

HOMOGENIZATION AND INFLUENCE OF FRAGMENTATION IN A BIOLOGICAL INVASION MODEL

MOHAMMAD EL SMAILY

Department of Mathematics, University of British Columbia
and Pacific Institute for the Mathematical Sciences
1984 Mathematics Road, V6T 1Z2, Vancouver, BC, Canada

FRANÇOIS HAMEL

Aix-Marseille Université, LATP, Faculté des Sciences et Techniques
Avenue Escadrille Normandie-Niemen, F-13397 Marseille Cedex 20, France
and Helmholtz Zentrum München, Institut für Biomathematik und Biometrie
Ingolstädter Landstrasse 1, D-85764 Neuherberg, Germany

LIONEL ROQUES

UR 546 Biostatistique et Processus Spatiaux, INRA, F-84000 Avignon, France

(Communicated by the associate editor name)

Dedicated to Professor Masayasu Mimura for his 65th birthday

ABSTRACT. In this paper, some properties of the minimal speeds of pulsating Fisher-KPP fronts in periodic environments are established. The limit of the speeds at the homogenization limit is proved rigorously. Near this limit, generically, the fronts move faster when the spatial period is enlarged, but the speeds vary only at the second order. The dependence of the speeds on habitat fragmentation is also analyzed in the case of the patch model.

1. Introduction and main hypotheses. In homogeneous environments, the probably most used population dynamics reaction-diffusion model is the Fisher-KPP model [13, 23]. In a one-dimensional space, it corresponds to the following equation

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + u(\mu - \nu u), \quad t > 0, \quad x \in \mathbb{R}. \quad (1)$$

The unknown $u = u(t, x)$ is the population density at time t and position x , and the positive constant coefficients D , μ and ν respectively correspond to the diffusivity (mobility of the individuals), the intrinsic growth rate and the susceptibility to crowding effects.

2000 *Mathematics Subject Classification.* Primary: 35B10, 35B27, 35K57; Secondary: 92B05.

Key words and phrases. Homogenization, fragmentation, reaction-diffusion model, pulsating fronts.

The authors are supported by the french “Agence Nationale de la Recherche” within the projects ColonSGS (second and third authors), PREFERED (all authors) and URTICLIM (third author). The second author is also indebted to the Alexander von Humboldt Foundation for its support.

A natural extension of this model to heterogeneous environments is the Shigesada-Kawasaki-Teramoto model [32],

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left(a_L(x) \frac{\partial u}{\partial x} \right) + u (\mu_L(x) - \nu_L(x)u), \quad t > 0, \quad x \in \mathbb{R}, \quad (2)$$

where the coefficients depend on the space variable x in a L -periodic fashion:

Definition 1.1 (L -periodicity). Let L be a positive real number. We say that a function $h : \mathbb{R} \rightarrow \mathbb{R}$ is L -periodic if

$$\forall x \in \mathbb{R}, \quad h(x + L) = h(x).$$

In this paper, we are concerned with the general equation:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left(a_L(x) \frac{\partial u}{\partial x} \right) + f_L(x, u), \quad t \in \mathbb{R}, \quad x \in \mathbb{R}. \quad (3)$$

The diffusion term a_L satisfies

$$a_L(x) = a(x/L),$$

where a is a $C^{2,\delta}(\mathbb{R})$ (with $\delta > 0$) 1-periodic function that satisfies

$$\exists 0 < \alpha_1 < \alpha_2, \quad \forall x \in \mathbb{R}, \quad \alpha_1 \leq a(x) \leq \alpha_2. \quad (4)$$

On other hand, the reaction term satisfies $f_L(x, \cdot) = f(x/L, \cdot)$, where $f := f(x, s) : \mathbb{R} \times \mathbb{R}_+ \rightarrow \mathbb{R}$ is 1-periodic in x , of class $C^{1,\delta}$ in (x, s) and C^2 in s . In this setting, both a_L and f_L are L -periodic in the variable x . Furthermore, we assume that:

$$\begin{cases} \forall x \in \mathbb{R}, & f(x, 0) = 0, \\ \exists M \geq 0, \forall s \geq M, \forall x \in \mathbb{R}, & f(x, s) \leq 0, \\ \forall x \in \mathbb{R}, & s \mapsto f(x, s)/s \text{ is decreasing in } s > 0. \end{cases} \quad (5)$$

Moreover, we set

$$\mu(x) := \lim_{s \rightarrow 0^+} f(x, s)/s,$$

and

$$\mu_L(x) := \lim_{s \rightarrow 0^+} f_L(x, s)/s = \mu\left(\frac{x}{L}\right).$$

The growth rate μ may be positive in some regions (favorable regions) or negative in others (unfavorable regions).

The stationary states $p(x)$ of (3) satisfy the equation

$$\frac{\partial}{\partial x} \left(a_L(x) \frac{\partial p}{\partial x} \right) + f_L(x, p) = 0, \quad x \in \mathbb{R}. \quad (6)$$

Under general hypotheses including those of this paper, and in any space dimension, it was proved in [4] that a necessary and sufficient condition for the existence of a positive and bounded solution p of (6) was the negativity of the principal eigenvalue $\rho_{1,L}$ of the linear operator

$$\mathcal{L}_0 : \Phi \mapsto -(a_L(x)\Phi')' - \mu_L(x)\Phi, \quad (7)$$

with periodicity conditions. In this case, the solution p was also proved to be unique, and therefore L -periodic. Actually, it is easy to see that the map $L \mapsto \rho_{1,L}$ is nonincreasing in $L > 0$, and even decreasing as soon as a is not constant (see the

proof of Lemma 3.1). Furthermore, $\rho_{1,L} \rightarrow -\int_0^1 \mu(x)dx$ as $L \rightarrow 0^+$. In this paper, in addition to the above-mentioned hypotheses, we make the assumption that

$$\int_0^1 \mu(x)dx > 0. \quad (8)$$

This assumption then guarantees that

$$\forall L > 0, \quad \rho_{1,L} < 0,$$

whence, for all $L > 0$, there exists a unique positive periodic and bounded solution p_L of (6). Notice that assumption (8) is immediately fulfilled if $\mu(x)$ is positive everywhere.

In this work, we are concerned with the propagation of pulsating traveling fronts which are particular solutions of the reaction-diffusion equation (3). Before going further on, we recall the definition of such solutions:

Definition 1.2 (Pulsating traveling fronts). A function $u = u(t, x)$ is called a pulsating traveling front propagating from right to left with an effective speed $c \neq 0$, if u is a classical solution of:

$$\begin{cases} \frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left(a_L(x) \frac{\partial u}{\partial x} \right) + f_L(x, u), & t \in \mathbb{R}, x \in \mathbb{R}, \\ \forall k \in \mathbb{Z}, \forall (t, x) \in \mathbb{R} \times \mathbb{R}, & u(t + \frac{kL}{c}, x) = u(t, x + kL), \\ 0 \leq u(t, x) \leq p_L(x), \\ \lim_{x \rightarrow -\infty} u(t, x) = 0 \text{ and } \lim_{x \rightarrow +\infty} u(t, x) - p_L(x) = 0, \end{cases} \quad (9)$$

where the above limits hold locally in t .

This definition has been introduced in [31, 32]. It has also been extended in higher dimensions with $p_L \equiv 1$ in [1] and [35], and with $p_L \neq 1$ in [5].

Under the above assumptions, it follows from [5] that there exists $c_L^* > 0$ such that pulsating traveling fronts satisfying (9) with a speed of propagation c exist if and only if $c \geq c_L^*$. Moreover, the pulsating fronts (with speeds $c \geq c_L^*$) are increasing in time t . Further uniqueness and qualitative properties are proved in [14, 15]. The value c_L^* is called the *minimal speed of propagation*. We refer to [2, 3, 11, 18, 25, 27, 28, 34] for further existence results and properties of the minimal speeds of KPP pulsating fronts. For existence, uniqueness, stability and further qualitative results for combustion or bistable nonlinearities in the periodic framework, we refer to [6, 7, 12, 16, 17, 19, 24, 26, 35, 36, 37, 38].

In the particular case of the Shigesada *et al* model (2), when $a(x) \equiv 1$, the effects of the spatial distribution of the function μ_L on the existence and global stability of a positive stationary state p_L of equation (2) have been investigated both numerically [30, 31] and theoretically [4, 8, 29]. In particular, as already noticed, enlarging the scale of fragmentation, i.e. increasing L , was proved to decrease the value of $\rho_{1,L}$. Biologically, this result means that larger scales have a positive effect on species persistence, for species whose dynamics is modelled by the Shigesada *et al* model.

The effects of the spatial distribution of the functions a_L and μ_L on the minimal speed of propagation c_L^* have not yet been investigated rigorously. This is a difficult problem, since the known variational formula for c_L^* bears on non-self-adjoint operators, and therefore, the methods used to analyze the dependence of $\rho_{1,L}$ on

fragmentation cannot be used in this situation. However, in the case of model (2), when $a_L \equiv 1$, $\nu_L \equiv 1$ and $\mu_L(x) = \mu(x/L)$, for a 1-periodic function μ taking only two values, Kinezaki *et al* [22] numerically observed that c_L^* was an increasing function of the parameter L . For sinusoidally varying coefficients, the relationships between c_L^* and L have also been investigated formally by Kinezaki, Kawasaki, Shigesada [21]. The case of a rapidly oscillating coefficient $a_L(x)$, corresponding to small L values, and the homogenization limit $L \rightarrow 0$, have been discussed in [19] and [38] for combustion and bistable nonlinearities $f(u)$.

The first aim of our work is to analyze rigorously the dependence of the speed of propagation c_L^* with respect to L , under the general setting of equation (3), for small L values. We determine the limit of the minimal speeds c_L^* as $L \rightarrow 0^+$ (the homogenization limit), and we also prove that near the homogenization limit, the species tends to propagate faster when the spatial period of the environment is enlarged. Next, in the case of an environment composed of patches of “habitat” and “non-habitat”, we consider the dependence of the minimal speed with respect to habitat fragmentation. We prove that fragmentation decreases the minimal speed.

2. Main results. In this section, we describe the main results of this paper. Unless otherwise mentioned, we make the assumptions of Section 1. The first theorem gives the limit of c_L^* as L goes to 0.

Theorem 2.1. *Let c_L^* be the minimal speed of propagation of pulsating traveling fronts solving (9). Then,*

$$\lim_{L \rightarrow 0^+} c_L^* = 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}, \quad (10)$$

where

$$\langle \mu \rangle_A = \int_0^1 \mu(x) dx \quad \text{and} \quad \langle a \rangle_H = \left(\int_0^1 (a(x))^{-1} dx \right)^{-1} = \langle a^{-1} \rangle_A^{-1}$$

denote the arithmetic mean of μ and the harmonic mean of a over the interval $[0, 1]$.

Formula (10) was derived formally in [33] for sinusoidally varying coefficients. Theorem 2.1 then provides a generalization of the formula in [33] and a rigorous analysis of the homogenization limit for general diffusion and growth rate profiles.

Remark 1. The previous theorem gives the limit of c_L^* as $L \rightarrow 0$ when the space dimension is 1. Theorem 3.3 of El Smaily [11] answered this issue in any dimensions N , but under an additional assumption of free divergence of the diffusion field (in the one-dimensional case considered here, this assumption reduces to $da/dx = 0$ in \mathbb{R}). Lastly, we refer to [6, 7, 16] for other homogenization limits with combustion-type nonlinearities.

Our second result describes the behavior of the function $L \mapsto c_L^*$, for small L values.

Theorem 2.2. *Let c_L^* be the minimal speed of propagation of pulsating traveling fronts solving (9). Then, the map $L \mapsto c_L^*$ is of class C^∞ in an interval $(0, L_0)$ for some $L_0 > 0$. Furthermore,*

$$\lim_{L \rightarrow 0^+} \frac{dc_L^*}{dL} = 0 \quad (11)$$

and

$$\lim_{L \rightarrow 0^+} \frac{d^2 c_L^*}{dL^2} = \gamma \geq 0. \quad (12)$$

Lastly, $\gamma > 0$ if and only if the function

$$\frac{\mu}{\langle \mu \rangle_A} + \frac{\langle a \rangle_H}{a}$$

is not identically equal to 2.

Corollary 1. *Under the notations of Theorem 2.2, it follows that if a is constant and μ is not constant, or if μ is constant and a is not constant, then $\gamma > 0$ and the speeds c_L^* are increasing with respect to L when L is close to 0.*

Remark 2. The question of the monotonicity of the map $L \mapsto c_L^*$ had also been studied under different assumptions in [11] (see Theorem 5.3). The author answered this question for a reaction-advection-diffusion equation over a periodic domain $\Omega \subseteq \mathbb{R}^N$, under an additional assumption on the diffusion coefficient (like in Remark 1, this assumption would mean again in our present setting that the diffusion coefficient $a(x)$ is constant over \mathbb{R}). Our result gives the behavior of the minimal speeds of propagation near the homogenization limit for general diffusion and growth rate coefficients. The condition $\gamma > 0$ is generically fulfilled, which means that, roughly speaking, the more oscillating the medium is, the slower the species moves. But the speeds vary only at the second order with respect to the period L . Based on numerical observations which have been carried out in [21] for special types of diffusion and growth rate coefficients, we conjecture that the monotonicity of c_L^* holds for all $L > 0$.

Lastly, we give a first theoretical evidence that habitat fragmentation, without changing the scale L , can decrease the minimal speed c^* . We here fix a period $L_0 > 0$.

We assume that $a \equiv 1$, and that $\mu_{L_0} := \mu_z$ takes only the two values 0 and $m > 0$, and depends on a parameter z . More precisely:

$$\begin{cases} \text{There exist } 0 \leq z \text{ and } l \in (0, L_0) \text{ such that } l + z \leq L_0, \\ \mu_z \equiv m \text{ on } [0, l/2] \cup [l/2 + z, l + z], \\ \mu_z \equiv 0 \text{ on } [l/2, l/2 + z] \cup [l + z, L_0]. \end{cases} \quad (13)$$

With this setting, the region where μ_z is positive, which can be interpreted as ‘‘habitat’’ in the Shigesada *et al* model, is of Lebesgue measure l in each period cell $[0, L_0]$. For $z = 0$, this region is simply an interval. However, whenever z is positive, this region is fragmented into two parts of same length $l/2$ (see Figure 1). Our next result means that this fragmentation into two parts reduces the speed c^* .

Theorem 2.3. *Let c_z^* be the minimal speed of propagation of pulsating traveling fronts solving (9), with $a_{L_0} \equiv 1$ and $\mu_{L_0} = \mu_z$ defined by (13). Assume that $l \in (3L_0/4, L_0)$. Then $z \mapsto c_z^*$ is decreasing in $[0, (L_0 - l)/2]$, and increasing in $[(L_0 - l)/2, L_0 - l]$.*

Remark 3. Note that, whenever $z > (L_0 - l)/2$, the two habitat components in the period cell $[l/2 + z, L_0 + l/2 + z]$ are at a distance smaller than $(L_0 - l)/2$ from each other. In fact, Theorem 2.3 proves that, when z varies in $(0, L_0 - l)$, c_z^* is all the larger as the minimal distance separating two habitat components is small, that is as the maximal distance between two consecutive habitat components is large.

Remark 4. Here, the function μ_z does not satisfy the general regularity assumptions of Section 1. However, c_z^* can still be interpreted as the minimal speed of propagation of weak solutions of (9), whose existence can be obtained by approaching μ_z with regular functions.

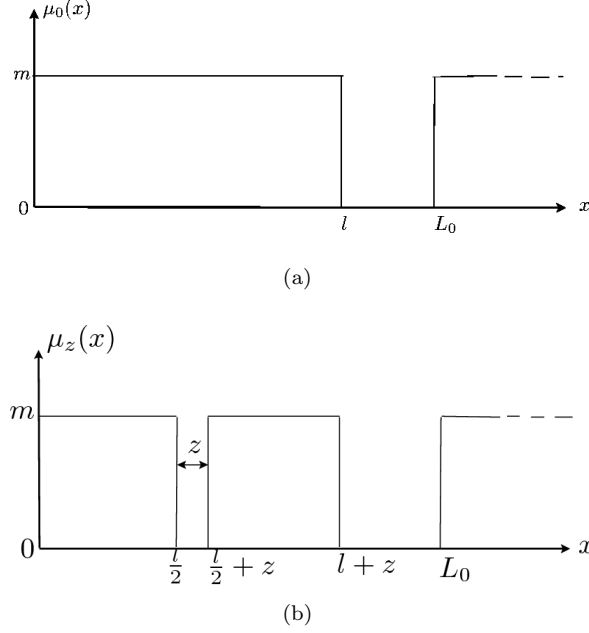


FIGURE 1. The L_0 -periodic function $x \mapsto \mu_z(x)$, (a): with $z = 0$; (b): with $z > 0$.

The main tool of this paper is a variational formulation for c_L^* involving elliptic eigenvalue problems which depend strongly on the coefficients a and f . Such a formulation was given in any space dimension in [3] in the case where the bounded stationary state p of the equation (3) is constant, and in [5] in the case of a general nonconstant bounded stationary state $p(x)$.

3. The homogenization limit: proof of Theorem 2.1. This proof is divided into three main steps.

Step 1: a rough upper bound for c_L^* . For each $L > 0$, the minimal speed c_L^* is positive and, from [5] (see also [3] in the case when $p \equiv 1$), it is given by the variational formula

$$c_L^* = \min_{\lambda > 0} \frac{k(\lambda, L)}{\lambda} = \frac{k(\lambda_L^*, L)}{\lambda_L^*}, \quad (14)$$

where $\lambda_L^* > 0$ and, for each $\lambda \in \mathbb{R}$ and $L > 0$, $k(\lambda, L)$ denotes the principal eigenvalue of the problem

$$(a_L \psi'_{\lambda, L})' + 2\lambda a_L \psi'_{\lambda, L} + \lambda a'_L \psi_{\lambda, L} + \lambda^2 a_L \psi_{\lambda, L} + \mu_L \psi_{\lambda, L} = k(\lambda, L) \psi_{\lambda, L} \text{ in } \mathbb{R}, \quad (15)$$

with L -periodicity conditions. In (15), $\psi_{\lambda, L}$ denotes a principal eigenfunction, which is of class $C^{2, \delta}(\mathbb{R})$, positive, unique up to multiplication by a positive constant, and L -periodic. Furthermore, it follows from Section 3 of [5] that the map $\lambda \mapsto k(\lambda, L)$ is convex and that $\frac{\partial k}{\partial \lambda}(0, L) = 0$ for each $L > 0$. Therefore, for each $L > 0$, the map $\lambda \mapsto k(\lambda, L)$ is nondecreasing in \mathbb{R}_+ and

$$\forall \lambda \geq 0, \forall L > 0, \quad k(\lambda, L) \geq k(0, L) = -\rho_{1, L} > 0 \quad (16)$$

under the notations of Section 1.

Multiplying (15) by $\psi_{\lambda,L}$ and integrating by parts over $[0, L]$, we get, due to the L -periodicity of a_L and $\psi_{\lambda,L}$:

$$k(\lambda, L) \int_0^L \psi_{\lambda,L}^2 = - \int_0^L a_L (\psi'_{\lambda,L})^2 + \lambda^2 \int_0^L a_L \psi_{\lambda,L}^2 + \int_0^L \mu_L \psi_{\lambda,L}^2,$$

for all $\lambda > 0$ and for all $L > 0$. Consequently,

$$\forall \lambda > 0, \forall L > 0, \quad k(\lambda, L) \leq \lambda^2 a_M + \mu_M, \quad (17)$$

where

$$a_M = \max_{x \in \mathbb{R}} a(x) > 0 \text{ and } \mu_M = \max_{x \in \mathbb{R}} \mu(x) > 0.$$

Using (14), we get that

$$\forall L > 0, \quad 0 < c_L^* \leq 2\sqrt{a_M \mu_M}. \quad (18)$$

Step 2: the sharp upper bound for c_L^* . For any $\lambda > 0$ and $L > 0$, consider the functions

$$\varphi_{\lambda,L}(x) := e^{\lambda x} \psi_{\lambda,L}(x), \quad x \in \mathbb{R}.$$

Since $\psi_{\lambda,L}$ is unique up to multiplication, we will assume in this step 2 that

$$\int_0^2 \varphi_{\lambda,L}^2(x) dx = 1. \quad (19)$$

The above choice ensures that

$$\int_0^2 \psi_{\lambda,L}^2(x) dx \leq \int_0^2 e^{2\lambda x} \psi_{\lambda,L}^2(x) dx = \int_0^2 \varphi_{\lambda,L}^2(x) dx = 1. \quad (20)$$

We are now going to prove that the families $(\psi_{\lambda,L})_{\lambda,L}$ and $(\varphi_{\lambda,L})_{\lambda,L}$ remain bounded in $H^1(0, 1)$ for L small enough and as soon as λ stays bounded. For each $L > 0$, we call

$$M_L = [1/L] + 1 \in \mathbb{N},$$

where $[1/L]$ stands for the integer part of $1/L$. Multiplying (15) by $\psi_{\lambda,L}$ and integrating by parts over $[0, M_L L]$, we get that

$$- \int_0^{M_L L} a_L \psi'_{\lambda,L}{}^2 + \int_0^{M_L L} \lambda^2 a_L \psi_{\lambda,L}^2 + \int_0^{M_L L} \mu_L \psi_{\lambda,L}^2 = k(\lambda, L) \int_0^{M_L L} \psi_{\lambda,L}^2.$$

Using (4), (16) and (17), it follows that

$$0 \leq \int_0^{M_L L} \psi'_{\lambda,L}{}^2 \leq \frac{1}{\alpha_1} \times (\lambda^2 a_M + \mu_M) \times \int_0^{M_L L} \psi_{\lambda,L}^2.$$

Since $1 < M_L L \leq 1 + L$ for all $L > 0$, we have that $1 < M_L L \leq 2$ for all $L \leq 1$. Thus, for all $0 < L \leq 1$,

$$\int_0^1 \psi'_{\lambda,L}{}^2 \leq \int_0^{M_L L} \psi'_{\lambda,L}{}^2 \text{ and } \int_0^{M_L L} \psi_{\lambda,L}^2 \leq \int_0^2 \psi_{\lambda,L}^2 \leq 1$$

from (20). It follows now that

$$\forall \lambda > 0, \forall 0 < L \leq 1, \quad \int_0^1 \psi'_{\lambda,L}{}^2 \leq \frac{\lambda^2 a_M + \mu_M}{\alpha_1}. \quad (21)$$

From (20) and (21), we conclude that, for any given $\Lambda > 0$, the family $(\psi_{\lambda,L})$ (with $0 < \lambda \leq \Lambda$ and $0 < L \leq 1$) is bounded in $H^1(0, 1)$. On the other hand,

$$\varphi'_{\lambda,L}(x) = \lambda \varphi_{\lambda,L}(x) + e^{\lambda x} \psi'_{\lambda,L}(x).$$

Owing to (19) and (21), we get:

$$\begin{aligned} \forall \lambda > 0, \forall L \leq 1, \|\varphi'_{\lambda,L}\|_{L^2(0,1)} &\leq \lambda \underbrace{\|\varphi_{\lambda,L}\|_{L^2(0,1)}}_{\leq 1} + e^\lambda \|\psi'_{\lambda,L}\|_{L^2(0,1)} \\ &\leq \lambda + e^\lambda \times \sqrt{\frac{\lambda^2 a_M + \mu_M}{\alpha_1}}. \end{aligned} \quad (22)$$

From (19) and (22), we obtain that, for any given $\Lambda > 0$, the family $(\varphi_{\lambda,L})$ (with $0 < \lambda \leq \Lambda$ and $0 < L \leq 1$) is bounded in $H^1(0,1)$ and that the family $(a_L \varphi'_{\lambda,L})_{0 < \lambda \leq \Lambda, 0 < L \leq 1}$ is bounded in $L^2(0,1)$ (due to (4)). Moreover,

$$\begin{aligned} (a_L \varphi'_{\lambda,L})' &= \lambda^2 a_L e^{\lambda x} \psi_{\lambda,L} + 2\lambda a_L e^{\lambda x} \psi'_L + \lambda a'_L e^{\lambda x} \psi_{\lambda,L} \\ &\quad + e^{\lambda x} a'_L \psi'_{\lambda,L} + e^{\lambda x} a_L \psi''_{\lambda,L}. \end{aligned}$$

Multiplying (15) by $e^{\lambda x}$, we then get

$$(a_L \varphi'_{\lambda,L})' + \mu_L \varphi_{\lambda,L} = k(\lambda, L) \varphi_{\lambda,L} \text{ in } \mathbb{R}. \quad (23)$$

Let

$$v_{\lambda,L}(x) = a_L(x) \varphi'_{\lambda,L}(x)$$

for all $\lambda > 0$, $L > 0$ and $x \in \mathbb{R}$. Pick any $\Lambda > 0$. One already knows that the family $(v_{\lambda,L})_{0 < \lambda \leq \Lambda, 0 < L \leq 1}$ is bounded in $L^2(0,1)$. Furthermore,

$$v'_{\lambda,L} + \mu_L \varphi_{\lambda,L} = k(\lambda, L) \varphi_{\lambda,L} \text{ in } \mathbb{R}. \quad (24)$$

Notice that the family $(k(\lambda, L))_{0 < \lambda \leq \Lambda, 0 < L \leq 1}$ is bounded from (16) and (17). From (19) and (24), it follows that the family $(v'_{\lambda,L})_{0 < \lambda \leq \Lambda, 0 < L \leq 1}$ is bounded in $L^2(0,1)$. Eventually, $(v_{\lambda,L})_{0 < \lambda \leq \Lambda, 0 < L \leq 1}$ is bounded in $H^1(0,1)$.

Pick now any sequence $(L_n)_{n \in \mathbb{N}}$ such that $0 < L_n \leq 1$ for all $n \in \mathbb{N}$, and $L_n \rightarrow 0^+$ as $n \rightarrow +\infty$. Choose any $\lambda > 0$ and any sequence $(\lambda_n)_{n \in \mathbb{N}}$ of positive numbers such that $\lambda_n \rightarrow \lambda$ as $n \rightarrow +\infty$. We claim that

$$k(\lambda_n, L_n) \rightarrow \lambda^2 \langle a \rangle_H + \langle \mu \rangle_A \text{ as } n \rightarrow +\infty, \quad (25)$$

where $\langle a \rangle_H = \left(\int_0^1 (a(x))^{-1} dx \right)$ and $\langle \mu \rangle_A = \int_0^1 \mu(x) dx$. To do so, call

$$\psi_n = \psi_{\lambda_n, L_n}, \quad \varphi_n = \varphi_{\lambda_n, L_n} \text{ and } v_n = v_{\lambda_n, L_n}.$$

It follows from the above computations that the sequences (ψ_n) and (v_n) are bounded in $H^1(0,1)$. Hence, up to extraction of a subsequence,

$$\psi_n \rightarrow \bar{\psi} \text{ and } v_n \rightarrow w \text{ as } n \rightarrow +\infty,$$

strongly in $L^2(0,1)$ and weakly in $H^1(0,1)$. By Sobolev injections, the sequence (ψ_n) is bounded in $C^{0,1/2}([0,1])$. But since each function ψ_n is L_n -periodic (with $L_n \rightarrow 0^+$), it follows from Arzela-Ascoli theorem that $\bar{\psi}$ has to be constant over $[0,1]$. Moreover, the boundedness of the sequence $(k(\lambda_n, L_n))_{n \in \mathbb{N}}$ implies that, up to extraction of another subsequence,

$$k(\lambda_n, L_n) \rightarrow \bar{k}(\lambda) \in \mathbb{R} \text{ as } n \rightarrow +\infty.$$

We denote this limit by $\bar{k}(\lambda)$, we will see later that indeed it depends only on λ . It follows now, from (24) after replacing (λ, L) by (λ_n, L_n) and passing to the limit as $n \rightarrow +\infty$, that

$$w' + \langle \mu \rangle_A e^{\lambda x} \bar{\psi} = \bar{k}(\lambda) \bar{\psi} e^{\lambda x} \text{ a.e. in } (0,1).$$

Notice indeed that $\mu_L \rightharpoonup \langle \mu \rangle_A$ as $L \rightarrow 0^+$ in $L^2(0, 1)$ weakly. Meanwhile,

$$\varphi'_n = \lambda_n e^{\lambda_n x} \psi_n + e^{\lambda_n x} \psi'_n = \frac{v_n}{a_{L_n}} \rightharpoonup \langle a^{-1} \rangle_A \quad w \text{ as } n \rightarrow +\infty,$$

weakly in $L^2(0, 1)$, where $\langle a^{-1} \rangle_A = \int_0^1 (a(x))^{-1} dx$. Thus, we obtain

$$w = \langle a^{-1} \rangle_A^{-1} \lambda e^{\lambda x} \bar{\psi} = \langle a \rangle_H \lambda e^{\lambda x} \bar{\psi}.$$

Consequently,

$$\lambda^2 \langle a \rangle_H \bar{\psi} + \langle \mu \rangle_A \bar{\psi} = \bar{k}(\lambda) \bar{\psi}.$$

Actually, since the functions ψ_n are L_n -periodic (with $L_n \rightarrow 0^+$) and converge to the constant $\bar{\psi}$ strongly in $L^2(0, 1)$, they converge to $\bar{\psi}$ in $L^2_{loc}(\mathbb{R})$. But

$$1 = \int_0^2 \varphi_n^2 \leq e^{4\lambda_n} \int_0^2 \psi_n^2 \leq e^{4M} \int_0^2 \psi_n^2,$$

where $M = \sup_{n \in \mathbb{N}} \lambda_n$. Hence, $\bar{\psi} \neq 0$ and

$$\lambda^2 \langle a \rangle_H + \langle \mu \rangle_A = \bar{k}(\lambda). \quad (26)$$

By uniqueness of the limit, one deduces that the whole sequence $(k(\lambda_n, L_n))_{n \in \mathbb{N}}$ converges to this quantity $\bar{k}(\lambda)$ as $n \rightarrow +\infty$, which proves the claim (25).

Now, take any sequence $L_n \rightarrow 0^+$ such that $c_{L_n}^* \rightarrow \limsup_{L \rightarrow 0^+} c_L^*$ as $n \rightarrow +\infty$. For each $\lambda > 0$ and for each $n \in \mathbb{N}$, one has

$$c_{L_n}^* \leq \frac{k(\lambda, L_n)}{\lambda}$$

from (14), whence

$$\limsup_{L \rightarrow 0^+} c_L^* = \lim_{n \rightarrow +\infty} c_{L_n}^* \leq \frac{\bar{k}(\lambda)}{\lambda} = \lambda \langle a \rangle_H + \frac{\langle \mu \rangle_A}{\lambda}.$$

Since this holds for all $\lambda > 0$, one concludes that

$$\limsup_{L \rightarrow 0^+} c_L^* \leq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}. \quad (27)$$

Step 3: the sharp lower bound for c_L^* . The aim of this step is to prove that

$$\liminf_{L \rightarrow 0^+} c_L^* \geq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$$

which would complete the proof of Theorem 2.1.

For each $L > 0$, the minimal speed c_L^* is given by (14) and the map $(0, +\infty) \ni \lambda \mapsto k(\lambda, L)/\lambda$ attains its minimum at $\lambda_L^* > 0$. We will prove that, for L small enough, the family (λ_L^*) is bounded from above and from below by $\bar{\lambda} > 0$ and $\underline{\lambda} > 0$ respectively. Namely, one has

Lemma 3.1. *There exist L_0 and $0 < \underline{\lambda} \leq \bar{\lambda} < +\infty$ such that*

$$\underline{\lambda} \leq \lambda_L^* \leq \bar{\lambda} \text{ for all } 0 < L \leq L_0.$$

The proof is postponed at the end of this section. Take now any sequence $(L_n)_n$ such that $0 < L_n \leq L_0$ for all n , and $L_n \rightarrow 0^+$ as $n \rightarrow +\infty$. From Lemma 3.1, there exists $\lambda^* > 0$ such that, up to extraction of a subsequence, $\lambda_{L_n}^* \rightarrow \lambda^*$ as $n \rightarrow +\infty$. One also has

$$c_{L_n}^* = \frac{k(\lambda_{L_n}^*, L_n)}{\lambda_{L_n}^*} \xrightarrow{n \rightarrow +\infty} \frac{\bar{k}(\lambda^*)}{\lambda^*} = \lambda^* \langle a \rangle_H + \frac{\langle \mu \rangle_A}{\lambda^*} \geq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$$

from (25) and (26). Therefore, $\liminf_{L \rightarrow 0^+} c_L^* \geq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$. Eventually,

$$\lim_{L \rightarrow 0^+} c_L^* = 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$$

and the proof of Theorem 2.1 is complete. \square

Proof of Lemma 3.1. Observe first that, for $\lambda = 0$ and for any $L > 0$, $k(0, L)$ is the principal eigenvalue of the problem

$$(a_L \phi_L')' + \mu_L \phi_L = k(0, L) \phi_L \text{ in } \mathbb{R},$$

and we denote $\phi_L = \psi_{0,L}$ a principal eigenfunction, which is L -periodic, positive and unique up to multiplication. In other words, $k(0, L) = -\rho_{1,L}$ under the notations of Section 1. Dividing the above elliptic equation by ϕ_L and integrating by parts over $[0, L]$, one gets

$$k(0, L) = \frac{1}{L} \int_0^L \frac{a_L \phi_L'^2}{\phi_L^2} + \int_0^1 \mu(x) dx \geq \langle \mu \rangle_A > 0.$$

On the other hand, as already recalled, $\frac{\partial k}{\partial \lambda}(0, L) = 0$ and the map $\lambda \mapsto k(\lambda, L)$ is convex for all $L > 0$. Therefore,

$$\forall \lambda > 0, \forall L > 0, k(\lambda, L) \geq k(0, L) \geq \langle \mu \rangle_A > 0.$$

Assume here that there exists a sequence $(L_n)_{n \in \mathbb{N}}$ of positive numbers such that $L_n \rightarrow 0^+$ and $\lambda_{L_n}^* \rightarrow 0^+$ as $n \rightarrow +\infty$. One then gets

$$c_{L_n}^* = \frac{k(\lambda_{L_n}^*, L_n)}{\lambda_{L_n}^*} \geq \frac{\langle \mu \rangle_A}{\lambda_{L_n}^*} \rightarrow +\infty \text{ as } n \rightarrow +\infty.$$

This is contradiction with (27). Thus, for $L > 0$ small enough, the family $(\lambda_L^*)_L$ is bounded from below by a positive constant $\underline{\lambda} > 0$ (actually, these arguments show that the whole family $(\lambda_L^*)_{L > 0}$ is bounded from below by a positive constant).

It remains now to prove that $(\lambda_L^*)_L$ is bounded from above when L is small enough. We assume, to the contrary, that there exists a sequence $L_n \rightarrow 0^+$ as $n \rightarrow +\infty$ such that $\lambda_{L_n}^* \rightarrow +\infty$ as $n \rightarrow +\infty$. Call

$$k_n = k(\lambda_{L_n}^*, L_n), \quad \psi_n(x) = \psi_{\lambda_{L_n}^*, L_n}(x)$$

and

$$\varphi_n(x) = \varphi_{\lambda_{L_n}^*, L_n}(x) = e^{\lambda_{L_n}^* x} \psi_n(x)$$

for all $n \in \mathbb{N}$ and $x \in \mathbb{R}$. Rewriting (23) for $\lambda = \lambda_{L_n}^*$ and for $L = L_n$, one consequently gets

$$\forall n \in \mathbb{N}, (a_{L_n} \varphi_n')' + \mu_{L_n} \varphi_n = k_n \varphi_n \text{ in } \mathbb{R}. \quad (28)$$

Owing to the positivity and the L_n -periodicity of the $C^2(\mathbb{R})$ eigenfunction ψ_n , it follows that

$$\forall n \in \mathbb{N}, \exists \theta_n \in [0, L_n], \psi_n(\theta_n) = \max_{x \in \mathbb{R}} \psi_n(x) = \max_{x \in [0, L_n]} \psi_n(x),$$

whence

$$\forall n \in \mathbb{N}, \psi_n'(\theta_n) = 0.$$

For each $n \in \mathbb{N}$, let $M_{L_n} = [1/L_n] + 1 \in \mathbb{N}$. Thus,

$$\forall n \in \mathbb{N}, \varphi_n'(\theta_n + M_{L_n} L_n) = \lambda_{L_n}^* e^{\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \psi_n(\theta_n).$$

Multiplying (28) by φ_n and integrating by parts over the interval $[\theta_n, \theta_n + M_{L_n} L_n]$, one then obtains

$$\underbrace{a_{L_n}(\theta_n + M_{L_n} L_n) \varphi_n'(\theta_n + M_{L_n} L_n) \varphi_n(\theta_n + M_{L_n} L_n) - a_{L_n}(\theta_n) \varphi_n'(\theta_n) \varphi_n(\theta_n)}_{A(n)} - \underbrace{\int_{\theta_n}^{\theta_n + M_{L_n} L_n} a_{L_n} \varphi_n'^2}_{B(n)} + \underbrace{\int_{\theta_n}^{\theta_n + M_{L_n} L_n} \mu_{L_n} \varphi_n^2}_{C(n)} = k_n \int_{\theta_n}^{\theta_n + M_{L_n} L_n} \varphi_n^2. \quad (29)$$

But, for each $n \in \mathbb{N}$, $M_{L_n} \in \mathbb{N}$ while a_{L_n} and ψ_n are L_n -periodic. Hence, $a_{L_n}(\theta_n + M_{L_n} L_n) = a_{L_n}(\theta_n)$, $\psi_n(\theta_n + M_{L_n} L_n) = \psi_n(\theta_n)$, and $\psi_n'(\theta_n + M_{L_n} L_n) = \psi_n'(\theta_n) = 0$. Then,

$$\begin{aligned} A(n) &= a_{L_n}(\theta_n) \lambda_{L_n}^* \psi_n^2(\theta_n) \left(e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} - e^{2\lambda_{L_n}^* \theta_n} \right) \\ &\geq \frac{\alpha_1}{2} \times \lambda_{L_n}^* \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \quad (\alpha_1 > 0 \text{ is given by (4)}), \end{aligned} \quad (30)$$

whenever n is large enough so that $2 \leq e^{2\lambda_{L_n}^* M_{L_n} L_n}$ (remember that $\lambda_{L_n}^* \rightarrow +\infty$ as $n \rightarrow +\infty$, by assumption). Meanwhile, for all $n \in \mathbb{N}$,

$$\begin{aligned} |C(n)| &\leq \int_{\theta_n}^{\theta_n + M_{L_n} L_n} \left| \mu\left(\frac{x}{L_n}\right) \right| e^{2\lambda_{L_n}^* x} \psi_n^2(x) dx \\ &\leq \mu_\infty \times \frac{\psi_n^2(\theta_n)}{2\lambda_{L_n}^*} \times e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)}, \end{aligned} \quad (31)$$

where $\mu_\infty = \max_{x \in \mathbb{R}} |\mu(x)|$. On the other hand, (14) and (18) yield

$$k_n \leq 2\sqrt{a_M \mu_M} \times \lambda_{L_n}^*$$

for all $n \in \mathbb{N}$, whence

$$\begin{aligned} k_n \int_{\theta_n}^{\theta_n + M_{L_n} L_n} \varphi_n^2 &= k_n \int_{\theta_n}^{\theta_n + M_{L_n} L_n} e^{2\lambda_{L_n}^* x} \psi_n^2(x) dx \\ &\leq \sqrt{a_M \mu_M} \times \psi_n^2(\theta_n) \times e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)}. \end{aligned} \quad (32)$$

Now, the term $B(n)$ can be estimated as follows

$$\begin{aligned} B(n) &= \sum_{j=0}^{M_{L_n}-1} \int_{\theta_n + jL_n}^{\theta_n + (j+1)L_n} a_{L_n} e^{2\lambda_{L_n}^* x} (\psi_n'(x) + \lambda_{L_n}^* \psi_n(x))^2 dx \\ &\leq \sum_{j=0}^{M_{L_n}-1} \alpha_2 e^{2\lambda_{L_n}^* (\theta_n + (j+1)L_n)} \int_{\theta_n + jL_n}^{\theta_n + (j+1)L_n} (\psi_n'(x) + \lambda_{L_n}^* \psi_n(x))^2 dx \\ &\hspace{15em} [\text{from (4)}] \\ &= \sum_{j=0}^{M_{L_n}-1} \alpha_2 e^{2\lambda_{L_n}^* (\theta_n + (j+1)L_n)} \int_0^{L_n} (\psi_n'(x) + \lambda_{L_n}^* \psi_n(x))^2 dx \end{aligned}$$

since ψ_n is L_n -periodic. One has

$$\int_0^{L_n} (\psi_n'(x) + \lambda_{L_n}^* \psi_n(x))^2 dx \leq \psi_n^2(\theta_n) \int_0^{L_n} \left(\frac{\psi_n'(x)}{\psi_n(x)} + \lambda_{L_n}^* \right)^2 dx.$$

We refer now to equation (15). Taking $\lambda = \lambda_{L_n}^*$, dividing this equation (15) by the L_n -periodic function ψ_n and then integrating by parts over the interval $[0, L_n]$, we

get

$$\int_0^{L_n} a_{L_n} \left(\frac{\psi'_n}{\psi_n} \right)^2 + 2\lambda_{L_n}^* \int_0^{L_n} a_{L_n} \frac{\psi'_n}{\psi_n} + \lambda_{L_n}^{*2} \int_0^{L_n} a_{L_n} + \int_0^{L_n} \mu_{L_n} = k_n L_n$$

for all $n \in \mathbb{N}$. Thus,

$$\int_0^{L_n} a_{L_n} \left(\frac{\psi'_n}{\psi_n} + \lambda_{L_n}^* \right)^2 + \underbrace{\int_0^{L_n} \mu_{L_n}}_{>0} = k_n L_n \leq 2\sqrt{a_M \mu_M} \times \lambda_{L_n}^* L_n.$$

Owing to (4), it follows that

$$\forall n \in \mathbb{N}, \int_0^{L_n} \left(\frac{\psi'_n}{\psi_n} + \lambda_{L_n}^* \right)^2 \leq \frac{2\sqrt{a_M \mu_M}}{\alpha_1} \times \lambda_{L_n}^* L_n.$$

Putting the above result into $B(n)$, we obtain, for all $n \in \mathbb{N}$,

$$\begin{aligned} B(n) &\leq \frac{2\alpha_2 \sqrt{a_M \mu_M}}{\alpha_1} \times \lambda_{L_n}^* L_n \psi_n^2(\theta_n) \sum_{j=0}^{M_{L_n}-1} e^{2\lambda_{L_n}^* (\theta_n + (j+1)L_n)} \\ &= \frac{2\alpha_2 \sqrt{a_M \mu_M}}{\alpha_1} \times \lambda_{L_n}^* L_n \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + L_n)} \times \frac{e^{2\lambda_{L_n}^* L_n M_{L_n}} - 1}{e^{2\lambda_{L_n}^* L_n} - 1} \\ &\leq \frac{2\alpha_2 \sqrt{a_M \mu_M}}{\alpha_1} \times \psi_n^2(\theta_n) \times \frac{\lambda_{L_n}^* L_n e^{2\lambda_{L_n}^* L_n}}{e^{2\lambda_{L_n}^* L_n} - 1} \times e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \\ &\leq \beta \times \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \times (\lambda_{L_n}^* L_n + 1), \end{aligned} \quad (33)$$

where $\beta = (2\alpha_2 \sqrt{a_M \mu_M} / \alpha_1) \times C$ and C is a positive constant such that

$$\forall x \geq 0, \frac{x e^{2x}}{e^{2x} - 1} \leq C \times (x + 1).$$

Lastly, let us rewrite equation (29) as

$$\forall n \in \mathbb{N}, A(n) + C(n) - k_n \int_{\theta_n}^{\theta_n + M_{L_n} L_n} \varphi_n^2 = B(n).$$

Together with (30), (31), (32) and (33), one concludes that there exists $n_0 \in \mathbb{N}$ such that for $n \geq n_0$,

$$\begin{aligned} &\frac{\alpha_1}{2} \times \lambda_{L_n}^* \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} - \mu_\infty \times \frac{\psi_n^2(\theta_n)}{2\lambda_{L_n}^*} \times e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \\ &- \sqrt{a_M \mu_M} \times \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \\ &\leq \beta \times \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)} \times (\lambda_{L_n}^* L_n + 1). \end{aligned} \quad (34)$$

Divide (34) by $\lambda_{L_n}^* \psi_n^2(\theta_n) e^{2\lambda_{L_n}^* (\theta_n + M_{L_n} L_n)}$. Then

$$\forall n \geq n_0, \frac{\alpha_1}{2} - \frac{\mu_\infty}{2(\lambda_{L_n}^*)^2} - \frac{\sqrt{a_M \mu_M}}{\lambda_{L_n}^*} \leq \beta \times \left(L_n + \frac{1}{\lambda_{L_n}^*} \right).$$

Passing to the limit as $n \rightarrow +\infty$, one has $L_n \rightarrow 0^+$ and $\lambda_{L_n}^* \rightarrow +\infty$, whence $\alpha_1 \leq 0$, which is impossible.

Therefore the assumption that $\lambda_{L_n}^* \rightarrow +\infty$ as $L_n \rightarrow 0^+$ is false and consequently the family $(\lambda_L^*)_L$ is bounded from above by some positive $\bar{\lambda} > 0$ whenever L is small (i.e. $0 < L \leq L_0$). This completes the proof of Lemma 3.1. \square

Remark 5. From Theorem 10, one concludes that the map $(0, +\infty) \ni L \mapsto c_L^*$ can be extended by continuity to the right at $L = 0^+$. Furthermore, for any sequence $(L_n)_n$ of positive numbers such that $L_n \rightarrow 0^+$ as $n \rightarrow +\infty$, one claims that the positive numbers $\lambda_{L_n}^*$ given in (14) converge to $\sqrt{\langle a \rangle_H^{-1} \langle \mu \rangle_A} = \sqrt{\langle a^{-1} \rangle_A \langle \mu \rangle_A}$ as $n \rightarrow +\infty$. Indeed

$$\forall n \in \mathbb{N}, c_{L_n}^* = \frac{k(\lambda_{L_n}^*, L_n)}{\lambda_{L_n}^*}$$

and Lemma 3.1 implies that, up to extraction of a subsequence, $\lambda_{L_n}^* \rightarrow \lambda^* > 0$. Passing to the limit as $n \rightarrow +\infty$ in the above equation and due (26) together with Step 2 of the proof of Theorem 10, one gets

$$2\sqrt{\langle a \rangle_H \langle \mu \rangle_A} = \frac{\bar{k}(\lambda^*)}{\lambda^*} = \lambda^* \langle a \rangle_H + \frac{\langle \mu \rangle_A}{\lambda^*},$$

whence $\lambda^* = \sqrt{\langle a \rangle_H^{-1} \langle \mu \rangle_A}$. Since the limit does not depend on any subsequence, one concludes that the limit of λ_L^* , as $L \rightarrow 0^+$, exists and

$$\lim_{L \rightarrow 0^+} \lambda_L^* = \sqrt{\langle a \rangle_H^{-1} \langle \mu \rangle_A} = \sqrt{\langle a^{-1} \rangle_A \langle \mu \rangle_A}.$$

Remark 6. As a matter of fact, the sharp lower bound

$$\liminf_{L \rightarrow 0^+} c_L^* \geq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$$

can be obtained by using another method.¹ It consists in proving that, if $(L_n)_{n \in \mathbb{N}}$ is a sequence of positive real numbers such that $\lim_{n \rightarrow +\infty} c_{L_n}^* = \liminf_{L \rightarrow 0^+} c_L^*$, then the solutions u_{L_n} of (9) with $L = L_n$ and speeds $c_{L_n}^*$ converge, after suitable normalization and up to extraction of a subsequence, to a solution u of the homogenized equation

$$\frac{\partial u}{\partial t} = \langle a \rangle_H \frac{\partial^2 u}{\partial x^2} + \langle f(\cdot, u) \rangle_A \quad (35)$$

such that $u(t, x) = U(x + ct)$, where $c = \liminf_{L \rightarrow 0^+} c_L^*$. Furthermore, U is increasing, $U(-\infty) = 0$, $U(+\infty)$ is the unique positive root of $\langle f(\cdot, U(+\infty)) \rangle_A = 0$. Since the function $u \mapsto \langle f(\cdot, u) \rangle_A / u$ is decreasing over $(0, +\infty)$ and since the minimal speed of usual travelling front for (35) is equal to $2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$, this implies that $\liminf_{L \rightarrow 0^+} c_L^* \geq 2\sqrt{\langle a \rangle_H \langle \mu \rangle_A}$.

This convergence result has its own interest. Actually, its proof requires technical extra-arguments which are too long to be included in details in the present paper and which will be the purpose of a forthcoming paper. We just sketch here the main ideas: (i) proof of the uniform convergence of the positive solutions p_{L_n} of (6) to the unique positive zero p of $\langle f(\cdot, p) \rangle_A = 0$, (ii) proof of $H_{loc}^1(\mathbb{R} \times \mathbb{R})$ estimates for the functions u_{L_n} , $a_{L_n} \frac{\partial u_{L_n}}{\partial x}$ and $\frac{\partial u_{L_n}}{\partial t}$, which are independent of n , (iii) passage to the limit, up to extraction of a subsequence, and convergence of the functions u_{L_n} to a travelling front $u(t, x) = U(x + ct)$ of (35), satisfying the right conditions at $\pm\infty$.

¹The authors thank the referee for pointing out this fact.

4. Monotonicity of the minimal speeds c_L^* near the homogenization limit.

This section is devoted to the proof of Theorem 2.2. Before going further in the proof, we recall that for each $L > 0$, the minimal speed c_L^* is given by the variational formula

$$c_L^* = \min_{\lambda > 0} \frac{k(\lambda, L)}{\lambda} = \frac{k(\lambda_L^*, L)}{\lambda_L^*},$$

where $\lambda_L^* > 0$ and $k(\lambda, L)$ is the principal eigenvalue of the elliptic equation (15). Notice that $k(\lambda, L)$ can be defined for all $\lambda \in \mathbb{R}$ and $L > 0$.

Step 1: properties of $k(\lambda, L)$ and definition of $\tilde{k}(\lambda, L)$. The principal eigenfunction $\psi_{\lambda, L}$ of (15) is L -periodic, positive and unique up to multiplication. Denote

$$\phi_{\lambda, L}(x) = \psi_{\lambda, L}(Lx)$$

for all $L > 0$, $\lambda \in \mathbb{R}$ and $x \in \mathbb{R}$. Each function $\phi_{\lambda, L}$ is 1-periodic, positive and it is the principal eigenfunction of

$$(a\phi'_{\lambda, L})' + 2L\lambda a\phi'_{\lambda, L} + L\lambda a'\phi_{\lambda, L} + L^2\lambda^2 a\phi_{\lambda, L} + L^2\mu\phi_{\lambda, L} = L^2k(\lambda, L)\phi_{\lambda, L},$$

associated to the principal eigenvalue $L^2k(\lambda, L)$. But the above problem can be defined for all $\lambda \in \mathbb{R}$ and $L \in \mathbb{R}$. That is, for each $(\lambda, L) \in \mathbb{R}^2$, there exists a unique principal eigenvalue $\tilde{k}(\lambda, L)$ and a unique (up to multiplication) principal eigenfunction $\tilde{\phi}(\lambda, L)$ of

$$(a\tilde{\phi}'_{\lambda, L})' + 2L\lambda a\tilde{\phi}'_{\lambda, L} + L\lambda a'\tilde{\phi}_{\lambda, L} + L^2\lambda^2 a\tilde{\phi}_{\lambda, L} + L^2\mu\tilde{\phi}_{\lambda, L} = \tilde{k}(\lambda, L)\tilde{\phi}_{\lambda, L}. \quad (36)$$

Furthermore, $\tilde{\phi}_{\lambda, L}$ is 1-periodic, positive and it can be normalized so that

$$\int_0^1 \tilde{\phi}_{\lambda, L}^2(x) dx = 1 \quad (37)$$

for all $(\lambda, L) \in \mathbb{R}^2$. By uniqueness of the principal eigenvalues, it follows that

$$\forall L > 0, \forall \lambda \in \mathbb{R}, \quad \tilde{k}(\lambda, L) = L^2k(\lambda, L)$$

and $\tilde{\phi}_{\lambda, L}$ and $\phi_{\lambda, L}$ are equal up to multiplication by positive constants for each $L > 0$ and $\lambda \in \mathbb{R}$.

Some useful properties of $k(\lambda, L)$ as $L \rightarrow 0^+$ shall now be derived from the study of the function \tilde{k} . Notice first that, since the coefficients of the left-hand side of (36) are analytic in (λ, L) , the function \tilde{k} is analytic, and from the normalization (37), the functions $\tilde{\phi}_{\lambda, L}$ also depend analytically in $H_{loc}^2(\mathbb{R})$ on the parameters λ and L (see [10, 20]). In particular, the function k is analytic in $\mathbb{R} \times (0, +\infty)$. Observe also that

$$\tilde{k}(\lambda, 0) = 0 \text{ and } \tilde{\phi}_{\lambda, 0} = 1 \text{ for all } \lambda \in \mathbb{R}.$$

Lastly, when λ is changed into $-\lambda$ or when L is changed into $-L$, then the operator in (36) is changed into its adjoint. But since the principal eigenvalues of the operator and its adjoint are identical, it follows that

$$\forall (\lambda, L) \in \mathbb{R}^2, \quad \tilde{k}(\lambda, L) = \tilde{k}(\lambda, -L) = \tilde{k}(-\lambda, L).$$

In particular, it follows that

$$\forall (i, j) \in \mathbb{N}^2, \quad \frac{\partial^i \tilde{k}}{\partial \lambda^i}(\lambda, 0) = \frac{\partial^i \partial^{2j+1} \tilde{k}}{\partial \lambda^i \partial L^{2j+1}}(\lambda, 0) = 0. \quad (38)$$

Therefore, for all $\bar{\lambda} \in \mathbb{R}$,

$$k(\lambda, L) = \frac{\tilde{k}(\lambda, L)}{L^2} \rightarrow \frac{1}{2} \times \frac{\partial^2 \tilde{k}}{\partial L^2}(\bar{\lambda}, 0) \text{ as } (\lambda, L) \rightarrow (\bar{\lambda}, 0^+).$$

But since this limit is equal to $\bar{k}(\bar{\lambda}) = \bar{\lambda}^2 < a >_H + < \mu >_A$ from Step 2 of the proof of Theorem 2.1, one then gets that

$$\frac{1}{2} \times \frac{\partial^2 \tilde{k}}{\partial L^2}(\bar{\lambda}, 0) = \bar{\lambda}^2 < a >_H + < \mu >_A \text{ for all } \bar{\lambda} \in \mathbb{R}. \quad (39)$$

It also follows from (38) that

$$\frac{\partial^2 k}{\partial \lambda^2}(\lambda, L) = \frac{1}{L^2} \times \frac{\partial^2 \tilde{k}}{\partial \lambda^2}(\lambda, L) \rightarrow \frac{1}{2} \times \frac{\partial^4 \tilde{k}}{\partial \lambda^2 \partial L^2}(\bar{\lambda}, 0) \text{ as } (\lambda, L) \rightarrow (\bar{\lambda}, 0^+). \quad (40)$$

From (39) and (40), one deduces that

$$\frac{\partial^2 k}{\partial \lambda^2}(\lambda, L) \rightarrow 2 < a >_H > 0 \text{ as } (\lambda, L) \rightarrow (\bar{\lambda}, 0^+). \quad (41)$$

Similarly, as $(\lambda, L) \rightarrow (\bar{\lambda}, 0^+)$,

$$\left\{ \begin{array}{l} \frac{\partial k}{\partial L}(\lambda, L) = \frac{\partial}{\partial L} \left(\frac{\tilde{k}(\lambda, L)}{L^2} \right) \rightarrow \frac{1}{6} \times \frac{\partial^3 \tilde{k}}{\partial L^3}(\bar{\lambda}, 0) = 0 \\ \frac{\partial^2 k}{\partial \lambda \partial L}(\lambda, L) = \frac{\partial}{\partial L} \left(\frac{1}{L^2} \times \frac{\partial \tilde{k}}{\partial \lambda}(\lambda, L) \right) \rightarrow \frac{1}{6} \times \frac{\partial^4 \tilde{k}}{\partial \lambda \partial L^3}(\bar{\lambda}, 0) = 0 \\ \frac{\partial^2 k}{\partial L^2}(\lambda, L) = \frac{\partial^2}{\partial L^2} \left(\frac{\tilde{k}(\lambda, L)}{L^2} \right) \rightarrow \frac{1}{12} \times \frac{\partial^4 \tilde{k}}{\partial L^4}(\bar{\lambda}, 0) \end{array} \right. \quad (42)$$

Remark 7. As a byproduct of the fact that \tilde{k} and k are even in λ , it follows that the minimal speed of pulsating fronts propagating from right to left (as in Definition 1.2) is the same as that of fronts propagating from left to right.

Step 2: properties of c_L^* and λ_L^* in the neighbourhood of $L = 0^+$. Let us first prove that, for each fixed $L > 0$, the positive real number $\lambda_L^* > 0$ given in (14) is unique. Indeed, if there are $0 < \lambda_1 < \lambda_2$ such that

$$c_L^* = \frac{k(\lambda_1, L)}{\lambda_1} = \frac{k(\lambda_2, L)}{\lambda_2} = \min_{\lambda > 0} \frac{k(\lambda, L)}{\lambda},$$

then $k(\lambda, L) = c_L^* \lambda$ for all $\lambda \in [\lambda_1, \lambda_2]$ since k is convex with respect to λ . Then $k(\lambda, L) = c_L^* \lambda$ for all $\lambda \in \mathbb{R}$ by analyticity of the map $\mathbb{R} \ni \lambda \mapsto k(\lambda, L)$. But $k(0, L) = -\rho_{1,L} > 0$, which gives a contradiction. Therefore, for each $L > 0$, λ_L^* is the unique minimum of the map $(0, +\infty) \ni \lambda \mapsto k(\lambda, L)/\lambda$.

Furthermore, we claim that $L \mapsto \lambda_L^*$ and $L \mapsto c_L^*$ are of class C^∞ in a right neighbourhood of $L = 0$. Indeed, by definition, λ_L^* satisfies

$$F(\lambda_L^*, L) := \frac{\partial k}{\partial \lambda}(\lambda_L^*, L) \times \lambda_L^* - k(\lambda_L^*, L) = 0. \quad (43)$$

The function $(\lambda, L) \mapsto F(\lambda, L)$ is of class C^∞ on $\mathbb{R} \times (0, +\infty)$ and $\frac{\partial F}{\partial \lambda}(\lambda, L) = \frac{\partial^2 k}{\partial \lambda^2}(\lambda, L) \times \lambda$. But

$$\lambda_L^* \rightarrow \lambda^* = \sqrt{< a >_H^{-1} < \mu >_A} > 0 \text{ as } L \rightarrow 0^+$$

from Remark 5, and

$$\frac{\partial^2 k}{\partial \lambda^2}(\lambda_L^*, L) \rightarrow 2 \langle a \rangle_H > 0 \text{ as } L \rightarrow 0^+$$

from (41). Therefore, from the implicit function theorem, the map $L \mapsto \lambda_L^*$ is of class C^∞ in an interval $(0, L_0)$ for some $L_0 > 0$. As a consequence of formula (14), the map $L \mapsto c_L^*$ is also of class C^∞ on $(0, L_0)$.

For each $L \in (0, L_0)$, one has

$$\begin{aligned} \frac{dc_L^*}{dL} &= \left(\frac{1}{\lambda_L^*} \times \frac{\partial k}{\partial \lambda}(\lambda_L^*, L) - \frac{k(\lambda_L^*, L)}{(\lambda_L^*)^2} \right) \times \frac{d\lambda_L^*}{dL} + \frac{1}{\lambda_L^*} \times \frac{\partial k}{\partial L}(\lambda_L^*, L) \\ &= \frac{1}{\lambda_L^*} \times \frac{\partial k}{\partial L}(\lambda_L^*, L) \end{aligned}$$

by definition of λ_L^* and formula (14). But $\lambda_L^* \rightarrow \lambda^* > 0$ and $\frac{\partial k}{\partial L}(\lambda_L^*, L) \rightarrow 0$ as $L \rightarrow 0^+$ from (42). Thus,

$$\frac{dc_L^*}{dL} \rightarrow 0 \text{ as } L \rightarrow 0^+.$$

On the other hand, it follows from (41), (42) and (43) that

$$\frac{d\lambda_L^*}{dL} = \frac{1}{\lambda_L^* \times \frac{\partial^2 k}{\partial \lambda^2}(\lambda_L^*, L)} \times \left(\frac{\partial k}{\partial L}(\lambda_L^*, L) - \lambda_L^* \times \frac{\partial^2 k}{\partial \lambda \partial L}(\lambda_L^*, L) \right) \rightarrow 0$$

as $L \rightarrow 0^+$. Therefore,

$$\begin{aligned} \frac{d^2 c_L^*}{dL^2} &= \frac{d\lambda_L^*}{dL} \times \left(-\frac{1}{(\lambda_L^*)^2} \times \frac{\partial k}{\partial L}(\lambda_L^*, L) + \frac{1}{\lambda_L^*} \times \frac{\partial^2 k}{\partial \lambda \partial L}(\lambda_L^*, L) \right) \\ &\quad + \frac{1}{\lambda_L^*} \times \frac{\partial^2 k}{\partial L^2}(\lambda_L^*, L) \\ &\rightarrow \frac{1}{12\lambda^*} \times \frac{\partial^4 \tilde{k}}{\partial L^4}(\lambda^*, 0) \text{ as } L \rightarrow 0^+, \end{aligned} \tag{44}$$

from (42).

Step 3: calculation of $\frac{\partial^4 \tilde{k}}{\partial L^4}(\lambda^*, 0)$. In this step, we fix $\lambda^* = \sqrt{\langle a \rangle_H^{-1} \langle \mu \rangle_A}$. Since the functions $\tilde{\phi}_{\lambda^*, L}$ depend analytically on $L \in \mathbb{R}$ in $H_{loc}^2(\mathbb{R})$, the expansion

$$\tilde{\phi}_{\lambda^*, L} = 1 + L\phi_1 + L^2\phi_2 + L^3\phi_3 + L^4\phi_4 + \dots$$

is valid in $H_{loc}^2(\mathbb{R})$ in a neighbourhood of $L = 0$, where $1 = \tilde{\phi}_{\lambda^*, 0}$ and

$$\phi_i = \frac{1}{i!} \times \frac{\partial^i \tilde{\phi}_{\lambda^*, L}}{\partial L^i} \Big|_{L=0}$$

for each $i \geq 1$. We now put this expansion into

$$\begin{aligned} (a\tilde{\phi}'_{\lambda^*, L})' + 2L\lambda^* a\tilde{\phi}'_{\lambda^*, L} + L\lambda^* a' \tilde{\phi}_{\lambda^*, L} + L^2(\lambda^*)^2 a\tilde{\phi}_{\lambda^*, L} + L^2 \mu \tilde{\phi}_{\lambda^*, L} \\ = \tilde{k}(\lambda^*, L) \tilde{\phi}_{\lambda^*, L} \end{aligned}$$

and remember that

$$\tilde{k}(\lambda^*, 0) = \frac{\partial \tilde{k}}{\partial L}(\lambda^*, 0) = \frac{\partial^3 \tilde{k}}{\partial L^3}(\lambda^*, 0) = 0$$

and

$$\frac{\partial^2 \tilde{k}}{\partial L^2}(\lambda^*, 0) = 2 \times [(\lambda^*)^2 \langle a \rangle_H + \langle \mu \rangle_A] = 4 \langle \mu \rangle_A$$

from (38) and (39). Since both $\tilde{\phi}_{\lambda^*, L}$ and $\tilde{k}(\lambda^*, L)$ depend analytically on L , it follows in particular that

$$\begin{cases} (a\phi_1)' + \lambda^* a' = 0, \\ (a\phi_2)' + 2\lambda^* a\phi_1' + \lambda^* a'\phi_1 + (\lambda^*)^2 a + \mu = 2 \langle \mu \rangle_A, \\ (a\phi_3)' + 2\lambda^* a\phi_2' + \lambda^* a'\phi_2 + (\lambda^*)^2 a\phi_1 + \mu\phi_1 = 2 \langle \mu \rangle_A \phi_1, \\ (a\phi_4)' + 2\lambda^* a\phi_3' + \lambda^* a'\phi_3 + (\lambda^*)^2 a\phi_2 + \mu\phi_2 \\ \qquad \qquad \qquad = 2 \langle \mu \rangle_A \phi_2 + \frac{1}{24} \times \frac{\partial^4 \tilde{k}}{\partial L^4}(\lambda^*, 0) \end{cases} \quad (45)$$

in \mathbb{R} . Furthermore, each function ϕ_i is 1-periodic and, by differentiating the normalization condition $\|\tilde{\phi}_{\lambda^*, L}\|_{L^2(0,1)}^2 = 1$ with respect to L at $L = 0$, it follows especially that

$$\int_0^1 \phi_1 = 0 \text{ and } \int_0^1 \phi_2 = -\frac{1}{2} \int_0^1 \phi_1^2.$$

It is then found that, for all $x \in \mathbb{R}$,

$$\phi_1(x) = \lambda^* \times \left(-x + \langle a \rangle_H \int_0^x \frac{1}{a(y)} dy - \frac{1}{2} \langle a \rangle_H \int_0^1 \frac{y}{a(y)} dy \right)$$

and

$$\begin{aligned} \phi_2'(x) &= \langle \mu \rangle_A \times \left[\frac{x}{a(x)} - \int_0^1 \frac{y}{a(y)} dy - \int_0^x \frac{1}{a(y)} dy - \frac{\langle a \rangle_H}{a(x)} \int_0^1 \frac{y}{a(y)} dy \right] \\ &\quad + \frac{1}{a(x)} \times \left[\langle a \rangle_H \int_0^1 \left(\frac{1}{a(y)} \int_0^y \mu(z) dz \right) dy - \int_0^x \mu(y) dy \right] \\ &\quad + (\lambda^*)^2 \left(x + \frac{1}{2} \right). \end{aligned}$$

Moreover, it follows from the third equation of (45) that, for all $x \in \mathbb{R}$,

$$\begin{aligned} a(x)\phi_3'(x) &= -2\lambda^* \int_0^x a(y)\phi_2'(y) dy - \lambda^* \int_0^x a'(y)\phi_2(y) dy \\ &\quad - (\lambda^*)^2 \int_0^x a(y)\phi_1(y) dy - \int_0^x \mu(y)\phi_1(y) dy \\ &\quad + 2 \langle \mu \rangle_A \int_0^x \phi_1(y) dy + \langle a \rangle_H c, \end{aligned}$$

where

$$\begin{aligned} c &= \int_0^1 \left[\frac{1}{a(y)} \times \left(2\lambda^* \int_0^y a(z)\phi_2'(z) dz + \lambda^* \int_0^y a'(z)\phi_2(z) dz + (\lambda^*)^2 \int_0^y a(z)\phi_1(z) dz \right. \right. \\ &\quad \left. \left. + \int_0^y \mu(z)\phi_1(z) dz - 2 \langle \mu \rangle_A \int_0^y \phi_1(z) dz \right) \right] dy \end{aligned}$$

On the other hand, by integrating the fourth equation of (45) over the interval $[0, 1]$, one gets that

$$\frac{1}{24} \times \frac{\partial^4 \tilde{k}}{\partial L^4}(\lambda^*, 0) = -2 \langle \mu \rangle_A \int_0^1 \phi_2 + \lambda^* \int_0^1 a\phi_3' + (\lambda^*)^2 \int_0^1 a\phi_2 + \int_0^1 \mu\phi_2. \quad (46)$$

Now, put all the previous calculations into (46). After a lengthy sequence of integrations by parts, it is finally found that

$$\frac{1}{24} \times \frac{\partial^4 \tilde{k}}{\partial L^4}(\lambda^*, 0) = \int_0^1 \frac{A(x)^2}{a(x)} dx - \langle a \rangle_H \left(\int_0^1 \frac{A(x)}{a(x)} dx \right)^2,$$

where

$$A(x) = \int_0^x \mu(y) dy + \langle \mu \rangle_A \langle a \rangle_H \int_0^x \frac{1}{a(y)} dy - 2 \langle \mu \rangle_A x.$$

From (44), it follows that

$$\frac{d^2 c_L^*}{dL^2} \rightarrow \gamma := 2 \sqrt{\langle a \rangle_H \langle \mu \rangle_A^{-1}} \times \left[\int_0^1 \frac{A(x)^2}{a(x)} dx - \langle a \rangle_H \left(\int_0^1 \frac{A(x)}{a(x)} dx \right)^2 \right]$$

as $L \rightarrow 0^+$. Cauchy-Schwarz inequality yields $\gamma \geq 0$. Furthermore, $\gamma = 0$ if and only if A is constant. But since $A(0) = 0$, the condition $\gamma = 0$ is equivalent to $A'(x) = 0$ for all x , which means that

$$\frac{\mu(x)}{\langle \mu \rangle_A} + \frac{\langle a \rangle_H}{a(x)} = 2 \quad \text{for all } x \in \mathbb{R}.$$

In particular, if μ is constant and a is not constant (resp. if a is constant and μ is not constant), then this condition is not satisfied, whence $\lim_{L \rightarrow 0^+} \frac{d^2 c_L^*}{dL^2} > 0$ in this case. That completes the proofs of Theorem 2.2 and Corollary 1. \square

Remark 8. In the case when $\langle \mu \rangle_A = 0$ and $\mu \not\equiv 0$, then $\rho_{1,L} < 0$ for each $L > 0$, and the minimal speed c_L^* of pulsating traveling fronts is well-defined and it is still positive. From the arguments developed in this section and in the previous one, one can check that, in this case,

$$c_L^* \rightarrow 0^+, \quad \lambda_L^* \rightarrow 0^+, \quad \frac{d\lambda_L^*}{dL} \rightarrow \sqrt{\frac{\beta}{\langle a \rangle_H}} > 0 \quad \text{and} \quad \frac{dc_L^*}{dL} \rightarrow 2\sqrt{\beta \langle a \rangle_H} > 0$$

as $L \rightarrow 0^+$, where

$$\beta = \int_0^1 \frac{A(x)^2}{a(x)} dx - \langle a \rangle_H \left(\int_0^1 \frac{A(x)}{a(x)} dx \right)^2 > 0$$

and $A(x) = \int_0^x \mu(y) dy$. Therefore, the speeds c_L^* are increasing in a right neighbourhood of $L = 0$ but, in this case, the variation is of the first order. Notice that the formula $\lim_{L \rightarrow 0^+} \frac{dc_L^*}{dL} = 2\sqrt{\beta \langle a \rangle_H}$ is coherent with the numerical calculations done by Kinezaki, Kawasaki and Shigesada in [21] (see Figure 3b with $\langle \mu \rangle_A = 0$, that is $A = 0$ under the notations of [21]).

5. Proof of Theorem 2.3 . As in the proofs of the previous theorems, we use the following formula for the minimal speed:

$$c_z^* = \min_{\lambda > 0} \frac{k_z(\lambda)}{\lambda} = \frac{k_z(\lambda_z^*)}{\lambda_z^*}, \quad (47)$$

where $k_z(\lambda)$ is defined as the unique real number such that there exists a positive L_0 -periodic function ψ satisfying:

$$\psi'' + 2\lambda \psi' + \lambda^2 \psi + \mu_z(x)\psi = k_z(\lambda)\psi \quad \text{in } (0, L_0). \quad (48)$$

Setting $\varphi(x) = e^{\lambda x}\psi(x)$, the above equation and periodicity conditions become equivalent to:

$$\begin{cases} \varphi'' + \mu_z(x)\varphi = k_z(\lambda)\varphi & \text{in } (0, L_0), \\ \varphi(L_0) = e^{\lambda L_0}\varphi(0), \\ \varphi'(L_0) = e^{\lambda L_0}\varphi'(0), \end{cases} \quad (49)$$

which therefore admits, for every positive λ , a unique solution $(\varphi, k_z(\lambda))$ with $\varphi > 0$ satisfying the normalisation condition $\varphi(0) = 1$.

Let $\lambda > 0$ be fixed. System (49), together with the normalization condition $\varphi(0) = 1$, is equivalent to:

$$\begin{cases} \varphi'' = (k_z(\lambda) - m)\varphi & \text{on } [0, l/2), \\ \varphi'' = k_z(\lambda)\varphi & \text{on } [l/2, l/2 + z), \\ \varphi'' = (k_z(\lambda) - m)\varphi & \text{on } [l/2 + z, l + z), \\ \varphi'' = k_z(\lambda)\varphi & \text{on } [l + z, L_0), \\ \varphi(0) = 1, \varphi(L_0) = e^{\lambda L_0}\varphi(0), \varphi'(L_0) = e^{\lambda L_0}\varphi'(0). \end{cases} \quad (50)$$

For each $z \in [0, L_0 - l]$, let λ_z^* be defined by the formula (47). We have the following lemma:

Lemma 5.1. *Assume that $l > 3L_0/4$. Then, for all $z \in [0, L_0 - l]$, we have $k_z(\lambda_z^*) > m$.*

Proof. Let us divide equation (48) by ψ and integrate by parts over $[0, L_0]$. Using the L_0 -periodicity of ψ , we obtain:

$$\int_0^{L_0} \frac{|\psi'|^2}{\psi^2} + L_0\lambda^2 + \int_0^{L_0} \mu_z(x)dx = L_0k_z(\lambda).$$

Thus,

$$k_z(\lambda) \geq \lambda^2 + \frac{1}{L_0} \int_0^{L_0} \mu_z(x)dx = \lambda^2 + m\frac{l}{L_0}. \quad (51)$$

From (47) and (51) and since, from (18), $c_z^* \leq 2\sqrt{m}$, we get:

$$(\lambda_z^*)^2 + m\frac{l}{L_0} \leq k_z(\lambda_z^*) \leq 2\lambda_z^*\sqrt{m}.$$

Thus, $(\lambda_z^*)^2 - 2\lambda_z^*\sqrt{m} + ml/L_0 \leq 0$, which implies that

$$\lambda_z^* \geq \sqrt{m} - \sqrt{m - ml/L_0}.$$

Using (51), we finally get

$$k_z(\lambda_z^*) \geq 2m(1 - \sqrt{1 - l/L_0}) > m,$$

as soon as $l > 3L_0/4$. \square

We now turn to the proof of Theorem 2.3 and we assume that $l \in (3L_0/4, L_0)$. Using the fact that $\varphi \in C^1(\mathbb{R})$, a straightforward but lengthy computation shows that, whenever $k_z(\lambda) > m$, system (50) is equivalent to

$$\frac{F(z, \lambda, k_z(\lambda))}{G(z, k_z(\lambda))} = 0,$$

where F and G are two functions, defined respectively in $[0, L_0 - l] \times (0, +\infty) \times [m, +\infty)$ and $[0, L_0 - l] \times [m, +\infty)$ by:

$$\begin{aligned} F(z, \lambda, s) = & 4(2s - m)\sqrt{s}\sqrt{s - m} \sinh(l\sqrt{s - m}) \sinh(\alpha\sqrt{s}) \\ & + m^2 \cosh(\beta\sqrt{s})(1 - \cosh(l\sqrt{s - m})) \\ & + 8(s^2 - ms)[\cosh(l\sqrt{s - m}) \cosh(\alpha\sqrt{s}) - \cosh(\lambda L_0)] \\ & + m^2 \cosh(\alpha\sqrt{s})(\cosh(l\sqrt{s - m}) - 1), \end{aligned} \quad (52)$$

and

$$\begin{aligned} G(z, s) = & m\sqrt{s} \cosh(l\sqrt{s - m}) [4 \sinh(\alpha\sqrt{s})(s/m - 1) \\ & + (\sinh(\alpha\sqrt{s}) - \sinh(\beta\sqrt{s})) (1 - 1/\cosh(l\sqrt{s - m}))] \\ & + m\sqrt{s - m} \sinh(l\sqrt{s - m}) \cosh(\alpha\sqrt{s}) \left[\frac{4s}{m} - 1 + \frac{\cosh(\beta\sqrt{s})}{\cosh(\alpha\sqrt{s})} \right], \end{aligned} \quad (53)$$

with $\alpha := L_0 - l$ and $\beta := L_0 - l - 2z$.

Each factor in the expression (53) is positive, as soon as $s > m$, for $z \in [0, L_0 - l]$. Thus, whenever $k_z(\lambda) > m$, system (50) is equivalent to the simpler equation

$$F(z, \lambda, k_z(\lambda)) = 0. \quad (54)$$

Furthermore, from Krein-Rutman theory, since the eigenfunction ψ in (48) is positive, $k_z(\lambda)$ is the largest real eigenvalue of the operator $\psi \mapsto \psi'' + 2\lambda \psi' + \lambda^2 \psi + \mu_z(x)\psi$. This result, implies that, for each $z \in [0, L_0 - l]$, and each $\lambda > 0$, $k_z(\lambda)$ is the largest real root of equation (54), as soon as $k_z(\lambda) > m$.

From equation (52), we easily see that

$$\lim_{s \rightarrow +\infty} F(z, \lambda, s) = +\infty, \quad (55)$$

for all $z \in [0, L_0 - l]$ and $\lambda > 0$. Moreover, differentiating (52) with respect to z , we obtain

$$\frac{\partial F}{\partial z}(z, \lambda, s) = 2m^2 \sqrt{s} \sinh(\sqrt{s}(L_0 - l - 2z)) [\cosh(l\sqrt{s - m}) - 1].$$

Thus, for all $s > m$, and $\lambda > 0$,

$$\frac{\partial F}{\partial z}(z, \lambda, s) > 0 \text{ for } z \in [0, (L_0 - l)/2], \quad (56)$$

and

$$\frac{\partial F}{\partial z}(z, \lambda, s) < 0 \text{ for } z \in ((L_0 - l)/2, L_0 - l].$$

Now, take $z_1 < z_2$ in $[0, (L_0 - l)/2]$, and assume that $c_{z_1}^* \leq c_{z_2}^*$. It follows from formula (47) that $k_{z_2}(\lambda) \geq c_{z_2}^* \lambda$, for all $\lambda > 0$. In particular,

$$k_{z_2}(\lambda_{z_1}^*) \geq c_{z_2}^* \lambda_{z_1}^* \geq c_{z_1}^* \lambda_{z_1}^* = k_{z_1}(\lambda_{z_1}^*). \quad (57)$$

From Lemma 5.1, we know that $k_{z_1}(\lambda_{z_1}^*) > m$. Thus, (57) implies $k_{z_2}(\lambda_{z_1}^*) > m$. From the above discussion, $k_{z_2}(\lambda_{z_1}^*)$ is therefore the largest real root of the equation $F(z_2, \lambda_{z_1}^*, k_{z_2}(\lambda_{z_1}^*)) = 0$, and, similarly, $k_{z_1}(\lambda_{z_1}^*)$ is the largest real root of $F(z_1, \lambda_{z_1}^*, k_{z_1}(\lambda_{z_1}^*)) = 0$. Using (55) and (56), and since $0 \leq z_1 < z_2 \leq (L_0 - l)/2$, we obtain $k_{z_2}(\lambda_{z_1}^*) < k_{z_1}(\lambda_{z_1}^*)$, which contradicts (57). Therefore, c_z^* is a decreasing function of z in $[0, (L_0 - l)/2]$. Similar arguments imply that c_z^* is an increasing function of z in $[(L_0 - l)/2, L_0 - l]$. This concludes the proof of Theorem 2.3. \square

REFERENCES

- [1] H. Berestycki and F. Hamel, *Front propagation in periodic excitable media*, Comm. Pure Appl. Math., **55** (2002), 949–1032. MR1900178
- [2] H. Berestycki, F. Hamel and N. Nadirashvili, *The principal eigenvalue of elliptic operators with large drift and applications to nonlinear propagation phenomena*, Comm. Math. Phys., **253** (2005), 451–480.
- [3] H. Berestycki, F. Hamel and N. Nadirashvili, *The speed of propagation for KPP type problems. I - Periodic framework*, J. Europ. Math. Soc., **7** (2005), 173–213. MR2127993
- [4] H. Berestycki, F. Hamel and L. Roques, *Analysis of the periodically fragmented environment model : I - Species persistence*, J. Math. Biol., **51** (2005), 75–113. MR2214420
- [5] 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., **84** (2005), 1101–1146. MR2155900
- [6] L.A. Caffarelli, K.-A. Lee and A. Mellet, *Singular limit and homogenization for flame propagation in periodic excitable media*, Arch. Ration. Mech. Anal., **172** (2004), 153–190. MR2058162
- [7] L.A. Caffarelli, K.-A. Lee and A. Mellet, *Homogenization and flame propagation in periodic excitable media: the asymptotic speed of propagation*, Comm. Pure Appl. Math., **59** (2006), 501–525. MR2199784
- [8] R.S. Cantrell and C. Cosner, “Spatial Ecology via Reaction-Diffusion Equations”, Series In Mathematical and Computational Biology, John Wiley and Sons, Chichester, Sussex UK, 2003. MR2191264
- [9] Y. Capdeboscq, *Homogenization of a neutronic critical diffusion problem with drift*, Proc. Royal Soc. Edinburgh, **132** (2002), 567–594. MR1912416
- [10] C. Conca and M. Vanninathan, *Homogenization of periodic structures via Bloch decomposition*, SIAM J. Appl. Math., **57** (1997), 1639–1659. MR1484944
- [11] M. El Smaily, *Pulsating travelling fronts: Asymptotics and homogenization regimes*, Europ. J. Appl. Math., **19** (2008), 393–434. MR2431698
- [12] P.C. Fife, “Mathematical Aspects of Reacting and Diffusing Systems”, Springer Verlag, 1979. MR0527914
- [13] R.A. Fisher, *The wave of advance of advantageous genes*, Ann. Eugenics, **7** (1937), 355–369.
- [14] F. Hamel, *Qualitative properties of monostable pulsating fronts : exponential decay and monotonicity*, J. Math. Pures Appl., **89** (2008), 355–399. MR2401143
- [15] F. Hamel and L. Roques, *Uniqueness, exponential behavior and stability of KPP pulsating fronts*, Preprint, 2008.
- [16] S. Heinze, *Homogenization of flame fronts*, Preprint IWR, Heidelberg, 1993.
- [17] S. Heinze, *Wave solution to reaction-diffusion systems in perforated domains*, Z. Anal. Anwendungen, **20** (2001), 661–670. MR1863939
- [18] S. Heinze, *Large convection limits for KPP fronts*, Preprint.
- [19] S. Heinze, G. Papanicolaou and A. Stevens, *Variational principles for propagation speeds in inhomogeneous media*, SIAM J. Appl. Math., **62** (2001), 129–148. MR1857539
- [20] T. Kato, “Perturbation Theory for Linear Operators”, 2nd edition, Springer, 1984. MR1335452
- [21] N. Kinezaki, K. Kawasaki and N. Shigesada, *Spatial dynamics of invasion in sinusoidally varying environments*, Popul. Ecol., **48** (2006), 263–270.
- [22] N. Kinezaki, K. Kawasaki, F. Takasu and N. Shigesada, *Modeling biological invasion into periodically fragmented environments*, Theor. Popul. Biol., **64** (2003), 291–302.
- [23] A.N. Kolmogorov, I.G. Petrovsky and N.S. Piskunov, *Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique*, Bull. Univ. État Moscou (Bjul. Moskovskogo Gos. Univ.), Sér. Inter. A, **1** (1937), 1–26.
- [24] H. Matano, *Traveling waves in spatially inhomogeneous diffusive media – The non-periodic case*, Preprint.
- [25] G. Nadin, *Pulsating traveling fronts in space-time periodic media*, C. R. Math. Acad. Sci. Paris, **346** (2008), 951–956. MR2449634
- [26] K.-I. Nakamura, *Effective speed of traveling wavefronts in periodic inhomogeneous media*, in “Proc. Workshop Nonlinear Partial Differential Equations and Related Topics”, Joint Research Center for Science and Technology of Ryukoku University, (1999), 53–60.

- [27] J. Nolen, M. Rudd and J. Xin, *Existence of KPP fronts in spatially-temporally periodic advection and variational principle for propagation speeds*, Dyn. Part. Diff. Eq., **2** (2005), 1–24. MR2142338
- [28] J. Nolen and J. Xin, *Existence of KPP type fronts in space-time periodic shear flows and a study of minimal speeds based on variational principle*, Disc. Cont. Dyn. Syst. - A, **13** (2005), 1217–1234. MR2166666
- [29] L. Roques and F. Hamel, *Mathematical analysis of the optimal habitat configurations for species persistence*, Math. Biosciences, **210** (2007), 34–59. MR2364810
- [30] L. Roques and R.S. Stoica, *Species persistence decreases with habitat fragmentation: an analysis in periodic stochastic environments*, J. Math. Biol., **55** (2007), 189–205. MR2322848
- [31] N. Shigesada and K. Kawasaki, “Biological Invasions: Theory and Practice”, Oxford Series in Ecology and Evolution, Oxford: Oxford University Press, 1997.
- [32] N. Shigesada, K. Kawasaki and E. Teramoto, *Traveling periodic waves in heterogeneous environments*, Theor. Popul. Biol., **30** (1986), 143–160.
- [33] N. Shigesada, K. Kawasaki and E. Teramoto, *The speeds of traveling frontal waves in heterogeneous environments*, in “Mathematical topics in population biology, morphogenesis and neurosciences” (eds. E. Teramoto and M. Yamaguti), Lecture Notes in Biomathematics, Springer, (1987), 87–97.
- [34] H.F. Weinberger, *On spreading speeds and traveling waves for growth and migration in periodic habitat*, J. Math. Biol., **45** (2002), 511–548. MR1943224
- [35] X. Xin, *Existence and uniqueness of travelling waves in a reaction-diffusion equation with combustion nonlinearity*, Indiana Univ. Math. J., **40** (1991), 985–1008.
- [36] X. Xin, *Existence and stability of travelling waves in periodic media governed by a bistable nonlinearity*, J. Dyn. Diff. Eq., **3** (1991), 541–573.
- [37] X. Xin, *Existence of planar flame fronts in convective-diffusive periodic media*, Arch. Ration. Mech. Anal., **121** (1992), 205–233.
- [38] X. Xin, *Analysis and modeling of front propagation in heterogeneous media*, SIAM Review, **42** (2000), 161–230.

Received September 2006; revised February 2007.

E-mail address: elsmaily@math.ubc.ca

E-mail address: francois.hamel@univ-cezanne.fr

E-mail address: lionel.roques@avignon.inra.fr