Pulsating fronts for Fisher-KPP systems with mutations as models in evolutionary epidemiology

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Contents

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Abstract

We consider a periodic reaction diffusion system which, because of competition between u and v, does not enjoy the comparison principle. It also takes into account mutations, allowing u to switch to v and vice versa. Such a system serves as a model in evolutionary epidemiology where two types of pathogens compete in a heterogeneous environment while mutations can occur, thus allowing coexistence.

We first discuss the existence of nontrivial positive steady states, using some bifurcation technics. Then, to sustain the possibility of invasion when nontrivial steady states exist, we construct pulsating fronts. As far as we know, this is the first such construction in a situation where comparison arguments are not available.

Key Words: reaction diffusion systems, pulsating fronts, evolutionary epidemiology, bifurcation technics, Bernstein gradient estimate, Harnack inequality.

AMS Subject Classifications: 35K57, 35B10, 92D15, 92D30.

1 Introduction

This work is concerned with the heterogeneous reaction diffusion system

$$\begin{cases} \partial_t u = \partial_{xx} u + u\left[r_u(x) - \gamma_u(x)(u+v)\right] + \mu(x)v - \mu(x)u, & t > 0,\, x \in \mathbb{R}, \\ \partial_t v = \partial_{xx} v + v\left[r_v(x) - \gamma_v(x)(u+v)\right] + \mu(x)u - \mu(x)v, & t > 0,\, x \in \mathbb{R}, \end{cases} \tag{1}$$

where r_u, r_v are periodic functions and γ_u, γ_v, μ are periodic positive functions. After discussing the existence of nontrivial steady states via bifurcation technics, we construct pulsating fronts, despite the lack of comparison principle for (1). Before going into mathematical details, let us describe the relevance of the the above system in evolutionary epidemiology.

System (1) describes a theoretical population divided into two genotypes with respective densities $u(t,x)$ and $v(t,x)$, and living in a one-dimensional habitat $x \in \mathbb{R}$. We assume that each genotype yields a different phenotype which also undergoes the influence of the environment. The difference in phenotype is expressed in terms of growth rate, mortality and competition, but we assume that the diffusion of the individuals is the same for each genotype. Finally, we take into account mutations occuring between the two genotypes.

The reaction coefficients r_u and r_v represent the intrinsic growth rates, which depend on the environment and take into account both birth and death rates. Notice that r_u and r_v may take some negative values, in deleterious areas where the death rate is greater than the birth rate. Function μ corresponds to the mutation rate between the two species. It imposes a truly *cooperative* dynamics in the small populations regime, and couples the dynamics of the two species. In particular, one expects that, at least for small mutation rates, *mutation aids survival and coexistence*. We also make the assumption that the mutation process is symmetric. From the mathematical point of view, this simplifies some of the arguments we use and improves the readability of the paper. We have no doubt that similar results hold in the non-symmetric case, though the proofs may be more involved.

In this context, the ability of the species to survive *globally in space* depends on the sign of the principal eigenvalue of the linearized operator around extinction $(0,0)$, as we will show further, which involves the coefficients r_u, r_v, μ.

Finally, γ_u and γ_v represent the strength of the competition (for e.g. a finite resource) between the two strains. The associated dynamics arises when populations begin to grow. It has no influence on the survival of the two species, but regulates the equilibrium densities of the two populations.

Such a framework is particularly suited to model the propagation of a pathogenic species within a population of hosts. Indeed system (1) can easily be derived from a host-pathogen microscopic model [26] in which we neglect the influence of the pathogen on the host's diffusion.

In a homogeneous environment the role of mutations, allowing survival for both u and v, has recently been studied by Griette and Raoul [25], through the system

$$\begin{cases} \partial_t u = \partial_{xx} u + u(1 - (u + v)) + \mu(v - u) \\ \partial_t v = \partial_{xx} v + rv\left(1 - \dfrac{u + v}{K}\right) + \mu(u - v). \end{cases}$$

On the other hand, it is known that the spatial structure has a great influence on host-parasites systems, both at the epidemiological and evolutionary levels [15], [7], [33]. In order to understand the influence of heterogeneities, we aim at studying steady states and propagating solutions, or *fronts*, of system (1).

Traveling fronts in homogeneous environments. In a homogeneous environment, propagation in reaction diffusion equations is typically described by *traveling waves*, namely solutions to the parabolic equation consisting of a constant profile shifting at a constant speed. This goes back to the seminal works [22], [31] on the Fisher-KPP equation

$$\partial_t u = \Delta u + u(1 - u),$$

a model for the spreading of advantageous genetic features in a population. The literature on traveling fronts for such homogeneous reaction diffusion equations is very large, see [22], [31], [5, 6], [21], [24], [13] among others. In such situations, many techniques based on the comparison principle — such as some monotone iterative schemes or the sliding method [14]— can be used to get *a priori* bounds, existence and monotonicity properties of the solution.

Nevertheless, when considering nonlocal effects or systems, the comparison principle may no longer be available so that the above techniques do not apply and the situation is more involved. One usually uses topological degree arguments to construct traveling wave solutions: see [12], [20], [2], [29] for the nonlocal Fisher-KPP equation, [4] for a bistable nonlocal equation, [3] for a nonlocal equation in an evolutionary context, [25] for a homogeneous system in an evolutionary context... Notice also that the boundary conditions are then typically understood in a weak sense, meaning that the wave connects 0 to "something positive" that cannot easily be identified: for example, in the nonlocal Fisher-KPP equation the positive steady state $u \equiv 1$ may present a Turing instability.

In a heterogeneous environment, however, it is unreasonable to expect the existence of such a solution. The particular type of propagating solution we aim at constructing in our periodic case is the so called *pulsating front*, first introduced by Xin [37] in the framework of flame propagation.

Pulsating fronts in heterogeneous environments. The definition of a pulsating front is the natural extension, in the periodic framework, of the aforementioned traveling waves. We

introduce a speed c and shift the origin with this speed to catch the asymptotic dynamics. Technically, a *pulsating front* (with speed c) is then a profile $(U(s, x), V(s, x))$ that is periodic in the space variable x, and that connects $(0, 0)$ to a non-trivial state, such that $(u(t, x), v(t, x)) := (U(x - ct, c), V(x - ct, x))$ solves (1). Equivalently, a pulsating front is a solution of (1) connecting $(0, 0)$ to a non-trivial state, and that satisfies the constraint

$$\left(u\left(t + \frac{L}{c}, x \right), v\left(t + \frac{L}{c}, x \right) \right) = (u(t, x - L), v(t, x - L)), \quad \forall (t, x) \in \mathbb{R}^2.$$

As far as monostable pulsating fronts are concerned, we refer among others to the seminal works of Weinberger [36], Berestycki and Hamel [8]. Let us also mention [30], [10], [27], [28] for related results.

One of the main difficulties we encounter when studying system (1) is that two main dynamics co-exist. On the one hand, when the population is small, (1) behaves like a cooperative system which enjoys a comparison principle. On the other hand, when the population is near a non-trivial equilibrium, (1) is closer to a competitive system. Since those dynamics cannot be separated, our system does not admit any comparison principle, and standard techniques such as monotone iterations cannot be applied. As far as we know, the present work is the first construction of pulsating fronts in a situation where comparison arguments are not available.

2 Main results and comments

2.1 Assumptions, linear material and notations

Periodic coefficients. Throughout this work, and even if not recalled, we always make the folllowing assumptions. Functions $r_u, r_v, \gamma_u, \gamma_v, \mu : \mathbb{R} \to \mathbb{R}$ are smooth and periodic with period $L > 0$. We assume further that γ_u, γ_v and μ are positive. We denote their bounds

$$\begin{array}{cccc} 0 < & \gamma^0 \leq & \gamma_u(x), \gamma_v(x) & \leq \gamma^\infty \\ 0 < & \mu^0 \leq & \mu(x) & \leq \mu^\infty \\ & r^0 \leq & r_u(x), r_v(x) & \leq r^\infty, \end{array}$$

for all $x \in \mathbb{R}$. Notice that r_u and r_v are allowed to take negative values, which is an additional difficulty, in particular in the proofs of Lemma 4.3 and Lemma 5.4. The fact that r_u, r_v do not have a positive lower bound is the main reason why we need to introduce several types of eigenvalue problems, see (19) and (34), to construct subsolutions of related problems.

On the linearized system around $(0, 0)$**.** We denote by A the symmetric matrix field arising after linearizing system (1) near the trivial solution $(0, 0)$, namely

$$A(x) := \begin{pmatrix} r_u(x) - \mu(x) & \mu(x) \\ \mu(x) & r_v(x) - \mu(x) \end{pmatrix}. \tag{2}$$

Since $A(x)$ has positive off-diagonal coefficients, the elliptic system associated with the linear operator $-\Delta - A(x)$ is cooperative, *fully coupled* and therefore satisfies the strong maximum principle as well as other convenient properties [17].

Remark 2.1 (Cooperative elliptic systems and comparison principle). Cooperative systems enjoy similar comparison properties as scalar elliptic operators. In particular, [17] and [19] show that the maximum principle holds for cooperative systems if the principal eigenvalue is positive. Moreover, Section 13 (see also the beginning of Section 14) of [17] shows that, for so-called *fully coupled systems* (which is the case of all the operators we will encounter since $\mu(x) \geq \mu^0 > 0$), the converse holds. These facts will be used for instance in the proof of Lemma 4.2.

Let us now introduce a principal eigenvalue problem that is necessary to enunciate our main results.

Definition 2.2 (Principal eigenvalue). We denote by λ_1 the principal eigenvalue of the stationary operator $-\Delta - A(x)$ with periodic conditions, where A is defined in (2).

In particular, we are equipped through this work with a principal eigenfunction $\Phi := \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ satisfying

$$\begin{cases} -\Phi_{xx} - A(x)\Phi = \lambda_1 \Phi \\ \Phi \text{ is } L\text{-periodic}, \quad \Phi \text{ is positive}, \quad \|\Phi\|_{\mathbf{L}^\infty} = 1. \end{cases} \tag{3}$$

For more details on principal eigenvalue for systems, we refer the reader to [17], in particular to Theorem 13.1 (Dirichlet boundary condition) which provides the principal eigenfunction. Furthermore, in the case of symmetric (self-adjoint) systems as the one we consider, the equivalent definition [19, (2.14)] provides some additional properties, in particular that the eigenfunction minimizes the Rayleigh quotient.

Function spaces. To avoid confusion with the usual function spaces, we denote the function spaces on a couple of functions with a bold font. Hence $\mathbf{L}^p(\Omega) := L^p(\Omega) \times L^p(\Omega)$ for $p \in [1, \infty]$ and $\mathbf{H}^q(\Omega) := H^q(\Omega) \times H^q(\Omega)$ for $q \in \mathbb{N}$ are equipped with the norms

$$\left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{L}^p} := \left\| \begin{pmatrix} \|u\|_{L^p} \\ \|v\|_{L^p} \end{pmatrix} \right\|_p, \quad \left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{H}^q} := \left\| \begin{pmatrix} \|u\|_{H^q} \\ \|v\|_{H^q} \end{pmatrix} \right\|_2.$$

Similarly, $\mathbf{C}^{\alpha,\beta} := C^{\alpha,\beta} \times C^{\alpha,\beta}$ for $\alpha \in \mathbb{N}$ and $\beta \in [0,1]$ is equipped with $\left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{C}^{\alpha,\beta}} :=$ $\max(\|u\|_{C^{\alpha,\beta}}, \|v\|_{C^{\alpha,\beta}})$ and $\mathbf{C}^\alpha := \mathbf{C}^{\alpha,0}$. The subscript of those spaces denotes a restriction to a subspace : $\mathbf{L}^p_{per}$, $\mathbf{H}^q_{per}$, $\mathbf{C}^0_{per}$, $\mathbf{C}^{0,1}_{per}$, $\mathbf{C}^1_{per}$ for L-periodic functions, $\mathbf{H}^1_0$ for functions that vanish on the boundary, etc. Those function spaces are Banach spaces, and $\mathbf{H}^1$, $\mathbf{H}^1_{per}$, $\mathbf{H}^1_0$, $\mathbf{L}^2$ and $\mathbf{L}^2_{per}$ have a canonical Hilbert structure.

2.2 Main results

As well-known in KPP situations, the sign of the principal eigenvalue λ_1 is of crucial importance for the fate of the population: we expect extinction when $\lambda_1 > 0$ and propagation (hence survival) when $\lambda_1 < 0$. To confirm this scenario, we first study the existence of a nontrivial nonnegative steady state of problem (1), that is a nontrivial nonnegative L-periodic solution to the system

$$\begin{cases} -p'' = (r_u(x) - \gamma_u(x)(p+q))p + \mu(x)q - \mu(x)p \\ -q'' = (r_v(x) - \gamma_v(x)(p+q))q + \mu(x)p - \mu(x)q. \end{cases} \tag{4}$$

Theorem 2.3 (On nonnegative steady states)**.** *If $\lambda_1 > 0$ then $(0,0)$ is the only nonnegative steady state of problem* (1).

On the other hand, if $\lambda_1 < 0$ then there exists a nontrivial positive steady state $(p(x) > 0, q(x) > 0)$ of problem (1).

Next we turn to the long time behavior of the Cauchy problem associated with (1). First, we prove extinction when the principal eigenvalue is positive.

Proposition 2.4 (Extinction)**.** *Assume $\lambda_1 > 0$. Let a nonnegative and bounded initial condition $(u^0(x), v^0(x))$ be given. Then, any nonnegative solution $(u(t,x), v(t,x)))$ of* (1) *starting from $(u^0(x), v^0(x))$ goes extinct exponentially fast as $t \to \infty$, namely*

$$\max\left(\|u(t, \cdot)\|_{L^\infty(\mathbb{R})}, \|v(t, \cdot)\|_{L^\infty(\mathbb{R})}\right) = O(e^{-\lambda_1 t}).$$

The proof of Proposition 2.4 is rather simple so we now present it. The cooperative parabolic system

$$\begin{cases} \partial_t \bar{u} = \partial_{xx}\bar{u} + (r_u(x) - \mu(x))\bar{u} + \mu(x)\bar{v} \\ \partial_t \bar{v} = \partial_{xx}\bar{v} + (r_v(x) - \mu(x))\bar{v} + \mu(x)\bar{u}, \end{cases} \tag{5}$$

enjoys the comparison principle, see [23, Theorem 3.2]. On the one hand, any nonnegative $(u(t,x), v(t,x))$ solution of (1) is a subsolution of (5). On the other hand one can check that $(M\varphi(x)e^{-\lambda_1 t}, M\psi(x)e^{-\lambda_1 t})$ — with (φ, ψ) the principal eigenfunction satisfying (3)— is a solution of (5) which is initially larger than (u^0, v^0), if $M > 0$ is sufficiently large. Conclusion then follows from the comparison principle.

The reverse situation $\lambda_1 < 0$ is much more involved. Since in this case we aim at controlling the solution from below, the nonlinear term in (1) has to be carefully estimated. In order to show that the population does invade the whole line when $\lambda_1 < 0$, we are going to construct pulsating fronts for (1).

Definition 2.5 (Pulsating front)**.** A pulsating front for (1) is a speed $c > 0$ and a classical positive solution $(u(t,x), v(t,x))$ to (1), which satisfy the constraint

$$\begin{pmatrix} u(t + \frac{L}{c}, x) \\ v(t + \frac{L}{c}, x) \end{pmatrix} = \begin{pmatrix} u(t, x - L) \\ v(t, x - L) \end{pmatrix}, \quad \forall (t,x) \in \mathbb{R}^2, \tag{6}$$

and supplemented with the boundary conditions

$$\liminf_{t \to +\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \lim_{t \to -\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{7}$$

locally uniformly w.r.t. x.

Following [10], we introduce a new set of variables that correspond to the frame of reference that follows the front propagation, that is $(s, x) := (x - ct, x)$. In these new variables, system (1) transfers into

$$\begin{cases} -(u_{xx} + 2u_{xs} + u_{ss}) - cu_s = (r_u(x) - \gamma_u(x)(u + v))u + \mu(x)v - \mu(x)u \\ -(v_{xx} + 2v_{xs} + v_{ss}) - cv_s = (r_v(x) - \gamma_v(x)(u + v))v + \mu(x)u - \mu(x)v, \end{cases} \tag{8}$$

and the constraint (6) is equivalent to the L-periodicity in x of the solutions to (8). An inherent difficulty to this approach is that the underlying elliptic operator, see the left-hand side member of system (8), is degenerate. This requires to consider a regularization of the operator and to derive a series of *a priori* estimates that do not depend on the regularization, see [8] or [10]. In addition to this inherent difficulty, the problem under consideration (1) does not admit a comparison principle, in contrast with the previous results on pulsating fronts. Nevertheless, as in the traveling wave case, if we only require boundary conditions in a weak sense — see (7) in Definition 2.5— then we can construct a pulsating front for (1) when the underlying principal eigenvalue is negative. This is the main result of the present paper since, as far as we know, this is the first construction of a pulsating front in a situation without comparison principle.

Theorem 2.6 (Construction of a pulsating front). *Assume $\lambda_1 < 0$. Then there exists a pulsating front solution to* (1).

As clear in our construction through the paper, the speed $c^* > 0$ of the pulsating front of Theorem 2.6 satisfies the bound

$$0 < c^* \leq \bar{c}^0 := \inf\{c \geq 0 : \exists \lambda > 0, \mu_{c,0}(\lambda) = 0\},$$

where $\mu_{c,0}(\lambda)$ is the first eigenvalue of the operator

$$S_{c,\lambda,0}\Psi := -\Psi_{xx} + 2\lambda\Psi_x + [\lambda(c - \lambda)Id - A(x)]\,\Psi$$

with L-periodic boundary conditions. In previous works on pulsating fronts [36], [8], [10], it is typically proved that $\bar{c}^0$ is actually the minimal speed of pulsating fronts (and that faster pulsating fronts $c > \bar{c}^0$ also exist). Nevertheless, those proofs seem to rely deeply on the fact that pulsating fronts, as in Definition 2.5, are increasing in time, which is far from obvious in our context without comparison. We conjecture that this remains true but, for the sake of conciseness, we leave it as an open question.

The paper is organized as follows. Section 3 is concerned with the proof of Theorem 2.3 on steady states. In particular the construction of nontrivial steady states requires an adaptation of some bifurcations results [34, 35], [18] that are recalled in Appendix, Section A. The rest of the paper is devoted to the proof of Theorem 2.6, that is the construction of a pulsating front. We first consider in Section 4 an ε-regularization of the degenerate problem (8) in a strip, where existence of a solution is proved by a Leray-Schauder topological degree argument. Then, in Section 5 we let the strip tend to $\mathbb{R}^2$ and finally let the regularization ε tend to zero to complete the proof of Theorem 2.6. This requires, among others, a generalization to elliptic systems of a Bernstein-type gradient estimate performed in [9], which is proved in Appendix, Section B.

3 Steady states

This section is devoted to the proof of Theorem 2.3. The main difficulty is to prove the existence of a positive steady state to (1) when $\lambda_1 < 0$. To do so, we shall use the bifurcation theory introduced in the context of Sturm-Liouville problems by Crandall and Rabinowitz [18], [34, 35]. Though an equivalent result may be obtained using a topological degree argument, this efficient theory shows clearly the relationship between the existence of solutions to the

nonlinear problem and the sign of the principal eigenvalue of the linearized operator near zero.

We shall first state and prove an independent theorem that takes advantage of the Krein-Rutman theorem in the context of a bifurcation originating from the principal eigenvalue of an operator. We will then use this theorem to show the link between the existence of a non-trivial positive steady state for (1), and the sign of the principal eigenvalue defined in (3).

3.1 Bifurcation result, a topological preliminary

We first prove a general bifurcation theorem, interesting by itself, which will be used as an end-point of the proof of Theorem 2.3. It consists in a refinement of the results in [18], [35, 34], under the additional assumption that the linearized operator satisfies the hypotheses of the Krein-Rutman Theorem. Our contribution is to show that the set of nontrivial fixed points only "meets" $\mathbb{R} \times \{0\}$ at point $(\frac{1}{\lambda_1(T)}, 0)$, with $\lambda_1(T)$ the principal eigenvalue of the linearized operator T.

This theorem is independent from the rest of the paper and we will thus use a different set of notations.

Theorem 3.1 (Bifurcation under Krein-Rutman assumption). *Let E be a Banach space. Let $C \subset E$ be a closed convex cone with nonempty interior $Int\, C \neq \varnothing$ and of vertex 0, i.e. such that $C \cap -C = \{0\}$. Let*

$$F : \quad \mathbb{R} \times E \quad \rightarrow \quad E$$
$$(\alpha, x) \quad \mapsto \quad F(\alpha, x)$$

be a continuous and compact operator, i.e. F maps bounded sets into relatively compact ones. Let us define

$$\mathcal{S} := \overline{\{(\alpha, x) \in \mathbb{R} \times E \backslash \{0\} : F(\alpha, x) = x\}}$$

the closure of the set of nontrivial fixed points of F, and

$$\mathbb{P}_{\mathbb{R}}\mathcal{S} := \{\alpha \in \mathbb{R} : \exists x \in C \backslash \{0\}, (\alpha, x) \in \mathcal{S}\}$$

the set of nontrivial solutions in C.
Let us assume the following.

1. $\forall \alpha \in \mathbb{R}$, $F(\alpha, 0) = 0$.

2. F is Fréchet differentiable near $\mathbb{R} \times \{0\}$ with derivative αT locally uniformly w.r.t. α, i.e. for any $\alpha_1 < \alpha_2$ and $\epsilon > 0$ there exists $\delta > 0$ such that

$$\forall \alpha \in (\alpha_1, \alpha_2), \ \|x\| \leq \delta \Rightarrow \|F(\alpha, x) - \alpha T x\| \leq \epsilon \|x\|.$$

3. T satisfies the hypotheses of Theorem A.1 (Krein-Rutman), i.e. $T(C \backslash \{0\}) \subset Int\, C$. We denote by $\lambda_1(T) > 0$ its principal eigenvalue.

4. $\mathcal{S} \cap (\{\alpha\} \times C)$ is bounded locally uniformly w.r.t. $\alpha \in \mathbb{R}$.

5. There is no fixed point on the boundary of C, i.e. $\mathcal{S} \cap (\mathbb{R} \times (\partial C \backslash \{0\})) = \varnothing$.

Then, either $\left(-\infty, \frac{1}{\lambda_1(T)}\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$ or $\left(\frac{1}{\lambda_1(T)}, +\infty\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$.

Proof. Let us first give a short overview of the proof. Since λ_1 is a simple eigenvalue, we know from Theorem A.2 that there exists a branch of nontrivial solutions originating from $\left(\frac{1}{\lambda_1}, 0\right)$. We will show that this branch is actually contained in $\mathbb{R} \times C$, thanks to Theorem A.3. Since it cannot meet $\mathbb{R} \times \{0\}$ except at $\left(\frac{1}{\lambda_1}, 0\right)$, it has to be unbounded, which proves our result.

Let us define

$$\mathcal{S}_C := \overline{\{(\alpha, x) \in \mathbb{R} \times (C\backslash\{0\}) : F(\alpha, x) = x\}}$$

which is a subset of $\mathcal{S}$, and $\alpha_1 := \frac{1}{\lambda_1(T)}$. We may call $(\alpha, x) \in \mathcal{S}_C$ a *degenerate* solution if $x \in \partial C$, and a *proper* solution otherwise.

Our first task is to show that the only degenerate solution is $\{(\alpha_1, 0)\}$. We first show $\mathcal{S}_C \cap (\mathbb{R} \times \partial C) \subset \{(\alpha_1, 0)\}$. Let $(\alpha, x) \in \mathcal{S}_C \cap (\mathbb{R} \times \partial C)$ be given. By item 5 we must have $x = 0$. Let $(\alpha_n, x_n) \to (\alpha, 0)$ such that $x_n \in C \setminus \{0\}$ and $F(\alpha_n, x_n) = x_n$. Let us define $y_n = \frac{x_n}{\|x_n\|} \in C \setminus \{0\}$. On the one hand since y_n is a bounded sequence and T is a compact operator, up to an extraction the sequence (Ty_n) converges to some z which, by item 3, must belong to C. On the other hand

$$y_n = \frac{x_n}{\|x_n\|} = \alpha_n Ty_n + \frac{F(\alpha_n, x_n) - \alpha_n Tx_n}{\|x_n\|} = \alpha z + o(1)$$

in virtue of items 1 and 2, so that in particular $z \neq 0$ and $\alpha \neq 0$. Since $y_n \to \alpha z$ and $Ty_n \to z$ we have $z = \alpha Tz$. Hence $z \in C \setminus \{0\}$ is an eigenvector for T associated with the eigenvalue $\frac{1}{\alpha}$ so that Theorem A.1 (Krein-Rutman) enforces $\alpha = \frac{1}{\lambda_1(T)} = \alpha_1$.

Next we aim at showing the reverse inclusion, that is $\{(\alpha_1, 0)\} \subset \mathcal{S}_C \cap (\mathbb{R} \times \partial C)$. We shall use the topologic results of Appendix A, namely Theorem A.2 and Theorem A.3. Let $z \in C$ be the eigenvector of T associated with $\lambda_1(T)$ such that $\|z\| = 1$, T^* the dual of T, and $l \in E'$ the eigenvector[2] of T^* associated with $\lambda_1(T)$ such that $\langle l, z \rangle = 1$, where $\langle \cdot, \cdot \rangle$ denotes the duality between E and its dual E'.

Now, for $\xi > 0$ and $\eta \in (0, 1)$, let us define

$$K^+_{\xi,\eta} := \{(\alpha, x) \in \mathbb{R} \times E : |\alpha - \alpha_1| < \xi, \langle l, x \rangle > \eta\|x\|\}.$$

The above sets are used to study the local properties of $\mathcal{S}$ near the branching point $(\alpha_1, 0)$. More precisely, it follows from Theorem A.3 that $\mathcal{S}\backslash\{(\alpha_1, 0)\}$ contains a nontrivial connex compound $\mathcal{C}^+_{\alpha_1}$ which is included in $K^+_{\xi,\eta}$ and near $(\alpha_1, 0)$:

$$\forall \xi > 0, \forall \eta \in (0, 1), \exists \zeta_0 > 0, \forall \zeta \in (0, \zeta_0), (\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset K^+_{\xi,\eta},$$

where

$$B_\zeta = \{(\alpha, x) \in \mathbb{R} \times E : |\alpha - \alpha_1| < \zeta, \|x\| < \zeta\}.$$

Moreover, $\mathcal{C}^+_{\alpha_1}$ satisfies the alternative in Theorem A.2. Let us show that $(\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset \mathbb{R} \times C$ for $\zeta > 0$ small enough, i.e.

$$\exists \zeta > 0, (\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset \mathbb{R} \times C. \tag{9}$$

To do so, assume by contradiction that there exists a sequence $(\alpha^n, x_n) \to (\alpha_1, 0)$ such that

$$\forall n \in \mathbb{N}, (\alpha^n, x_n) \in \mathcal{C}^+_{\alpha_1} \text{ and } x_n \notin C.$$

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[2] Let us recall that according to the Fredholm alternative, we have $\dim \ker(I - \lambda T) = \dim \ker(I - \lambda T^*) < \infty$ so that each eigenvalue of T is an eigenvalue of T^* with the same multiplicity.

Writing $\frac{x_n}{\|x_n\|} = \alpha^n T \frac{x_n}{\|x_n\|} + \frac{F(\alpha^n, x_n) - \alpha^n T x_n}{\|x_n\|}$ and reasoning as above, we see that (up to extraction) the sequence $\left(\frac{x_n}{\|x_n\|}\right)$ converges to some w such that $Tw = \frac{1}{\alpha_1} w = \lambda_1(T) w$. As a result $w = z$ or $w = -z$ (recall that z is the unique eigenvector of T such that $z \in C$ and $\|z\| = 1$). But the property $\langle l, x_n \rangle \geq \eta \|x_n\|$ enforces $\frac{x_n}{\|x_n\|} \to z$. Since $\frac{x_n}{\|x_n\|} \notin C$ and $z \in Int\, C$, this is a contradiction. Hence (9) is proved.

Since $\mathcal{C}_{\alpha_1}^+$ is connected and $\mathcal{C}_{\alpha_1}^+ \cap (\mathbb{R} \times \partial C) = \varnothing$ by item 5, we deduce from (9) that $\mathcal{C}_{\alpha_1}^+ \subset \mathcal{S}_C$. Moreover, since by definition $\{(\alpha_1, 0)\} \in \overline{\mathcal{C}_{\alpha_1}^+}$ and $\mathcal{S}_C$ is closed, we have

$$\{(\alpha_1, 0)\} \subset \mathcal{S}_C \cap (\mathbb{R} \times \partial C).$$

We have then established that $\{(\alpha_1, 0)\}$ is the only degenerate solution in C i.e. $\mathcal{S}_C \cap (\mathbb{R} \times \partial C) = \{(\alpha_1, 0)\}$. Applying Theorem A.3 near $\{(\alpha_1, 0)\}$, there exists a branch $\mathcal{C}_{\alpha_1}^+$ of solutions such that $\{(\alpha_1, 0)\} \subset \overline{\mathcal{C}_{\alpha_1}^+}$. By the above argument, $\mathcal{C}_{\alpha_1}^+ \subset \mathcal{S}_C$. Since $\mathcal{C}_{\alpha_1}^+$ cannot meet $\mathbb{R} \times \{0\}$ at $(\alpha, 0) \neq (\alpha_1, 0)$, it follows from Theorem A.3 that $\mathcal{C}_{\alpha_1}^+$ is unbounded. It therefore follows from item 4 that there exists a sequence $(\alpha^n, x^n) \in \mathcal{C}_{\alpha_1}^+$ with $|\alpha^n| \to \infty$. Since $\mathcal{C}_{\alpha_1}^+$ contains only proper solutions (i.e. $\mathcal{C}_{\alpha_1}^+ \cap (\mathbb{R} \times \partial C) = \varnothing$), the projection $P_{\mathbb{R}}(\mathcal{C}_{\alpha_1}^+)$ of $\mathcal{C}_{\alpha_1}^+$ on $\mathbb{R}$ is included in $\mathbb{P}_{\mathbb{R}}\mathcal{S}$. Finally, the continuity of the projection $P_{\mathbb{R}}$ and the fact that $\mathcal{C}_{\alpha_1}^+$ is connected show that either $(\alpha_1, \alpha^n) \subset P_{\mathbb{R}}(\mathcal{C}_{\alpha_1}^+)$ or $(\alpha^n, \alpha_1) \subset P_{\mathbb{R}}(\mathcal{C}_{\alpha_1}^+)$, depending on $\alpha_1 \leq \alpha^n$ or $\alpha^n \leq \alpha_1$. Letting $n \to \infty$ proves Theorem 3.1. $\qquad\square$

3.2 A priori estimates on steady states

In order to meet the hypotheses of Theorem 3.1 in subsection 3.3, we prove some *a priori* estimates on stationary solutions. We have in mind to apply Theorem 3.1 in the cone of nonnegativity of $\mathbf{L}^\infty(\mathbb{R})$. Specifically, Lemma 3.2 will be used to meet item 4 (the solutions are locally bounded), and Lemma 3.3 will be used to meet item 5 (there is no solution on the boundary of the cone).

Lemma 3.2 (Uniform upper bound). *There exists a constant $C = C(r^\infty, \mu^\infty, \gamma^0) > 0$ such that any nonnegative periodic solution (p, q) to (4) satisfies $p(x) \leq C$ and $q(x) \leq C$, for all $x \in \mathbb{R}$.*

Proof. Let $\begin{pmatrix} p \\ q \end{pmatrix}$ be a solution to system (4), so that

$$\begin{cases} -p'' & \leq & p(r_u - \gamma_u p) + q(\mu - \gamma_u p) \\ -q'' & \leq & q(r_v - \gamma_v q) + p(\mu - \gamma_v q). \end{cases} \tag{10}$$

Let us define $C := \max\left(\frac{r^\infty}{\gamma^0}, \frac{\mu^\infty}{\gamma^0}\right) > 0$. Denote by x_0 a point where p reaches its maximum, so that $-p''(x_0) \geq 0$. Assume by contradiction that $p(x_0) > C$. Then, in virtue of (10), one has $-p''(x_0) \leq p(x_0)(r_u(x_0) - \gamma_u(x_0)C) < 0$, which is a contradiction. Thus $p \leq C$. Inequality $q \leq C$ is proved the same way. $\qquad\square$

Lemma 3.3 (Positivity of solutions). *Any nonnegative periodic solution (p, q) to (4) such that $(p, q) \not\equiv (0, 0)$ actually satisfies $p(x) > 0$ and $q(x) > 0$, for all $x \in \mathbb{R}$.*

Proof. Write

$$\begin{cases} -p'' & \geq & p(r_u - \mu - \gamma_u(p + q)) \\ -q'' & \geq & q(r_v - \mu - \gamma_v(p + q)), \end{cases}$$

and the result is a direct application of the strong maximum principle. $\qquad\square$

3.3 Proof of the result on steady states

We are now in the position to prove Theorem 2.3.

The $\lambda_1 > 0$ case. Let (p, q) be a nonnegative steady state solving (4). We need to show that $(p, q) \equiv (0, 0)$. Let us recall that $\Phi = \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ is the principal eigenfunction solving (3). From Lemma 3.2, we can define

$$C_0 := \inf \left\{ C \geq 0 : \forall x \in \mathbb{R}, \begin{pmatrix} p(x) \\ q(x) \end{pmatrix} \leq C \begin{pmatrix} \varphi(x) \\ \psi(x) \end{pmatrix} \right\}. \tag{11}$$

Let us assume by contradiction that $C_0 > 0$. Hence, without loss of generality, $p - C_0\varphi$ attains a zero maximum value at some point $x_0 \in \mathbb{R}$, and $q - C_0\psi \leq 0$ at this point. But, from (3) and (4) we get

$$\begin{cases} -(p - C_0\varphi)'' - (r_u(x) - \mu(x))(p - C_0\varphi) = \mu(x)(q - C_0\psi) - \gamma_u(p+q)p - \lambda_1 C_0\varphi < 0 \\ -(q - C_0\psi)'' - (r_v(x) - \mu(x))(q - C_0\psi) = \mu(x)(p - C_0\varphi) - \gamma_v(p+q)q - \lambda_1 C_0\psi < 0. \end{cases}$$

Evaluating the first inequality at point x_0 yields $(p - C_0\varphi)''(x_0) > 0$, which is a contradiction since x_0 is a local maximum for $p - C_0\varphi$. As a result $C_0 = 0$ and $(p, q) \equiv (0, 0)$. □

The reverse situation $\lambda_1 < 0$, where we need to prove the existence of a nontrivial steady state, is more involved. We shall combine our *a priori* estimates of subsection 3.2 with our bifurcation result, namely Theorem 3.1. We will also use the $\lambda_1 > 0$ case. We want to stress eventually that we will use the notations introduced in subsection 2.1, in particular for functional spaces.

Before starting the proof itself, we would like to present briefly the core of the argument we use. We introduce a new parameter $\beta \in \mathbb{R}$ and look at the modified system

$$\begin{cases} -p'' = p(r_u + \beta - \gamma_u(p+q)) + \mu(q - p) \\ -q'' = q(r_v + \beta - \gamma_v(p+q)) + \mu(p - q) \end{cases} \tag{12}$$

which is system (4) with r_u (resp. r_v) replaced by $r_u + \beta$ (resp. $r_v + \beta$). We apply Theorem 3.1 to system (12) with the bifurcation parameter β. There exists then a branch of solutions originating from $\beta = \lambda_1$, and which spans to $\beta \to +\infty$ since the eigenvalue of the linearization of system (12) is *positive* for $\beta < \lambda_1$ (i.e. no solution exists for $\beta \in (-\infty, \lambda_1)$). In particular there exists a solution for $\beta = 0$ since $\lambda_1 < 0$. Let us make this argument rigorous.

The $\lambda_1 < 0$ case. We start with the following lemma.

Lemma 3.4 (Fréchet differentiability). *Let*

$$f \begin{pmatrix} p \\ q \end{pmatrix} := \begin{pmatrix} -\gamma_u(p+q)p \\ -\gamma_v(p+q)q \end{pmatrix}.$$

Then, the induced operator $\mathbf{L}^{\infty}_{per}(\mathbb{R}) \longrightarrow \mathbf{L}^{\infty}_{per}(\mathbb{R})$ is Fréchet differentiable at $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ with derivative $0_{\mathbf{L}^{\infty}}$.

Proof. We need to show that

$$\left\| f \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} = o\left(\left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \right)$$

as $\left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \to 0$. We have

$$\left\| f \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \leq \gamma^\infty \left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \| p + q \|_{L^\infty_{per}(\mathbb{R})} \leq 2\gamma^\infty \left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})}^2$$

which proves the lemma. $\qquad\square$

We are now in the position to complete the proof of Theorem 2.3. It follows from classical theory that, for $M > 0$ large enough, the problem

$$\begin{cases} -\begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}'' - A(x) \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} + M \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} = \begin{pmatrix} p \\ q \end{pmatrix} \\ \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} \in \mathbf{H}^1_{per} \end{cases} \tag{13}$$

has a unique weak solution $\begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}$, for each $\begin{pmatrix} p \\ q \end{pmatrix} \in \mathbf{L}^2_{per}$. Let us call L_M^{-1} the associated operator, namely

$$L_M^{-1}: \quad \begin{array}{ccc} \mathbf{L}^2_{per} & \to & \mathbf{H}^1_{per} \\ \begin{pmatrix} p \\ q \end{pmatrix} & \mapsto & \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}. \end{array}$$

Notice that, assuming $M > -\lambda_1$, the principal eigenvalue associated with problem (13) is $\lambda_1' := \lambda_1 + M > 0$, and recall that the actual algebraic eigenvalue $\lambda_1(L_M^{-1})$ of the operator L_M^{-1} is given by

$$\lambda_1(L_M^{-1}) = \frac{1}{\lambda_1'} > 0.$$

From elliptic regularity, the restriction of L_M^{-1} to $\mathbf{L}^\infty_{per}(\mathbb{R})$ maps $\mathbf{L}^\infty_{per}(\mathbb{R})$ into $\mathbf{C}^{0,\theta}_{per}(\mathbb{R})$, $0 < \theta < 1$, and L_M^{-1} is therefore a compact operator on $\mathbf{L}^\infty_{per}(\mathbb{R})$. Hence,

$$F: \quad \begin{array}{ccc} \mathbb{R} \times \mathbf{L}^\infty_{per}(\mathbb{R}) & \to & \mathbf{L}^\infty_{per}(\mathbb{R}) \\ \left(\alpha, \begin{pmatrix} p \\ q \end{pmatrix} \right) & \mapsto & L_M^{-1}\left(f \begin{pmatrix} p \\ q \end{pmatrix} + \alpha \begin{pmatrix} p \\ q \end{pmatrix} \right) \end{array}$$

is a continuous and compact map, to which we aim at applying Theorem 3.1. Let us recall that the cone of nonnegativity

$$C := \left\{ \begin{pmatrix} p \\ q \end{pmatrix} \in \mathbf{L}^\infty_{per}(\mathbb{R}) : \begin{pmatrix} p \\ q \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\}$$

is, as required by Theorem 3.1, a closed convex cone of vertex 0 and nonempty interior in $\mathbf{L}^\infty_{per}$. Finally, we want to stress that solutions to $F\left(\alpha, \begin{pmatrix} p \\ q \end{pmatrix} \right) = \begin{pmatrix} p \\ q \end{pmatrix}$ are classical solutions to the system

$$-\begin{pmatrix} p \\ q \end{pmatrix}'' - A(x) \begin{pmatrix} p \\ q \end{pmatrix} = f \begin{pmatrix} p \\ q \end{pmatrix} + (\alpha - M) \begin{pmatrix} p \\ q \end{pmatrix} \tag{14}$$

which is equivalent to system (12) with $\beta = \alpha - M$, where α is the bifurcation parameter. Let us check that all assumptions of Theorem 3.1 are satisfied.

1. Clearly we have $\forall \alpha \in \mathbb{R}, F\left(\alpha, \begin{pmatrix} 0 \\ 0 \end{pmatrix}\right) = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$.

2. From Lemma 3.4 and the composition rule for derivatives, F is Fréchet differentiable near $\mathbb{R} \times \left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\}$ with derivative αL_M^{-1} locally uniformly w.r.t. α.

3. From the comparison principle (available for L_M^{-1} since $\lambda_1' > 0$, see [17]), L_M^{-1} satisfies the hypotheses of the Krein-Rutman Theorem, namely $L_M^{-1}(C \setminus \{0\}) \subset Int\, C$.

4. Lemma 3.2 shows that, for any $\alpha_* < \alpha^*$, $\mathcal{S} \cap (\alpha_*, \alpha^*) \times C$ is bounded (in view of system (12), the constant C defined in the proof of Lemma 3.2 is locally bounded w.r.t. α).

5. From Lemma 3.3, any nonnegative fixed point is positive, i.e. $\mathcal{S} \cap (\mathbb{R} \times (\partial C \setminus \{0\})) = \varnothing$.

We may now apply Theorem 3.1 which states that either $\mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing$ for any $\alpha \in (\lambda_1', +\infty)$ or $\mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing$ for any $\alpha \in (-\infty, \lambda_1')$. Invoking the case of positive principal eigenvalue (see the begininning of the present subsection), we see that there is no nonnegative nontrivial fixed points when $\alpha < \lambda_1'$. As a result we have

$$\forall \alpha \in (\lambda_1', +\infty), \mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing.$$

In particular, since $\lambda_1' = M + \lambda_1 < M$, there exists a positive fixed point for $\alpha = M$, which is a classical solution of (14). This completes the proof of Theorem 2.3. $\qquad\square$

4   Towards pulsating fronts: the problem in a strip

We have established above the existence of a nontrivial periodic steady state $(p(x) > 0, q(x) > 0)$ when the first eigenvalue of the linearized stationary problem λ_1 is negative. The rest of the paper is devoted to the construction of a pulsating front, see Definition 2.5, when $\lambda_1 < 0$.

In order to circumvent the degeneracy of the elliptic operator in (8) we need to introduce a regularization via a small positive parameter ε. Also, in order to gain compactness, the system (8) posed in $(s, x) \in \mathbb{R}^2$ (recall that $s = x - ct$) is first reduced to a strip $(s, x) \in (-a, a) \times \mathbb{R}$ (recall the periodicity in the x variable).

More precisely, let us first define the constants $a_0^* > 0$ (minimal size of the strip in the s variable on which we impose a normalization), $\nu_0 > 0$ (maximal normalization), and $K_0 > 0$ by

$$a_0^* := 2\sqrt{\frac{5}{-\lambda_1}}, \qquad \nu_0 := \min\left(1, \frac{-\lambda_1}{4\gamma^\infty}, \min_{x \in \mathbb{R}}(p(x), q(x))\right),$$

$$K_0 := \max\left(\frac{8\gamma^\infty \max_{x \in \mathbb{R}}(p(x) + q(x))}{-\lambda_1}, 1 + \max_{x \in \mathbb{R}}\left(\frac{p(x)}{q(x)}, \frac{q(x)}{p(x)}\right)\right).$$

Also we define the strip $\Omega_0 := (-a_0, a_0) \times \mathbb{R}$ for $a_0 \geq a_0^*$.

Theorem 4.1 (A solution of the regularized problem in a strip). *Assume $\lambda_1 < 0$. Let $a_0 > a_0^*$, $0 < \nu < \nu_0$ and $K > K_0$ be given. Then there is $C > 0$ such that, for any $\varepsilon \in (0, 1)$, there is $\bar{a} = \bar{a}^\varepsilon > 0$ (whose definition can be found in Lemma 4.3 item 4) such that: for any*

$a \geq a_0 + \bar{a}$, *there exist a L-periodic in x and positive $(u(s,x), v(s,x))$, bounded by C, and a speed $c \in (0, \bar{c}^{\varepsilon} + \varepsilon)$, solving the following mixed Dirichlet-periodic problem on the domain $\Omega := (-a, a) \times \mathbb{R}$*

$$\begin{cases} L_{\varepsilon} u - c u_s = u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \Omega \\ L_{\varepsilon} v - c v_s = v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \Omega \\ (u,v)(-a,x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u,v)(a,x) = (0,0), \quad \forall x \in \mathbb{R} \\ \sup_{\Omega_0} (u+v) = \nu, \end{cases} \tag{15}$$

where $L_{\varepsilon} := -\partial_{xx} - 2\partial_{xs} - (1+\varepsilon)\partial_{ss}$ and the speed $\bar{c}^{\varepsilon} \geq 0$ is defined in Lemma 4.2.

This whole section is concerned with the proof of Theorem 4.1. In order to use a topological degree argument, we transform continuously our problem until we get a simpler problem for which we know how to compute the degree explicitly.

Our first homotopy allows us to get rid of the competitive behaviour of the system. Technically we interpolate the nonlinear terms $-\gamma_u uv$, $-\gamma_v uv$ with the linear terms $-\gamma_u u \frac{q}{K}$, $-\gamma_v v \frac{p}{K}$ respectively, to obtain system (20) which is truly cooperative. In particular, since the boundary condition at $s = -a$ is a supersolution to (20), we can prove the existence of a unique solution to (20) for each $c \in \mathbb{R}$ via a monotone iteration technique, the monotonicity of the constructed solutions and further properties. Nevertheless we still need to compute the degree explicitly, to which end we use a second homotopy that interpolates the right-hand side of (20) with a linear term, and then a third homotopy to get rid of the coupling between the speed c and the profiles u and v. At this point we are equipped to compute the degree. For related arguments in a traveling wave context, we refer teh reader to [12], [3, 4], [25].

The role of the a priori estimates in subsections 4.1, 4.2 and 4.3 is to ensure that there is no solution on the boundary of the open sets that we choose to contain our problem, and thus that the degree is a constant along our path. In subsection 4.4, we complete the proof of Theorem 4.1.

Before that, we need to establish some properties on the upper bound $\bar{c}^{\varepsilon}$ for the speed in Theorem 4.1.

Lemma 4.2 (On the upper bound for the speed). *Let*

$$S_{c,\lambda,\varepsilon}\Psi := -\Psi_{xx} + 2\lambda\Psi_x + [\lambda(c - (1+\varepsilon)\lambda)Id - A(x)]\Psi,$$

and define

$$\bar{c}^{\varepsilon} = \inf \{c \geq 0, \exists \lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\}, \tag{16}$$

where $\mu_{c,\varepsilon}(\lambda)$ is the first eigenvalue of the operator $S_{c,\lambda,\varepsilon}$ with L-periodic boundary conditions. Then the following holds.

1. *For any $\varepsilon \in (0,1)$, we have $\bar{c}^{\varepsilon} < +\infty$.*

2. *We have $\bar{c}^{\varepsilon} = \min \{c \geq 0, \exists \lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\}$.*

3. *$\varepsilon \mapsto \bar{c}^{\varepsilon}$ is nondecreasing.*

Proof.   1. We need to prove that the set in the right-hand side of (16) is non-empty. We first notice that $\mu_{c,\varepsilon}(0) = \lambda_1 < 0$ for any $c > 0$. Next, for the eigenfunction $\Phi := \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ solving (3), we have $S_{c,\lambda,\varepsilon}\Phi = \lambda_1\Phi + 2\lambda\Phi_x + \lambda(c - (1 + \varepsilon)\lambda)\Phi$. In particular for $\lambda = \frac{c}{2}$, we have

$$S_{c,\frac{c}{2},\varepsilon}\Phi \geq (\lambda_1 + \frac{c^2}{4}(1 - \varepsilon))\Phi + c\Phi_x \geq \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

as soon as $c \geq c_*$ where $c_* > 0$ depends only on the quantities $\min(\varphi, \psi)$, $\|\Phi_x\|_{\mathbf{L}^\infty}$ and $-\lambda_1$. It therefore follows from [17, Theorem 13.1, item c] that $\mu_{c_*,\varepsilon}\left(\frac{c_*}{2}\right) \geq 0$. Since the principal eigenvalue of $S_{c,\lambda,\varepsilon}$ is continuous[3] with respect to λ (and c), there exists $\lambda \in (0, \frac{c_*}{2}]$ such that $\mu_{c_*,\varepsilon}(\lambda) = 0$, which proves that (16) is well-posed.

2. For the eigenfunction Φ solving (3), we have

$$S_{c,\lambda,\varepsilon}\Phi \leq 2\lambda\Phi_x - \lambda^2\left(1 + \varepsilon - \frac{c}{\lambda}\right)\Phi < \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

as soon as $\lambda \geq \lambda_*$ where $\lambda_* > 0$ depends only on $\min(\varphi, \psi)$, $\|\Phi_x\|_{\mathbf{L}^\infty}$, and an upper bound for c. Hence the maximum principle does not hold for $S_{c,\lambda,\varepsilon}$, and it follows from [17, Theorem 14.1] that $\mu_{c,\varepsilon}(\lambda) \leq 0$.

Now, we consider sequences $c_n \searrow \bar{c}^\varepsilon$, and $\lambda_n \geq 0$ such that $\mu_{c_n,\varepsilon}(\lambda_n) = 0$. From the above, we have $\lambda_n \leq \lambda_*$ so that, up to extraction, $\lambda_n \to \lambda_\infty$. From the continuity of the principal eigenvalue, we deduce that $\mu_{\bar{c}^\varepsilon,\varepsilon}(\lambda_\infty) = 0$, and the infimum in (16) is attained.

3. Let $\varepsilon' \leq \varepsilon$ and $c > 0$ such that there is a positive solution Θ to $S_{c,\lambda,\varepsilon}\Theta = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$. Then $S_{c,\lambda,\varepsilon'}\Theta = (\varepsilon - \varepsilon')\lambda^2\Theta \geq \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ so that, as in the proof of item 1, there exists $0 < \lambda' \leq \lambda$ such that $\mu_{c,\varepsilon'}(\lambda') = 0$. Thus

$$\{c \geq 0, \exists\lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\} \subset \{c \geq 0, \exists\lambda > 0, \mu_{c,\varepsilon'}(\lambda) = 0\}.$$

Taking the infimum on c yields $\bar{c}^{\varepsilon'} \leq \bar{c}^\varepsilon$.
Lemma 4.2 is proved. $\qquad\square$

4.1   Estimates along the first homotopy

Let us recall that the role of the first homotopy is to get rid of the competition of our original problem ($\tau = 1$), so that the classical comparison methods become available for $\tau = 0$. Notice that it is crucial that the Dirichlet condition at $s = -a$ is a supersolution for the $\tau = 0$ problem, in order to apply a sliding method in the following subsection. Hence, for $0 \leq \tau \leq 1$,

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[3]This property is potentially false in general but has a simple proof in our setting. Take a sequence of operators $T_n \to T$ that send a proper cone C into $K \subset \text{Int } C$ with K compact, i.e. $T_n(C) \subset K$ and $T(C) \subset K$. Assume that the series of normalized eigenvectors $x_n \in C$ s.t. $T_n x_n = \lambda_n x_n$ diverges, then we can extract to sequences $x_n^1 \to y \in C$ and $x_n^2 \to z \in C$ with $y \neq z$. Extracting further, there exists μ and ν s.t. $Ty = \mu y$ and $Tz = \nu z$ which is a contradiction since $y \neq z$. Hence the continuity of the eigenvalue.

we consider the problem

$$\begin{cases} L_\varepsilon u - cu_s = u[r_u - \gamma_u(u + (\tau v + (1-\tau)\frac{q}{K}))] + \mu v - \mu u \\ L_\varepsilon v - cv_s = v[r_v - \gamma_v((\tau u + (1-\tau)\frac{p}{K}) + v)] + \mu u - \mu v \\ (u,v)(-a,x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u,v)(a,x) = (0,0), \quad \forall x \in \mathbb{R}, \end{cases} \tag{17}$$

along with the normalization condition $\sup_{\Omega_0} (u + v) = \nu$.

Lemma 4.3 (A priori estimates along the first homotopy). *Let a nonnegative* $(u,v) \in \mathbf{C}^1_{per}(\Omega)$ *(where* $\Omega = (-a,a) \times \mathbb{R}$ *and the periodicity is understood only w.r.t. the* $x \in \mathbb{R}$ *variable) and* $c \in \mathbb{R}$ *solve* (17), *with* $0 \le \tau \le 1$. *Then*

1. (u,v) *is a classical solution to* (17), *i.e.* $(u,v) \in \mathbf{C}^2(\overline{\Omega})$.

2. *The positive constant* $C := \max(\frac{2r^\infty}{\gamma^0}, K\max(p+q))$ *is such that*

$$u(s,x) + v(s,x) \le C, \quad \forall(s,x) \in \overline{\Omega} = [-a,a] \times \mathbb{R}.$$

3. (u,v) *is positive in* Ω.

4. *Let* $\lambda_0 > 0$ *and* $\Phi_0(x) = \begin{pmatrix} \Phi_u(x) \\ \Phi_v(x) \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ *be such that* $S_{\bar{c}^\varepsilon, \lambda_0, \varepsilon}\Phi_0 = 0$ *and* $\|\Phi_0\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} = 1$. *Define* $\bar{a} = \bar{a}^\varepsilon := \max(-\frac{1}{\lambda_0}\ln\left(\frac{\nu\min(\Phi_u,\Phi_v)}{4K\max(p,q)}\right), 1)$. *Then if* $a \ge a_0 + \bar{a}$ *and* $c \ge \bar{c}^\varepsilon$, *we have* $\sup_{\Omega_0} (u+v) < \frac{\nu}{2}$.

5. *If* $c = 0$ *and* $a \ge a_0 + 1$ *then*

$$\sup_{\Omega_0} (u+v) \ge \frac{-\lambda_1^\varepsilon}{\gamma^\infty} - \frac{\max(p+q)}{K}, \tag{18}$$

where λ_1^ε *is the principal eigenvalue of the operator* $L_\varepsilon - A(x)$ *with Dirichlet condition in* s *and* L-periodic *condition in* x, *in the domain* Ω_0, *as defined in* (19).

Proof.   1. This is true from classical elliptic regularity. We omit the details.

2. In view of (17), the sum $S := u + v$ satisfies

$$\begin{aligned} L_\varepsilon S - cS_s &= r_u u + r_v v - \gamma_u u(u + (1-\tau)\frac{q}{K} + \tau v) - \gamma_v v(v + (1-\tau)\frac{p}{K} + \tau u) \\ &\le r^\infty S - \gamma^0(u^2 + v^2). \end{aligned}$$

Since $S^2 = u^2 + 2uv + v^2 \le 2(u^2 + v^2)$, we have

$$L_\varepsilon S - cS_s \le \frac{\gamma^0}{2} S \left(\frac{2r^\infty}{\gamma^0} - S \right).$$

Since the maximum principle holds for the operator $L_\varepsilon - c\partial_s$ independently of c and $\varepsilon > 0$, S cannot have an interior local maximum which is greater than $\frac{2r^\infty}{\gamma^0}$. This along with the boundary conditions $S(-a,x) = K(p(x) + q(x))$, $S(a,x) = 0$ proves item 2.

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3. Assume that there exists $(s_0, x_0) \in (-a, a) \times \mathbb{R}$ such that $u(s_0, x_0) = 0$. Since

$$L_\varepsilon u - c u_s \geq u \left[r_u(x) - \gamma_u(x) \left(u + \left(\tau v + (1 - \tau) \frac{q}{K} \right) \right) - \mu(x) \right],$$

the strong maximum principle enforces $u \equiv 0$ which contradicts the boundary condition at $s = -a$. The same argument applies to v.

4. Let $\zeta(s, x) := B e^{-\lambda_0 s} \Phi_0(x)$, $B > 0$. Then we have

$$L_\varepsilon \zeta - c \zeta_s = B e^{-\lambda_0 s} \left(S_{\bar{c}^\varepsilon, \lambda_0, \varepsilon} \Phi_0 + A(x) \Phi_0 + \lambda_0 (c - \bar{c}^\varepsilon) \Phi_0 \right) = A(x) \zeta + \lambda_0 (c - \bar{c}^\varepsilon) \zeta \geq A(x) \zeta$$

so that ζ is a strict supersolution to problem (17). By item 2, one can define

$$B_0 := \inf \left\{ B > 0, \forall (s, x) \in [-a, a] \times \mathbb{R}, \begin{pmatrix} u(s, x) \\ v(s, x) \end{pmatrix} \leq \zeta(s, x) \right\} > 0$$

and $\zeta_0(s, x) = \begin{pmatrix} \zeta_u(s, x) \\ \zeta_v(s, x) \end{pmatrix} := B_0 e^{-\lambda_0 s} \Phi_0(x)$. From the strong maximum principle in $(-a, a) \times \mathbb{R}$, and the $s = a$ boundary condition, the touching point has to lie on $s = -a$. Thus there exists x_0 such that either $\zeta_u(-a, x_0) = u(-a, x_0)$ or $\zeta_v(-a, x_0) = v(-a, x_0)$. In any case one has $B_0 \leq K e^{-\lambda_0 a} \frac{\max(p, q)}{\min(\Phi_u, \Phi_v)}$, which in in turn implies

$$\sup_{\Omega_0} (u + v) \leq 2 B_0 e^{\lambda_0 a_0} \leq 2K \frac{\max(p, q)}{\min(\Phi_u, \Phi_v)} e^{-\lambda_0 (a - a_0)} \leq 2K \frac{\max(p, q)}{\min(\Phi_u, \Phi_v)} e^{-\lambda_0 \bar{a}} \leq \frac{\nu}{2},$$

in view of the definition of $\bar{a}$. This proves item 4.

5. Assume by contradiction that $\sup_{\Omega_0} (u + v) < \frac{-\lambda_1^\varepsilon}{\gamma^\infty} - \frac{\max(p + q)}{K}$ (which in particular enforces $\lambda_1^\varepsilon < 0$). Then, in $(-a_0, a_0) \times \mathbb{R}$, we have

$$\begin{cases} L_\varepsilon u &= (r_u - \mu - \gamma_u (u + \tau v + (1 - \tau) \frac{q}{K})) u + \mu v \geq (r_u - \mu + \lambda_1^\varepsilon) u + \mu v \\ L_\varepsilon v &= (r_v - \mu - \gamma_v (v + \tau u + (1 - \tau) \frac{p}{K})) v + \mu u \geq (r_v - \mu + \lambda_1^\varepsilon) v + \mu u. \end{cases}$$

Denote by $\Phi^\varepsilon(s, x) := \begin{pmatrix} \bar{\varphi}(s, x) \\ \bar{\psi}(s, x) \end{pmatrix}$ the principal eigenvector associated with λ_1^ε (vanishing at $s = \pm a_0$, L periodic in x) normalized by $\|\bar{\Phi}^\varepsilon\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} = 1$, see problem (19). Define

$$A_0 := \max\{A > 0 : A\bar{\varphi}(s, x) \leq u(s, x) \text{ and } A\bar{\psi}(s, x) \leq v(s, x), \forall (s, x) \in [-a_0, a_0] \times \mathbb{R}\}.$$

Then we have $A_0 \bar{\varphi} \leq u$, $A_0 \bar{\psi} \leq v$, with equality at at least one point for at least one equation, say $A_0 \bar{\varphi}(s_0, x_0) = u(s_0, x_0)$ for some $-a_0 < s_0 < a_0$ and $x_0 \in \mathbb{R}$. But

$$L_\varepsilon(u - A_0 \bar{\varphi}) - (r_u - \mu + \lambda_1^\varepsilon)(u - A_0 \bar{\varphi}) \geq \mu(v - A_0 \bar{\psi}) \geq 0,$$

so that the strong maximum principle enforces $u \equiv A_0 \bar{\varphi}$, which is a contradiction since u is positive on $(-a, a) \times \mathbb{R}$ and $\bar{\varphi}$ vanishes on $\{\pm a_0\} \times \mathbb{R}$. A similar argument leads to a contradiction in the case $v(s_0, x_0) = A_0 \bar{\psi}(s_0, x_0)$. This proves item 5.

Lemma 4.3 is proved. □

Item 5 of the above lemma is relevant only when $\lambda_1^\varepsilon < 0$, which is actually true if $a_0 > 0$ is large enough, as proved below. Let us denote by λ_1^ε, $\Phi^\varepsilon(s, x)$ the principal eigenvalue, eigenfunction solving the mixed Dirichlet-periodic eigenproblem

$$
\begin{cases}
L_\varepsilon \Phi^\varepsilon = A(x)\Phi^\varepsilon + \lambda_1^\varepsilon \Phi^\varepsilon & \text{in } \Omega_0 = (-a_0, a_0) \times \mathbb{R} \\
\Phi^\varepsilon(-a_0, x) = \Phi^\varepsilon(a_0, x) = 0 & \forall x \in \mathbb{R} \\
\Phi^\varepsilon(s, x) \quad \text{is periodic w.r.t. } x \\
\Phi^\varepsilon > \begin{pmatrix} 0 \\ 0 \end{pmatrix} \text{ in } \Omega_0 = (-a_0, a_0) \times \mathbb{R}.
\end{cases} \tag{19}
$$

Lemma 4.4 (An estimate for λ_1^ε). *We have $\lambda_1^\varepsilon \leq \lambda_1 + \frac{5}{2a_0^2}(1 + \varepsilon)$.*

Proof. Since the matrix $A(x)$ is symmetric, we are equipped with the Rayleigh quotient

$$
\lambda_1^\varepsilon = \inf_{w \in H_{0,per}^1 \times H_{0,per}^1} \frac{\int_{(-a_0,a_0) \times (0,L)} \left({}^t w_x w_x + 2\, {}^t w_x w_s + (1+\varepsilon)\, {}^t w_s w_s - {}^t w A(x) w \right) \, \mathrm{d}s \mathrm{d}x}{\int_{(-a_0,a_0) \times (0,L)} {}^t w w \, \mathrm{d}s \mathrm{d}x}.
$$

Let us denote $\Phi(x) = \begin{pmatrix} \varphi(x) \\ \psi(x) \end{pmatrix}$ the principal eigenvector solving (3), and define

$$
\bar{\Phi} := \|\Phi\|_{\mathbf{L}_{per}^2}^{-1} \Phi.
$$

We define the test function $w(s, x) := \eta(s)\bar{\Phi}(x)$, with $\eta(s) := \sqrt{\frac{15}{16a_0^5}}(a_0 - s)(a_0 + s)$, so that $\int_{(-a_0,a_0)} \eta^2(s)ds = 1$. Noticing that $\int {}^t w_x w_s \mathrm{d}x \mathrm{d}s = 0$, we get

$$
\lambda_1^\varepsilon \leq \int_{(0,L)} ({}^t \bar{\Phi}_x \bar{\Phi}_x - {}^t \bar{\Phi} A(x) \bar{\Phi})(x) \mathrm{d}x + \int_{(-a_0,a_0)} (1+\varepsilon)\eta_s^2(s)\mathrm{d}s = \lambda_1 + \frac{5}{2a_0^2}(1+\varepsilon),
$$

which shows the result. $\qquad\square$

Remark 4.5 (Consistency of the choice of parameters in Theorem 4.1). Let us say a word on the choice of the positive parameters (a_0^*, ν_0, K_0) in Theorem 4.1. First, the choice of a_0^* and Lemma 4.4 imply that $\lambda_1^\varepsilon \leq \frac{3\lambda_1}{4}$ for any $\varepsilon \in (0, 1)$ and $a_0 \geq a_0^*$. Then, (18) and the choices of K_0, ν_0 imply that, for $c = 0$,

$$
\sup_{\Omega_0} (u + v) \geq \frac{-\lambda_1}{2\gamma^\infty} \geq 2\nu_0.
$$

In particular, item 5 in Lemma 4.3 gives a true lower bound for $\sup_{\Omega_0} (u + v)$ in the case $c = 0$.

4.2 Estimates for the end-point $\tau = 0$ of the first homotopy

We introduce the problem

$$
\begin{cases}
L_\varepsilon u - cu_s = u(r_u - \gamma_u(u + \frac{q}{K})) + \mu v - \mu u \\
L_\varepsilon v - cv_s = v(r_v - \gamma_v(\frac{p}{K} + v)) + \mu u - \mu v \\
(u, v)(-a, x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\
(u, v)(a, x) = (0, 0), \quad \forall x \in \mathbb{R},
\end{cases} \tag{20}
$$

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which corresponds to (17) with $\tau = 0$ and for which comparison methods are available. In this subsection we derive refined estimates for (20) that will allow us to enlarge the domain on which the degree is computed, which is necessary for the second homotopy that we will perform.

Lemma 4.6 (On problem (20)). *1. For each $c \in \mathbb{R}$, there exists a unique nonnegative solution (u, v) to (20), which satisfies*

$$\forall (s, x) \in \Omega, \quad 0 < u(s, x) < Kp(x) \text{ and } 0 < v(s, x) < Kq(x). \tag{21}$$

2. Let $c \in \mathbb{R}$ and (u, v) the nonnegative solution to (20). Then u and v are nonincreasing in s.

3. The mapping $c \mapsto \begin{pmatrix} u \\ v \end{pmatrix}$ is decreasing, where (u, v) is the unique nonnegative solution to (20).

Proof. In this proof we denote

$$f : \left(x, \begin{pmatrix} u \\ v \end{pmatrix} \right) \mapsto \begin{pmatrix} u(r_u(x) - \gamma_u(x)(u + \frac{q}{K})) + \mu(x)v - \mu(x)u \\ v(r_v(x) - \gamma_v(x)(\frac{p}{K} + v)) + \mu(x)u - \mu(x)v \end{pmatrix} \tag{22}$$

so that (20) is recast $L_\varepsilon \begin{pmatrix} u \\ v \end{pmatrix} - c \begin{pmatrix} u \\ v \end{pmatrix}_s = f\left(x, \begin{pmatrix} u \\ v \end{pmatrix} \right)$. We select $M > 0$ large enough so that $f(x, \cdot) + M Id$ is uniformly nondecreasing on $[0, C]^2$, with C the constant from Lemma 4.3, that is

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} \leq \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} \leq \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} \leq \begin{pmatrix} C \\ C \end{pmatrix} \Rightarrow f\left(x, \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} \right) - f\left(x, \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} \right) \geq -M \begin{pmatrix} u_2 - u_1 \\ v_2 - v_1 \end{pmatrix},$$

for all $x \in \mathbb{R}$.

1. We first claim that $(s, x) \mapsto (Kp(x), Kq(x))$ is a strict supersolution to problem (20). Since $K \geq K_0$, we have $p + q < Kp \leq Kp + \frac{q}{K}$ so that

$$\begin{aligned} L_\varepsilon(Kp) - c(Kp)_s &= -(Kp)'' \\ &= (Kp)(r_u(x) - \gamma_u(x)(p + q)) + \mu(x)Kq - \mu(x)Kp \\ &> (Kp)(r_u(x) - \gamma_u(x)(Kp + \frac{q}{K})) + \mu(x)(Kq) - \mu(x)(Kp), \end{aligned}$$

and similarly

$$L_\varepsilon(Kq) - c(Kq)_s > (Kq)(r_v(x) - \gamma_v(x)(\frac{p}{K} + Kq)) + \mu(x)(Kp) - \mu(x)(Kq),$$

which proves the claim. Obviously, $(s, x) \mapsto \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ is a strict subsolution to problem (20) because of the boundary condition at $s = -a$. Since system (20) is cooperative, the classical monotone iteration method shows that, for any $c \in \mathbb{R}$, there exists at least a solution (u, v) to problem (20) which satisfies (21).

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Next, in order to prove uniqueness, let (u,v) and $(\tilde{u},\tilde{v})$ be two nonnegative solutions to (20), such that $(u,v) \neq (\tilde{u},\tilde{v})$. Then, for any $0 < \zeta < 1$, $(U^\zeta, V^\zeta) := (\zeta u, \zeta v)$ satisfies

$$
\begin{cases}
L_\varepsilon U^\zeta - cU_s^\zeta &= U^\zeta(r_u - \gamma_u \frac{q}{K} - \mu - \frac{\gamma_u(x)}{\zeta}U^\zeta) + \mu(x)V^\zeta \\
&< U^\zeta(r_u - \gamma_u \frac{q}{K} - \mu - \gamma_u(x)U^\zeta) + \mu(x)V^\zeta \\
L_\varepsilon V^\zeta - cV_s^\zeta &= V^\zeta(r_v - \gamma_v \frac{p}{K} - \mu - \frac{\gamma_v(x)}{\zeta}V^\zeta) + \mu(x)U^\zeta \\
&< V^\zeta(r_v - \gamma_v \frac{p}{K} - \mu - \gamma_v(x)V^\zeta) + \mu(x)U^\zeta \\
(U^\zeta, V^\zeta)(-a,x) = (\zeta K p(x), \zeta K q(x)) &\leq (Kp(x), Kq(x)) \\
(U^\zeta, V^\zeta)(a,x) = (0,0),
\end{cases}
$$

and is therefore a strict subsolution to problem (20). From Hopf lemma we know that $(\tilde{u}_s, \tilde{v}_s)(a,x) < (0,0)$ so that we can define

$$\zeta_0 := \sup\{\zeta > 0 : (U^\zeta, V^\zeta)(s,x) < (\tilde{u}, \tilde{v})(s,x), \forall (s,x) \in \Omega\} > 0.$$

Then we have $(0,0) \leq (U^{\zeta_0}, V^{\zeta_0}) \leq (\tilde{u}, \tilde{v}) \leq (C,C)$. Assume by contradiction that $\zeta_0 < 1$. Then we have

$$
\begin{cases}
L_\varepsilon(\tilde{u} - U^{\zeta_0}) - c(\tilde{u} - U^{\zeta_0})_s + M(\tilde{u} - U^{\zeta_0}) &\geq 0 \\
L_\varepsilon(\tilde{v} - V^{\zeta_0}) - c(\tilde{v} - V^{\zeta_0})_s + M(\tilde{v} - V^{\zeta_0}) &\geq 0 \\
(\tilde{u} - U^{\zeta_0}, \tilde{v} - V^{\zeta_0})(-a,x) \geq (0,0) \\
(\tilde{u} - U^{\zeta_0}, \tilde{v} - V^{\zeta_0})(a,x) = (0,0).
\end{cases}
$$

From Hopf lemma we deduce

$$((\tilde{u} - U^{\zeta_0})_s, (\tilde{v} - V^{\zeta_0})_s)(a,x) < (0,0)$$

so that there exists $(s_0, x_0) \in (-a,a) \times \mathbb{R}$ such that, say, $\tilde{u}(s_0, x_0) = U^{\zeta_0}(s_0, x_0)$. From the strong maximum principle we deduce $\tilde{u} \equiv U^{\zeta_0}$, which is a contradiction in view of the boundary condition at $s = -a$. We conclude that $\zeta_0 \geq 1$ and thus $(u,v) \leq (\tilde{u}, \tilde{v})$. Then exchanging the roles of (u,v) and $(\tilde{u}, \tilde{v})$ in the above argument, we get that $(\tilde{u}, \tilde{v}) \leq (u,v)$ so that finally $(\tilde{u}, \tilde{v}) = (u,v)$. This is in contradiction with our initial hypothesis. We conclude that the nonnegative solution to equation (20) is unique.

2. For given $c \in \mathbb{R}$, let (u,v) be the solution to (20). In order to use a sliding technique, we define
$$(u^t(s,x), v^t(s,x)) := (u(s+t,x), v(s+t,x))$$

for $t > 0$ and $(s,x) \in [-a, a-t] \times \mathbb{R}$. From the boundary conditions, there is $\delta > 0$ such that

$$\forall t \in (2a - \delta, 2a), \forall (s,x) \in (-a, a-t) \times \mathbb{R}, \quad u^t(s,x) < u(s,x) \text{ and } v^t(s,x) < v(s,x).$$

In particular, one can define

$$t_0 := \inf\{t > 0, \forall (s,x) \in [-a, a-t], \ u^t(s,x) \leq u(s,x) \text{ and } v^t(s,x) \leq v(s,x)\}.$$

Assume by contradiction that $t_0 > 0$. Then there exists $(s_0, x_0) \in (-a, a-t_0) \times \mathbb{R}$ such that, say, $u^{t_0}(s_0, x_0) = u(s_0, x_0)$ (notice that $s_0 = -a$ and $s_0 = a - t_0$ are prevented by (21)). Since we have

$$L_\varepsilon \begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} - c\begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix}_s + M\begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} = (f + M)\begin{pmatrix} u^{t_0} \\ v^{t_0} \end{pmatrix} - (f + M)\begin{pmatrix} u \\ v \end{pmatrix} \leq 0$$

and $\begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} \leq 0$, the strong maximum principle implies $u^{t_0} \equiv u$, which contradicts $0 < u < Kp$. We conclude that $t_0 = 0$, which means that u and v are nonincreasing in s.

3. Let (c, u, v) and $(\tilde{c}, \tilde{u}, \tilde{v})$ two solutions of equation (20) with $c < \tilde{c}$. As above, we define

$$(\tilde{u}^t(s, x), \tilde{v}^t(s, x)) := (\tilde{u}(s + t, x), \tilde{v}(s + t, x)),$$

and

$$t_0 := \inf\{t > 0, \forall (s, x) \in [-a, a - t], \ \tilde{u}^t(s, x) \leq u(s, x) \text{ and } \tilde{v}^t(s, x) \leq v(s, x)\}.$$

Assume by contradiction that $t_0 > 0$. Then there again exists $(s_0, x_0) \in (-a, a - t_0) \times \mathbb{R}$ such that, say, $\tilde{u}^{t_0}(s_0, x_0) = u(s_0, x_0)$. Moreover we have

$$\begin{aligned}
L_\varepsilon \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix} &- c \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix}_s + M \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix} \\
&= (f + M) \begin{pmatrix} \tilde{u}^{t_0} \\ \tilde{v}^{t_0} \end{pmatrix} - (f + M) \begin{pmatrix} u \\ v \end{pmatrix} + (\tilde{c} - c) \begin{pmatrix} \tilde{u}^{t_0} \\ \tilde{v}^{t_0} \end{pmatrix}_s \\
&\leq \begin{pmatrix} 0 \\ 0 \end{pmatrix},
\end{aligned}$$

since $\tilde{u}_s \leq 0$ and $\tilde{v}_s \leq 0$ (recall that $\tilde{u}$ and $\tilde{v}$ are decreasing), so that we again derive a contradiction. As a result $t_0 = 0$, that is $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \leq \begin{pmatrix} u \\ v \end{pmatrix}$ and then $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix}$ from the strong maximum principle.

The lemma is proved. $\qquad\square$

4.3 Estimates along the second homotopy

The second homotopy allows us to get rid of the nonlinearity and the coupling in u and v at the expense of an increased linear part. For $0 \leq \tau \leq 1$, we consider

$$\begin{cases}
L_\varepsilon u - cu_s = \tau \left(u \left(r_u - \gamma_u \frac{q}{K} - \mu - \gamma_u u \right) + \mu v \right) - (1 - \tau)\mathcal{C}u \\
L_\varepsilon v - cv_s = \tau \left(v \left(r_v - \gamma_v \frac{p}{K} - \mu - \gamma_v v \right) + \mu u \right) - (1 - \tau)\mathcal{C}v \\
(u, v)(-a, x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\
(u, v)(a, x) = (0, 0), \quad \forall x \in \mathbb{R},
\end{cases} \tag{23}$$

with

$$\mathcal{C} := -\min_{x \in \mathbb{R}} \left(r_u(x) - \gamma_u(x) \left(\frac{q(x)}{K} + C \right) - \mu(x), r_v(x) - \gamma_v(x) \left(\frac{p(x)}{K} + C \right) - \mu(x), 0 \right) \tag{24}$$

where C is as in Lemma 4.3 item 2.

Lemma 4.7 (A priori estimates along the second homotopy)**.** *Let a nonnegative $(u, v) \in \mathbf{C}^1_{per}(\Omega)$ (where $\Omega = (-a, a) \times \mathbb{R}$ and the periodicity is understood only w.r.t. the $x \in \mathbb{R}$ variable) and $c \in \mathbb{R}$ solve (23), with $0 \leq \tau \leq 1$. Then*

1. (u, v) is a classical solution to (23), i.e. $(u, v) \in \mathbf{C}^2(\overline{\Omega})$.

2. We have
$$u(s, x) + v(s, x) \leq C, \quad \forall (s, x) \in \overline{\Omega} = [-a, a] \times \mathbb{R}.$$

3. (u, v) is positive in Ω.

4. If $a \geq a_0 + \bar{a}$ and $c \geq \bar{c}^\varepsilon$, we have $\sup\limits_{\Omega_0} (u + v) < \frac{\nu}{2}$, where $\bar{a}$ is as in Lemma 4.3 item 4.

5. There exists $\underline{c} = \underline{c}(a) \geq 0$ such that if $c \leq -\underline{c}(a)$ then $\sup\limits_{\Omega_0} (u + v) > \nu$.

Proof. Items 1, 2, 3 and 4 can be proved as in Lemma 4.3. We therefore omit the details, and only focus on item 5.

From item 2 and the choice of $\mathcal{C}$ we see that, for any $0 \leq \tau \leq 1$,
$$L_\varepsilon u - c u_s + \mathcal{C} u \geq 0, \quad u(-a, x) = K p(x), \quad u(a, x) = 0.$$

Now, let $\alpha_\pm := \frac{-c \pm \sqrt{c^2 + 4(1+\varepsilon)\mathcal{C}}}{2(1+\varepsilon)}$ and $m := K \min\limits_{x \in \mathbb{R}} (p(x), q(x)) > 0$. Then the function $\theta(s, x) = \theta(s) := m \frac{e^{\alpha_- s + \alpha_+ a} - e^{\alpha_+ s + \alpha_- a}}{e^{(\alpha_+ - \alpha_-)a} - e^{(\alpha_- - \alpha_+)a}}$ solves
$$L_\varepsilon \theta - c \theta_s + \mathcal{C} \theta = 0, \quad \theta(-a) = m, \quad \theta(a) = 0.$$

From the comparison principle, we infer that $u(s, x) \geq \theta(s)$, and similarly $v(s, x) \geq \theta(s)$, for all $(s, x) \in (-a, a) \times \mathbb{R}$. As a result $\sup\limits_{\Omega_0} (u + v) \geq 2 \sup_{(-a_0, a_0)} \theta \geq 2\theta(0)$.

Next, for $c \leq -c^1(a) := -\frac{1+\varepsilon}{a} \ln 4$ one has $e^{(\alpha_- - \alpha_+)a} \leq \frac{1}{4}$ so that
$$\theta(0) \geq m \frac{e^{\alpha_+ a} - e^{\alpha_- a}}{e^{(\alpha_+ - \alpha_-)a}} = m e^{\alpha_- a} \left(1 - e^{(\alpha_- - \alpha_+)a}\right) \geq m \frac{3 e^{\alpha_- a}}{4}.$$

Next, thanks to a Taylor expansion, we have
$$\alpha_- = \frac{-c}{2(1+\varepsilon)} \left(1 - \sqrt{1 + \frac{4(1+\varepsilon)\mathcal{C}}{c^2}}\right) = \frac{-c}{2(1+\varepsilon)} \left(-\frac{2(1+\varepsilon)\mathcal{C}}{c^2} + o\left(\frac{1}{c^2}\right)\right) = \frac{\mathcal{C}}{c} + o\left(\frac{1}{|c|}\right)$$

so that there exists $c^2 = c^2(a) > 0$ such that for any $c \leq -c^2(a)$ we have $e^{\alpha_- a} > \frac{2}{3}$. As a result when $c \leq -\underline{c}(a) := -\max(c^1(a), c^2(a))$, we have
$$\sup\limits_{\Omega_0} (u + v) \geq m \geq \nu_0 > \nu,$$

which proves item 5. □

4.4 Proof of Theorem 4.1

Equipped with the above estimates, we are now in the position to prove Theorem 4.1 using three homotopies and the Leray Schauder topological degree. To do so, let us define the following open subset of $\mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$

$$\Gamma := \left\{ \left(c, \begin{pmatrix} u \\ v \end{pmatrix}\right) \in \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) : c \in (0, \bar{c}^\varepsilon + \varepsilon), \begin{pmatrix} 0 \\ 0 \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix} < \begin{pmatrix} C \\ C \end{pmatrix} \text{ in } \Omega \right\}$$

where $\Omega = (-a, a) \times \mathbb{R}$, and $C > 0$ is the constant defined in Lemma 4.3 item 2.

- We develop the first homotopy argument. For $0 \leq \tau \leq 1$, let us define the operator

$$F_\tau : \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \quad \rightarrow \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$$

where $F_\tau \left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) = \left(\tilde{c}, \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \right)$, with

$$\tilde{c} = c + \sup_{\Omega_0} (\tilde{u} + \tilde{v}) - \nu$$

and $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}$ is the unique solution in $\mathbf{C}^1_{per}(\Omega)$ of the linear problem

$$\begin{cases} L_\varepsilon \tilde{u} - c\tilde{u}_s &= u(r_u - \gamma_u(u + (\tau v + (1 - \tau)\frac{q}{K}))) + \mu v - \mu u \\ L_\varepsilon \tilde{v} - c\tilde{v}_s &= v(r_v - \gamma_v((\tau u + (1 - \tau)\frac{p}{K}) + v)) + \mu u - \mu v \\ (u, v)(-a, x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u, v)(a, x) = (0, 0), \quad \forall x \in \mathbb{R}. \end{cases}$$

From standard elliptic estimates, for any $0 \leq \tau \leq 1$, F_τ maps $\mathbf{C}^1_{per}(\Omega)$ into $\mathbf{C}^2_{per}(\overline{\Omega})$, which shows that F_τ is a compact operator in $\mathbf{C}^1_{per}(\Omega)$. Moreover F_τ depends continuously on the parameter $0 \leq \tau \leq 1$. The Leray-Schauder topological argument can thus be applied: in order to prove that the degree is independent of the parameter τ, it suffices to show that there is no fixed point of F_τ on the boundary $\partial \Gamma$, which will be a consequence of estimates in subsection 4.1. Indeed, let $\left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) = (c, u, v)$ be a fixed point of F_τ in $\overline{\Gamma}$.

1. From Lemma 4.3, Lemma 4.4 and Remark 4.5 we know that if $c = 0$ then $\sup_{\Omega_0} (u + v) > \nu$ so that $\tilde{c} > c$, which is absurd. That shows $c \neq 0$.

2. From Lemma 4.3 we know that if $c \geq \bar{c}^\varepsilon$ then $\sup_{\Omega_0} (u + v) < \nu$ so that $\tilde{c} < c$, which is absurd. That shows $c < \bar{c}^\varepsilon + \varepsilon$.

3. From Lemma 4.3 we know that $u < C$ and $v < C$.

4. From Lemma 4.3 and the boundary condition at $s = -a$, we know that $u > 0$ and $v > 0$ in $[-a, a) \times \mathbb{R}$. Moreover, we know from Hopf lemma that $\forall x \in \mathbb{R}$, $u_s(a, x) < 0$ and $v_s(a, x) < 0$.

As a result, $(c, u, v) \notin \partial \Gamma$ so that

$$\deg(Id - F_1, \Gamma, 0) = \deg(Id - F_0, \Gamma, 0). \tag{25}$$

- We now consider the second homotopy. For $0 \leq \tau \leq 1$, let us define the operator

$$G_\tau : \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \quad \rightarrow \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$$
$$\left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) \quad \mapsto \quad \left(\tilde{c}, \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \right)$$

with again

$$\tilde{c} = c + \sup_{\Omega_0} (\tilde{u} + \tilde{v}) - \nu$$

and $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}$ is the unique solutions in $\mathbf{C}^1_{per}(\Omega)$ of the linear problem

$$
\begin{cases}
L_\varepsilon \tilde{u} - c\tilde{u}_s + (1-\tau)\mathcal{C}\tilde{u} &= \tau \left(u \left(r_u - \gamma_u \frac{q}{K} - \mu - \gamma_u u \right) + \mu v \right) \\
L_\varepsilon \tilde{v} - c\tilde{v}_s + (1-\tau)\mathcal{C}\tilde{v} &= \tau \left(v \left(r_v - \gamma_v \frac{p}{K} - \mu - \gamma_v v \right) + \mu u \right) \\
(u,v)(-a,x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\
(u,v)(a,x) = (0,0), \quad \forall x \in \mathbb{R},
\end{cases}
$$

and $\mathcal{C}$ is defined by (24). Notice that G_τ is a continuous family of compact operators and that $G_1 = F_0$. From Lemma 4.3 and Lemma 4.6, we see that there is no fixed point of F_0 such that $c \leq 0$ since $c \mapsto \begin{pmatrix} u \\ v \end{pmatrix}$ is nonincreasing. As a result enlarging Γ into

$$
\tilde{\Gamma} := \left\{ \left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) \in \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) : c \in (-\underline{c}(a), \bar{c}^\varepsilon + \varepsilon), \begin{pmatrix} 0 \\ 0 \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix} < \begin{pmatrix} C \\ C \end{pmatrix} \text{ in } \Omega \right\},
$$

with $\underline{c}(a) \geq 0$ as in Lemma 4.7, does not alter the degree, that is

$$
\deg(Id - F_0, \Gamma, 0) = \deg(Id - F_0, \tilde{\Gamma}, 0) = \deg(Id - G_1, \tilde{\Gamma}, 0). \tag{26}
$$

Next, using the estimates of Lemma 4.7 and Hopf lemma as above, we see that there is no fixed point of G_τ on the boundary $\partial\tilde{\Gamma}$. We have then

$$
\deg(Id - G_1, \tilde{\Gamma}, 0) = \deg(Id - G_0, \tilde{\Gamma}, 0). \tag{27}
$$

Now G_0 is independent of (u,v). Since $L_\varepsilon - c\partial_s + \mathcal{C}Id$ is invertible for each $c \in \mathbb{R}$, there exists exactly one solution of (23) with $\tau = 0$ for each $c \in \mathbb{R}$, which we denote (u_c, v_c). Thanks to a sliding argument, which we omit here, the solutions to (23) with $\tau = 0$ are nonincreasing in s and $c \mapsto (u_c, v_c)$ is decreasing, so that there exists a unique $c \in (-\underline{c}(a), \bar{c}^\varepsilon + \varepsilon)$, which we denote c_0, such that (c_0, u_{c_0}, v_{c_0}) is a fixed point to G_0.

• Finally a third homotopy allows us to compute the degree. For $0 \leq \tau \leq 1$, let us define the operator $H_\tau : \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \to \mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$ by

$$
H_\tau(c, u, v) = \left(c + \sup_{\Omega_0} (u_c + v_c) - \nu, \tau u_c + (1-\tau)u_{c_0}, \tau v_c + (1-\tau)v_{c_0} \right).
$$

Noticing that $H_1 = G_0$ and that, again, H_τ has no fixed point on the boundary $\partial\tilde{\Gamma}$, we obtain

$$
\deg(Id - G_0, \tilde{\Gamma}, 0) = \deg(Id - H_1, \tilde{\Gamma}, 0) = \deg(Id - H_0, \tilde{\Gamma}, 0). \tag{28}
$$

Then since H_0 has separated variables and $c \mapsto \sup_{\Omega_0} (u_c + v_c)$ is decreasing, we see that

$$
\deg(Id - H_0, \tilde{\Gamma}, 0) = 1. \tag{29}
$$

• Combining (25), (26), (27), (28) and (29), we get $\deg(Id - F_1, \Gamma, 0) = 1$, which shows the existence of a solution to (15) in $\mathbf{C}^1_{per}(\Omega)$. Theorem 4.1 is proved. $\qquad \square$

5 Pulsating fronts

From the previous section, we are equipped with a solution to (15) in the strip $(-a, a) \times \mathbb{R}$. From the estimates of Theorem 4.1 and standard elliptic estimates, we can — up to a subsequence— let $a \to \infty$ and then recover, for any $0 < \varepsilon < 1$, a speed $0 < c = c^\varepsilon < \bar{c}^\varepsilon + \varepsilon$ and smooth profiles $(0,0) < (u(s,x), v(s,x)) = (u^\varepsilon(s,x), v^\varepsilon(s,x)) < (C, C)$ solving

$$\begin{cases} -u_{xx} - 2u_{xs} - (1+\varepsilon)u_{ss} - cu_s &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \mathbb{R}^2 \\ -v_{xx} - 2v_{xs} - (1+\varepsilon)v_{ss} - cv_s &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \mathbb{R}^2 \\ (u,v)(s, \cdot) \quad \text{is } L\text{-periodic} \\ \sup_{\Omega_0} (u+v) = \nu. \end{cases} \tag{30}$$

Let us mention again that, because of the lack of comparison, we do not know that the above solution is decreasing in s, in sharp contrast with the previous results on pulsating fronts [36], [8], [30], [10], [27], [28]. To overcome this lack of monotony, further estimates will be required.

Now, the main difficulty is to show that, letting $\varepsilon \to 0$, we recover a nonzero speed and thus a pulsating front. To do so, it is not convenient to use the (s, x) variables, and we therefore switch to functions

$$\tilde{u}(t, x) := u(x - ct, x), \quad \tilde{v}(t, x) := v(x - ct, x), \quad (t, x) \in \mathbb{R}^2,$$

which are consistent with Definition 2.5 of a pulsating front. Hence, after dropping the tildes, (30) is recast

$$\begin{cases} -\frac{\varepsilon}{c^2} u_{tt} - u_{xx} + u_t &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \mathbb{R}^2 \\ -\frac{\varepsilon}{c^2} v_{tt} - v_{xx} + v_t &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \mathbb{R}^2 \\ \sup_{x - ct \in (-a_0, a_0)} u(t,x) + v(t,x) = \nu. \end{cases} \tag{31}$$

Also the L periodicity for (30) is transferred into the constraint (6) for (31). Moreover, up to a translation, we can assume w.l.o.g. that the solution to (31) satisfies

$$\sup_{x \in (-a_0, a_0)} (u(0,x) + v(0,x)) = \nu. \tag{32}$$

Also, though t can be interpreted as a time, we would like to stress out that (31) is not a Cauchy problem.

Our first goal in this section is to let $\varepsilon \to 0$ in (31) and get the following.

Theorem 5.1 (Letting the regularization tend to zero)**.** *There exist a speed $0 < c \le \bar{c}^0 := \lim_{\varepsilon \to 0} \bar{c}^\varepsilon$ (see Lemma 4.2) and positive profiles (u, v) solving, in the classical sense,*

$$\begin{cases} u_t - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu(v - u) & \text{in } \mathbb{R}^2 \\ v_t - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu(u - v) & \text{in } \mathbb{R}^2, \end{cases} \tag{33}$$

satisfying the constraint (6) and, for some $a_0 > 0$, the normalization

$$\sup_{x - ct \in (-a_0, a_0)} (u + v) = \nu.$$

The present section is organized as follows. After proving further estimates on solutions to (31) in subsection 5.1, we prove Theorem 5.1 in subsection 5.2, the main difficulty being to exclude the possibility of a standing wave. Finally, in subsection 5.3 we conclude the construction of a pulsating front, thus proving our main result Theorem 2.6.

5.1 Lower estimates on solutions to (31)

We start by showing a uniform lower bound on the solutions to (31) that have a positive lower bound. The argument relies on the sign of the eigenvalue λ_1, or more precisely that of the first eigenvalue to the stationary Dirichlet problem in large bouded domains. For $b > 0$, we denote (λ_1^b, Φ^b) with $\Phi^b(x) := \begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}$ the unique eigenpair solving

$$\begin{cases} -\Phi_{xx}^b - A(x)\Phi^b = \lambda_1^b \Phi^b \\ \varphi^b(x) > 0, \ \psi^b(x) > 0, \quad x \in (-b, b) \\ \varphi^b(\pm b) = \psi^b(\pm b) = 0, \end{cases} \tag{34}$$

and $\|\Phi^b\|_{\mathbf{L}^\infty(-b,b)} = 1$. From Lemma C.1, we know that $\lambda_1^b \to \lambda_1 < 0$ when $b \to \infty$. We can thus select $a_1 > a_0^*$, with a_0^* as in Theorem 4.1, large enough so that

$$b \geq a_1 \Rightarrow \lambda_1^b \leq \frac{3\lambda_1}{4}. \tag{35}$$

Also, from Hopf lemma we have $C^b := \sup_{x \in (-b,b)} \left(\frac{\varphi^b(x)}{\psi^b(x)}, \frac{\psi^b(x)}{\varphi^b(x)} \right) < +\infty.$

Lemma 5.2 (A uniform lower estimate). *Let $(u(t,x), v(t,x))$ be a classical positive solution to*

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} = u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \mathbb{R}^2 \\ \beta v_t - \kappa v_{tt} - v_{xx} = v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \mathbb{R}^2, \end{cases} \tag{36}$$

with $\kappa \geq 0$ and $\beta \in \mathbb{R}$. Let also $b \geq a_1$ and Φ^b the solution to (34).
Then there exists a constant $\alpha_0 = \alpha_0(\mu^0, \gamma^\infty, \lambda_1^b, C^b) > 0$ such that if

$$\inf_{(t,x) \in \mathbb{R} \times (-b,b)} \min(u(t,x), v(t,x)) > 0$$

then

$$\forall (t,x) \in \mathbb{R} \times (-b,b), \quad \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha_0 \Phi^b(x).$$

Proof. Let $0 < \eta \leq 1$ be given. For $\alpha > 0$, we define

$$\begin{pmatrix} U^{\alpha,\eta}(t,x) \\ V^{\alpha,\eta}(t,x) \end{pmatrix} := \alpha(1 - \eta t^2) \begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}.$$

Then for small $\alpha < \min \left(\inf_{(t,x) \in \mathbb{R} \times (-b,b)} u, \inf_{(t,x) \in \mathbb{R} \times (-b,b)} v \right)$ we have $\begin{pmatrix} U^{\alpha,\eta}(t,x) \\ V^{\alpha,\eta}(t,x) \end{pmatrix} \leq \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix}$ for all $(t,x) \in \mathbb{R} \times (-b,b)$, whereas for large $\alpha > \frac{\max(u(0,0), v(0,0))}{\min(\varphi^b(0), \psi^b(0))}$ one has $\begin{pmatrix} U^{\alpha,\eta}(0,0) \\ V^{\alpha,\eta}(0,0) \end{pmatrix} > \begin{pmatrix} u(0,0) \\ v(0,0) \end{pmatrix}$. Thus we can define

$$\alpha_0^\eta = \alpha_0 := \sup \left\{ \alpha > 0, \forall (t,x) \in \mathbb{R} \times (-b,b), \begin{pmatrix} U^{\alpha,\eta}(t,x) \\ V^{\alpha,\eta}(t,x) \end{pmatrix} \leq \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \right\} > 0.$$

Assume by contradiction that

$$\alpha_0 \leq \alpha_0^* := \min\left(1, \frac{\mu^0}{2\gamma^\infty}, \frac{-\lambda_1^b}{2(1+2C^b)\gamma^\infty}\right).$$

There exists a touching point $(t_0, x_0) \in (-\sqrt{\eta}, \sqrt{\eta}) \times (-b, b)$ such that either $u(t_0, x_0) = U^{\alpha_0, \eta}(t_0, x_0)$ or $v(t_0, x_0) = V^{\alpha_0, \eta}(t_0, x_0)$. Assume $u(t_0, x_0) = U^{\alpha_0, \eta}(t_0, x_0)$ for instance. Then $u - U^{\alpha_0, \eta}$ reaches a zero minimum at (t_0, x_0) so that

$$
\begin{aligned}
0 &\geq \beta\,(u - U^{\alpha_0, \eta})_t - \kappa\,(u - U^{\alpha_0, \eta})_{tt} - (u - U^{\alpha_0, \eta})_{xx} \\
&= (\beta u_t - \kappa u_{tt} - u_{xx}) + \alpha_0(1 - \eta t_0^2)\varphi_{xx}^b + 2\alpha_0\beta\eta t_0\varphi^b - 2\alpha_0\kappa\eta\varphi^b
\end{aligned}
$$

at point (t_0, x_0). Using (34) and (36) yields

$$0 \geq u(r_u - \mu - \gamma_u(u + v)) + \mu v - \alpha_0(1 - \eta t_0^2)(\varphi^b(r_u - \mu + \lambda_1^b) + \mu\psi^b) + 2\alpha_0\eta\varphi^b(\beta t_0 - \kappa)$$

at point (t_0, x_0), and since $u(t_0, x_0) = \alpha_0(1 - \eta t_0^2)\varphi^b(x_0)$ we end up with

$$0 \geq u_0[-\lambda_1^b - \gamma_u(x_0)(u_0 + v_0)] + \mu(x_0)[v_0 - \alpha_0(1 - \eta t_0^2)\psi^b(x_0)] + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa), \quad (37)$$

with the notations $u_0 = u(t_0, x_0)$, $v_0 = v(t_0, x_0)$. Now two cases may occur.

• Assume first that $v_0 \leq 2\alpha_0(1 - \eta t_0^2)\psi^b(x_0)$. Then we have

$$v_0 \leq 2\alpha_0(1 - \eta t_0^2)\frac{\psi^b(x_0)}{\varphi^b(x_0)}\varphi^b(x_0) \leq 2C^b u_0,$$

and since $v_0 - \alpha_0(1 - \eta t_0^2)\psi^b(x_0) \geq 0$, we deduce from (37) that

$$\gamma_u(x_0)(1 + 2C^b)u_0^2 \geq -\lambda_1^b u_0 + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa),$$

which in turn implies

$$\gamma^\infty(1 + 2C^b)\alpha_0 \geq \gamma_u(x_0)(1 + 2C^b)u_0 \geq -\lambda_1^b + \frac{2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa)}{u_0} \geq -\lambda_1^b - \frac{2\eta}{\inf u}(|\beta||t_0| + \kappa),$$

since $\alpha_0 \leq 1$ and $\varphi^b \leq 1$. Since $|t_0| \leq \frac{1}{\sqrt{\eta}}$, one then has

$$\alpha_0 \geq \frac{-\lambda_1^b}{(1 + 2C^b)\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta| + \kappa}{(1 + 2C^b)\gamma^\infty \inf u}. \quad (38)$$

• On the other hand, assume $v_0 \geq 2\alpha_0(1 - \eta t_0^2)\psi^b(x_0)$. Then we deduce from (37) that

$$
\begin{aligned}
\gamma_u(x_0)u_0^2 &\geq -\lambda_1^b u_0 + \frac{\mu(x_0)}{2}(v_0 - 2\alpha_0(1 - \eta t_0^2)\psi^b(x_0)) + v_0\left(\frac{\mu(x_0)}{2} - \gamma_u(x_0)u_0\right) \\
&\quad + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa) \\
&\geq -\lambda_1^b u_0 + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa),
\end{aligned}
$$

since $\gamma_u u \leq \gamma_u \alpha_0^* \leq \frac{\mu^0}{2}$. Arguing as in the first case, we end up with

$$\alpha_0 \geq \frac{-\lambda_1^b}{\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta| + \kappa}{\gamma^\infty \inf u}. \quad (39)$$

From (38) , (39) and the symmetric situation where $v(t_0, x_0) = V^{\alpha_0, \eta}(t_0, x_0)$, we deduce that, in any case,

$$\alpha_0 \geq \frac{-\lambda_1^b}{(1 + 2C^b)\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta| + \kappa}{\gamma^\infty \inf(u, v)}. \tag{40}$$

One sees that for

$$0 < \eta < \eta^* := \min\left(1, \left(\frac{-\lambda_1^b \inf(u, v)}{4(|\beta| + \kappa)(1 + 2C^b)}\right)^2\right),$$

inequality (40) is a contradiction since it implies $\alpha_0 > \alpha_0^*$. Hence we have shown that for any $0 < \eta < \eta^*$ one has $\alpha_0 = \alpha_0^\eta > \alpha_0^*$. In particular

$$\forall \eta \in (0, \eta^*), \forall (t, x) \in \mathbb{R} \times (-b, b), \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} \geq \alpha_0^*(1 - \eta t^2)\begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}.$$

Taking the limit $\eta \to 0$, we then obtain

$$\forall (t, x) \in \mathbb{R} \times (-b, b), \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} \geq \alpha_0^* \Phi^b(x),$$

which concludes the proof of Lemma 5.2. $\qquad\square$

Next we establish a forward-in-time lower estimate for solutions of the (possibly degenerate) problem (41). The proof is based on the same idea as in Lemma 5.2, but it is here critical that the coefficient β of the time-derivative has the right sign. Roughly speaking, the following lemma asserts that once a population has reached a certain threshold on a large enough set, it cannot fall under that threshold at a later time.

Lemma 5.3 (A forward-in-time lower estimate). *Let $(u(t, x), v(t, x))$ be a classical positive solution to*

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} &= u(r_u - \gamma_u(u + v)) + \mu v - \mu u \quad in\ \mathbb{R}^2 \\ \beta v_t - \kappa v_{tt} - v_{xx} &= v(r_v - \gamma_v(u + v)) + \mu u - \mu v \quad in\ \mathbb{R}^2, \end{cases} \tag{41}$$

with $\kappa \geq 0$ and $\beta \geq 0$. Let also $b \geq a_1$ and Φ^b the solution to (34).
Then there exists a constant $\alpha_0 = \alpha_0(\mu^0, \gamma^\infty, \lambda_1^b, C^b) > 0$ such that if $0 < \alpha < \alpha_0$ and

$$\forall x \in (-b, b),\ \alpha\Phi^b(x) < \begin{pmatrix} u(0, x) \\ v(0, x) \end{pmatrix}, \tag{42}$$

then

$$\forall t > 0, \forall x \in (-b, b),\ \alpha\Phi^b(x) \leq \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix}.$$

Proof. Let

$$0 < \alpha < \alpha_0 := \min\left(1, \frac{-\lambda_1^b}{2(1 + 2C^b)\gamma^\infty}, \frac{\mu^0}{2\gamma^\infty}\right)$$

and assume (42). For $\eta > 0$ we define

$$\zeta(t, x) = \begin{pmatrix} \zeta_u(t, x) \\ \zeta_v(t, x) \end{pmatrix} := \alpha(1 - \eta t)\begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}.$$

From (42), we can define

$$\eta_0 := \inf \left\{ \eta \in \mathbb{R} : \forall t \geq 0, \forall x \in [-b, b], \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} \geq \zeta(t, x) \right\}.$$

Assume by contradiction that $\eta_0 > 0$. Then there exists $t_0 > 0$ and $x_0 \in (-b, b)$ such that, say, $u(t_0, x_0) = \zeta_u(t_0, x_0)$. Then at point (t_0, x_0) we have

$$0 \geq \beta(u - \zeta_u)_t - \kappa(u - \zeta_u)_{tt} - (u - \zeta_u)_{xx} = u(r_u - \gamma_u(u + v)) + \mu(v - u) + \zeta_{u_{xx}} + \beta\alpha\eta\varphi^b.$$

Using (34) and $u(t_0, x_0) = \alpha(1 - \eta_0 t_0)\varphi^b(x_0)$, we end up with

$$0 \geq u_0(-\lambda_1^b - \gamma_u(x_0)(u_0 + v_0)) + \mu(x_0)(v_0 - \zeta_v(t_0, x_0)), \tag{43}$$

with the notations $u_0 = u(t_0, x_0)$, $v_0 = v(t_0, x_0)$ and thanks to $\beta \geq 0$. Now two cases may occur.

- Assume first that $v_0 \leq 2\zeta_v(t_0, x_0)$. Then $v_0 \leq 2\frac{\zeta_v(t_0, x_0)}{\zeta_u(t_0, x_0)}\zeta_u(t_0, x_0) \leq 2C^b\zeta_u(t_0, x_0) = 2C^b u_0$, so that (43) yields (recall that $v_0 \geq \zeta_v(t_0, x_0)$)

$$\gamma_u(x_0)(1 + 2C^b)u_0^2 \geq \gamma_u(x_0)(u_0 + v_0)u_0 \geq -\lambda_1^b u_0.$$

As a result $u_0 > \alpha_0$, which is a contradiction.

- Assume now that $v_0 \geq 2\zeta_v(t_0, x_0)$. Then we deduce from (43) that

$$\gamma_u(x_0)u_0^2 \geq -\lambda_1^b u_0 + v_0\left(\frac{\mu(x_0)}{2} - \gamma_u(x_0)u_0\right) + \frac{\mu(x_0)}{2}(v_0 - 2\zeta_v(t_0, x_0))$$

$$\geq -\lambda_1^b u_0 + \frac{1}{2}\mu(x_0)(v_0 - 2\zeta_v(t_0, x_0)),$$

since $u_0 \leq \alpha_0 \leq \frac{\mu^0}{2\gamma^\infty}$. As a result $u_0 \geq \frac{-\lambda_1^b}{\gamma^\infty} > \alpha_0$, which is also a contradiction.

Thus $\eta_0 \leq 0$ and in particular

$$\forall t > 0, \forall x \in (-b, b), \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} \geq \alpha \begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix},$$

which concludes the proof of Lemma 5.3. $\qquad\qquad\square$

5.2 Proof of Theorem 5.1

In this subsection, we prove that a well-chosen series of solutions to equation (31) cannot converge, as $\varepsilon \to 0$, to a standing wave ($c = 0$). In other words, we prove Theorem 5.1, making a straightforward use of the crucial Lemma 5.4. The rough idea of the proof of Lemma 5.4 is that a standing wave cannot stay in the neighborhood of 0 for a long time. Hence the normalization allows us to prevent a sequence of solutions from converging to a standing wave, provided ν is chosen small enough. Notice also that the interior gradient estimate for elliptic systems of Lemma B.1 will be used.

In the sequel we select $a_1 > a_0^*$ as in (35), recall that $\lambda_1^{a_1}$ denotes the eigenvalue of problem (34) in the domain $(-a_1, a_1)$, and define

$$\nu^* := \frac{1}{2}\min(\nu_0, \underline{\nu}) > 0,$$

where $\underline{\nu} := \alpha_0 \inf_{x \in (-a_0^*, a_0^*)} \min(\varphi^{a_1}(x), \psi^{a_1}(x))$, with $\alpha_0 > 0$ the constant in Lemma 5.2 in the domain $(-a_1, a_1)$.

Lemma 5.4 (Nonzero limit speed). *Let $(\varepsilon_n, c_n, u^n(t,x), v^n(t,x))$ be a sequence such that $\varepsilon_n > 0$, $\varepsilon_n \to 0$, $c_n \neq 0$, (u^n, v^n) is a positive solution to problem (31) with $\varepsilon = \varepsilon_n$, $c = c_n$, $0 < \nu < \nu^*$ and $a_0 > a_1$. Then*

$$\liminf_{n \to \infty} c_n > 0. \tag{44}$$

Proof. Assume by contradiction that there is a sequence as in Lemma 5.4 with $\lim c_n = 0$. Define the sequence $\kappa_n := \frac{\varepsilon_n}{c_n^2} > 0$ which, up to an extraction, tends to $+\infty$, or to some $\kappa \in (0, +\infty)$ or to 0. In each case we are going to construct a couple of functions (u, v) that shows a contradiction. We refer to [8] or to [10] for a similar trichotomy.

Case 1: $\kappa_n \to +\infty$. Defining $(\tilde{u}^n, \tilde{v}^n)(t,x) := (u^n, v^n)(\sqrt{\kappa_n} t, x)$, problem (31) is recast

$$\begin{cases} -u^n_{tt} - u^n_{xx} + \frac{1}{\sqrt{\kappa_n}} u^n_t &= u^n(r_u - \gamma_u(u^n + v^n)) + \mu v^n - \mu u^n \\ -v^n_{tt} - v^n_{xx} + \frac{1}{\sqrt{\kappa_n}} v^n_t &= v^n(r_v - \gamma_v(u^n + v^n)) + \mu u^n - \mu v^n \\ \sup_{x - \sqrt{\varepsilon_n} t \in (-a_0, a_0)} u^n(t,x) + v^n(t,x) = \nu, \end{cases} \tag{45}$$

where we have dropped the tildes. From standard elliptic estimates, this sequence converges, up to an extraction, to a classical nonnegative solution (u, v) of

$$\begin{cases} -u_{tt} - u_{xx} &= u(r_u - \gamma_u(u + v)) + \mu v - \mu u \\ -v_{tt} - v_{xx} &= v(r_v - \gamma_v(u + v)) + \mu u - \mu v, \end{cases} \tag{46}$$

and since (u^n, v^n) satisfies the third equality in (45) together with (32), (u, v) satisfies $\sup_{(t,x) \in \mathbb{R} \times (-a_0, a_0)} (u + v) = \nu$. In particular, (u, v) is nontrivial and thus positive by the strong maximum principle.

Now, applying Lemma 5.3 to (u, v) with $\alpha := \frac{1}{2} \min \left(\inf_{x \in (-a_0, a_0)} (u(0,x), v(0,x)), \alpha_0 \right) > 0$, we get

$$\forall t > 0, \forall x \in (-a_0, a_0), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \Phi^{a_0}(x).$$

Next, thanks to standard elliptic estimates, the sequence

$$(u^n(t,x), v^n(t,x)) := (u(t + n, x), v(t + n, x))$$

converges, up to an extraction, to a solution (u, v) of (46) — that we denote again by (u, v) — which satisfies

$$\sup_{(t,x) \in \mathbb{R} \times (-a_0, a_0)} (u + v) = \nu, \tag{47}$$

and

$$\forall (t,x) \in \mathbb{R} \times (-a_0, a_0), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \Phi^{a_0}(x).$$

In particular, since $a_0 > a_1$, the latter implies

$$\inf_{(t,x) \in \mathbb{R} \times (-a_1, a_1)} \min(u, v) > 0. \tag{48}$$

Case 2: $\kappa_n \to \kappa \in (0, +\infty)$. Thanks to standard elliptic estimates, the sequence (u^n, v^n) converges, up to an extraction, to a solution (u, v) of

$$\begin{cases} -\kappa u_{tt} - u_{xx} + u_t &= u(r_u - \gamma_u(u + v)) + \mu v - \mu u \\ -\kappa v_{tt} - v_{xx} + v_t &= v(r_v - \gamma_v(u + v)) + \mu u - \mu v, \end{cases} \tag{49}$$

and since (u^n, v^n) satisfies the third equality in (31) together with (32), (u, v) satisfies $\sup\limits_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u + v) = \nu$. In particular, (u, v) is nontrivial and thus positive by the strong maximum principle.

Now, using Lemma 5.3 and a positive large shift in time exactly as in Case 1, we end up with a solution (u, v) to (49) which satisfies (47) and (48).

Case 3: $\kappa_n \to 0$. In this case, the elliptic operator becomes degenerate as $n \to \infty$, so that we cannot use the standard elliptic theory. The idea is then to use a Bernstein interior gradient estimate for elliptic systems that we present and prove in Appendix B.

Applying Lemma B.1 to the series (u^n, v^n) solving (31), we get a uniform L^∞ bound for (u_x^n, v_x^n). Furthermore by differentiating (31) with respect to x, we see that (u_x^n, v_x^n) solves a system for which Lemma B.1 still applies. As a result, we get a uniform L^∞ bound for (u_{xx}^n, v_{xx}^n).

Let us show that there is also a uniform L^∞ bound for (u_t^n, v_t^n). From the uniform bounds found above, we can write

$$u_t^n - \kappa_n u_{tt}^n = F^n(t, x).$$

Let $F := \max(1, \sup_n \|F^n\|_{L^\infty(\mathbb{R}^2)}) < +\infty$. Assume by contradiction that there is a point (t_0, x_0) where $u_t^n(t_0, x_0) > 2F$. From the above equation we deduce that $u_t^n(t, x_0) > 2F$ remains valid for $t \geq t_0$, and thus

$$\kappa_n u_{tt}^n(t, x_0) > F, \quad \forall t \geq t_0.$$

Integrating twice, we get

$$u^n(t, x_0) \geq F\left(2(t - t_0) + \frac{1}{2\kappa_n}(t - t_0)^2\right) - \|u^n\|_{L^\infty}, \quad \forall t \geq t_0.$$

Letting $t \to \infty$ we get that u^n is unbounded, a contradiction. Thus, $u_t^n(t, x) \leq 2F$ for any $(t, x) \in \mathbb{R}^2$ and, in a straightforward way, $|u_t^n(t, x)|, |v_t^n(t, x)| \leq 2F$ for any $(t, x) \in \mathbb{R}^2$.

Since we have uniform L^∞ bounds for (u^n, v^n), (u_x^n, v_x^n) and (u_t^n, v_t^n), there are u and v in $H_{loc}^1(\mathbb{R}^2)$ such that, up to a subsequence,

$$(u^n, v^n) \to (u, v) \text{ in } L_{loc}^\infty(\mathbb{R}^2), \quad (u_x^n, v_x^n, u_t^n, v_t^n) \rightharpoonup (u_x, v_x, u_t, v_t) \text{ in } L_{loc}^2(\mathbb{R}^2) \text{ weak}.$$

As a result, letting $n \to \infty$ into (31) yields

$$\begin{cases} u_t - u_{xx} &= u(r_u - \gamma_u(u + v)) + \mu v - \mu u \\ v_t - v_{xx} &= v(r_v - \gamma_v(u + v)) + \mu u - \mu v \end{cases} \tag{50}$$

in a weak sense. From parabolic regularity, (u, v) is actually a classical solution to (50). Since the convergence occurs locally uniformly (32) and since (u^n, v^n) satisfies the third equality in (31) together with (32), (u, v) satisfies $\sup\limits_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u + v) = \nu$. In particular, (u, v) is nontrivial and thus positive by the strong maximum principle.

Now, using Lemma 5.3 and a positive large shift in time as in Case 1 (parabolic estimates replacing elliptic estimates), we end up with a solution (u, v) to (50) which satisfies (47) and (48).

Conclusion. In any of the three above cases, we have constructed a classical solution (u, v) to $(\beta \geq 0, \kappa \geq 0)$

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} &= u(r_u - \gamma_u(u + v)) + \mu v - \mu u \\ \beta v_t - \kappa v_{tt} - v_{xx} &= v(r_v - \gamma_v(u + v)) + \mu u - \mu v, \end{cases}$$

which satisfies (47) and (48). Applying Lemma 5.2, we find that (recall that $a_1 > a_0^*$)

$$\inf_{\mathbb{R} \times (-a_0^*, a_0^*)} (u, v) \geq \alpha_0 \inf_{(-a_0^*, a_0^*)} (\varphi^{a_1}, \psi^{a_1}) = \underline{\nu}.$$

But, since $a_0 > a_0^*$ the above implies

$$\sup_{\mathbb{R} \times (-a_0, a_0)} (u + v) \geq 2 \inf_{\mathbb{R} \times (-a_0^*, a_0^*)} (u, v) \geq 2\underline{\nu} > \nu^* > \nu,$$

which contradicts (47). Lemma 5.4 is proved. $\qquad\square$

We are now in the position to prove Theorem 5.1.

Proof of Theorem 5.1. From the beginning of Section 5 and Lemma 5.4 we can consider a sequence $(\varepsilon_n, c_n, u^n(t, x), v^n(t, x))$ such that $\varepsilon_n > 0$, $\varepsilon_n \to 0$, $0 < c_n \leq \bar{c}^{\varepsilon_n} + \varepsilon_n$, (u^n, v^n) is a positive solution to problem (31) with $\varepsilon = \varepsilon_n$, $c = c_n$, $\nu < \nu^*$ and $a_0 > a_1$, satisfying the constraint (6), and the crucial fact

$$\lim_{n \to \infty} c_n > 0. \tag{51}$$

Notice that, as a by-product, this shows that $\bar{c}^0 := \lim_{\varepsilon \to 0} \bar{c}^\varepsilon > 0$ (see Lemma 4.2). We can now repeat the argument in the proof of Lemma 5.4 Case 3 and extract a sequence (u^n, v^n) which converges to a classical solution (u, v) of equation (33), satisfying the normalization

$$\sup_{x - ct \in (-a_0, a_0)} (u + v) = \nu$$

as well as the constraint (6). Theorem 5.1 is proved. $\qquad\square$

5.3 Proof of Theorem 2.6

We are now close to conclude the proof of our main result of construction of a pulsating front, Theorem 2.6. From Theorem 5.1, it only remains to prove the boundary conditions (7), namely

$$\liminf_{t \to +\infty} \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \lim_{t \to -\infty} \begin{pmatrix} u(t, x) \\ v(t, x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \text{locally uniformly w.r.t. } x,$$

to match Definition 2.5 of a pulsating front. The former is derived by another straighforward application of Lemma 5.3, while the latter is proved below. Hence, Theorem 2.6 is proved. $\qquad\square$

Lemma 5.5 (Zero limit behavior). *For $a_1 > a_0^*$ and $\nu^* > 0$ as in subsection 5.2, let $c > 0$ and (u, v) be as in Theorem 5.1, satisfying in particular the normalization* $\displaystyle\sup_{x - ct \in (-a_0, a_0)} (u + v) = \nu$ *with $\nu < \nu^*$ and $a_0 > a_1$. Then*

$$\lim_{t \to -\infty} \max(u, v)(t, x) \to 0, \quad \text{locally uniformly w.r.t. } x.$$

Proof. We first claim that $\displaystyle\inf_{\mathbb{R}\times(-a_0,a_0)}\min(u,v) = 0$. Indeed if this is not the case then, in particular, $\displaystyle\inf_{\mathbb{R}\times(-a_1,a_1)}\min(u,v) > 0$, and we derive a contradiction via Lemma 5.2 by a straightforward adaptation of the Conclusion of the proof of Lemma 5.4, because $\mathbb{R}\times(-a_1,a_1)$ intersects $\{(t,x) : x - ct \in (-a_0,a_0)\}$.

Now let $a > a_0$ be given and assume by contradiction that there is $m > 0$ and a sequence $t_n \to -\infty$ such that $\displaystyle\sup_{x\in(-a,a)}\max(u,v)(t_n,x) \geq m$. Thanks to the Harnack inequality for parabolic systems, see [23, Theorem 3.9], there is $C > 0$ such that

$$\forall n \in \mathbb{N}, \quad \inf_{x\in(-a,a)}\min(u,v)(t_n+1,x) \geq \frac{1}{C}\sup_{x\in(-a,a)}\max(u+v)(t_n,x) \geq \frac{m}{C}.$$

We now use our forward-in-time lower estimate, see Lemma 5.3, in $(-a,a)$ and with $\alpha := \frac{1}{2}\min(\alpha_0, \frac{m}{C}) > 0$ to get

$$\forall n \in \mathbb{N}, \ \forall t > t_n + 1, \ \forall x \in (-a,a), \quad \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \begin{pmatrix} \varphi^a(x) \\ \psi^a(x) \end{pmatrix}.$$

Since $t_n \to -\infty$ and $a > a_0$, the above implies

$$\inf_{(t,x)\in\mathbb{R}\times(-a_0,a_0)}\min(u,v)(t,x) \geq \alpha \inf_{x\in(-a_0,a_0)}(\varphi^a,\psi^a)(x) > 0.$$

This is a contradiction and the lemma is proved. $\qquad\square$

A   Topological theorems

Let us first recall the classical Krein-Rutman theorem.

Theorem A.1 (Krein-Rutman theorem)**.** *Let E be a Banach space. Let $C \subset E$ be a closed convex cone of vertex 0, such that $C \cap -C = \{0\}$ and $Int\,C \neq \varnothing$. Let $T : E \to E$ be a linear compact operator such that $T(C\backslash\{0\}) \subset Int\,C$.*

Then, there exists $u \in Int\,C$ and $\lambda_1 > 0$ such that $Tu = \lambda_1 u$. Moreover, if $Tv = \mu v$ for some $v \in C\backslash\{0\}$, then $\mu = \lambda_1$. Finally, we have

$$\lambda_1 = \max\{|\mu|, \mu \in \sigma(T)\},$$

and the algebraic and geometric multiplicity of λ_1 are both equal to 1.

We now quote some results on the structure of the solution set for nonlinear eigenvalue problems in a Banach space, more specifically when bifurcation occurs. For more details and proofs, we refer the reader to the works of Rabinowitz [34, 35], Crandall and Rabinowitz [18]. See also earlier related results of Krasnosel'skii [32] and the book of Brown [16].

Theorem A.2 (Bifurcation from eigenvalues of odd multiplicity)**.** *Let E be a Banach space. Let $F : \mathbb{R} \times E \to E$ be a (possibly nonlinear) compact operator such that*

$$\forall \lambda \in \mathbb{R}, \ F(\lambda, 0) = 0.$$

Assume that F is Fréchet differentiable near $(\lambda, 0)$ with derivative λT. Let us define

$$\mathcal{S} := \overline{\{(\lambda, x) \in \mathbb{R} \times E \backslash \{0\} : F(\lambda, x) = x\}}.$$

Let us assume that $\frac{1}{\mu} \in \sigma(T)$ is of odd multiplicity.

Then there exists a maximal connex compound $\mathcal{C}_\mu \subset \mathcal{S}$ such that $(\mu, 0) \in \mathcal{C}_\mu$ and either

1. *$\mathcal{C}_\mu$ is not bounded in $\mathbb{R} \times E$, or*

2. *there exists $\mu^* \neq \mu$ with $\frac{1}{\mu^*} \in \sigma(T)$ and $(\mu^*, 0) \in \mathcal{C}_\mu$.*

When the eigenvalue is simple, one can actually refine the above result as follows.

Theorem A.3 (Bifurcation from simple eigenvalues)**.** *Let the assumptions of Theorem A.2 hold. Assume further that $\frac{1}{\mu} \in \sigma(T)$ is simple. Let T^* be the dual of T, and $l \in E'$ an eigenvector of T^* associated with $\frac{1}{\mu}$ with $\|l\| = 1$ (recall that $\frac{1}{\mu}$ is of multiplicity 1 for both T and T^*). Let us define*

$$K_{\xi, \eta}^+ := \{(\lambda, u) \in \mathbb{R} \times E, |\lambda - \mu| < \xi, \langle l, u \rangle > \eta \|u\|\}, \quad K_{\xi, \eta}^- := -K_{\xi, \eta}^+.$$

Then $\mathcal{C}_\mu \backslash \{(\mu, 0)\}$ contains two connex compounds $\mathcal{C}_\mu^+$ and $\mathcal{C}_\mu^-$ which satisfy

$$\forall \nu \in \{+, -\}, \forall \xi > 0, \forall \eta \in (0, 1), \exists \zeta_0 > 0, \forall \zeta \in (0, \zeta_0), (\mathcal{C}_\mu^\nu \cap B_\zeta) \subset K_{\xi, \eta}^\nu,$$

where $B_\zeta := \{(\lambda, u) \in \mathbb{R} \times E, |\lambda - \mu| < \zeta, \|u\| < \zeta\}$ is the ball of center $(\mu, 0)$ and radius ζ. Moreover, both $\mathcal{C}_\mu^+$ and $\mathcal{C}_\mu^-$ satisfies the alternative in Theorem A.2.

B   A Bernstein-type interior gradient estimate for elliptic systems

We present here some L^∞ gradient estimates for regularizations of degenerate elliptic systems, which are uniform with respect to the regularization parameter $\kappa \geq 0$. The result below generalizes the result of Berestycki and Hamel [9], which is concerned with scalar equations.

Lemma B.1 (Interior gradient estimates)**.** *Let Ω be an open subset of $\mathbb{R}^2$. Let $f, g : \Omega \times \mathbb{R}^2 \to \mathbb{R}$ be two C^1 functions with bounded derivatives. Let $0 \leq \kappa \leq 1$ and $(u(y, x), v(y, x))$ be a solution of the class C^3 of the system*

$$\begin{cases} -\kappa u_{yy} - u_{xx} + u_y &= f(y, x, u, v) \quad &\text{in } \Omega, \\ -\kappa v_{yy} - v_{xx} + v_y &= g(y, x, u, v) \quad &\text{in } \Omega. \end{cases} \tag{52}$$

Then, for all $(y, x) \in \Omega$,

$$|u_x(y, x)|^2 + |v_x(y, x)|^2 + \kappa |u_y(y, x)|^2 + \kappa |v_y(y, x)|^2 \leq C \left(1 + \frac{1}{(dist((y, x), \partial\Omega))^2} \right)$$

where

$$C = C(\|u\|_{L^\infty(B)} + \|v\|_{L^\infty(B)}, osc_B u, osc_B v, \|f\|_{C^{0,1}(B \times [\underline{u}, \overline{u}] \times [\underline{v}, \overline{v}])}, \|g\|_{C^{0,1}(B \times [\underline{u}, \overline{u}] \times [\underline{v}, \overline{v}])}),$$

with B the ball of center (y, x) and radius $\frac{dist((y,x), \partial\Omega)}{2}$ in $\mathbb{R}^2$, $\underline{u} := \inf_B u$, $\overline{u} := \sup_B u$, $\underline{v} := \inf_B v$, $\overline{v} := \sup_B v$. In particular, this estimate is independent on the regularization parameter $0 \leq \kappa \leq 1$.

Proof. Let h be the smooth function defined on $\mathbb{R}$ by

$$h(z) := \begin{cases} \exp\left(\frac{z^2}{z^2-1}\right) & |z| < 1 \\ 0 & |z| \geq 1. \end{cases}$$

Let us then define $C_0 := \max(\|h\|_{L^\infty}, \|h'\|_{L^\infty}, \|h''\|_{L^\infty})$ and $\zeta(Y, X) := h\left(\frac{\sqrt{Y^2+X^2}}{2}\right)$.

Let $(y_0, x_0) \in \Omega$ be a given point, $d_0 := dist((y_0, x_0), \partial\Omega)$, $d := \min\left(\frac{d_0}{2}, 1\right)$, B_0 the ball of center (y_0, x_0) and radius d. Let χ be the function defined by

$$\forall (y, x) \in \mathbb{R}^2, \quad \chi(y, x) := \zeta\left(\frac{y - y_0}{d}, \frac{x - x_0}{d}\right).$$

Finally, let P^u and P^v be defined in Ω by

$$\begin{aligned}
P^u(y, x) &:= \chi^2(y, x)(u_x^2(y, x) + \kappa u_y^2(y, x)) + \lambda u^2(y, x) + \rho e^{x-x_0} \\
P^v(y, x) &:= \chi^2(y, x)(v_x^2(y, x) + \kappa v_y^2(y, x)) + \lambda v^2(y, x) + \rho e^{x-x_0},
\end{aligned}$$

where $\lambda > 0$ and $\rho > 0$ are constants to be fixed later. Our goal is to apply the maximum principle to the function $P := P^u + P^v$ for convenient values of λ and ρ. We present below the computations on P^u only and reflect them on P^v.

We first compute the partial derivatives of P^u and get

$$\begin{aligned}
P_y^u &= 2\chi_y\chi u_x^2 + 2\chi^2 u_{xy}u_x + 2\kappa(\chi_y\chi u_y^2 + \chi^2 u_{yy}u_y) + 2\lambda u_y u \\
P_{yy}^u &= 2(\chi_{yy}\chi + \chi_y^2)u_x^2 + 8\chi_y\chi u_{xy}u_x + 2\chi^2(u_{xyy}u_x + u_{xy}^2) \\
&\quad + \kappa[2(\chi_{yy}\chi + \chi_y^2)u_y^2 + 8\chi_y\chi u_{yy}u_y + 2\chi^2(u_{yyy}u_y + u_{yy}^2)] \\
&\quad + 2\lambda(u_{yy}u + u_y^2) \\
P_{xx}^u &= 2(\chi_{xx}\chi + \chi_x^2)u_x^2 + 8\chi_x\chi u_{xx}u_x + 2\chi^2(u_{xxx}u_x + u_{xx}^2) \\
&\quad \kappa[2(\chi_{xx}\chi + \chi_x^2)u_y^2 + 8\chi_x\chi u_{xy}u_y + 2\chi^2(u_{yxx}u_y + u_{yx}^2)] \\
&\quad + 2\lambda(u_{xx}u + u_x^2) + \rho e^{x-x_0}.
\end{aligned}$$

Let $M := \partial_y - \kappa\partial_{yy} - \partial_{xx}$. Then we have

$$\begin{aligned}
MP^u &= 2\left[\chi_y\chi - \kappa(\chi_{yy}\chi + \chi_y^2) - (\chi_{xx}\chi + \chi_x^2)\right]u_x^2 \\
&\quad + 2\kappa\left[\chi_y\chi - \kappa(\chi_{yy}\chi + \chi_y^2) - (\chi_{xx}\chi + \chi_x^2)\right]u_y^2 \\
&\quad + 2\chi^2\left[u_{xy} - \kappa u_{xyy} - u_{xxx}\right]u_x \\
&\quad + 2\kappa\chi^2\left[u_{yy} - \kappa u_{yyy} - u_{yxx}\right]u_y \\
&\quad - 2\left[\kappa(\chi^2 u_{xy}^2 + 4\chi_y\chi u_{xy}u_x) + (\chi^2 u_{xx}^2 + 4\chi_x\chi u_{xx}u_x)\right] \\
&\quad - 2\kappa[\kappa(4\chi_y\chi u_y u_{yy} + \chi^2 u_{yy}^2) + (4\chi_x\chi u_y u_{xy} + \chi^2 u_{xy}^2)] \\
&\quad + 2\lambda\left[(u_y - \kappa u_{yy} - u_{xx})u - \kappa u_y^2 - u_x^2\right] \\
&\quad - \rho e^{x-x_0}.
\end{aligned}$$

We now reformulate some of the lines of the above equality, starting with lines three and four. We differentiate the first equation of system (52) with respect to x to obtain

$$\begin{aligned}
2\chi^2\left[u_{xy} - \kappa u_{xyy} - u_{xxx}\right]u_x &= 2\chi^2(f_x + u_x f_u + v_x f_v)u_x \\
&\leq \chi^2(u_x^2 + f_x^2) + 2\chi^2 u_x^2|f_u| + \chi^2(u_x^2 + v_x^2)|f_v|,
\end{aligned}$$

and then with respect to y to get

$$
\begin{aligned}
2\chi^2\left[u_{yy} - \kappa u_{yyy} - u_{yxx}\right]u_y & = 2\chi^2(f_y + u_y f_u + v_y f_v)u_y \\
& \leq \chi^2(u_y^2 + f_y^2) + 2\chi^2 u_y^2|f_u| + \chi^2(u_y^2 + v_y^2)|f_v|.
\end{aligned}
$$

As far as lines five and six are concerned, we use the factorizations

$$
\begin{aligned}
\chi^2 u_{xy}^2 + 4\chi_y \chi u_{xy} u_x & = (\chi u_{xy} + 2\chi_y u_x)^2 - 4\chi_y^2 u_x^2 \\
\chi^2 u_{xx}^2 + 4\chi_x \chi u_{xx} u_x & = (\chi u_{xx} + 2\chi_x u_x)^2 - 4\chi_x^2 u_x^2 \\
\chi^2 u_{yy}^2 + 4\chi_y \chi u_{yy} u_y & = (\chi u_{yy} + 2\chi_y u_y)^2 - 4\chi_y^2 u_y^2 \\
\chi^2 u_{xy}^2 + 4\chi_x \chi u_{xy} u_y & = (\chi u_{xy} + 2\chi_x u_y)^2 - 4\chi_x^2 u_y^2.
\end{aligned}
$$

For line seven, we use the first equation in (52) to write $(u_y - \kappa u_{yy} - u_{xx})u = fu$. As a result, we collect

$$
\begin{aligned}
MP^u & \leq 2\left[\chi_y\chi - \kappa\chi_{yy}\chi - \chi_{xx}\chi + 3\chi_x^2 + 3\kappa\chi_y^2 + \chi^2\left(|f_u| + \tfrac{1+|f_v|}{2}\right) - \lambda\right](u_x^2 + \kappa u_y^2) \\
& \quad + 2\lambda fu + \chi^2(v_x^2 + \kappa v_y^2)|f_v| + \chi^2(f_x^2 + \kappa f_y^2) - \rho e^{x-x_0},
\end{aligned}
$$

and, similarly,

$$
\begin{aligned}
MP^v & \leq 2\left[\chi_y\chi - \kappa\chi_{yy}\chi - \chi_{xx}\chi + 3\chi_x^2 + 3\kappa\chi_y^2 + \chi^2\left(|g_v| + \tfrac{1+|g_u|}{2}\right) - \lambda\right](v_x^2 + \kappa v_y^2) \\
& \quad + 2\lambda gv + \chi^2(u_x^2 + \kappa u_y^2)|g_u| + \chi^2(g_x^2 + \kappa g_y^2) - \rho e^{x-x_0}.
\end{aligned}
$$

Notice that $|\chi| \leq C_0$, $|\chi_x|, |\chi_y| \leq \frac{C_0}{d}$, $|\chi_{xx}|, |\chi_{yy}| \leq \frac{C_0}{d^2}$ and recall that $\kappa, d \leq 1$. Hence, putting everything together, we arrive at

$$
\begin{aligned}
MP & \leq \left(20\frac{C_0^2}{d^2} + 4C_0^2(\|f\|_{C^{0,1}} + \|g\|_{C^{0,1}}) + C_0^2 - \lambda\right)(u_x^2 + v_x^2 + \kappa u_y^2 + \kappa v_y^2) \\
& \quad + 2\lambda(\|f\|_{L^\infty} + \|g\|_{L^\infty})(\|u\|_{L^\infty} + \|v\|_{L^\infty}) + 2C_0^2(\|f\|_{C^{0,1}}^2 + \|g\|_{C^{0,1}}^2) - 2\rho e^{x-x_0}.
\end{aligned}
$$

It is now time to specify

$$
\begin{cases}
\lambda & = 20\frac{C_0^2}{d^2} + 4C_0^2(\|f\|_{C^{0,1}} + \|g\|_{C^{0,1}}) + C_0^2 > 0 \\
\rho & = \frac{e}{2}\left[2\lambda(\|f\|_{L^\infty} + \|g\|_{L^\infty})(\|u\|_{L^\infty} + \|v\|_{L^\infty}) + 2C_0^2(\|f\|_{C^{0,1}}^2 + \|g\|_{C^{0,1}}^2) + 1\right] > 0.
\end{cases}
$$

As a result we have $MP(y, x) < 0$ for all $(y, x) \in B_0$ (since then $x - x_0 \geq -1$). The maximum principle then implies

$$
P(y_0, x_0) \leq \max_{(y,x)\in\partial B_0} P(y, x).
$$

Since $\chi(y_0, x_0) = 1$ and $\chi(y, x) = 0$ when $(y, x) \in \partial B_0$, the above inequality implies

$$
\begin{aligned}
(u_x^2 + v_x^2 + \kappa u_y^2 + \kappa v_y^2)(y_0, x_0) & \leq \lambda(\|u\|_{L^\infty}^2 + \|v\|_{L^\infty}^2) - \lambda(u^2 + v^2)(y_0, x_0) + 2\rho e \\
& \leq 2\lambda(\|u\|_{L^\infty} \, osc_{B_0}(u) + \|v\|_{L^\infty} osc_{B_0}(v)) + 2\rho e \\
& \leq K\{(\|u\|_{L^\infty} + \|v\|_{L^\infty})(osc_{B_0}(u) + osc_{B_0}(v) \\
& \quad + \|f\|_{C^{0,1}} + \|g\|_{C^{0,1}}) + \|f\|_{C^{0,1}}^2 + \|g\|_{C^{0,1}}^2 + 1\}\left(1 + \frac{1}{d^2}\right)
\end{aligned}
$$

using the expressions of λ and ρ above, for a universal positive constant $K > 0$ and where the $C^{0,1}$ norms of f, g are taken on $B_0 \times [\inf_{B_0} u, \sup_{B_0} u] \times [\inf_{B_0} v, \sup_{B_0} v]$. This proves the lemma. $\qquad\square$

C Dirichlet and periodic principal eigenvalues

We prove here that the principal eigenvalue with Dirichlet boundary conditions in a ball converges to the principal eigenvalue with periodic boundary conditions, when the radius tends to $+\infty$.

Lemma C.1 (Dirichlet and periodic principal eigenvalues). *Let $A \in L^\infty(\mathbb{R}; \mathcal{S}_2(\mathbb{R}))$ be a symmetric cooperative matrix field that is periodic with period $L > 0$. Let λ_1 be the principal eigenvalue of the operator $-\partial_{xx} - A(x)$ with periodic boundary conditions, that is*

$$-\begin{pmatrix}\varphi \\ \psi\end{pmatrix}'' - A(x)\begin{pmatrix}\varphi \\ \psi\end{pmatrix} = \lambda_1\begin{pmatrix}\varphi \\ \psi\end{pmatrix}, \tag{53}$$

with $\varphi, \psi \in H^1_{per}$ and $\varphi > 0, \psi > 0$. For $R > 0$, let λ_1^R be the principal eigenvalue of the operator $-\partial_{xx} - A(x)$ with Dirichlet boundary conditions on $(-R, R)$, that is

$$-\begin{pmatrix}\varphi^R \\ \psi^R\end{pmatrix}'' - A(x)\begin{pmatrix}\varphi^R \\ \psi^R\end{pmatrix} = \lambda_1^R\begin{pmatrix}\varphi^R \\ \psi^R\end{pmatrix}, \tag{54}$$

with $\varphi^R, \psi^R \in H^1_0(-R, R)$ and $\varphi^R > 0, \psi^R > 0$. Then, there exists $C > 0$ depending only on A such that, for all $R > 0$,

$$\lambda_1 \leq \lambda_1^R \leq \lambda_1 + \frac{C}{R}.$$

Proof. Without loss of generality we assume $L = 1$. Inequality $\lambda_1 \leq \lambda_1^R$ is very classical, see [11, Proposition 4.2] or [1, Proposition 3.3] for instance, and we omit the details. Also, the same classical argument yields that $R \mapsto \lambda_1^R$ is nonincreasing so it is enough to prove $\lambda_1^R \leq \lambda_1 + \frac{C}{R}$ when $R = 2, 3, \dots$.

We consider a smooth auxiliary function $\eta : \mathbb{R} \to \mathbb{R}$ satisfying

$$\eta \equiv 1 \text{ on } (-\infty, 0], \ 0 < \eta < 1 \text{ on } (0, 1), \ \eta \equiv 0 \text{ on } [1, \infty).$$

Since the operator in (54) is self-adjoint in the domain $(-R, R)$, the principal eigenvalue λ_1^R is given by the Rayleigh quotient

$$\lambda_1^R = \inf_{\Psi \in \mathbf{H}^1_0(-R,R), \Psi \neq 0} Q(\Psi, \Psi), \quad Q(\Psi, \Psi) := \frac{\int_{-R}^R ({}^t\Psi_x \Psi_x - {}^t\Psi A(x)\Psi)\mathrm{d}x}{\int_{-R}^R {}^t\Psi\Psi\mathrm{d}x}.$$

In particular we have $\lambda_1^R \leq Q(\Theta, \Theta)$, with Θ the $\mathbf{H}^1_0(-R, R)$ test function defined by

$$\Theta(x) := \eta(-R + 1 - x)\eta(-R + 1 + x)\Phi(x), \quad \Phi(x) := \begin{pmatrix}\varphi(x) \\ \psi(x)\end{pmatrix},$$

where φ, ψ are as in (53), with the normalization $\int_0^1 {}^t\Phi\Phi\mathrm{d}x = 1$. We then have $Q(\Theta, \Theta) = Q^1(\Theta) + Q^2(\Theta)$, where

$$Q^1(\Theta) := \frac{\int_{|x| \leq R-1}({}^t\Theta_x\Theta_x - {}^t\Theta A(x)\Theta)\mathrm{d}x}{\int_{-R}^R {}^t\Theta\Theta\mathrm{d}x}, \quad Q^2(\Theta) := \frac{\int_{R-1 \leq |x| \leq R}({}^t\Theta_x\Theta_x - {}^t\Theta A(x)\Theta)\mathrm{d}x}{\int_{-R}^R {}^t\Theta\Theta\mathrm{d}x}.$$

We write

$$Q^1(\Theta) = \frac{\int_{|x| \leq R-1}({}^t\Theta_x\Theta_x - {}^t\Theta A(x)\Theta)\mathrm{d}x}{\int_{|x| \leq R-1}{}^t\Theta\Theta\mathrm{d}x} \frac{\int_{-(R-1)}^{R-1}{}^t\Theta\Theta\mathrm{d}x}{\int_{-R}^{R}{}^t\Theta\Theta\mathrm{d}x} = \lambda_1 \frac{\int_{-(R-1)}^{R-1}{}^t\Theta\Theta\mathrm{d}x}{\int_{-R}^{R}{}^t\Theta\Theta\mathrm{d}x},$$

thanks to $\Theta \equiv \Phi \equiv \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ on $(-(R-1), R-1)$ and the 1-periodicity of φ, ψ (recall that $R-1$ is an integer). As a result

$$|Q^1(\Theta) - \lambda_1| = |\lambda_1| \frac{\int_{R-1<|x|<R}{}^t\Theta\Theta\mathrm{d}x}{\int_{-R}^{R}{}^t\Theta\Theta\mathrm{d}x} \leq |\lambda_1| \frac{\int_{R-1<|x|<R}{}^t\Phi\Phi\mathrm{d}x}{\int_{-(R-1)}^{R-1}{}^t\Phi\Phi\mathrm{d}x} = |\lambda_1| \frac{1}{R-1},$$

since $0 \leq \eta \leq 1$. On the other hand one can see that, for a constant $C_2 > 0$ depending only on $\|\eta'\|_{L^\infty(\mathbb{R})}$ and $\|A\|_{L^\infty(\mathbb{R};\mathcal{S}_2(\mathbb{R}))}$,

$$\left| \int_{R-1<|x|<R} ({}^t\Theta_x\Theta_x - {}^t\Theta A(x)\Theta)\mathrm{d}x \right| \leq C_2 \int_{R-1<|x|<R} ({}^t\Phi\Phi + {}^t\Phi_x\Phi_x)\mathrm{d}x$$

$$= 2C_2 \int_{0<|x|<1} ({}^t\Phi\Phi + {}^t\Phi_x\Phi_x)\mathrm{d}x =: C_2'$$

so that

$$|Q^2(\Theta)| \leq \frac{C_2'}{\int_{-R}^{R}{}^t\Theta\Theta\mathrm{d}x} \leq \frac{C_2'}{\int_{-(R-1)}^{R-1}{}^t\Phi\Phi\mathrm{d}x} = \frac{C_2'}{(2R-2)\int_0^1 {}^t\Phi\Phi\mathrm{d}x} = \frac{C_2'}{(2R-2)}.$$

This concludes the proof of the lemma. $\qquad\qquad\square$

References

[1] M. Alfaro, H. Berestycki, and G. Raoul, *The effect of climate shift on a species submitted to dispersion, evolution, growth and nonlocal competition*, submitted.

[2] M. Alfaro and J. Coville, *Rapid traveling waves in the nonlocal Fisher equation connect two unstable states*, Appl. Math. Lett., 25 (2012), pp. 2095–2099.

[3] M. Alfaro, J. Coville, and G. Raoul, *Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypic trait*, Comm. Partial Differential Equations, 38 (2013), pp. 2126–2154.

[4] ——, *Bistable travelling waves for nonlocal reaction diffusion equations*, Discrete Contin. Dyn. Syst., 34 (2014), pp. 1775–1791.

[5] D. G. Aronson and H. F. Weinberger, *Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation*, in Partial differential equations and related topics (Program, Tulane Univ., New Orleans, La., 1974), Springer, Berlin, 1975, pp. 5–49. Lecture Notes in Math., Vol. 446.

[6] ——, *Multidimensional nonlinear diffusion arising in population genetics*, Adv. in Math., 30 (1978), pp. 33–76.

[7] B. Ashby, S. Gupta, and A. Buckling, *Spatial structure mitigates fitness costs in host-parasite coevolution.*, The American Naturalist, 183 (2014), pp. E64–E74. PMID: 24561607.

[8] H. Berestycki and F. Hamel, *Front propagation in periodic excitable media*, Comm. Pure Appl. Math., 55 (2002), pp. 949–1032.

[9] ——, *Gradient estimates for elliptic regularizations of semilinear parabolic and degenerate elliptic equations*, Comm. Partial Differential Equations, 30 (2005), pp. 139–156.

[10] H. Berestycki, F. Hamel, and L. Roques, *Analysis of the periodically fragmented environment model. II. Biological invasions and pulsating travelling fronts*, J. Math. Pures Appl. (9), 84 (2005), pp. 1101–1146.

[11] H. Berestycki, F. Hamel, and L. Rossi, *Liouville-type results for semilinear elliptic equations in unbounded domains*, Ann. Mat. Pura Appl. (4), 186 (2007), pp. 469–507.

[12] H. Berestycki, G. Nadin, B. Perthame, and L. Ryzhik, *The non-local Fisher-KPP equation: travelling waves and steady states*, Nonlinearity, 22 (2009), pp. 2813–2844.

[13] H. Berestycki, B. Nicolaenko, and B. Scheurer, *Traveling wave solutions to combustion models and their singular limits*, SIAM J. Math. Anal., 16 (1985), pp. 1207–1242.

[14] H. Berestycki and L. Nirenberg, *On the method of moving planes and the sliding method*, Bol. Soc. Brasil. Mat. (N.S.), 22 (1991), pp. 1–37.

[15] A. Best, S. Webb, A. White, and M. Boots, *Host resistance and coevolution in spatially structured populations*, Proceedings of the Royal Society of London B: Biological Sciences, 278 (2011), pp. 2216–2222.

[16] R. F. Brown, *A topological introduction to nonlinear analysis*, Birkhäuser Boston, Inc., Boston, MA, second ed., 2004.

[17] J. Busca and B. Sirakov, *Harnack type estimates for nonlinear elliptic systems and applications*, Ann. Inst. H. Poincaré Anal. Non Linéaire, 21 (2004), pp. 543–590.

[18] M. G. Crandall and P. H. Rabinowitz, *Bifurcation from simple eigenvalues*, J. Functional Analysis, 8 (1971), pp. 321–340.

[19] L. Damascelli and F. Pacella, *Symmetry results for cooperative elliptic systems via linearization*, SIAM J. Math. Anal., 45 (2013), pp. 1003–1026.

[20] J. Fang and X.-Q. Zhao, *Monotone wavefronts of the nonlocal Fisher-KPP equation*, Nonlinearity, 24 (2011), pp. 3043–3054.

[21] P. C. Fife and J. B. McLeod, *The approach of solutions of nonlinear diffusion equations to travelling front solutions*, Arch. Ration. Mech. Anal., 65 (1977), pp. 335–361.

[22] R. A. Fisher, *The wave of advance of advantageous genes*, Ann. of Eugenics, 7 (1937), pp. 355–369.

[23] J. FÖLDES AND P. POLÁČIK, *On cooperative parabolic systems: Harnack inequalities and asymptotic symmetry*, Discrete Contin. Dyn. Syst., 25 (2009), pp. 133–157.

[24] R. A. GARDNER, *Existence and stability of travelling wave solutions of competition models: a degree theoretic approach*, J. Differential Equations, 44 (1982), pp. 343–364.

[25] Q. GRIETTE AND G. RAOUL, *Existence and qualitative properties of travelling waves for an epidemiological model with mutations*, J. Differential Equations, 260 (2016), pp. 7115–7151.

[26] Q. GRIETTE, G. RAOUL, AND S. GANDON, *Virulence evolution at the front line of spreading epidemics*, Evolution, 69 (2015), pp. 2810–2819.

[27] F. HAMEL, *Qualitative properties of monostable pulsating fronts: exponential decay and monotonicity*, J. Math. Pures Appl. (9), 89 (2008), pp. 355–399.

[28] F. HAMEL AND L. ROQUES, *Uniqueness and stability properties of monostable pulsating fronts*, J. Eur. Math. Soc. (JEMS), 13 (2011), pp. 345–390.

[29] F. HAMEL AND L. RYZHIK, *On the nonlocal Fisher-KPP equation: steady states, spreading speed and global bounds*, Nonlinearity, 27 (2014), pp. 2735–2753.

[30] W. HUDSON AND B. ZINNER, *Existence of traveling waves for reaction diffusion equations of Fisher type in periodic media*, in Boundary value problems for functional-differential equations, World Sci. Publ., River Edge, NJ, 1995, pp. 187–199.

[31] A. N. KOLMOGOROV, I. G. PETROVSKY, AND N. S. PISKUNOV, *Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique*, Bull. Univ. Etat Moscou, Sér. Inter. A 1 (1937), pp. 1–26.

[32] M. A. KRASNOSEL'SKII, *Topological methods in the theory of nonlinear integral equations*, Translated by A. H. Armstrong; translation edited by J. Burlak. A Pergamon Press Book, The Macmillan Co., New York, 1964.

[33] S. LION AND S. GANDON, *Evolution of spatially structured host-parasite interactions*, Journal of Evolutionary Biology, 28 (2015), pp. 10–28.

[34] P. H. RABINOWITZ, *A note on a nonlinear eigenvalue problem for a class of differential equations*, J. Differential Equations, 9 (1971), pp. 536–548.

[35] ——, *Some global results for nonlinear eigenvalue problems*, J. Functional Analysis, 7 (1971), pp. 487–513.

[36] H. F. WEINBERGER, *On spreading speeds and traveling waves for growth and migration models in a periodic habitat*, J. Math. Biol., 45 (2002), pp. 511–548.

[37] J. XIN, *Front propagation in heterogeneous media*, SIAM Rev., 42 (2000), pp. 161–230.