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BY

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Spreading speeds in slowly oscillating environments

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Abstract

In this paper, we derive exact asymptotic estimates of the spreading speeds of solutions of some reaction-diffusion models in periodic environments with very large periods. Contrarily to the other limiting case of rapidly oscillating environments, there was previously no explicit formula in the case of slowly oscillating environments. The knowledge of these two extremes permits to quantify the effect of environmental fragmentation on the spreading speeds. On the one hand, our analytical estimates and numerical simulations reveal speeds which are higher than expected for Shigesada-Kawasaki-Teramoto models with Fisher-KPP reaction terms in slowly oscillating environments. On the other hand, spreading speeds in very slowly oscillating environments are proved to be 0 in the case of models with strong Allee effects; such an unfavorable effect of aggregation is merely seen in reaction-diffusion models.

Keywords. Spreading speeds; Reaction-diffusion; Fragmentation; Periodic environment; Allee effect.

1 Introduction

In this paper, we are concerned with quantitative estimates of the spreading speeds of solutions of some reaction-diffusion models in heterogeneous and slowly oscillating

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environments. More precisely, we study models of the type

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f_L(x, u), \quad t > 0,\ x \in \mathbb{R}, \tag{1.1}$$

where the diffusion coefficient D is a given positive constant and the reaction term f_L is L-periodic in x. In this limit as $L \to +\infty$, we are interested in the large-time speed of propagation of the region where the solutions of the Cauchy problem with compactly supported initial data are away from 0.

For reaction terms of the type $f_L(x, u) = u(\mu_L(x) - \gamma_L(x)u)$, this equation corresponds to the Shigesada-Kawasaki-Teramoto (SKT) model (Shigesada et al., 1986), which is a natural extension of the classical Fisher and Kolmogorov-Petrovsky-Piskunov model (Fisher, 1937; Kolmogorov et al., 1937) to heterogeneous environments. In this context, u can be interpreted as a population density, while μ_L and γ_L respectively correspond to intrinsic growth rate and intraspecific competition coefficients. Some spreading properties of the solutions of such space-periodic equations have been studied, since the work of Freidlin and Gärtner (1979). In particular, if μ_L is nonnegative and not identically zero, there is a spreading speed $w_L^* \geq 0$, such that, if the initial population density is compactly supported and not identically equal to 0, any observer who travels with a speed larger than w_L^* will see the population density go to 0, whereas any observer traveling with a speed smaller than w_L^* will see the density approach a positive state, which is in general heterogeneous (see formula (2.5) below for the precise statements).

For the SKT model, the homogenization limit of rapidly oscillating media – corresponding to small values of L – has been fully investigated (El Smaily et al., 2009; Kinezaki et al., 2006). The spreading speed has been proved to converge to the spreading speed in an averaged environment, with the growth rate μ_L being replaced by its average value $\overline{\mu_L}$. The dependence of the spreading speed on the parameter L has also been recently analyzed: the speed was found to be an increasing function of the period L, first numerically for some specific examples in Kinezaki et al. (2003); Shigesada and Kawasaki (1997), and then analytically for the general case in Nadin (2010).

In the present paper, we derive, in the case of SKT patch models[1], an explicit formula for the limit of the spreading speed as L becomes very large. The limiting case that we consider here, that of slowly oscillating media, should be at least as interesting as the limit of rapidly oscillating media. Indeed, the precise knowledge of these two extreme cases enables us to estimate whether the spatial structure of the environment has a significant effect on the spreading speeds. Though propagation in slowly varying media has been studied through probabilistic arguments in Freidlin (1985), under assumptions more general than periodicity of the coefficients, previous

[1] In patch models, one assumes a mosaic of differentiated environments, each of which having a relatively well defined structure which one might consider as homogeneous. This involves an equation with piecewise constant coefficients, see hypothesis (H3) below.

theoretical studies do not offer explicit formulae for the limiting spreading speeds. They do not either focus on the dependence of the spreading speeds with respect to the oscillations of the medium.

The analytical results of Section 2 reveal significant increase of the spreading speeds in slowly oscillating environments for the SKT model (see formula (2.7) below and the particular cases stated after Theorem 2.1). To understand this, we numerically compute in Section 3 the solution of the SKT model in such environments. These computations suggest that this speed enhancement is linked to the "infinite speed of propagation" of the solutions of reaction-diffusion equations. The numerical results also tend to confirm that the high spreading speeds found in slowly oscillating media are caused by the growth of the tail of the solution, sent by diffusion far from the leading edge of the solution. To counterbalance the effects caused by this infinite speed of propagation, we consider reaction terms taking into account the Allee effect. In the case of a strong Allee effect, numerical computations then show a very different pattern of dependence between the spreading speeds and the period L. We even prove rigorously a result of independent interest, namely that, under a general condition on the Allee effect, propagation may be blocked when the period L is large enough (see Theorem 3.2 below). Lastly, in Section 4, we prove the analytical results which are stated in Sections 2 and 3 for the SKT model and the one with a strong Allee effect.

2 An explicit formula for the spreading speed in slowly oscillating media for the SKT model

For the derivation of the limit of the spreading speed as $L \to +\infty$, we place ourselves under hypotheses slightly more general than those of the SKT model. We set $f_L(x,\cdot) = f(x/L,\cdot)$, where $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$, $(x,s) \mapsto f(x,s)$ is a function which is 1-periodic in x (thus f_L is L-periodic in x). Moreover, we assume that

$$\begin{cases} \forall\, x \in \mathbb{R}, \quad f(x,0) = 0, \\ \exists\, M \geq 0,\ \forall\, s \geq M,\ \forall\, x \in \mathbb{R}, \quad f(x,s) \leq 0, \\ \forall\, x \in \mathbb{R}, \quad s \mapsto \dfrac{f(x,s)}{s} \text{ is decreasing in } s > 0. \end{cases} \tag{H1}$$

By analogy with the SKT model, we set

$$\mu(x) := \lim_{s \to 0^+} \frac{f(x,s)}{s} \quad \text{and} \quad \mu_L(x) := \mu\left(\frac{x}{L}\right).$$

It is worth noticing that the growth rate μ is not assumed to be nonnegative, it may actually change sign. But we always assume that μ is bounded.

Under hypothesis (H1), and assuming that f was of class $C^{1,\delta}$ in (x,s) and C^2 in s, it was proved by Berestycki et al. (2005a) that a necessary and sufficient condition for the existence of a positive and bounded stationary solution p_L of (1.1) was the negativity of the principal eigenvalue $\rho_{1,L}$ of the linear operator

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

with periodicity conditions. The principal eigenvalue $\rho_{1,L}$ is characterized by the existence and uniqueness (up to multiplication) of a positive and L-periodic function ϕ_L solving $\mathcal{L}_0\phi_L = \rho_{1,L}\phi_L$ in $\mathbb{R}$. In this case, the solution p_L was also proved to be unique, and therefore L-periodic. Moreover, the solution $u(t,x)$ of (1.1) was proved to converge to p_L, uniformly on all compact subsets of $\mathbb{R}$, as $t \to +\infty$, given any bounded and continuous initial condition $u(0,\cdot) = u_0 \geq 0$, with $u_0 \not\equiv 0$. In the sequel, we may therefore assume that

$$\rho_{1,L} < 0. \tag{H2$_a$}$$

In fact, a comparison with the Dirichlet-Laplace eigenvalue (see e.g. Roques and Hamel, 2007, Appendix E) shows that for large enough periods L, (H2$_a$) is automatically fulfilled provided that μ is positive somewhere. Thus, for our analysis in slowly oscillating media, we may assume, instead of (H2$_a$):

$$\mu^+ := \text{esssup}_{x\in[0,1]}\mu(x) > 0. \tag{H2$_b$}$$

The notion of spreading speeds is closely related to the existence of pulsating traveling fronts of the reaction-diffusion equation (1.1). The definition of pulsating traveling fronts, which is recalled below, has been introduced in Shigesada et al. (1986) (it has also been extended in higher dimensions in Berestycki and Hamel, 2002; Berestycki et al., 2005b; Xin, 1991). More precisely, a function $u : \mathbb{R}\times\mathbb{R} \to \mathbb{R}$, $(t,x) \mapsto u(t,x)$, defined for all time $t \in \mathbb{R}$, is called a pulsating traveling front propagating from left to right with an effective speed $c \neq 0$ for problem (1.1) if it satisfies

$$\begin{cases} \forall\, z\in\mathbb{Z},\ \forall\,(t,x)\in\mathbb{R}\times\mathbb{R}, \quad u\left(t+\dfrac{zL}{c},x\right) = u(t,x-zL), \\ \forall\,(t,x)\in\mathbb{R}\times\mathbb{R}, \quad 0 \leq u(t,x) \leq p_L(x), \\ \displaystyle\lim_{x\to-\infty} u(t,x) - p_L(x) = 0 \text{ and } \lim_{x\to+\infty} u(t,x) = 0, \end{cases} \tag{2.2}$$

where the above limits hold locally in t. Under the above assumptions (H1) and (H2$_a$), it follows from Berestycki et al. (2005b) that there exists a minimal speed $c_L^* > 0$ such that pulsating traveling fronts satisfying (2.2) with a speed of propagation c exist if and only if $c \geq c_L^*$. Moreover, c_L^* is characterized by the following formula:

$$c_L^* = \min_{\lambda>0} \frac{k_L(\lambda)}{\lambda}, \tag{2.3}$$

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

$$D\,\psi'' + 2\,\lambda\, D\,\psi' + \lambda^2\, D\,\psi + \mu_L(x)\,\psi = k_L(\lambda)\,\psi \ \text{ in } \mathbb{R}. \tag{2.4}$$

Uniqueness (up to shifts in time) of the fronts with any given speed $c \geq c_L^*$ has been proved recently (Hamel and Roques, 2010). We refer to Bages et al. (2008); Berestycki et al. (2005a,b); El Smaily (2008); Heinze (2005); Liang et al. (2010); Ryzhik and Zlatos (2007); Xin (2000); Zlatos (2010), for further results and asymptotic and stability properties of such pulsating fronts, and to Nadin (2009); Nolen et al. (2005); Nolen and Xin (2005), for the study of pulsating traveling fronts in time-periodic media.

The minimal speed of pulsating traveling fronts does not immediately appear as a fundamental notion in population ecology, but it turns out to be closely related to the more intuitive notion of spreading speed. Indeed, it is known (Berestycki et al., 2008; Freidlin and Gärtner, 1979; Weinberger, 2002) that, under assumptions (H1) and ($H2_a$), there exists a spreading speed, $w_L^* \geq 0$ such that, given any nonzero compactly supported and nonnegative initial density $u(0, x)$, the solution u of (1.1) satisfies

$$\begin{cases} u(t, x + ct) \underset{t \to +\infty}{\longrightarrow} 0, & \text{for all } x \in \mathbb{R} \text{ and } |c| > w_L^*, \\ u(t, x + ct) \underset{t \to +\infty}{\longrightarrow} p_L(x), & \text{for all } x \in \mathbb{R} \text{ and } c \in (-w_L^*, w_L^*). \end{cases} \tag{2.5}$$

In the one-dimensional case considered here, this spreading speed w_L^* is precisely equal to the minimal speed c_L^*, that is

$$w_L^* = c_L^*.$$

This result is not true in general in higher dimensions (Berestycki et al., 2005b) (see also Berestycki et al., 2008, for further spreading properties in non-periodic media).

As above mentioned, the homogenization limit as $L \to 0$ has been investigated by El Smaily et al. (2009). More precisely, under the assumption that $\overline{\mu} = \int_0^1 \mu(x)dx \geq 0$ and μ is not constant, it is known that $\rho_{1,L} < 0$ for each $L > 0$ and that

$$c_0^* := \lim_{L \to 0^+} c_L^* = 2\sqrt{D\,\overline{\mu}}. \tag{2.6}$$

In this paper, we are interested in the limit of slowly oscillating media, that is the limit of the spreading speeds $w_L^* = c_L^*$ as $L \to +\infty$. This limit exists and is finite since the speeds c_L^* are known to be bounded and nondecreasing with respect to the period L (Nadin, 2010). We denote this limit by c_∞^*, that is

$$c_L^* \underset{L \to +\infty}{\longrightarrow} c_\infty^*.$$

For the first result of this paper, we restrict our analysis to the case of a patch model, where the function $\mu(x) = \partial f / \partial s(x, 0)$ takes only two values μ^+ and μ^- with $\mu^+ \geq \mu^-$ and $\mu^+ > 0$. Namely, we assume that:

$$\begin{cases} \mu(x) = \mu^+ \text{ if } x \in [0, \theta), \\ \mu(x) = \mu^- \text{ if } x \in [\theta, 1), \end{cases} \tag{H3}$$

for some $\theta \in (0,1)$, which corresponds to the proportion of favorable patches in the environment.[2] The assumption $\mu^+ > 0$, that is (H2$_b$), implies that $\rho_{1,L} < 0$ for large L, whence the positive spreading speeds $w_L^* = c_L^*$ are well-defined for large L. Though simple, models with this type of growth rate function have aroused much interest in the recent literature (Cantrell and Cosner, 2003; Kawasaki and Shigesada, 2007; Kinezaki et al., 2003; Shigesada and Kawasaki, 1997; Shigesada et al., 1986).

Our first mathematical result, the proof of which is given in Section 4, is the following

Theorem 2.1. *Under hypotheses* (H1), (H2$_b$) *and* (H3), *the limit c_∞^* of c_L^* as $L \to +\infty$ is given by*

$$c_\infty^* = \sqrt{D} \min_{\lambda \geq (1-\theta)\sqrt{\mu^+ - \mu^-}} \frac{j^{-1}(\lambda)}{\lambda}, \tag{2.7}$$

where the function $j : [\mu^+, +\infty) \to [(1-\theta)\sqrt{\mu^+ - \mu^-}, +\infty)$ is defined by

$$\forall\, m \geq \mu^+, \quad j(m) = \theta\sqrt{m - \mu^+} + (1-\theta)\sqrt{m - \mu^-}$$

and $j^{-1} : [(1-\theta)\sqrt{\mu^+ - \mu^-}, +\infty) \to [\mu^+, +\infty)$ denotes the reciprocal of the function j.

Let us now comment and give some applications of Theorem 2.1. Notice first that if $\mu^+ = \mu^- =: \mu_0 > 0$ is constant, then $j(m) = \sqrt{m - \mu_0}$ for all $m \geq \mu_0$ and formula (2.7) reduces to the classical homogeneous Fisher-KPP formula $c_\infty^* = 2\sqrt{D\,\mu_0} = c_L^*$, which holds for all $L > 0$. It is also noteworthy that, in the heterogeneous case, Theorem 2.1 leads to an explicit formula for c_∞^*, in terms of the parameters μ^+, μ^- and θ. For general values of θ, this explicit formula is very lengthy, and thus not presented here. In some particular cases, however, Theorem 2.1 leads to simple formulae for c_∞^*. For instance, when

$$\theta = \frac{1}{2},$$

that is when the ratio between the length of the favorable region and that of the unfavorable region is unitary in each periodicity cell, we get:

$$c_\infty^* = 4\sqrt{D} \times \frac{(\mu^+)^2 + (\mu^-)^2 + (\mu^+ + \mu^-)\sqrt{\triangle}}{(\mu^+ + \mu^- + 2\sqrt{\triangle})^{\frac{3}{2}}}, \tag{2.8}$$

with $\triangle = (\mu^+)^2 + (\mu^-)^2 - \mu^+\mu^-$. If, in addition to $\theta = 1/2$, we also assume that $\mu^- = -\mu^+$, we simply get

$$c_\infty^* = \left(\frac{2}{\sqrt{3}}\right)^{\frac{3}{2}} \sqrt{D\,\mu^+},$$

[2]Here, the functions μ_L do not satisfy the regularity assumptions $\mu_L \in C^{0,\delta}$ used in the abovementioned references. However, c_L^* can still be interpreted as the minimal speed of propagation of weak solutions of (1.1) and (2.2), whose existence can be obtained by approaching μ_L with regular functions.

whereas $c_L^* \to c_0^* = 2\sqrt{D\,\overline{\mu}} = 0$ as $L \to 0$ (compare also with a homogeneous environment, with $\mu \equiv \mu^+$, which leads to $c_L^* = c_\infty^* = 2\sqrt{D\,\mu^+} > (2/\sqrt{3})^{3/2} \times \sqrt{D\,\mu^+}$). On the other hand, if we set $\mu^- = -n\,\mu^+$ in (2.8), we get

$$c_\infty^* = 2\sqrt{\frac{D\,\mu^+}{n}} + O\left(\frac{1}{n^{3/2}}\right) \quad \text{as } n \to +\infty.$$

Lastly, in the case $\mu^- = 0$, formula (2.8) reduces to:

$$c_\infty^* = \frac{8}{9}\sqrt{3\,D\,\mu^+}.$$

In this last case, we have $c_0^* = 2\sqrt{D\,\overline{\mu}} = \sqrt{2\,D\,\mu^+}$, whence $c_\infty^* = (4\sqrt{6}/9) \times c_0^*$, independently of μ^+.

Thus, as already emphasized and as illustrated in the above examples, the limiting spreading speed c_∞^* involves an explicit and in general lengthy dependence on the parameters μ^+, μ^- and θ. What is more surprising is that formula (2.7) and the subsequent ones are not the ones which one could have had in mind at first sight. Actually, under hypotheses (H1) and (H3), one could have expected c_∞^* to be close to an harmonic mean of the two speeds corresponding to the two homogeneous environments, respectively with $\mu \equiv \mu^+$ and $\mu \equiv \mu^-$, whenever these speeds exist (i.e. when $\mu^+ \geq \mu^- > 0$). Indeed, for large values of L, we could have expected the solution to spread approximately at the constant speeds $2\sqrt{D\mu^+}$ and $2\sqrt{D\mu^-}$ in the favorable and unfavorable patches, respectively. Thus, the average spreading speed would have been approximately equal to $h = L/(T_L^+ + T_L^-)$, where T_L^+ and T_L^- respectively correspond to the required times to cross the distances θL and $(1-\theta)L$ at speeds $2\sqrt{D\,\mu^+}$ and $2\sqrt{D\,\mu^-}$, respectively. This would have led to:

$$h = \frac{2\sqrt{D\,\mu^+\,\mu^-}}{\theta\sqrt{\mu^-} + (1-\theta)\sqrt{\mu^+}},$$

that is the harmonic mean between the speeds $2\sqrt{D\mu^+}$ and $2\sqrt{D\mu^-}$ with coefficients θ and $1-\theta$. However, it turns out that this value is even smaller than the spreading speed in the homogenization limit as $L \to 0$, namely

$$h < c_0^* = 2\sqrt{D\,\overline{\mu}} = 2\sqrt{D\,(\theta\mu^+ + (1-\theta)\mu^-)}$$

as soon as $\mu^- < \mu^+$, as follows from Jensen's inequality, together with the convexity of the function $x \mapsto 1/\sqrt{x}$ and h is therefore far lower than c_∞^*. Actually, the reason for the increase of the spreading speeds in slowly oscillating media can be easily understood from the numerical simulations and interpretations given in the next section.

We also mention that a result of Freidlin (1985), obtained through probabilistic arguments and under some technical assumptions, leads to the following formula for c_∞^* :

$$c_\infty^* = \lim_{t \to +\infty} \frac{X(t)}{t},$$

where $X(t)$ is defined by

$$\sup_{\phi \in E_{t,X(t)}} \left\{ \int_0^t \left[\mu(\phi(s)) - \frac{1}{4D} (\phi'(s))^2 \right] ds \right\} = 0,$$

and, for every $t \geq$ and $Y \in \mathbb{R}$,

$$E_{t,Y} = \{\phi \in C([0,t] : \mathbb{R}), \text{ with } \phi(0) = Y \text{ and } \phi(t) = 0\}.$$

This formula bears on a variational equation which gives $X(t)$ in an implicit manner, and thus it is more difficult to use, both analytically and numerically, than formulae of type (2.7).

Theorem 2.1 corresponds to the case of patchy environments, that is hypothesis (H3). However, formula (2.7) leads us to formulate the following conjecture in the case of general heterogeneous environments:

Conjecture 2.2. *For any bounded and periodic function μ, such that* (H1) *and* ($H2_b$) *are satisfied, we have*

$$c_\infty^* = \sqrt{D} \min_{\lambda \geq \int_0^1 \sqrt{M - \mu(x)}\, dx} \frac{j^{-1}(\lambda)}{\lambda}, \tag{2.9}$$

where $M = esssup_{x \in \mathbb{R}} \mu(x)$ and the function $j : [M, +\infty) \to \left[\int_0^1 \sqrt{M - \mu(x)}\, dx, +\infty \right)$ is defined by

$$\forall\, m \geq M, \quad j(m) = \int_0^1 \sqrt{m - \mu(x)}\, dx.$$

This conjecture was successfully checked numerically on several examples: $\mu(x) = \sin(2\pi x)$, $\mu(x) = 2 \sin(2\pi x)$, $\mu(x) = \sin^2(2\pi x)$, $\mu(x) = 1 + \sin(2\pi x)$, $\mu(x) = 1 + \cos(2\pi x) \sin(2\pi x)$, with $D = 1$. Both the numerical simulations and formula (2.9) lead to the following values of c_∞^*, respectively: 1.11, 1.57, 1.49, 2.11 and 2.03. On the other hand, in rapidly oscillating environments, the speeds c_L^* converge as $L \to 0$ to $2\sqrt{D\,\overline{\mu}} = 0$, 0, $\sqrt{2}$, 2 and 2 respectively.

Conjecture 2.2 for heterogeneous reaction-diffusion-advection equations will be studied in the forthcoming paper by Hamel et al. (2010), with an approach based on viscosity solutions for some Hamilton-Jacobi equations.

An important by-product of the analysis of the limit of large oscillating media is the study of spreading speeds in media with large reaction terms. More precisely, replace the reaction term f with $B\,f$ in (1.1), that is consider the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + B\, f(x,u), \quad t > 0,\ x \in \mathbb{R}, \tag{2.10}$$

where B is a positive parameter. Let $c^*(B)$ denote the minimal speed of pulsating traveling fronts propagating from left to right for problem (2.10), in the same sense as (2.2) with $L = 1$ and p_L being replaced with the unique positive 1-periodic stationary state of (2.10), when it exists (the existence is guaranteed for all $B > 0$ if $\overline{\mu} \geq 0$ and

$\mu \not\equiv 0$). The speeds $c^*(B)$ are also the large-time spreading speeds, in the sense of (2.5), of all solutions of (2.10) with nonnegative and nonzero compactly supported initial data. In Berestycki et al. (2005b), the limit of large reactions $B\,f$ as $B \to +\infty$ was considered and it was proved there that, under the hypotheses $\overline{\mu} \geq 0$ and (H2$_b$), the spreading speeds $c^*(B)$ satisfy:

$$\frac{1}{2}\sqrt{D\,\mu^+} \leq \liminf_{B\to+\infty} \frac{c^*(B)}{\sqrt{B}} \leq \limsup_{B\to+\infty} \frac{c^*(B)}{\sqrt{B}} \leq 2\sqrt{D\,\mu^+}, \tag{2.11}$$

where $\mu^+ = \text{esssup}_{\mathbb{R}}\mu$. One could therefore legitimately ask whether, in the limit of large amplitudes, the normalized speeds $c^*(B)/\sqrt{B}$ depend only on μ^+. In fact, this is not true in general, as the following result shows:

Proposition 2.3. *Under hypotheses* (H1), (H2$_b$)*, there holds*

$$\lim_{B\to+\infty} \frac{c^*(B)}{\sqrt{B}} = c^*_\infty. \tag{2.12}$$

Notice that this result, which is proved in Section 4, works in the general case of a growth rate μ which may not be of the patch type (H3). As already observed from the above examples in the case of the patch model (H3), we clearly see that c^*_∞ in general depends not only on μ^+, but also on θ and μ^- (see also Conjecture 2.2 above for general non-patchy environments). In other words, the limit of $c^*(B)/\sqrt{B}$ for problem (2.10) does not depend only on μ^+. Nevertheless, an interesting consequence of (2.11) and (2.12) is that, under the additional assumption $\overline{\mu} \geq 0$, the inequality

$$c^*_\infty \geq \frac{1}{2}\sqrt{D\,\mu^+}$$

holds true automatically. This explains why, in the above numerical examples, the difference $c^*_\infty - c^*_0$ was higher for high values of μ^+, especially when $\overline{\mu} = 0$.

Remark 2.4. To complete this section, we mention that formulae closely related to (2.7) or (2.9) can be derived for other types of models. For instance, Kawasaki and Shigesada (2007) considered the integro-difference model:

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} J(x-y) g_L(y, N_t(y))dy, \quad t \in \mathbb{N},\ x \in \mathbb{R}, \tag{2.13}$$

where the dispersal kernel J is an exponential damping function $J(s) = \frac{1}{2}e^{-|s|}$, and the growth function is

$$g_L(x, N) = N\mu_L(x)e^{-N}.$$

Assuming that the linear conjecture (Mollison, 1991; van den Bosch et al., 1990) held, that is that the propagation speed v^*_L (which is defined in Kawasaki and Shigesada, 2007, as an average speed of range expansion, see (3.17) below) was the same as that of the linear model where g_L is replaced by its derivative at $N = 0$, they obtained a variational formula for this speed v_L^*. Using arguments similar to those of Section 4, we conjecture that the limit as $L \to +\infty$ of the spreading speed in the case of model (2.13) is given by the following formula:

$$v_L^* \underset{L\to+\infty}{\longrightarrow} v_\infty^* = \min_{\lambda \in \left[(1-\theta)\sqrt{1-\mu^-/\mu^+},1\right)} -\frac{\ln\left(j^{-1}(\lambda)\right)}{\lambda},$$

where the function $j : [0, 1/\mu^+] \to [(1-\theta)\sqrt{1-\mu^-/\mu^+}, 1]$ is defined by

$$\forall\, m \in \left[0, \frac{1}{\mu^+}\right], \quad j(m) = \theta\sqrt{1 - m\,\mu^+} + (1-\theta)\sqrt{1 - m\,\mu^-}.$$

In the particular case $\mu^+ = 2$, $\mu^- = 1$, and $\theta = 1/2$, we obtain, for this model, $v_\infty^* \simeq 1.36 \times v_0^*$. In this case, as for model (1.1), slowly oscillating environments thus lead to significantly higher speeds than rapidly oscillating ones.

3 Numerical computations and comparison with models taking into account the Allee effect

In this section, we present some numerical simulations which have been carried out on the SKT model with large periods and we compare them to other models with Allee effect.

3.1 Shigesada-Kawasaki-Teramoto model

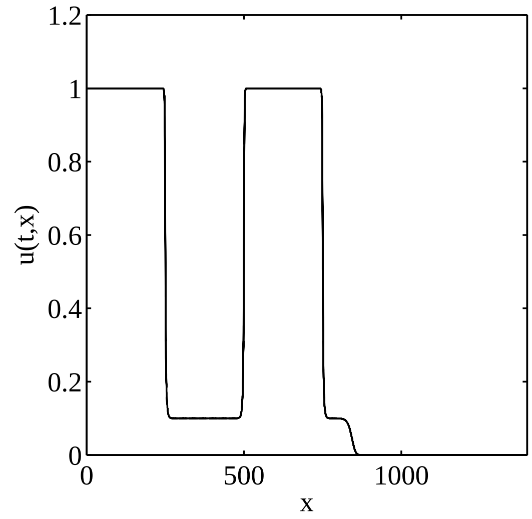
What are the reasons for such an increasing behavior of the spreading speed with respect to the period L, leading to significantly increased speeds in very slowly oscillating environments, compared to rapidly oscillating ones? Is this reasonable from an ecological viewpoint?

We could expect that for most individual based models (IBMs) (Gross et al., 1992; Kareiva and Shigesada, 1983; Marsh and Jones, 1988; Turchin, 1998) in such a periodic environment, too large unfavorable regions should be associated with reduced spreading speeds. Indeed, imagine the case of very unfavorable regions, where no individual can reproduce, and where the death rate is very high. The probability that an individual manages to cross such regions without dying is very low, especially for large L. If the mean time required for this region to be crossed by some individual increases super-linearly with L, the spreading speed should decrease with L, and even converge to 0 as $L \to +\infty$.

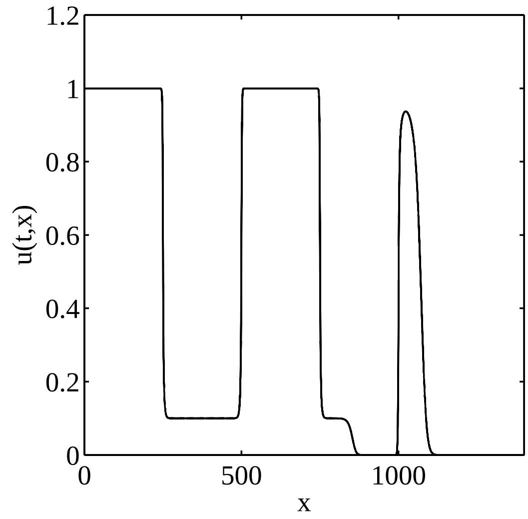
Even if the diffusion part

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}$$

of equation (1.1) can be obtained as the macroscopic limit of uncorrelated random walks (see e.g. Okubo and Levin, 2002; Turchin, 1998), this model, and more generally reaction-diffusion models with non-degenerate diffusion, behave quite differently,



(a) $t = 580$



(b) $t = 600$

Figure 1: Profile of the solution $u(t,x)$, at two successive times, $t = 580$ and $t = 600$, starting from a compactly supported initial condition $u(0,x)$ and with $\mu^+ = 1$, $\mu^- = 0.1$, $D = 1$, $\theta = 1/2$ and $L = 500$.

compared to IBMs. Indeed, because of strong parabolic maximum principle, even with compactly supported initial population density $u(0,x)$ which is not identically equal to 0, the solution $u(t,x)$ of (1.1) becomes strictly positive at all points $x \in \mathbb{R}$ as soon as $t > 0$. This phenomenon, sometimes referred to as "infinite speed of propagation", may have an important impact on the dependence of c_L^* with respect to L, especially for large L.

Figure 1 depicts the profile of the solution $u(t,x)$ at two successive times, starting with a compactly supported initial condition, and for $L = 500$. We observe that the favorable patch beginning at $x = 1000$ becomes invaded before the full invasion of the preceding unfavorable patch $[750, 1000)$. This phenomenon emphasizes the key role played by infinite speed of propagation in such a slowly oscillating environment, and the *pulled* nature of SKT solutions (Stokes, 1976; van Saarloos, 2003): the very low population density "sent" by diffusion in the favorable patch starting at $x = 1000$ reacts and becomes significant before the leading edge of the front-like solution attains this region.

Moreover, another effect, which may seem a bit paradoxal, makes the spreading speeds larger in very slowly environments, at least under some appropriate conditions on the coefficients $\mu^\pm$. Namely, we have computed, for a large value of L, the value of the mean speed c_f inside a favorable patch, that is the ratio between the distance $\theta\, L$ and the time spent by the solution to cross this favorable region (see Remark 3.1 for more details on the way this speed was computed). One could then wonder if this speed is reduced or increased compared to a homogeneous favorable environment (with

$\mu \equiv \mu^+$). The result of these computations, with the reaction term

$$f_L(x,u) = u(\mu_L(x) - u)$$

are presented in Fig. 2. We can observe that, in the case presented here, the speed c_f is larger than $2\sqrt{D\,\mu^+}$. Therefore, the presence of unfavorable regions, though it decreases the (global) asymptotic spreading speed c_L^*, increases the speed of propagation in the remaining favorable regions, compared to a homogeneous environment. Let us give a mathematical interpretation of this observation in the case when $\theta = 1/2$. At large time, the solution u of (1.1) behaves like a pulsating traveling front $\varphi_L^*(x - c_L^* t + o(t), x)$ with minimal speed c_L^*, around the position $c_L^* t - o(t)$ as $t \to +\infty$ (Weinberger, 2002). This pulsating traveling front $\varphi_L^*(s,x)$ converges to 0 like

$$\varphi_L^*(s,x) \sim s\, e^{-\lambda_L^* s}\, \phi_L^*(x) \quad \text{as } s \to +\infty,$$

where ϕ_L^* is positive and L-periodic (Hamel, 2008). It actually follows from (2.7) that

$$\lambda_L^* \underset{L\to+\infty}{\longrightarrow} \lambda_\infty^* = \frac{1}{2}\sqrt{D \times (\mu^+ + \mu^- + 2\sqrt{\triangle})},$$

where $\triangle = (\mu^+)^2 + (\mu^-)^2 - \mu^+\mu^-$ is as in (2.8). On the other hand, the front $\varphi_+^*(s)$ with minimal speed $c_+^* = 2\sqrt{D\,\mu^+}$ in the homogeneous environment with $\mu \equiv \mu^+$ in $\mathbb{R}$ behaves like $\varphi_+^*(s) \sim C\,s\,e^{-\lambda_+^* s}$ as $s \to +\infty$, where C is a positive constant, and $\lambda_+^* = \sqrt{D\,\mu^+}$. But $0 < \lambda_\infty^* < \lambda_+^*$ as soon as $\mu^+ > \mu^- > -5\,\mu^+/3$. Therefore, under this condition, in the heterogeneous environment with large period L, the limiting pulsating front φ_L^* has an exponential behavior which decays slower than that of the homogeneous traveling front in the homogeneous environment with $\mu \equiv \mu^+$. But it is well-known (Bramson, 1983) that in a homogeneous environment a solution with an exponential decay slower than that of the minimal front moves at a larger speed at large time. As a consequence, when the period L of the heterogeneous environment is very large, the solution u of (1.1) eventually moves in the favorable region at a faster speed than the minimal speed $2\sqrt{D\,\mu^+}$ of the homogeneous front, provided that $\mu^+ > \mu^- > -5\,\mu^+/3$.

Remark 3.1. For the computation of c_f, the average speed in the favorable part of the environment for the SKT model, we placed ourselves in the favorable patch $C^+ = [600, 700)$, and we defined

$$c_f := \frac{\text{length}(C^+)}{t_2 - t_1}, \tag{3.14}$$

where

$$t_1 = \inf\left\{t \geq 0,\ \sup_{x\in C^+} u(t,x) \geq \frac{\mu^-}{2}\right\} \text{ and } t_2 = \inf\left\{t,\ \inf_{x\in C^+} u(t,x) \geq \frac{\mu^-}{2}\right\}.$$

Thus $t_2 - t_1$ corresponds to the time required for C^+ to be filled by a density at least equal to $\mu^-/2$. This duration $t_2 - t_1$ is known to be finite since $u_L(t,x) \to p_L(x) \geq \mu^-$ as $t \to +\infty$, uniformly on compact sets (Berestycki et al., 2005a).

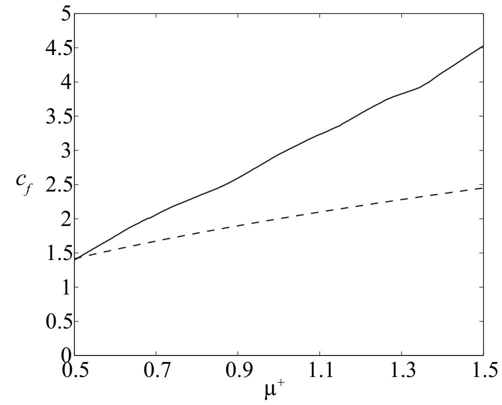


Figure 2: Solid line: average speed of propagation c_f in the favorable patch $[600, 700)$, for values of μ^+ in $[0.5, 1.5]$. Dashed line: spreading speed $c^* = 2\sqrt{D\mu^+}$ in a homogeneous favorable environment with $\mu \equiv \mu^+$. We fixed $L = 200$, $\mu^- = 0.5$, $D = 1$, $\theta = 1/2$.

3.2 Model with Allee effect

To counterbalance the effects caused by the infinite speed of propagation, common to all models of the type (1.1), we may assume that the growth term $f_L(x, u)$ is negative at low densities u. This corresponds to an Allee effect.

Allee effect occurs when, for each x, the *per capita* growth rate, $f(x, u)/u$, reaches its peak at a strictly positive population density. At low densities, the *per capita* growth rate may then become negative (strong Allee effect). Allee effect is known in many species (Allee, 1938; Dennis, 1989; Veit and Lewis, 1996), and results from several processes which can co-occur (Berec et al., 2007), such as diminished chances of finding mates at low densities (Mccarthy, 1997), fitness decrease due to consanguinity or decreased visitation rates by pollinators for some plant species (Groom, 1998).

In reaction-diffusion models, Allee effects are generally modeled by equations of bistable type (Fife, 1979; Turchin, 1998):

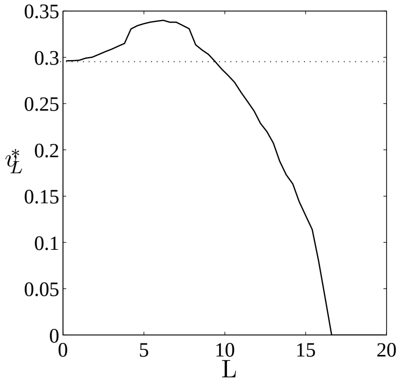
$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + u(1-u)(u-\rho), \quad t > 0, \ x \in \mathbb{R}. \tag{3.15}$$

In order to study the effects of an oscillating environment, we study an extension of (3.15) to a heterogeneous environment, proposed by Roques et al. (2008):

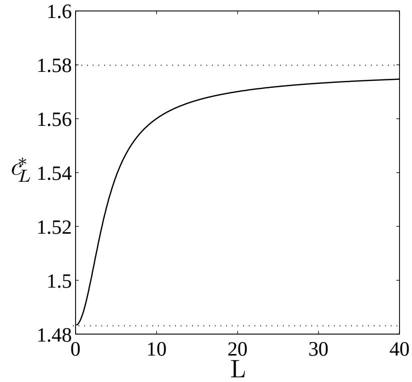
$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + u\left[(1-u)(u-\rho) + \nu_L(x)\right], \quad t > 0, \ x \in \mathbb{R}. \tag{3.16}$$

In this situation, the *per capita* growth rate, $(1-u)(u-\rho) + \nu_L(x)$ depends on u and on the location x, and is negative at low densities if $\text{esssup}_{x\in\mathbb{R}}\nu_L(x) < \rho$. We assume that $\nu_L(x) = \nu(x/L)$, where ν is a 1-periodic function defined by:

$$\begin{cases} \nu(x) = \nu^+ \text{ if } x \in [0, \theta), \\ \nu(x) = \nu^- \text{ if } x \in [\theta, 1), \end{cases} \tag{H4}$$



(a)



(b)

Figure 3: a) Average speed of range expansion v_L^* of the solution of the model (3.16) with Allee effect, in terms of the period L. The dotted line corresponds to the spreading speed in an averaged environment, where ν has been replaced by $\overline{\nu}$. We fixed $\nu^+ = 0$, $\nu^- = -0.3$, $\rho = 10^{-2}$, $D = 1$ and $\theta = 1/2$, and a threshold $u^* = 0.1$. b) Spreading speed c_L^* of the solution of (1.1), under hypotheses (H1-H3), as a function of L. The bottom dotted line corresponds to the homogenization limit (2.6). The top dotted line corresponds to the limit (2.8). We fixed $\mu^+ = 1$, $\mu^- = 0.1$, $D = 1$ and $\theta = 1/2$.

and the parameters $\theta \in (0, 1)$ and $\nu^- \leq \nu^+ < \rho$ are given.

Starting from a compactly supported initial condition u_0, we have computed the average speed v_L^* of range expansion, defined by

$$v_L^* = \lim_{t \to +\infty} \frac{x^*(t)}{t}, \tag{3.17}$$

where

$$x^*(t) = \max\left(0, \sup\left\{x \in \mathbb{R} \text{ such that } u(t,x) > u^*\right\}\right), \tag{3.18}$$

for some fixed small threshold $u^* > 0$. Notice that for problem (3.16), the existence of pulsating traveling front and the existence of a spreading speed, in the sense of (2.5) and independently of u_0 (provided that spreading occurs), are still open questions. However, if such a spreading speed exists, then it has to be equal to v_L^*.

This speed v_L^* was numerically computed (see Remark 3.1 below) for increasing values of L. The results of the simulations are presented in Fig. 3 a), together with the SKT speed c_L^* (Fig. 3 b). As in the SKT case, the homogenization limit $v_0^* = \lim_{L \to 0} v_L^*$ seems to be equal to the spreading speed in an averaged environment (existence of a spreading speed is known in the homogeneous case, see Aronson and Weinberger, 1975), where ν is replaced with its arithmetic mean $\overline{\nu}$. Moreover, for small values of L, v_L^* is increasing, denoting a detrimental effect of very rapidly oscillating environments on the propagation speeds. On the other hand, contrarily to the SKT case, the speed v_L^* is a decreasing function of L, for L large enough. Too large values of L even lead to propagation failure irrespectively of the size of the supports of the initial conditions, and in this case $v_L^* = 0$.

As a matter of fact, this blocking phenomenon can also be viewed as a consequence of the following result which is of independent interest and which holds in a more general setting.

Theorem 3.2. *Let $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$, $(x, s) \mapsto f(x, s)$ be a function which is locally bounded in $\mathbb{R}_+ \times \mathbb{R}$, locally Lipschitz-continuous with respect to s uniformly with respect to x, 1-periodic in x and satisfies*

$$\left\{\begin{array}{l} \forall\, x \in \mathbb{R}, \quad f(x,0) = 0, \\ \exists\, M \geq 0, \ \ \forall\, s \geq M, \ \ \forall\, x \in \mathbb{R}, \quad f(x,s) \leq 0, \\ \exists\, \alpha > 0, \ \beta \in (0,M), \quad \forall\, (x,s) \in \mathbb{R} \times [0,\beta], \quad f(x,s) \leq -\alpha\, s, \\ \exists\, 0 \leq a < b \leq 1, \ \ \exists \xi \in (0,M), \ \ \exists\, g \in C^1([0,M];\mathbb{R}) \ \ \text{such that} \\ \qquad\qquad g(0) = g(\xi) = g(M) = 0, \ g'(0) < 0, \ g'(M) < 0, \\ \qquad\qquad g < 0 \ \text{on} \ (0,\xi), \ g > 0 \ \text{on} \ (\xi, M), \ \displaystyle\int_0^M g(s)\, ds < 0, \\ \qquad\qquad \forall\, (x,s) \in [a,b] \times [0,M], \quad f(x,s) \leq g(s). \end{array}\right. \tag{3.19}$$

Set $f_L(x, s) = f(x/L, s)$. Then, there exists $L^* > 0$ large enough such that, for any $L \geq L^*$ and for any nonnegative bounded compactly supported function u_0, the solution u of

$$\left\{\begin{array}{l} \dfrac{\partial u}{\partial t} = D\dfrac{\partial^2 u}{\partial x^2} + f_L(x,u) \quad t > 0, \ x \in \mathbb{R}, \\ u(0,x) = u_0(x) \end{array}\right. \tag{3.20}$$

satisfies $v_L^* = 0$, irrespectively of the choice of $u^* > 0$ in (3.18).

Roughly speaking Theorem 3.2 means that if f_L has a steady state 0 which is strictly stable uniformly with respect to x and if f_L is bounded from above on a sufficiently large space interval by a space-independent bistable function g for which 0 is the most stable zero, then propagation fails. Of course, the same conclusion holds for the spreading speed to the left, which is defined by replacing the maximum and supremum in (3.18) with minimum and infimum. It is immediate to see that assumption (3.19) is satisfied for the model (3.16) under hypotheses (H4) with the choice of parameters $\nu^{\pm}$ and ρ given in Fig. 3 b).

Remark 3.3. To compute the solutions u of the SKT model and of the model (3.16) with Allee effect, which are necessary for the computation of the speeds c_f and v_L^*, we used a second-order finite elements method. The estimation of the position $x^*(t)$, defined in (3.18), and of the times t_2 and t_1 in (3.14), depend on the accuracy of this numerical method (observe the lack of smoothness of the curves in Fig. 3 a) and Fig. 2). On the other hand, in the SKT case, the speed c_L^* was directly computed through formula (2.3). This was made possible thanks to formula (4.28) below. This method was observed to be very accurate. Furthermore, compared to other methods (Kinezaki et al., 2006; Shigesada and Kawasaki, 1997), it has the great advantage of being adaptable to any type of growth rate μ (and not necessarily step functions).

4 Proofs of the results

In this section, we prove the mathematical results announced in this paper. We begin with the SKT model and we then deal with the model taking into account a strong Allee effect.

4.1 Slowly oscillating media and the case of large reaction for the SKT model

This subsection is devoted to the proof of Theorem 2.1 and Proposition 2.3 on the limiting spreading speeds in environments with very slow oscillations or very large reaction terms.

Proof of Theorem 2.1. Assume that hypotheses (H1), (H2$_b$) and (H3) with $\mu^- < \mu^+$ are satisfied. Let $L_0 > 0$ be such that, for all $L \geq L_0$, the hypothesis (H2$_a$) is fulfilled, that is $\rho_{1,L} < 0$ (we recall that, because of (H2$_b$), such a L_0 exists). Hence, the spreading speeds $c^*_L = w^*_L$ for (1.1) are well-defined for all $L \geq L_0$. Remember that c^*_L is equal to $c^*_L = \min_{\lambda>0} k_L(\lambda)/\lambda$ from (2.3), where $k_L(\lambda)$ is the principal eigenvalue of (2.4). We shall then establish some estimates on $k_L(\lambda)$ for large values of L.

Let us first collect some general properties of the function $(\lambda, L) \mapsto k_L(\lambda)$, which can actually be defined over $\mathbb{R} \times (0, +\infty)$.

Proposition 4.1. *The function $(\lambda, L) \mapsto k_L(\lambda)$ is analytic in $\mathbb{R} \times (0, +\infty)$, convex and even with respect to the variable $\lambda \in \mathbb{R}$, and nondecreasing with respect to the variable $L > 0$. Furthermore, $k_L(0) = -\rho_{1,L}$ and*

$$\overline{\mu} + D\,\lambda^2 < k_L(\lambda) < \mu^+ + D\,\lambda^2 \tag{4.21}$$

for all $(\lambda, L) \in \mathbb{R} \times (0, +\infty)$. Lastly, for each $L > 0$, there exists a unique $\gamma_L > 0$ such that

$$k_L(\gamma_L) = \mu^+, \quad k_L(\lambda) < \mu^+ \text{ for all } \lambda \in [0, \gamma_L), \quad k_L(\lambda) > \mu^+ \text{ for all } \lambda \in (\gamma_L, +\infty),$$

and the map $L \mapsto \gamma_L$ is nonincreasing in $(0, +\infty)$.

Proof. The analyticity of $k_L(\lambda)$ follows from the simplicity of the principal eigenvalue of (2.4) (see El Smaily et al., 2009; Kato, 1984). The evenness with respect to λ holds because $k_L(-\lambda)$ is the principal eigenvalue of the adjoint operator. The convexity in λ

has been proved in Berestycki et al. (2005b), Section 3. The monotonicity with respect to L follows from Nadin (2010) and the formula $k_L(0) = -\rho_{1,L}$ holds by definition of $\rho_{1,L}$.

Let us now establish (4.21). To do so, divide equation (2.4) by ψ and integrate by parts over $[0, L]$. Using the L-periodicity of ψ, we obtain:

$$D \int_0^L \frac{|\psi'|^2}{\psi^2} + L\, D\, \lambda^2 + \int_0^L \mu_L(x) dx = L\, k_L(\lambda).$$

Thus $\overline{\mu} + D\,\lambda^2 < k_L(\lambda)$ since ψ is not constant (because μ is not constant either). Next, integrating (2.4) by parts over $[0, L]$, we easily get $k_L(\lambda) < \mu^+ + \lambda^2 D$.

The existence and uniqueness of $\gamma_L > 0$ such that $k_L(\gamma_L) = \mu^+$ follows from (4.21) applied at $\lambda = 0$ and $+\infty$, and from the convexity of the $k_L(\lambda)$ with respect to λ. Furthermore, $k_L(\lambda) < \mu^+$ for all $\lambda \in [0, \gamma_L)$ and $k_L(\lambda) > \mu^+$ for all $\lambda \in (\gamma_L, +\infty)$. Lastly, since $L \mapsto k_L(\lambda)$ is nondecreasing for each $\lambda \in \mathbb{R}$, one gets that the map $L \mapsto \gamma_L$ is nonincreasing over $(0, +\infty)$. $\square$

From formula (2.3) and the monotonicity of $k_L(\lambda)$ with respect to L, as already noticed by Nadin (2010), it follows that the function $[L_0, +\infty) \ni L \mapsto c^*_L$ is nondecreasing. Moreover, formulae (2.3) and (4.21) also imply that c^*_L is bounded from above by $2\sqrt{D\,\mu^+}$, for all $L \geq L_0$. Thus we can define the real number

$$c^*_\infty := \lim_{L\to+\infty} c^*_L \; > 0. \tag{4.22}$$

Similarly, for each $\lambda \in \mathbb{R}$, we can define the real numbers

$$k_\infty(\lambda) := \lim_{L\to+\infty} k_L(\lambda) \; \in [\overline{\mu} + D\,\lambda^2, \mu^+ + D\,\lambda^2]$$

and

$$\gamma_\infty := \lim_{L\to+\infty} \gamma_L \; \geq 0. \tag{4.23}$$

Let us now set, for all $\lambda > 0$ and $L > 0$,

$$c_L(\lambda) = \frac{k_L(\lambda)}{\lambda} \;\text{ and }\; c_\infty(\lambda) = \frac{k_\infty(\lambda)}{\lambda}.$$

The following two lemmas deal with the properties of the functions c_∞ and k_∞.

Lemma 4.2. *There exists*

$$\lambda^*_\infty \in (0, +\infty) \cap \left[\frac{\sqrt{\mu^+} - \sqrt{\mu^+ - \overline{\mu}}}{\sqrt{D}}, \frac{\sqrt{\mu^+} + \sqrt{\mu^+ - \overline{\mu}}}{\sqrt{D}} \right] \tag{4.24}$$

such that the continuous function $\lambda \mapsto c_\infty(\lambda)$ is nonincreasing in $(0, \lambda^*_\infty]$ and nondecreasing in $[\lambda^*_\infty, +\infty)$. Moreover, $c_\infty(0^+) = c_\infty(+\infty) = +\infty$ and $c_\infty(\lambda^*_\infty) = c^*_\infty$.

Proof. From Proposition 4.1, we can write

$$c_L'(\lambda) = \frac{k_L'(\lambda)}{\lambda} - \frac{k_L(\lambda)}{\lambda^2}$$

for all $L \geq L_0$. Thus, $\lim_{\lambda\to 0^+} c_L'(\lambda) = -\infty$ for all $L \geq L_0$, from hypothesis (H2$_a$). Let λ_L^* be defined by

$$\lambda_L^* = \sup\big\{\lambda > 0 \text{ such that } c_L \text{ is decreasing in } (0,\lambda)\big\}.$$

We also have

$$c_L(0^+) = \lim_{\lambda\to 0^+} \frac{k_L(\lambda)}{\lambda} = +\infty \tag{4.25}$$

because of hypothesis (H2$_a$), for $L \geq L_0$. Furthermore, using (4.21), we get that

$$\lim_{\lambda\to+\infty} c_L(\lambda) = +\infty. \tag{4.26}$$

Thus, $\lambda_L^* \in (0,+\infty)$, and $c_L'(\lambda_L^*) = 0$. Moreover, for all $\lambda > 0$,

$$c_L''(\lambda) = \frac{k_L''(\lambda)}{\lambda} - 2\frac{c_L'(\lambda)}{\lambda} \geq -2\frac{c_L'(\lambda)}{\lambda}$$

from the convexity of $k_L(\lambda)$ with respect to λ. Thus, it follows that $c_L'(\lambda) \geq 0$ for all $\lambda \in [\lambda_L^*,+\infty)$. Hence, the map $\lambda \mapsto c_L(\lambda)$ is decreasing in $(0,\lambda_L^*)$, and nondecreasing in $[\lambda_L^*,+\infty)$. From formula (2.3), we obtain

$$c_L(\lambda_L^*) = c_L^*. \tag{4.27}$$

On the other hand, using (4.21), and since $c_L^* \leq 2\sqrt{D\mu^+}$, we obtain

$$D\,(\lambda_L^*)^2 + \overline{\mu} \leq k_L(\lambda_L^*) \leq 2\lambda_L^*\sqrt{D\,\mu^+}.$$

As a consequence,

$$\lambda_L^* \in \left[\frac{\sqrt{\mu^+} - \sqrt{\mu^+ - \overline{\mu}}}{\sqrt{D}}, \frac{\sqrt{\mu^+} + \sqrt{\mu^+ - \overline{\mu}}}{\sqrt{D}}\right]. \tag{4.28}$$

Furthermore, since $c_{L_0}(\lambda) \leq c_L(\lambda) \leq \mu^+/\lambda + D\,\lambda$ for all $L \geq L_0$ and $\lambda > 0$, with $c_{L_0}(0^+) = +\infty$, it follows that $\liminf_{L\to+\infty} \lambda_L^* > 0$. Indeed, choose any $\underline{\lambda} > 0$ such that

$$\forall\,\lambda' \in (0,\underline{\lambda}],\quad c_{L_0}(\lambda') > 2\sqrt{D\,\mu^+} = \min_{\lambda>0}\left(\frac{\mu^+}{\lambda} + D\,\lambda\right).$$

Since $c_L(\lambda) \geq c_{L_0}(\lambda)$ for all $\lambda > 0$ and $L \geq L_0$, it follows from the above properties of λ_L^* that $\lambda_L^* \geq \underline{\lambda}$ for all $L \geq L_0$.

Thus, there exists an increasing sequence $(L_n)_{n\in\mathbb{N}}$ of positive real numbers such that $\lim_{n\to+\infty} L_n = +\infty$ and $\lambda_{L_n}^* \to \lambda_\infty^*$ as $n \to +\infty$, where λ_∞^* satisfies (4.24). Moreover, the function $\lambda \mapsto c_\infty(\lambda)$ is nonincreasing in $(0,\lambda_\infty^*)$ and nondecreasing in $(\lambda_\infty^*,+\infty)$. Lastly, all functions $\lambda \mapsto k_L(\lambda)$ are convex, and so is the function $\lambda \mapsto$

$k_\infty(\lambda)$. Hence, it is continuous in $\mathbb{R}$ and so is the function $\lambda \mapsto c_\infty(\lambda)$ in $(0,+\infty)$. Since $c_{L_n}(\lambda) \to c_\infty(\lambda)$ as $n \to +\infty$ in a monotone way for each $\lambda > 0$, Dini's theorem implies that the convergence of $c_{L_n}(\lambda)$ to $c_\infty(\lambda)$ as $n \to +\infty$ is local uniform with respect to $\lambda \in (0,+\infty)$. Thus,

$$c_\infty(\lambda^*_\infty) = \lim_{n\to+\infty} c_{L_n}(\lambda^*_{L_n})$$

and therefore, from (4.27) and the definition (4.22), one concludes that $c_\infty(\lambda^*_\infty) = c^*_\infty$. Lastly, the equalities $c_\infty(0^+) = c_\infty(+\infty) = +\infty$ follow from (4.25) and (4.26) satisfied for each $L \geq L_0$, and from the monotonicity with respect to L. □

We shall now use the structure of equation (2.4) with the patch model (H3) in order to derive the key-equation fulfilled by $k_\infty(\lambda)$ for all $\lambda > \gamma_\infty$, where $\gamma_\infty \in [0,+\infty)$ has been defined in (4.23).

Lemma 4.3. *For each $\lambda > \gamma_\infty$, there holds $k_\infty(\lambda) > \mu^+$ and $k_\infty(\lambda)$ satisfies the equation*

$$\theta\sqrt{k_\infty(\lambda) - \mu^+} + (1-\theta)\sqrt{k_\infty(\lambda) - \mu^-} = \lambda\sqrt{D}. \tag{4.29}$$

Proof. First, for any $\lambda \in \mathbb{R}$, setting $\varphi(x) = e^{\lambda x}\psi(x)$, the equation (2.4), with the periodicity conditions, becomes equivalent to:

$$\begin{cases} D\varphi'' + \mu_L(x)\varphi &= k_L(\lambda)\varphi \text{ in } \mathbb{R}, \\ \varphi(L) &= e^{\lambda L}\varphi(0), \\ \varphi'(L) &= e^{\lambda L}\varphi'(0), \\ \varphi &> 0 \text{ in } \mathbb{R}, \end{cases} \tag{4.30}$$

which therefore admits a unique solution $(\varphi, k_L(\lambda))$ with $\varphi > 0$ satisfying the normalization condition $\varphi(0) = 1$. The function φ is of class $C^1(\mathbb{R})$ and of class C^2 on the intervals $(0, \theta L)$ and $(\theta L, L)$ and their integer shifts. Because of (H3), system (4.30), together with the normalization condition $\varphi(0) = 1$, is equivalent to:

$$\begin{cases} D\varphi'' &= (k - \mu^+)\,\varphi \text{ on } (0,\theta L), \\ D\varphi'' &= (k - \mu^-)\,\varphi \text{ on } (\theta L, L), \\ \varphi(0) &= 1,\ \varphi(L) = e^{\lambda L}\varphi(0), \\ \varphi'(L) &= e^{\lambda L}\varphi'(0) \\ \varphi &> 0 \text{ in } \mathbb{R}, \end{cases} \tag{4.31}$$

with $k = k_L(\lambda)$.

Now, a straightforward but lengthy computation shows that, for each $\lambda \in \mathbb{R}$ and $L > 0$,

$$\Big[\exists\, k > \mu^+ \text{ and } \varphi \in C^1(\mathbb{R}) \text{ satisfying (4.31)}\Big] \Leftrightarrow \Big[F(\lambda, L, k) = 0\Big], \tag{4.32}$$

where the function $F:\mathbb{R}\times(0,+\infty)\times(\mu^+,+\infty)$, $(\lambda,L,k)\mapsto F(\lambda,L,k)$ is defined by

$$\begin{aligned} F(\lambda,L,k) &= (\mu^++\mu^--2k)\sinh\left(\theta L\sqrt{\tfrac{k-\mu^+}{D}}\right)\sinh\left((1-\theta)L\sqrt{\tfrac{k-\mu^-}{D}}\right) \\ &\quad +2\sqrt{k-\mu^+}\sqrt{k-\mu^-}\times \\ &\qquad\times\left[\cosh(\lambda L)-\cosh\left(\theta L\sqrt{\tfrac{k-\mu^+}{D}}\right)\cosh\left((1-\theta)L\sqrt{\tfrac{k-\mu^-}{D}}\right)\right]. \end{aligned} \tag{4.33}$$

Fix now any real number λ such that $\lambda>\gamma_\infty$. It follows from Proposition 4.1 that, for all L large enough, $k_L(\lambda)>\mu^+$. Since $k_L(\lambda)$ is nondecreasing with respect to L, one gets that $k_\infty(\lambda)>\mu^+$. Moreover,

$$F(\lambda,L,k_L(\lambda))=0. \tag{4.34}$$

If $\theta\sqrt{k_\infty(\lambda)-\mu^+}+(1-\theta)\sqrt{k_\infty(\lambda)-\mu^-}<\lambda\sqrt{D}$, then, by comparing the exponentially large terms in (4.34) and passing to the limit as $L\to\infty$, we obtain

$$\sqrt{k_\infty(\lambda)-\mu^+}\sqrt{k_\infty(\lambda)-\mu^-}=0,$$

which is impossible. On the other hand, if $\theta\sqrt{k_\infty(\lambda)-\mu^+}+(1-\theta)\sqrt{k_\infty(\lambda)-\mu^-}>\lambda\sqrt{D}$, then we get that

$$(\mu^++\mu^--2k_\infty(\lambda))-2\sqrt{k_\infty(\lambda)-\mu^+}\sqrt{k_\infty(\lambda)-\mu^-}=0,$$

which is impossible since the left-hand side is negative.

Finally, we therefore have $\theta\sqrt{k_\infty(\lambda)-\mu^+}+(1-\theta)\sqrt{k_\infty(\lambda)-\mu^-}=\lambda\sqrt{D}$. □

It remains to identify the real number γ_∞ and to show that λ^*_∞, given in Lemma 4.2, is larger than γ_∞:

Lemma 4.4. *There holds*

$$0<\gamma_\infty=(1-\theta)\sqrt{\frac{\mu^+-\mu^-}{D}}<\lambda^*_\infty.$$

Proof. Remember that $k_L(\gamma_L)=\mu^+$ and that $\gamma_L\to\gamma_\infty\geq 0$ as $L\to+\infty$. Since $k_L(\lambda)\to k_\infty(\lambda)$ as $L\to+\infty$ in a monotone way for each $\lambda\in\mathbb{R}$ and since the function k_∞ is convex whence continuous, Dini's theorem implies that the convergence $k_L(\lambda)\to k_\infty(\lambda)$ as $L\to+\infty$ is local uniform with respect to $\lambda\in\mathbb{R}$. Thus,

$$k_\infty(\gamma_\infty)=\mu^+.$$

But since equation (4.29) is also satisfied at $\lambda=\gamma_\infty$ by continuity of k_∞, it follows that

$$\gamma_\infty=(1-\theta)\sqrt{\frac{\mu^+-\mu^-}{D}}>0.$$

On the other hand, since formula (4.29) holds for all $\lambda \geq \gamma_\infty$, one gets that the right-derivative $k'_\infty(\gamma_\infty^+)$ of the convex function k_∞ at γ_∞ is equal to $k'_\infty(\gamma_\infty^+) = 0$. Therefore, the map $\lambda \mapsto c_\infty(\lambda) = k_\infty(\lambda)/\lambda$ has a right-derivative at γ_∞ and

$$c'_\infty(\gamma_\infty^+) = -\frac{k_\infty(\gamma_\infty)}{\gamma_\infty^2} = -\frac{\mu^+}{\gamma_\infty^2} < 0.$$

Since the function $\lambda \mapsto c_\infty(\lambda)$ is nondecreasing in $[\lambda_\infty^*, +\infty)$ from Lemma 4.2, one gets that $\gamma_\infty < \lambda_\infty^*$. □

Remark 4.5. Since the function k_∞ is convex and $k_\infty(0) \leq \mu^+$ from Proposition 4.1, it follows again from the convexity of k_∞ that $k_\infty(\lambda) = \mu^+$ for all $\lambda \in [0, \gamma_\infty]$, whence $c_\infty(\lambda) = \mu^+/\lambda$ in the interval $[0, \gamma_\infty]$.

Conclusion of the proof of Theorem 2.1. From Lemmata 4.2 and 4.4, we have

$$c_\infty^* = \min_{\Lambda > 0} \frac{k_\infty(\Lambda)}{\Lambda} = \min_{\Lambda \geq \gamma_\infty = (1-\theta)\sqrt{(\mu^+ - \mu^-)/D}} \frac{k_\infty(\Lambda)}{\Lambda},$$

where $k_\infty(\Lambda)$ is defined by (4.29) for all $\Lambda \geq \gamma_\infty$ from Lemma 4.3 and the continuity of k_∞. Therefore, by setting $\lambda = \Lambda\sqrt{D}$, it follows that

$$c_\infty^* = \sqrt{D} \min_{\lambda \geq (1-\theta)\sqrt{\mu^+ - \mu^-}} \frac{j^{-1}(\lambda)}{\lambda},$$

where $j(m) = \theta\sqrt{m - \mu^+} + (1-\theta)\sqrt{m - \mu^-}$ for all $m \geq \mu^+$. The proof of Theorem 2.1 is thereby complete. □

Proof of Proposition 2.3. The proof bears on a classical rescaling argument (see e.g. Nadin, 2010). Indeed, consider equation (2.4) with any $L > 0$ and $\lambda \in \mathbb{R}$, and set $\phi(x) = \psi(Lx)$. Let us make explicit the relationship between $k_L(\lambda)$ and μ by writing $k_L(\lambda, \mu)$ instead of $k_L(\lambda)$. We get that

$$D\,\phi'' + 2\,L\,\lambda\,D\,\phi' + L^2\,\lambda^2\,D\,\phi + L^2\,\mu\,\phi = L^2\,k_L(\lambda, \mu)\,\phi,\ \ x \in \mathbb{R}$$

and ϕ is 1-periodic and positive in $\mathbb{R}$. We deduce that $k_1(L\lambda, L^2\mu) = L^2 k_L(\lambda, \mu)$, and therefore

$$\frac{k_L(\lambda, \mu)}{\lambda} = \frac{1}{L} \times \frac{k_1(L\lambda, L^2\mu)}{L\lambda}.$$

From formula (2.3), it follows that

$$c^*(B) = \min_{\lambda' > 0} \frac{k_1(\lambda', B\mu)}{\lambda'} = \sqrt{B} \times \min_{\lambda > 0} \frac{k_{\sqrt{B}}(\lambda, \mu)}{\lambda} = \sqrt{B} \times c^*_{\sqrt{B}}.$$

Thus, we obtain that $c^*(B)/\sqrt{B}$ converges to c_∞^* as $B \to +\infty$. □

4.2 Propagation failure in the case of strong Allee effect

This subsection is devoted to the

Proof of Theorem 3.2. Let f, M, α, β, a, b, ξ and g be as in (3.19). Thus, there exists a function $h \in C^1([0, M+2]; \mathbb{R})$ which is larger than $f(x, \cdot)$ around 0 and larger than g on $[0, M]$, and which is bistable on $[0, M+2]$ with zero mass, that is

$$\begin{cases} h(0) = h(\xi) = h(M+2) = 0, \;\; h'(0) < 0, \;\; h'(M+2) < 0, \\ h < 0 \text{ on } (0, \xi), \;\; h > 0 \text{ on } (\xi, M+2), \;\; \displaystyle\int_0^{M+2} h(s)\, ds = 0, \\ \exists\, \beta' \in (0, \beta], \;\; \forall\, s \in [0, \beta'], \quad -\alpha\, s \le h(s), \\ \forall\, s \in [0, M], \quad g(s) \le h(s). \end{cases}$$

In particular, it follows from (3.19) that

$$\begin{cases} \forall\, (x, s) \in [a, b] \times [0, M+2], & f(x, s) \le h(s), \\ \forall\, (x, s) \in \mathbb{R} \times [0, \beta'], & f(x, s) \le h(s). \end{cases} \tag{4.35}$$

It is then well-known (Aronson and Weinberger, 1975; Fife, 1979) that there exists a stationary front connecting 0 to $M+2$ for problem (1.1) with nonlinearity h, namely there exists a unique C^2 function $\phi : \mathbb{R} \to (0, M+2)$ such that

$$\begin{cases} D\, \phi'' + h(\phi) = 0 \text{ on } \mathbb{R}, \\ \phi(-\infty) = M+2, \;\; \phi(0) = M+1, \;\; \phi(+\infty) = 0, \;\; \phi' < 0 \text{ on } \mathbb{R}. \end{cases}$$

The condition $\phi(0) = M+1$ is a normalization condition which guarantees the uniqueness of ϕ. Since $0 < \beta' \le M < M+1$, there exists a unique $A > 0$ such that $\phi(A) = \beta'$. Now, set

$$L^* = \frac{A}{b-a} > 0,$$

and let us check that the conclusion of Theorem 3.2 holds with this value L^*.

To do so, let L be any positive real number such that $L \ge L^*$, let u_0 be any bounded nonnegative and compactly supported function, let u denote the solution of the Cauchy problem (3.20) and let us prove that u cannot move to the right too far at large time because it is blocked from above by a suitable stationary supersolution in a neighborhood of $+\infty$.

Notice first that, since $f_L(x, s) \le 0$ for all $(x, s) \in \mathbb{R} \times [M, +\infty)$, the maximum principle implies that $u(t, x) \le v(t, x)$ for all $t \ge 0$ and $x \in \mathbb{R}$, where v denotes the solution of the heat equation

$$\frac{\partial v}{\partial t} = D \frac{\partial^2 v}{\partial x^2} \tag{4.36}$$

with initial condition $v_0(x) = \max(u_0(x), M)$. But $v_0 - M$ is bounded and compactly supported. Hence there exists a time $T \ge 0$ such that $v(t, x) - M \le 1$ for all $(t, x) \in$

$[T,+\infty) \times \mathbb{R}$. Therefore,

$$\forall\,(t,x) \in [T,+\infty) \times \mathbb{R}, \quad u(t,x) \le M+1. \tag{4.37}$$

Define

$$M' = \max(\|u_0\|_{L^\infty(\mathbb{R})}, M)$$

and observe that the constant M' is a supersolution for the problem (3.20), since $f_L(x,M') \le 0$ for all $x \in \mathbb{R}$. Therefore, $u \le M'$ in $[0,+\infty) \times \mathbb{R}$. Remember also that u is everywhere nonnegative since it is at initial time and since $f_L(x,0) = 0$ for all $x \in \mathbb{R}$. Since $f_L(x,s)$ is locally Lipschitz-continuous with respect s uniformly in x, there exists a constant $k > 0$ such that $f_L(x,s) \le k\,s$ for all $(x,s) \in \mathbb{R} \times [0,M']$. The maximum principle yields

$$\forall\,(t,x) \in [0,+\infty) \times \mathbb{R}, \quad u(t,x) \le e^{kt} w(t,x),$$

where w is the solution of the heat equation (4.36) with initial condition $w_0 = u_0$. But since w_0 is bounded and compactly supported, there exists $B > 0$ such that

$$\forall\,(t,x) \in [0,T] \times [B,+\infty), \quad w(t,x) \le e^{-kT} \times (M+1).$$

It follows that

$$\forall\,(t,x) \in [0,T] \times [B,+\infty), \quad u(t,x) \le M+1.$$

Together with (4.37), one gets that

$$\forall\,(t,x) \in [0,+\infty) \times [B,+\infty), \quad u(t,x) \le M+1. \tag{4.38}$$

Fix now $N \in \mathbb{N}$ such that

$$(a+N)\,L \ge B \;\text{ and }\; \text{supp}(u_0) \cap [(a+N)L,+\infty) = \emptyset,$$

where $\text{supp}(u_0)$ denotes the support of u_0. Set

$$\forall\,x \in \mathbb{R}, \quad \overline{\phi}(x) = \phi(x-(a+N)L).$$

Let us show that $\overline{\phi}$ is a supersolution for the Cauchy problem (3.20) for $(t,x) \in [0,+\infty) \times [(a+N)L,+\infty)$. Notice first that $\overline{\phi} > 0 = u_0$ in $[(a+N)L,+\infty)$ due to the choice of N. Furthermore, for all $t \ge 0$,

$$u(t,(a+N)L) \le M+1 = \phi(0) = \overline{\phi}((a+N)L)$$

because of (4.38) and $(a+N)L \ge B$. On the other hand, for all $x \in [(a+N)L,(b+N)L]$, there holds

$$D\,\overline{\phi}''(x) + f_L(x,\overline{\phi}(x)) = D\,\overline{\phi}''(x) + f\left(\frac{x}{L},\overline{\phi}(x)\right) \le D\,\overline{\phi}''(x) + h(\overline{\phi}(x)) = 0$$

from the definition of $\overline{\phi}$, from the first property of (4.35) and since f is 1-periodic in x. Lastly, for all $x \in [(b+N)L, +\infty)$, one has

$$x - (a+N)L \geq (b-a)L \geq (b-a)L^* = A$$

from the choice of L^*, whence

$$0 < \overline{\phi}(x) = \phi(x - (a+N)L) \leq \phi(A) = \beta'$$

since ϕ is decreasing. Thus, for all $x \in [(b+N)L, +\infty)$,

$$f_L(x, \overline{\phi}(x)) = f\left(\frac{x}{L}, \overline{\phi}(x)\right) \leq h(\overline{\phi}(x))$$

from the second property of (4.35), whence

$$D\,\overline{\phi}''(x) + f_L(x, \overline{\phi}(x)) \leq D\,\overline{\phi}''(x) + h(\overline{\phi}(x)) = 0.$$

Eventually, $D\,\overline{\phi}''(x) + f_L(x, \overline{\phi}(x)) \leq 0$ for all $x \geq (a+N)L$ and the maximum principle implies that

$$\forall\,(t,x) \in [0,+\infty) \times [(a+N)L, +\infty), \quad 0 \leq u(t,x) \leq \overline{\phi}(x) = \phi(x - (a+N)L).$$

Since $\phi(+\infty) = 0$, one concludes that $v_L^* = 0$, where v_L^* is defined in (3.17), irrespectively of the value $u^* > 0$ used in (3.18). The proof of Theorem 3.2 is thereby complete. □

5 Concluding remarks

We derived in Theorem 2.1 an exact formula for the spreading speed c_∞^* of the solution to the SKT patch model, in the limit of slowly oscillating environments. This formula enables explicit computation of c_∞^*, and comparison with rapidly oscillating environments. For several examples, under the hypotheses of the patch model, and under more general hypotheses, or for an integro-difference model introduced by Kawasaki and Shigesada (2007), we found significantly increased speeds in slowly varying environments, especially when the growth term has a large amplitude and a low average.

The numerical computations of Section 3.1 show that, for the SKT model, this pattern of dependence of the spreading speed with respect to the spatial period is strongly related to the infinite speed of propagation, common to models of the type (1.1) and to integro-difference models of the type (2.13) with non-compactly supported dispersal kernels. Indeed, we observed that very low population densities sent by diffusion in the favorable patches far from the leading edge of the front-like solution react and become significant before the leading edge of the solution attains this region (Fig. 1), emphasizing the *pulled* nature of the solutions of the SKT model.

Such a phenomenon should not appear for *pushed* solutions, and especially if the growth term remains negative whenever the population density is below a certain threshold, i.e. when a strong Allee effect occurs. Indeed, the density sent by diffusion too far from the leading edge of the solution will stay below this threshold, and will thereby not contribute to the progression of the invasion. In such case, the computations of Section 3.2 and Theorem 3.2 show that, when the period increases too much, the average speed of range expansion of the solution decreases and eventually becomes equal to 0. To our knowledge, the example presented here is the first one to show a decreasing relationship between aggregation of patches and propagation speeds, for reaction-diffusion models. Moreover, it reinforces our belief that, in the SKT model, a key element to explain the increase of the spreading speed in slowly oscillating environments is the infinite speed of propagation of the solution.

Reaction-diffusion models like (1.1) are often interpreted as if they were hydrodynamic limits of individual based models (IBMs). And this can indeed be proved rigourously, for instance in the simple case $f \equiv 0$. However, by nature, IBMs cannot exhibit infinite speed of propagation. We can therefore expect them to behave quite differently. For instance, in many situations, as discussed in Section 3.1, we could expect the spreading speed (to be defined rigorously for this kind of model) to decrease with L, and to converge to 0 as $L \to +\infty$.

The solutions of the SKT model exhibit other interesting spreading properties, which should not appear in IBMs. For instance, the unfavorable regions lead to an overall decreased speed compared to a homogeneous favorable environment, but to an increased speed in the favorable regions, compared to the homogeneous entirely favorable medium (Fig. 2).

Is it a strength or a weakness of this type of model to be able to exhibit growth of the very low population density which is dispersed by diffusion at long distance? Shall this be compensated systematically by assuming an Allee effect, by considering degenerate diffusion (which may lead to compactly supported solutions see e.g. Vázquez, 2007), or by using telegraph equation (see e.g. Turchin, 1998, for a biological interpretation), wave equations or other hyperbolic equations, when one wants to study the effects of the spatial heterogeneities on the spreading speed? We believe that the answer depends on the organisms we want to model.

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