^2 \, d\xi d\theta \leq \frac{K_0 c^*}{a} + \theta_{\min}\int_{J_1} \left|m'\right|^2 \, d\xi d\theta \\ &\qquad + \int g_\tau(\theta)\left(\mu^2 + m^2\right)\chi'' \, d\xi d\theta + c^*\int \left(\mu^2 + m^2\right)\chi' d\xi d\theta + 4r|\Theta| K_0^2. \end{aligned}$$

Thus, we obtain our first energy estimate: $\mu \in H^1([-a,a]\times\Theta)$ with a uniform bound of order $\mathcal{O}\left(K_0(a)^2\right)$ uniformly:

$$\min\left(\frac{\theta_{\min}}{2},1\right)\int_{J_1}\left(|\partial_\xi\mu|^2+|\partial_\theta\mu|^2\right)d\xi d\theta \le C(|\Theta|,\theta_{\min},\chi)\left(1+K_0(a)^2\right)\,, \tag{3.19}$$

nH1

as soon as $a \ge \frac{1}{2}$.

We now come to the proof that $\partial_\theta\mu$ is also in $H^1((-a,a)\times\Theta)$. We differentiate (3.13) with respect to θ for this purpose. Here, we use crucially that ν is a function of the variable ξ only. Note that we cannot expect that $\mu \in H^2([-a,a]\times\Theta)$ with a bound of order $\mathcal{O}\left(K_0(a)^2\right)$ at this stage. But we need additional elliptic regularity in the variable θ only.

$$\forall(\xi,\theta)\in(-a,a)\times\Theta,\qquad -c\partial_{\xi\theta}\mu-\tau\partial_{\xi\xi}\partial\mu-g_\tau(\theta)\partial_{\xi\xi\theta}\mu-\alpha\partial_{\theta\theta\theta}\mu=r\partial_\theta\mu(1-\nu)\,. \tag{3.20}$$

eq:n_theta

We use the cut-off function $\widetilde{\chi}(\xi)=\chi(\xi_0+2(\xi-\xi_0))$, for which $\operatorname{supp}\widetilde{\chi}\subset J_1$, and $\chi(\xi)=1$ on $J_{1/2}=(\xi_0-1/4,\xi_0+1/4)$. Multiplying (3.20) by $\widetilde{\chi}\partial_\theta\mu$, we get after integration by parts

$$\int_{J_1}\tau\partial_\xi\mu\partial_{\theta\xi}\mu\widetilde{\chi}\,d\xi d\theta+\int_{J_1}\tau\partial_\xi\mu\partial_\theta\mu\widetilde{\chi}'\,d\xi d\theta+\int_{J_1}g_\tau(\theta)\partial_{\xi\theta}\mu\partial_\theta\mu\widetilde{\chi}'\,d\xi d\theta$$
$$+\int_{J_1}g_\tau(\theta)\left|\partial_{\xi\theta}\mu\right|^2\widetilde{\chi}\,d\xi d\theta+\alpha\int_{J_1}\left|\partial_{\theta\theta}\mu\right|^2\widetilde{\chi}\,d\xi d\theta\le r\int_{J_1}\left|\partial_\theta\mu\right|^2\widetilde{\chi}\,d\xi d\theta+c\int_{J_1}\widetilde{\chi}'\frac{|\partial_\theta\mu|^2}{2}d\xi d\theta.$$

Notice that all the boundary terms vanish since $\partial_\theta\mu=0$ on all segments of the boundary. Using the H^1 estimate (3.19) obtained previously for μ, we deduce

testntheta2

$$\frac{\theta_{\min}}{2}\int_{J_{1/2}}\left|\partial_{\theta\xi}\mu\right|^2d\xi d\theta+\alpha\int_{J_{1/2}}\left|\partial_{\theta\theta}\mu\right|^2d\xi d\theta\le\left(r+\frac{c^*}{2}\|\widetilde{\chi}'\|_\infty\right)\int_{J_1}\left|\partial_\theta\mu\right|^2d\xi d\theta+\frac{1}{2\theta_{\min}}\int_{J_1}\left|\partial_\xi\mu\right|^2d\xi d\theta$$
$$+\frac{1}{2}\int_{J_1}\left(|\partial_\xi\mu|^2+|\partial_\theta\mu|^2\right)|\widetilde{\chi}'|\,d\xi d\theta+\frac{1}{2}\int\theta\left|\partial_\theta\mu\right|^2\widetilde{\chi}''\,d\xi d\theta$$

from which we conclude

$$\min\left(\frac{\theta_{\min}}{2},1\right)\int_{J_1}\left(|\partial_{\xi\theta}\mu|^2+|\partial_{\theta\theta}\mu|^2\right)d\xi d\theta\le\overline{C}(\Theta,\theta_{\min},\chi)\left(1+K_0(a)^2\right)\,. \tag{3.21}$$

nthetaH1

This crucial computation proves that $\partial_\theta\mu$ also belongs to $H^1((-a,a)\times\Theta)$.

 # Step 2: Improved regularity of the trace $\mu(\xi,\cdot)$.

We aim to control the regularity of the partial function $\theta\mapsto\mu(\xi_0,\theta)$. For this purpose we use a trace embedding inequality with higher derivatives, namely if both μ and $\partial_\theta\mu$ belongs to $H^1((-a,a)\times\Theta)$, then the trace function $\mu(\xi_0,\cdot)$ belongs to $H^{3/2}_\theta$. More precisely, there exists a constant C_{tr} such that

$$\|\mu(\xi_0,\cdot)\|^2_{H^{3/2}_\theta}\le C_{tr}\left(\|\partial_\theta\mu\|^2_{H^1_{x,\theta}}+\|\mu\|^2_{H^1_{x,\theta}}\right)\,.$$

Combining the previous inequality with estimates (3.19) and (3.21) of # Step 1, we deduce that

$$\|\mu(\xi_0,\cdot)\|^2_{H^{3/2}_\theta}\le C\left(1+K_0(a)^2\right)\,.$$

On the other hand, the interpolation inequality [1, Theorem 5.9, p.141] gives a constant C_{int} such that

$$\|\mu(\xi_0,\cdot)\|_{L^\infty_\theta}\le C_{int}\|\mu(\xi_0,\cdot)\|^{1/2}_{L^1_\theta}\|\mu(\xi_0,\cdot)\|^{1/2}_{H^{3/2}_\theta}$$

Recall from # Step 0, that $\nu(\xi_0)=\|\mu(\xi_0,\cdot)\|_{L^1_\theta}\le 1$. As a consequence, we obtain

$$K_0(a)^4=\|\mu(\xi_0,\cdot)\|^4_{L^\infty_\theta}\le C\left(1+K_0(a)^2\right)\,,$$

for some constant C, depending only on Θ, $\theta_{\min}$, and χ. Therefore, $K_0(a)$ is bounded uniformly with respect to $a>0$. This concludes the proof of Lemma 12.

□

3.5 Resolution of the problem in the slab.

We now finish the proof of the existence of solutions of (3.13). As previously explained, it consists in a Leray-Schauder topological degree argument. All uniform estimates derived in the previous Sections are key points to obtain *a priori* estimates on steady states of suitable operators. We then simplify the problem with homotopy invariances. We begin with a very classical problem: the construction of KPP travelling waves for the Fisher-KPP equation in a slab.

propKPP **Lemma 13.** *Let us consider the following Fisher-KPP problem in the slab $(-a, a)$:*

$$\begin{cases} -c\partial_\xi \nu - \theta_{min}\partial_{\xi\xi}\nu = r\nu(1-\nu)\,, & \xi \in (-a,a)\,, \\ \nu(-a) = 1\,, \quad \nu(a) = 0\,. \end{cases}$$

One has the following properties:

1. *For a given c, there exists a unique decreasing solution $\nu^c \in [0,1]$. Moreover, the function $c \to \nu^c$ is continuous and decreasing.*

2 2. *There exists $\varepsilon^* > 0$ (independent of a) such that the solution with $c = 0$ satisfies $\nu_{c=0}(0) > \varepsilon^*$.*

3 3. *For all $\varepsilon > 0$, there exists $a(\varepsilon)$ such that for all $c > 2\sqrt{r\theta_{min}}$, $\nu(0) < \varepsilon$ for $a \geq a(\varepsilon)$.*

4. *As a corollary of 2 and 3, for all $\varepsilon < \varepsilon^*$, there exists a unique $c_0 \in [0, 2\sqrt{r\theta_{min}}]$ such that $\nu_{c_0}(0) = \varepsilon$ for $a \geq a(\varepsilon)$.*

Proof of Lemma 13. The existence and uniqueness of solutions follows from [4]. By classical maximum principle arguments, $\nu \leq 1$. The inequality $\nu \geq 0$ is not as easily obtained. One needs to truncate the non-linearity replacing $\nu(1-\nu)$ by $\nu_+(1-\nu)$. We refer to Lemma 15 were the same argument is exposed.

The solution is necessarily decreasing since

$$\forall \xi \in (-a,a), \qquad \partial_\xi\left(e^{\frac{c}{\theta_{min}}\xi}\partial_\xi \nu\right) \leq 0,$$

and $\partial_\xi\nu(-a) \leq 0$. By classical arguments, the application $c \to \nu^c$ is continuous. For the decreasing character, we write, for $c_1 < c_2$ and $v := \nu_2 - \nu_1$:

$$-c_2\partial_\xi v - \theta_{min}\partial_{\xi\xi} v = (1 - (\nu_1 + \nu_2))\, v + (c_2 - c_1)\,\partial_\xi \nu_1,$$

so that v satisfies

$$\begin{cases} -c_2\partial_\xi v - \theta_{min}\partial_{\xi\xi} v \leq (1 - (\nu_1 + \nu_2))\, v, & \xi \in (-a,a)\,, \\ v(-a) = 0\,, \quad v(a) = 0\,. \end{cases}$$

The comparison principle then yields that $v \leq 0$, that is $\nu_2 \leq \nu_1$. The proofs of Lemmas 9 and 11 can be adapted to prove the remainder of the Lemma.

□

With this ε^* in hand, we can state the main Proposition:

slabsol **Proposition 14. (Solution in the slab).** *Let $\varepsilon < \min(\varepsilon_0, \varepsilon^*)$. There exists $C_0 > 0$ and $a_0(\varepsilon) > 0$ such that for all $a \geq a_0$, the slab problem (3.13) with the normalization condition $\nu(0) = \varepsilon$ has a solution (c, μ) such that*

$$\|\mu\|_{L^\infty([-a,a]\times\Theta)} \leq C_0, \qquad c \in \,]\,0, c^*\,]\,.$$

Proof of Proposition 14. Given a non negative function $\mu(\xi,\theta)$ satisfying the boundary conditions

$$\forall (\xi,\theta) \in [-a,a]\times\Theta, \qquad \partial_\theta\mu(\xi,\theta_{\min}) = \partial_\theta\mu(\xi,\theta_{\max}) = 0, \qquad \mu(-a,\theta) = |\Theta|^{-1}\,, \qquad \mu(a,\theta) = 0\,. \quad (3.22)$$ boundv

we consider the one-parameter family of problems on $(-a,a)\times\Theta$:

$$\begin{cases} -c\partial_\xi Z^\tau - g_\tau(\theta)\partial_{\xi\xi}Z^\tau - \alpha\partial_{\theta\theta}Z^\tau = r\mu_+(1-\nu_\mu)\,, & (\xi,\theta)\in(-a,a)\times\Theta,\\ \partial_\theta Z^\tau(\xi,\theta_{\min}) = \partial_\theta Z^\tau(\xi,\theta_{\max}) = 0\,, & \xi\in(-a,a),\\ Z^\tau(-a,\theta) = |\Theta|^{-1}, Z^\tau(a,\theta)=0, & \theta\in\Theta. \end{cases} \tag{3.23}$$

eq:tauslab

We have here introduced the notation ν_μ to emphasize that it corresponds to the density associated to μ and not to Z^τ. We have also introduced the function "positive part", defined as

$$\forall x\in\mathbb{R}, \qquad x_+ := x\mathbf{1}_{x\geq 0}.$$

We introduce the map

$$\mathcal{K}_\tau : (c,\mu)\to(\varepsilon-\nu_\mu(0)+c, Z^\tau)\,,$$

where Z_τ is the solution of the previous linear system (3.23). The ellipticity of the system (3.23) gives that the map $\mathcal{K}_\tau$ is a compact map from $\left(X=\mathbb{R}\times\mathcal{C}^{1,\beta}\left((-a,a)\times\Theta\right), \|(c,\mu)\| = \max\left(|c|, \|\mu\|_{\mathcal{C}^{1,\beta}}\right)\right)$ onto itself ($\forall\beta\in(0,1)$). Moreover, it depends continuously on the parameter $\tau\in[0,1]$. Before going any further, we shall prove that a fixed point (c,μ) of $\mathcal{K}_\tau$ gives a solution of $P_{\tau,a}$. For this purpose, one needs to check that such a fixed point defines a *nonnegative* density μ. We enlighten this property in the next Lemma.

positivity

Lemma 15. *A fixed point (c,μ) of $\mathcal{K}_\tau$ gives a solution of $P_{\tau,a}$.*

Proof of Lemma 15. Such a fixed point solves

$$\begin{cases} -c\partial_\xi \mu - g_\tau(\theta)\partial_{\xi\xi}\mu - \alpha\partial_{\theta\theta}\mu = r\mu_+(1-\nu_\mu)\,, & (\xi,\theta)\in(-a,a)\times\Theta,\\ \partial_\theta \mu(\xi,\theta_{\min}) = \partial_\theta \mu(\xi,\theta_{\max}) = 0\,, & \xi\in(-a,a),\\ \mu(-a,\theta) = |\Theta|^{-1}\,, \quad \mu(a,\theta)=0\,, & \theta\in\Theta. \end{cases}$$

with $\nu := \int_\Theta \mu(\cdot,\theta)d\theta$ and the supplementary renormalization condition $\nu(0)=\varepsilon$. It remains to show that μ is then nonnegative. We play with the maximum principle as in [8]. Suppose that μ attains a negative minimum at some point (ξ_0,θ_0). Necessarily, $\xi_0\neq\pm a$ due to the imposed Dirichlet boundary conditions, and the Neumann boundary condition in θ rules out $\theta_0\in\partial\Theta$ by the strong maximum principle. Moreover, if $(\xi_0,\theta_0)\in(-a,a)\times\Theta$, then by continuity of μ, one can find an open set $\mathcal{V}\subset(-a,a)\times\Theta$ containing (ξ_0,θ_0) such that one has,

$$\forall(\xi,\theta)\in\mathcal{V}, \qquad -c\partial_\xi\mu - g_\tau(\theta)\partial_{\xi\xi}\mu - \alpha\partial_{\theta\theta}\mu = 0.$$

By the strong maximum principle, this would imply that μ is a negative constant, which is impossible. □

We emphasize that all the estimates done previously are not perturbed. Solving the problem P_a (3.13) is equivalent to proving that the kernel of $\mathrm{Id}-\mathcal{K}_1$ is non-trivial. We can now apply the Leray-Schauder theory.

We define the open set for $\delta>0$,

$$\mathcal{B} = \left\{\ (c,\mu)\mid 0<c<c^*+\delta,\ \|\mu\|_{\mathcal{C}^{1,\beta}((-a,a)\times\Theta)} < C_0+\delta\right\}.$$

The different a priori estimates of Lemmas 9, 10, 11, 12 give that for all $\tau\in[0,1]$ and sufficiently large a, the operator $\mathrm{Id}-\mathcal{K}_\tau$ cannot vanish on the boundary of $\mathcal{B}$. Indeed, if it vanishes on $\partial\mathcal{B}$, there exists a solution (c,μ) of (3.13) which also satisfies $c\in\{0,c^*+\delta\}$ or $\|\mu\|_{\mathcal{C}^{1,\beta}((-a,a)\times\Theta)} = C_0+\delta$ and $\nu(0)=\varepsilon$. But this is ruled out by the condition $\varepsilon<\varepsilon_0$, due to Lemmas 9, 10, 11, 12. It yields by the homotopy invariance that

$$\forall\tau\in[0,1]\,,\quad \deg\left(\mathrm{Id}-\mathcal{K}_1,\mathcal{B},0\right) = \deg\left(\mathrm{Id}-\mathcal{K}_\tau,\mathcal{B},0\right) = \deg\left(\mathrm{Id}-\mathcal{K}_0,\mathcal{B},0\right).$$

We now need to compute $\deg\left(\mathrm{Id}-\mathcal{K}_0,\mathcal{B},0\right)$. This will be done with two supplementary homotopies. We need these two homotopies to write $\mathrm{Id}-\mathcal{K}_0$ as a tensor of two applications whose degree with respect to $\mathcal{B}$ and 0 are computable. We first define, with $\nu_{Z^0}(\cdot) = \int_\Theta Z^0(\cdot,\theta)d\theta$:

$$\mathcal{M}_\tau : (c,v)\to\left(c-(1-\tau)\nu_v(0)-\tau\nu_{Z^0}(0)+\varepsilon, Z^0\right)$$

If there exists $(c,\mu)\in\partial\mathcal{B}$ such that $\mathcal{M}_\tau(c,\mu)=(c,\mu)$, then (c,μ) is such that $Z^0=\mu$ and $\nu_{Z^0}(0)=\varepsilon$. However, such a fixed point (c,μ) then satisfies

$$\begin{cases} -c\partial_\xi\mu-\theta_{min}\partial_{\xi\xi}\mu-\partial_{\theta\theta}\mu=r\mu(1-\nu)\,, & \xi\in(-a,a)\times\Theta,\\ \partial_\theta\mu(\xi,\theta_{\min})=\partial_\theta\mu(\xi,\theta_{\max})=0\,, & \xi\in(-a,a),\\ \mu(-a,\theta)=|\Theta|^{-1},\quad \mu(a,\theta)=0, & \theta\in\Theta, \end{cases} \tag{3.24}$$

eq:vKPP

which is now closely linked to the standard Fisher-KPP equation. Indeed, after integration w.r.t θ, ν satisfies

$$\begin{cases} -c\partial_\xi\nu-\theta_{min}\partial_{\xi\xi}\nu=r\nu(1-\nu)\,, & \xi\in(-a,a),\\ \nu(-a)=1\,,\quad \nu(a)=0\,, \end{cases} \tag{3.25}$$

eq:tauslab2

and $\nu(0)=\varepsilon$. Given a (unique) solution ν of (3.25) after Lemma 13, we can solve the equation for v. The solution of (3.24) is then unique thanks to the maximum principle, and reads $\mu(\xi,\theta)=\frac{\nu(\xi)}{|\Theta|}$. As a consequence, such a fixed point cannot belong to $\partial\mathcal{B}$ after all *a priori* estimates of Lemma 13. Thus, by the homotopy invariance and $\mathcal{K}_0=\mathcal{M}_0$, we have

$$\deg\left(\mathrm{Id}-\mathcal{K}_0,\mathcal{B},0\right)=\deg\left(\mathrm{Id}-\mathcal{M}_1,\mathcal{B},0\right).$$

The concluding arguments are now the same as in [8]. Up to the end of the proof, we shall exhibit the dependency of Z^0 in c: $Z^0=Z_c$. We now define our last homotopy by the formula

$$\mathcal{N}_\tau:(c,\mu)\to\left(c+\varepsilon-\nu_{Z_c}(0),\tau Z_c+(1-\tau)Z_{c_0}\right),$$

where c_0 is the unique $c\in[0,2\sqrt{r\theta_{\min}}]$ such that $\nu_{Z_c}(0)=\varepsilon$, for $\varepsilon<\varepsilon^*$ and $a(\varepsilon)$ sufficiently large (see again Lemma 13). If $\mathcal{N}_\tau$ has a fixed point, then necessarily $\varepsilon=\nu_{Z_c}(0)$ and $\mu=\tau Z_c+(1-\tau)Z_{c_0}$. This gives $\mu=Z_{c_0}$ by uniqueness of the speed c_0. Again, such a μ cannot belong to $\partial\mathcal{B}$ (we recall that $c_0<2\sqrt{r\theta_{min}}<c^*$ after (2.7)). By homotopy invariance and $\mathcal{M}_1=\mathcal{N}_1$:

$$\deg\left(\mathrm{Id}-\mathcal{K}_1,\mathcal{B},0\right)=\deg\left(\mathrm{Id}-\mathcal{K}_0,\mathcal{B},0\right)=\deg\left(\mathrm{Id}-\mathcal{M}_1,\mathcal{B},0\right)=\deg\left(\mathrm{Id}-\mathcal{N}_0,\mathcal{B},0\right).$$

Finally, the operator $\left(\mathrm{Id}-\mathcal{N}_0\right)(c,\mu)=\left(\nu_{Z_c}(0)-\varepsilon,\mu-Z_{c_0}\right)$ is such that $\deg\left(\mathrm{Id}-\mathcal{N}_0,\mathcal{B},0\right)=-1$. Indeed, the degree of the first component is -1 as it is a decreasing function of c, and the degree of the second one is 1.

We conclude that $\deg\left(\mathrm{Id}-\mathcal{K}_1,\mathcal{B},0\right)=-1$. Therefore it has a non-trivial kernel whose elements are solution of the slab problem. This proves the Proposition.

□

ofileminspeed

4 Construction of spatial travelling waves with minimal speed c^*.

In this Section, we now use the solution of the slab problem (3.13) given by Proposition 14 to construct a wave solution with minimal speed c^*. For this purpose, we first pass to the limit in the slab to obtain a profile in the whole space $\mathbb{R}\times\Theta$. Then we prove that this profile necessarily travels with speed c^*.

4.1 Construction of a spatial travelling wave in the full space.

convslab **Lemma 16.** *Let $\varepsilon<\min\left(\varepsilon_0,\varepsilon^*\right)$. There exists $c_0\in[0,c^*]$ such that the system*

$$\begin{cases} -c_0\partial_\xi\mu-\theta\partial_{\xi\xi}\mu-\alpha\partial_{\theta\theta}\mu=r\mu(1-\nu), & (\xi,\theta)\in\mathbb{R}\times\Theta,\\ \partial_\theta\mu(\xi,\theta_{\min})=\partial_\theta\mu(\xi,\theta_{\max})=0, & \xi\in\mathbb{R}, \end{cases} \tag{4.26}$$

convslab2

has a non-negative solution $\mu\in\mathcal{C}_b^2\left(\mathbb{R}\times\Theta\right)$ satisfying $\nu(0)=\varepsilon$.

Proof of Lemma 16. For sufficiently large $a > a_0(\varepsilon)$, Proposition 14 gives a solution (c^a, μ^a) of (3.13) which satisfies $c^a \in [0, c^*]$, $\|\mu^a\|_{L^\infty((-a,a)\times\Theta)} \leq K_0$ and $\nu^a(0) = \varepsilon$. As a consequence,

$$\|\nu^a\|_{L^\infty((-a,a))} \leq |\Theta| K_0.$$

The elliptic regularity [22] implies that for all $\beta > 0$, $\|\mu^a\|_{\mathcal{C}^{1,\beta}((-a,a)\times\Theta)} \leq C$ for some $C > 0$ uniform in a. Then, the Ascoli theorem gives that possibly after passing to a subsequence $a_n \to +\infty$, (c^a, μ^a) converges towards $(c_0, \mu) \in [0, c^*] \times \mathcal{C}^{1,\beta}(\mathbb{R}\times\Theta)$ which satisfies (4.26) and $\nu(0) = \varepsilon$.

□

Remark 17. *We do not obtain after the proof that* $\sup \nu \leq 1$*, and nothing is known about the behaviors at infinity at this stage. Nevertheless, we have an uniform bound* $\|\nu\|_{L^\infty(\mathbb{R})} \leq |\Theta| K_0$*.*

4.2 The profile is travelling with the minimal speed c^*.

inf **Lemma 18. (Lower bound on the infimum).** *There exists $\delta > 0$ such that any solution (c, μ) of*

$$\begin{cases} -\theta \partial_{\xi\xi}\mu - \alpha \partial_{\theta\theta}\mu - c\partial_\xi \mu = r(1-\nu)\mu, & (\xi,\theta) \in \mathbb{R}\times\Theta, \\ \partial_\theta \mu(\xi, \theta_{\min}) = \partial_\theta \mu(\xi, \theta_{\max}) = 0, & \xi \in \mathbb{R}, \end{cases}$$

with $c \in [0, c^*]$, ν bounded and $\inf_{\xi\in\mathbb{R}} \nu(\xi) > 0$ satisfies $\inf_{\xi\in\mathbb{R}} \nu(\xi) > \delta$.

Proof of Lemma 18. We again adapt an argument from [2] to our context. By the Harnack inequality of Proposition 8, one has

$$\forall\, (\xi, \theta, \theta') \in \mathbb{R}\times\Theta^2, \qquad \mu(\xi,\theta) \leq C(\xi)\mu(\xi,\theta'). \tag{4.27}$$ Hn

Since (1.2) is invariant by translation in space, and the renormalization $\nu(0) = \varepsilon$ is not used in the proof of the Harnack inequality, we can take a constant $C(\xi)$ which is independent from ξ [22]. This yields

$$\forall\, (\xi,\theta) \in \mathbb{R}\times\Theta, \qquad -\theta\partial_{\xi\xi}\mu(\xi,\theta) - \alpha\partial_{\theta\theta}\mu(\xi,\theta) - c\partial_\xi\mu(\xi,\theta) \geq r(1 - C\Theta\mu(\xi,\theta))\mu(\xi,\theta).$$

Hence, μ is a super solution of some elliptic equation with local terms only. For $\eta > 0$ arbitrarily given, we define the family of functions

$$\psi_m(\xi,\theta) = m\left(1 - \eta\xi^2\right) Q^*(\theta).$$

From the uniform L^∞ estimate on μ, there exists M large enough such that $\psi_M(0,\theta) > \mu(0,\theta)$. Moreover, by assumption we have $\psi_m \leq \mu$ for $m = \frac{\inf_{\mathbb{R}} \nu}{C|\Theta| \|Q^*\|_\infty} > 0$. As a consequence, we can define

$$m_0 := \sup\{m > 0, \quad \forall(\xi,\theta) \in \mathbb{R}\times\Theta, \quad \psi_m(\xi,\theta) \leq \mu(\xi,\theta)\}.$$

As in previous same ideas, see Lemmas 9 and 11, there exists (x_0, θ_0) such that $\mu - \psi_{m_0}$ has a zero minimum at this point. We have clearly that $\xi_0 \in \left[-\frac{1}{\sqrt{\eta}}; \frac{1}{\sqrt{\eta}}\right]$ since ψ_m is negative elsewhere. We have, at (ξ_0, θ_0):

$$\begin{aligned} 0 &\geq -\theta_0\partial_{\xi\xi}\left(\mu - \psi_{m_0}\right) - \alpha\partial_{\theta\theta}\left(\mu - \psi_{m_0}\right) - c\partial_\xi\left(\mu - \psi_{m_0}\right), \\ &\geq r\left(1 - C|\Theta|\mu\right)\mu + \theta_0\partial_{\xi\xi}\left(\psi_{m_0}\right) + \alpha\partial_{\theta\theta}\left(\psi_{m_0}\right) + c\partial_\xi\left(\psi_{m_0}\right), \\ &\geq r\left(1 - C|\Theta|\mu\right)\mu - 2\eta m_0\theta_0 Q^*(\theta_0) - \left(-\lambda^* c^* + \theta_0(\lambda^*)^2 + r\right)\psi_{m_0}(\xi_0,\theta_0) - 2c\eta\xi_0 m_0 Q^*(\theta_0), \\ &\geq \mu(\xi_0,\theta_0)\left(\lambda^* c^* - \theta_0(\lambda^*)^2 - rC|\Theta|\mu(\xi_0,\theta_0)\right) - 2m_0 Q^*(\theta_0)\left(\eta\theta_0 + \eta\xi_0 c\right). \end{aligned}$$

It follows from $\mu(\xi_0,\theta_0) \geq \frac{\nu(\xi_0)}{C|\Theta|}$ (4.27), from the inequalities $|\xi_0| \leq \frac{1}{\sqrt{\eta}}$, $c \leq c^*$, $m_0 \leq M$ and the fact that for all $\theta_0 \in \Theta$, the quantity $c^* - \theta_0\lambda^* - \theta_{\min}\lambda^*$ is positive (see (2.8)) that

$$\begin{aligned} \mu(\xi_0,\theta_0) &\geq \frac{\lambda^*\left(c^* - \theta_0\lambda^*\right)}{rC|\Theta|} - \frac{2M\|Q^*\|_\infty\left(\eta\theta_{\max} + \sqrt{\eta}c^*\right)}{r\nu(\xi_0)}, \\ &\geq \frac{\theta_{\min}\left(\lambda^*\right)^2}{rC|\Theta|} - \frac{2M\|Q^*\|_\infty\left(\sqrt{\eta}c^* + \eta\theta_{\max}\right)}{r\left(\inf_{\xi\in\mathbb{R}}\nu\right)}. \end{aligned}$$

Recalling $\inf_{\xi\in\mathbb{R}} \nu > 0$ and taking arbitrarily small values of $\eta > 0$, we have necessarily $\mu(\xi_0, \theta_0) \geq \frac{\theta_{min}(\lambda^*)^2}{2Cr|\Theta|}$. Since μ and ψ_{m_0} coincide at (ξ_0, θ_0), we have $m_0 \geq \frac{\theta_{min}(\lambda^*)^2}{2rC|\Theta|\|Q^*\|_\infty}$. The definition of m_0 now gives

$$\forall(\xi,\theta) \in \mathbb{R}\times\Theta, \qquad \mu(\xi,\theta) \geq \frac{\theta_{min}\,(\lambda^*)^2}{2C|\Theta|r\|Q^*\|_\infty}\left(1-\eta\xi^2\right)Q^*(\theta).$$

Since η is arbitrarily small, we have necessarily $\nu(\xi) \geq \delta := \frac{\theta_{min}(\lambda^*)^2}{2C|\Theta|r\|Q^*\|_\infty}$ for all $\xi \in \mathbb{R}$.

□

We deduce from this Lemma that up to choosing $\varepsilon < \delta$, the solution necessarily satisfies $\inf_{\mathbb{R}} \nu(\xi) = 0$. Since this infimum cannot be attained, we have necessarily $\liminf_{\xi\to+\infty} \nu(\xi) = 0$ (up to $\xi \to -\xi$ and $c \to -c$). We now prove that this enforces $c = c^*$ for our wave. For this purpose, we show that a solution going slower than c^* cannot satisfy the lim inf condition by a sliding argument.

prop:minspeed **Proposition 19.** *Any solution (c,μ) of the system*

$$\begin{cases} -\theta\partial_{\xi\xi}\mu - \alpha\partial_{\theta\theta}\mu - c\partial_\xi\mu = r\mu(1-\nu), & (\xi,\theta)\in\mathbb{R}\times\Theta, \\ \partial_\theta\mu(\xi,\theta_{\min}) = \partial_\theta\mu(\xi,\theta_{\max}) = 0, & \xi\in\mathbb{R}, \end{cases} \tag{4.28}$$

eq:minspeed

with $c \geq 0$ and $\inf_{\xi\in\mathbb{R}} \nu(\xi) = 0$ satisfies necessarily $c \geq c^*$.

As a consequence, the solution given after Lemma 16 goes with the speed c^*. This latter speed appears to be the minimal speed of existence of nonnegative travelling waves, similarly as for the Fisher KPP equation.

Proof of Proposition 19. We again play with subsolutions. By analogy with the Fisher-KPP equation, we shall use oscillating fronts associated with speed $c < c^*$ to "push" solutions of (4.28) up to the speed c^*. We now proceed like in [12].

Let us now consider the following spectral problem :

$$\begin{cases} \alpha Q_\lambda(\theta)'' + \left(-\lambda c + \theta\lambda^2 + r - s\right)Q_\lambda(\theta) = 0\,, \\ Q_\lambda'(\theta_{min}) = Q_\lambda'(\theta_{max}) = 0\,. \end{cases} \tag{4.29}$$

eq:eigenpbs

When $s = 0$ we know from Proposition 5 that for $c = c^*$ there exists some real $\lambda^* > 0$ such that the spectral problem is solvable with a positive eigenvector. Moreover, the minimal speed is increasing with respect to r. Indeed, for all $r_1 < r_2$ and $\lambda > 0$, one has

$$\lambda c_{r_1}(\lambda) = r_1 + \lambda^2\theta_{\max} - \gamma(\lambda) < r_2 + \lambda^2\theta_{\max} - \gamma(\lambda) = \lambda c_{r_2}(\lambda)$$

and thus $c^*_{r_1} < c^*_{r_2}$.

Now suppose by contradiction that $c < c^*$. Take $c < \bar{c} < c^*$, $s > 0$. One can choose $s = s(\bar{c}) > 0$ such that $\bar{c}$ is the minimal speed of the spectral problem (4.29).

Let us now consider (4.29) for complex values of λ. The analytic perturbation theory, see [24, Chapter 7, §1, §2, §3], yields that the eigenvalues are analytic in λ at least in a neighborhood of the real axis. As a consequence, by the Rouché theorem we know that taking $\bar{c}$ sufficiently close to c, there exists $\lambda_c := \lambda_R + i\lambda_I \in \mathbb{C}$ with $\mathrm{Re}(\lambda_c) > 0$ such that there exists $Q_{\lambda_c} : \Theta \mapsto \mathbb{C}$ which solves the spectral problem (4.29) (with $s = s(\bar{c})$). The local analyticity ensures that $\mathrm{Re}\left(Q_{\lambda_c}\right) > 0$ when $\bar{c}$ is sufficiently close to c, since $\mathrm{Re}\left(Q_{\lambda_{\bar{c}}}\right) > 0$.

Let us now define the real function

$$\psi(\xi,\theta) := \mathrm{Re}\left(e^{-\lambda_c\xi}Q_{\lambda_c}(\theta)\right) = e^{-\lambda_R\xi}\left[\mathrm{Re}\left(Q_{\lambda_c}(\theta)\right)\cos(\lambda_I\xi) + \mathrm{Im}\left(Q_{\lambda_c}(\theta)\right)\sin(\lambda_I\xi)\right].$$

By construction, one has

$$-\theta\partial_{\xi\xi}\psi - \alpha\partial_{\theta\theta}\psi - c\partial_\xi\psi - r\psi = -s(\bar{c})\psi.$$

Thus, for all $m \geq 0$, the function $v := \mu - m\psi$ satisfies

$$-\theta\partial_{\xi\xi}v - \alpha\partial_{\theta\theta}v - c\partial_\xi v - rv = ms(\bar{c})\psi - r\nu(\xi)\mu.$$

For all $\theta \in \Theta$, one has $\psi(0,\theta) > 0$ and $\psi\left(\pm\frac{\pi}{\lambda_I},\theta\right) < 0$. As a consequence, there exists an open subdomain $\mathcal{D} \subset \Omega := \left[-\frac{\pi}{\lambda_I},\frac{\pi}{\lambda_I}\right] \times \Theta$ such that $\psi > 0$ on $\mathcal{D}$ and ψ vanishes on the boundary $\partial\mathcal{D}$.

There now exists m_0 such that v attains a zero minimum at $(z_0,\theta_0) \in \mathcal{D}$. If $\theta_0 \in \Theta$, one deduces $\nu(z_0) \geq \frac{s(\bar{c})}{r}$. It could happen that $\theta_0 \in \partial\Theta$ but in this case the latter conclusion remains true thanks to the Neumann boundary conditions satisfied by ψ. From the Harnack estimate of Proposition 8, there exists a constant C which depends on $|\mathcal{D}|$ such that one has for all $\xi \in \mathbb{R}$,

$$\forall(z,\theta,\theta') \in \mathcal{D} \times \Theta, \qquad \mu(z+\xi,\theta) \leq C\mu(\xi,\theta')$$

Integrating this estimate over Θ, we conclude that $\nu(0) \geq \frac{s(\bar{c})}{rC}$.

We now want to translate the argument in space. For this purpose, we define, for $\zeta \in \mathbb{R}$, the function $h(\xi,\theta) := \mu(\xi+\zeta,\theta)$. It also satisfies (4.28). As a consequence, for all $\zeta \in \mathbb{R}$, $\nu(\zeta) = \int_\Theta h(0,\theta)d\theta \geq \frac{s(\bar{c})}{rC}$. We emphasize that the renormalization $\nu(0) = \varepsilon$, which is the only reason for which (3.13) is not invariant by translation, is not used here. We then obtain $\inf_{\xi\in\mathbb{R}} \nu(\xi) \geq \frac{s(\bar{c})}{rC}$. This contradicts the property $\inf_{\xi\in\mathbb{R}} \nu(\xi) = 0$.

□

4.3 The profile has the required limits at infinity.

limits **Proposition 20.** *Any solution (c,μ) of the system*

$$\begin{cases} -\theta\partial_{\xi\xi}\mu - \alpha\partial_{\theta\theta}\mu - c\partial_\xi\mu = r\mu(1-\nu), & (\xi,\theta) \in \mathbb{R}\times\Theta, \\ \partial_\theta\mu(\xi,\theta_{\min}) = \partial_\theta\mu(\xi,\theta_{\max}) = 0, & \xi \in \mathbb{R}, \end{cases}$$

with $c \geq 0$ and $\nu(0) = \varepsilon$ satisfies

1. *There exists $m > 0$ such that $\forall\xi \in]-\infty,0]$, $\mu(\xi,\cdot) > mQ(\cdot)$,*
2. $\lim_{\xi\to+\infty}\mu(\xi,\cdot) = 0$.

Proof of Proposition 20. We again adapt to our case an argument from [2]. By the Harnack inequality applied on $[-1,0]\times\Theta$, there exists $\widetilde{C}$ such that one has

$$\inf_{(\xi,\theta)\in[-1,0]\times\Theta} \mu(\xi,\theta) \geq \frac{\varepsilon}{\widetilde{C}|\Theta|}, \tag{4.30}$$ HHn

recalling $\nu(0) = \varepsilon$. Also recalling

$$\forall(\xi,\theta,\theta') \in \mathbb{R}\times\Theta^2, \qquad \mu(\xi,\theta) \leq C\mu(\xi,\theta'),$$

we obtain

$$\forall(\xi,\theta) \in \mathbb{R}\times\Theta, \qquad -\theta\partial_{\xi\xi}\mu(\xi,\theta) - \alpha\partial_{\theta\theta}\mu(\xi,\theta) - c\partial_\xi\mu(\xi,\theta) \geq r(1 - C|\Theta|\mu(\xi,\theta))\mu(\xi,\theta).$$

Let us define, for $m = \frac{1}{2}\min\left(\frac{\varepsilon}{|\Theta|\widetilde{C}\|Q^*\|_\infty}, \frac{\theta_{min}(\lambda^*)^2}{rC\|Q^*\|_\infty|\Theta|}\right)$ and $\eta > 0$ arbitrarily given, the function

$$\psi_\eta(\xi,\theta) = m\,(1+\eta\xi)\,Q^*(\theta).$$

on $]-\infty,0]\times\Theta$. We have,

$$\forall(\xi,\theta) \in]-\infty,-1]\times\Theta, \qquad \psi_1(\xi,\theta) = m\,(1+\xi)\,Q^*(\theta) \leq 0 \leq \mu(\xi,\theta).$$

Moreover, for $(\xi,\theta) \in]-1,0] \times \Theta$, using (4.30), we have

$$\psi_1(\xi,\theta) = m\,(1+\xi)\,Q^*(\theta) \le m\|Q^*\|_\infty \le \frac{1}{2}\frac{\varepsilon\|Q^*\|_\infty}{|\Theta|\widetilde{C}\|Q^*\|_\infty} \le \inf_{\xi\in[-1,0]\times\Theta} \mu(\xi,\theta) \le \mu(\xi,\theta).$$

As a consequence we can define

$$\eta_0 := \min\{\eta > 0, \forall (\xi,\theta) \in]-\infty,0] \times \Theta, \psi_\eta(\xi,\theta) \le \mu(\xi,\theta)\} \in [0,1].$$

We will now prove that $\eta_0 = 0$ by contradiction. Suppose that $\eta_0 > 0$. We apply the same technique as in the proofs of Lemmas 9 and 11: there exists (ξ_0,θ_0) such that $\mu - \psi_{\eta_0}$ has a zero minimum at this point. Moreover, we have $\xi_0 \in \left[-\frac{1}{\eta_0}; 0\right]$ since ψ_η is negative elsewhere. Moreover, ξ_0 cannot be 0 since this would give $\mu(0,\theta_0) = mQ^*(\theta_0) \le \frac{1}{2}\frac{\varepsilon}{|\Theta|\widetilde{C}}$ and this would contradict (4.30). We have, at (ξ_0,θ_0):

$$\begin{aligned}
0 &\ge -\theta\partial_{\xi\xi}\left(\mu - \psi_{\eta_0}\right) - \alpha\partial_{\theta\theta}\left(\mu - \psi_{\eta_0}\right) - c\partial_\xi\left(\mu - \psi_{m_0}\right) \\
&\ge r\left(1 - C\Theta\mu\right)\mu + \theta\partial_{\xi\xi}\psi_{\eta_0} + \alpha\partial_{\theta\theta}\psi_{\eta_0} + c\partial_\xi\psi_{m_0} \\
&\ge r\left(1 - C\Theta\mu\right)\mu - \psi_{\eta_0}(\xi_0,\theta_0)\left(-\lambda^* c^* + \theta_0\left(\lambda^*\right)^2 + r\right) + cm_0\eta Q^*(\theta_0) \\
&\ge \mu(\xi_0,\theta_0)\left(\lambda^* c^* - \theta_0(\lambda^*)^2 - rC|\Theta|\mu(\xi_0,\theta_0)\right) + cm_0\eta Q^*(\theta_0) \\
&\ge \mu(\xi_0,\theta_0)\left(\lambda^* c^* - \theta_0(\lambda^*)^2 - rC|\Theta|\mu(\xi_0,\theta_0)\right)
\end{aligned}$$

It yields

$$\frac{\theta_{min}(\lambda^*)^2}{rC|\Theta|} \le \mu(\xi_0,\theta_0) = \psi_{\eta_0}(\xi_0,\theta_0) \le m\|Q^*\|_\infty.$$

and this contradicts the very definition of m. As a consequence, $\eta_0 = 0$ and

$$\forall (\xi,\theta) \in \mathbb{R}^- \times \Theta, \qquad \mu(\xi,\theta) \ge mQ^*(\theta)$$

In particular, $\inf_{\mathbb{R}^-} \nu \ge m$ holds.

We now prove that $\lim_{\xi\to+\infty} \mu(\xi,\cdot) = 0$. It is sufficient to prove that $\lim_{\xi\to\infty} \nu(\xi) = 0$. Suppose that there exists δ a subsequence $\xi_n \to +\infty$ such that $\forall n \in \mathbb{N}$, $\nu(\xi_n) \ge \delta$. Adapting the preceding proof we obtain that for all $n \in \mathbb{N}$,

$$\forall (\xi,\theta) \in]-\infty,\xi_n] \times \Theta, \qquad \nu(\xi) \ge \frac{1}{2}\min\left(\frac{\delta}{|\Theta|\widetilde{C}\|Q^*\|_\infty}, \frac{\theta_{min}(\lambda^*)^2}{rC\|Q^*\|_\infty|\Theta|}\right). \tag{4.31}$$

last

Hence (4.31) is true for all $\xi \in \mathbb{R}$ and Lemma 18 gives the contradiction since the normalization ε is well chosen.

□

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References

Adams [1] Adams, Robert A. and Fournier, John J. F., *Sobolev spaces*, Pure and Applied Mathematics (Amsterdam), Elsevier/Academic Press, Amsterdam, 2003.

Alfaro [2] M. Alfaro, J. Coville, and G. Raoul. *Travelling waves in a nonlocal equation as a model for a population structured by a space variable and a phenotypical trait.* To appear in Comm. Partial Differential Equations.

Arnold [3] A. Arnold, L. Desvillettes and C. Prevost, *Existence of nontrivial steady states for populations structured with respect to space and a continuous trait*, Comm. Pure Appl. Anal. **11** (2012), no. 1, 83–96.

Aronson [4] D. G. Aronson and H. F. Weinberger, *Multidimensional nonlinear diffusion arising in population genetics*, Adv. in Math. 30 (1978), no. 1, 33–76.

Benichou [5] O. Benichou, V. Calvez, N. Meunier and R. Voituriez, *Front acceleration by dynamic selection in Fisher population waves*, Phys. Rev. E 86, 041908 (2012).

cki-Chapuisat [6] H. Berestycki and G. Chapuisat, *Travelling fronts guided by the environment for reaction-diffusion equations*, preprint arXiv:1206.6575.

estycki-Hamel [7] H. Berestycki and F. Hamel, *Generalized transition waves and their properties*, Comm. Pure Appl. Math. 65, (2012), no. 5, 592–648.

estycki-Nadin [8] H. Berestycki, G. Nadin, B. Perthame and L. Ryzhik, *The non-local Fisher-KPP equation: travelling waves and steady states*, Nonlinearity **22** (2009), no. 12, 2813–2844.

Bouin [9] E. Bouin, V. Calvez, N. Meunier, S. Mirrahimi, B. Perthame, G. Raoul, and R. Voituriez. *Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration.* C. R. Math. Acad. Sci. Paris, 350(15-16):761–766, 2012.

Bouin-2 [10] E. Bouin, *Revisiting the WKB approach for front propagation in kinetic equations.* In preparation.

Bouin-Calvez [11] E. Bouin, V. Calvez, *A kinetic eikonal equation*, C. R. Math. Acad. Sci. Paris **350** (2012), 243–248.

-Calvez-Nadin [12] E. Bouin, V. Calvez, G. Nadin, *Front propagation in a kinetic reaction-transport equation*, preprint arXiv:1307.8325, 2013.

alvez-Nadin-2 [13] E. Bouin, V. Calvez, G. Nadin, *Hyperbolic travelling waves driven by growth*, To appear in M3AS, 2013.

uin-Mirrahimi [14] E. Bouin, S. Mirrahimi, *A Hamilton-Jacobi approach for a model of population structured by space and trait*, preprint arXiv:1307.8332, 2013.

Champagnat [15] N. Champagnat et S. Méléard, *Invasion and adaptive evolution for individual-based spatially structured populations*, J. Math. Biol. 55 (2007), no. 2, 147–188.

oville-Davila [16] J. Coville, J. Dávila and S. Martínez, *Pulsating fronts for nonlocal dispersion and KPP nonlinearity*, Ann. Inst. H. Poincaré Anal. Non Linéaire 30 (2013), no. 2, 179–223.

ille-Dupaigne [17] J. Coville and L. Dupaigne, *On a non-local reaction diffusion equation arising in population dynamics*, Proc. Roy. Soc. Edinburgh Sect. A 137 (2007), no. 4, 727–755.

Desvillettes [18] L. Desvillettes, R. Ferrière et C. Prévost, *Infinite dimensional reaction-diffusion for population dynamics*, preprint CMLA (2004).

Dockery [19] J. Dockery, V. Hutson, K. Mischaikow, M. Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol. 37 (1) (1998) 61–83.

Ferriere [20] N. Champagnat, R. Ferrière, S. Méléard, *From individual stochastic processes to macroscopic models in adaptive evolution*, Stoch. Models 24 (Suppl. 1) (2008) 2–44.

Fisher [21] R.A. Fisher, *The advance of advantageous genes*, Ann. Eugenics **65** (1937), 335–369.

Gilbarg [22] Gilbarg, David, and Trudinger, Neil S., *Elliptic partial differential equations of second order*, Springer Berlin ; New York, 1998.

Hamel [23] F. Hamel, L. Ryzhik, *On the nonlocal Fisher-KPP equation: steady states, spreading speed and global bounds*, preprint http://arxiv.org/abs/1307.3001.

Kato [24] Kato, Tosio, *Perturbation theory for linear operators*, Classics in Mathematics, Reprint of the 1980 edition, Springer-Verlag, Berlin, 1995,

Kokko [25] H. Kokko, A. López-Sepulcre, *From individual dispersal to species ranges: perspectives for a changing world*, Science 313 (5788) (2006) 789–791.

Kolmogorov [26] A.N. Kolmogorov, I.G. Petrovsky, N.S. Piskunov, *Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique*, Moskow Univ. Math. Bull. **1** (1937), 1–25.

Nadin [27] G. Nadin, *travelling fronts in space-time periodic media*, J. Math. Pures Appl. (9) 92 (2009), no. 3, 232–262.

Nolen [28] J. Nolen and L. Ryzhik, *travelling waves in a one-dimensional heterogeneous medium*, Ann. Inst. H. Poincaré Anal. Non Linéaire 26 (2009), no. 3, 1021–1047.

Perthame [29] B. Perthame, *Transport Equations in Biology*, Frontiers in Mathematics, Birkhäuser Basel, 2007.

Phillips [30] B.L. Phillips, G.P. Brown, J.K. Webb, R. Shine, *Invasion and the evolution of speed in toads*, Nature 439 (7078) (2006) 803.

Ronce [31] O. Ronce, *How does it feel to be like a rolling stone? Ten questions about dispersal evolution*, Annu. Rev. Ecol. Syst. 38 (2007) 231–253.

Shen [32] W. Shen and A. Zhang, *travelling wave solutions of spatially periodic nonlocal monostable equations*, ArXiv e-prints, (2012). http://arxiv.org/abs/1202.2452

Shine [33] R. Shine, G.P. Brown, B.L. Phillips, *An evolutionary process that assembles phenotypes through space rather than through time*, Proc. Natl. Acad. Sci. USA 108 (14) (2011) 5708–5711.

Simmons [34] A.D. Simmons, C.D. Thomas, *Changes in dispersal during species' range expansions*, Amer. Nat. 164 (2004) 378–395.

Thomas [35] Thomas, C. D. and Bodsworth, E. J. and Wilson, R. J. and Simmons, A. D. and Davies, Z. G. and Musche, M. and Conradt, L., *Ecological and evolutionary processes at expanding range margins*, Nature **411**, 577-581 (2001).

Xin [36] J. Xin, *Front propagation in heterogeneous media*, SIAM Rev. 42, (2000), no. 2, 161–230.