Travelling waves for diffusive and strongly competitive systems: Relative motility and invasion speed

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Our interest here is to find the invader in a two species, diffusive and competitive Lotka–Volterra system in the particular case of travelling wave solutions. We investigate the role of diffusion in homogeneous domains. We might expect *a priori* two different cases: strong interspecific competition and weak interspecific competition. In this paper, we study the first one and obtain a clear conclusion: the invading species is, up to a fixed multiplicative constant, the more diffusive one.

1 Introduction

Competitive reaction–diffusion systems have been widely studied in the last few years. These mathematical models are motivated by numerous applications: ecology, chemistry, genetics, etc. In general, the mathematical formulations of this problem are, for some spatial domain Ω (not necessarily bounded), some $n \in \mathbb{N}$ and some positive constants $\left(d_i, r_i, a_i, k_{i,j}\right)_{i,j \in \{1,\dots,n\}}$

$$\forall i \in \{1, \dots, n\} \quad \partial_t u_i = d_i \Delta_x u_i + u_i \left(r_i - a_i u_i - \sum_{j \neq i} k_{i,j} u_j \right) \text{ in } \Omega \times (0, +\infty). \quad (1.1)$$

One tough question is how their solutions and, when they exist, the long-time steady states, depend on the diffusion rates $(d_i)_{i \in \{1,\dots,n\}}$. Asymptotically, how do the species (if we see these as continuous approximations of some population-dynamics problems) represented by the densities $(u_i)_{i \in \{1,\dots,n\}}$ share the domain Ω? Basically, in the neighbourhood of any spatial point x, two cases may occur: either only one species persists (exclusion case) or two or more persist (coexistence case). In the exclusion case, the only persistent species is called invading species. *A priori*, all the parameters participate in the determination

of this invader: number of species n, heterogeneity of Ω, boundedness of Ω, boundary conditions, intrinsic growth rates $(r_i)_{i \in \{1,\dots,n\}}$, interspecific competition rates $(k_{i,j})_{i,j \in \{1,\dots,n\}}$, intraspecific competition rates $(a_i)_{i \in \{1,\dots,n\}}$ and of course diffusion rates $(d_i)_{i \in \{1,\dots,n\}}$.

The dependency on diffusion rates is a very open general problem. Previous works show clearly that a very general result is for the moment unachievable and that we have to consider in each study a specific case for the other parameters of the problem. A key work in this area is the paper by Dockery *et al.* [6]. They proved that, when Ω is bounded, heterogeneous, with Neumann boundary conditions and when $k_{i,j} = 1$ for all $i,j \in \{1,\dots,n\}$, the less motile species – that is the one with the lower diffusion rate – is the invading species. Their result relies fundamentally on the heterogeneity, the basic idea being that each species loses the individuals trying to invade unfavourable areas while, in favourable areas, the competition helps the more concentrated one, that is the less diffusive one.

We leave the extension of Dockery's result for different $(k_{i,j})_{i,j \in \{1,\dots,n\}}$ to others and wonder if a similar result can be obtained in homogeneous domains (bounded or not).

Actually, it is quite tough to guess heuristically what could happen in homogeneous domains. Indeed, on one hand, the more diffusive species might be able to ignore its competitors long enough and invade the whole territory while eliminating the competitors slowly. On the other hand, the more concentrated species – that is the less diffusive one – might benefit from the maxim "unity is strength" and eliminate slowly the dispersed competitors and, asymptotically, invade the domain. It is well-known that diffusion tends to bring unexpected results. In any case, if something can revert the invasion, we expect it to be the competition. With this in mind, we decide to focus first on the infinite competition limit which should amplify the effects of competition.

Many papers limit their study to the case $n = 2$ (and so will we) because then the system becomes monotonic and is therefore much simpler to study than the general case. We will not use the monotonicity explicitly but it will be the underlying mechanism behind many results.

When $n = 2$, the PDE system can be rewritten as

$$\begin{cases} \partial_t u = d_1 \Delta_x u + u\,(r_1 - a_1 u - k_1 v) & \text{in} \quad \Omega \times (0, +\infty), \\ \partial_t v = d_2 \Delta_x v + v\,(r_2 - a_2 v - k_2 u) & \text{in} \quad \Omega \times (0, +\infty). \end{cases}$$

When there is no diffusion at all, this system becomes an ODE system. Then, the steady state $(u,v) = (0,1)$ (resp. $(u,v) = (1,0)$) is stable when $\frac{k_1 r_2}{r_1 a_2} > 1$ (resp. $\frac{k_2 r_1}{r_2 a_1} > 1$), unstable when $\frac{k_1 r_2}{r_1 a_2} < 1$ (resp. $\frac{k_2 r_1}{r_2 a_1} > 1$). Our interest lies in the bistable case and more precisely in the so-called "strong competition case" where $\frac{k_1 r_2}{r_1 a_2}$ and $\frac{k_2 r_1}{r_2 a_1}$ are much larger than 1. In the monostable case, only one species is a "strong" competitor.

The infinite competition limit ($k_1 \to +\infty$ and $\frac{k_1}{k_2}$ constant) has been studied by Dancer *et al.* in 1999 in the case of bounded domains with Neumann boundary conditions [5] (they also investigated Dirichlet conditions five years later [4]). They obtained a free boundary Stefan problem and, under regularity assumptions, a spatial segregation with an explicit condition on the interface. In 2007, Nakashima and Wakasa [13] studied the generation of interfaces for such systems and obtained a similar free boundary condition.

It is worth mentioning that the spatial segregation in multi-dimensional domains for

elliptic PDE yields highly non-trivial issues. It can be either approached as a free boundary problem (Dancer [5], Quitalo [14]) or as an optimal partition problem (Conti [2, 3]), but in both cases it is really a problem in itself, which requires additional assumptions on the initial conditions and a lot of work.

Therefore, our interest goes to unbounded homogeneous domains. Reaction–diffusion studies in such domains usually conjecture the existence of propagation fronts and, when their existence can be rigorously proved, derive from them some information on the dynamics of the system and the long-time steady state. Here, it is important to recall that the main underlying assumption with propagation fronts is that, when the initial conditions are well-chosen, the solutions of the PDE asymptotically "behave like" the travelling wave solution. We refer to Gardner [8] for such results for finite k. We will not treat this aspect of the problem in this paper but will indeed investigate travelling wave solutions.

A straightforward consequence of the travelling wave approach is that it reduces the multi-dimensional $\Omega \times \mathbb{R}_+^\star$ to $\mathbb{R}$. The problem becomes one-dimensional, that is an ODE problem, and thus all the free boundary issues vanish. Our hope is to find a similar spatial segregation limit, with an explicit condition on the interface connecting the invasion speed of the travelling wave to the diffusion rates. We know from Gardner [8] and Kan-On [10] that the invasion speed is constant and bounded by the Fisher–KPP's speeds [11] of the species. Can we use the infinite competition limit to derive its sign and therefore know which species invades the other? Will unity be strength?

It is important to remark that the invasion speed is not linearly determined here. Actually, a linearization near $(0, 1)$ or $(1, 0)$ yields no condition on the invasion speed and the linearized speed cannot be defined as usual. As far as we know, the linear determinacy for competition–diffusion systems is useful only with a specific class of monostable problems (Huang [9], Lewis [12]).

In the next section, we fully pose the problem, enunciate our final result and recall that the problem is well-posed. The third and main section is dedicated to a compactness result and the convergence to a limit problem which is similar in many ways to the one Dancer *et al.* obtained. Eventually, the last section explicits the relation between the speed and the diffusion rates.

2 Formulation of the problem and main theorem

In this first section, we present the PDE problem studied in this article, give its ecological interpretation and enunciate our main result. We also check quickly that the problem is well-posed.

2.1 Model

2.1.1 *Reaction–diffusion system*

We first consider the following one-dimensional Lotka–Volterra competition–diffusion problem:

$$\begin{cases} \partial_t \mu = d_1 \partial_{xx}\mu + \mu (r_1 - a_1\mu - k_1\rho) & \text{in} \quad \mathbb{R} \times (0, +\infty), \\ \partial_t \rho = d_2 \partial_{xx}\rho + \rho (r_2 - a_2\rho - k_2\mu) & \text{in} \quad \mathbb{R} \times (0, +\infty), \end{cases}$$

where $d_1, d_2, r_1, r_2, a_1, a_2, k_1, k_2$ are positive constants with ecological meaning (diffusion rates, intrinsic growth rates, intraspecific competition rates, interspecific competition rates). We assume, without loss of generality, that $\frac{k_2 a_2}{r_2^2} \geqslant \frac{k_1 a_1}{r_1^2}$.

Let $k = \frac{k_1 r_2}{a_2 r_1} > 0$, $\alpha = \frac{k_2 a_2 r_1}{k_1 a_1 r_2} > 0$, $d = \frac{d_2}{d_1} > 0$, $r = \frac{r_2}{r_1} > 0$ and

$$(u_k, v_k) : (x, t) \mapsto \left(\frac{a_1}{r_1} \mu \left(\sqrt{\frac{d_1}{r_1}} x, \frac{1}{r_1} t \right), \frac{a_2}{r_2} \rho \left(\sqrt{\frac{d_1}{r_1}} x, \frac{1}{r_1} t \right) \right).$$

We get

$$\begin{cases} \partial_t u_k = \partial_{xx} u_k + u_k (1 - u_k) - k u_k v_k & \text{in} \quad \mathbb{R} \times (0, +\infty), \\ \partial_t v_k = d \partial_{xx} v_k + r v_k (1 - v_k) - \alpha k u_k v_k & \text{in} \quad \mathbb{R} \times (0, +\infty). \end{cases}$$

As soon as $k > 1$ (which will always be assumed thereafter), $\frac{\alpha k}{r} > 1$, that is the system is bistable. Indeed, the free assumption $\frac{k_2 a_2}{r_2^2} \geqslant \frac{k_1 a_1}{r_1^2}$ we made earlier ensures that $\frac{\alpha}{r} \geqslant 1$.

A priori, the parameters k, α, d and r can take any positive value. Let $\mathscr{P}(k, \alpha, d, r)$ denote this generic PDE problem. Our interest lies in the limit, as $k \to +\infty$, of the set of problems $\{\mathscr{P}(k, \alpha, d, r)\}_{k > 1}$ (associated with a given (α, d, r)) (hence the notation u_k and v_k).

Moreover, going back to the initial parameters, this means that we actually consider a larger class of ecological problems than just $k_1 \to +\infty$ and $\frac{k_1}{k_2}$ constant. Indeed, the only restrictions are that $\frac{d_2}{d_1}$, $\frac{r_2}{r_1}$ and $\frac{k_2 a_2}{k_1 a_1}$ are fixed along the whole class. For example, the limit $k \to +\infty$ may correspond to the following:

- k_2 proportional (with a fixed constant along the whole class) to k_1 and $k_1 \to +\infty$ with a_1 and a_2 fixed (along the whole class);
- $k_1 \to +\infty$ and a_1 proportional to $\frac{1}{k_1}$ with a_2 and k_2 fixed;
- a_2 proportional to a_1 and $a_1 \to 0$ with k_1 and k_2 fixed.

2.1.2 *Travelling wave system*

Searching for a travelling wave of the variable $\xi = x - c_k t$, where $c_k \in \mathbb{R}$ is the unknown invasion speed, the problem is eventually rewritten as

$$\begin{cases} -u_k'' - c_k u_k' = u_k (1 - u_k) - k u_k v_k & \text{in} \quad \mathbb{R} \\ -d v_k'' - c_k v_k' = r v_k (1 - v_k) - \alpha k u_k v_k & \text{in} \quad \mathbb{R} \\ u_k(-\infty) = 1, \ u_k(+\infty) = 0 \\ v_k(-\infty) = 0, \ v_k(+\infty) = 1 \\ \qquad u_k' < 0 & \text{in} \quad \mathbb{R} \\ \qquad v_k' > 0 & \text{in} \quad \mathbb{R}. \end{cases} \tag{2.1}$$

It is well-known that natural selection tends to differentiate the niches of competing species. The travelling wave solution corresponds to the case where u_k lives essentially in the left half-space while v_k lives essentially in the right half-space. In such a situation, it seems obvious that one species might chase the other and invade the abandoned territory. The whole point of this article is to determine this species, or equivalently, the sign of the invasion speed. Indeed

(1) $c_k > 0$ iff u_k chases v_k;

(2) $c_k < 0$ iff v_k chases u_k.

Of course, we aim to find a result depending on the value of d. Thus in the following pages, when we focus on the dependency of c_k on d, we write $c_{k,d}$; otherwise, when d is fixed, we simply write c_k.

2.2 "Unity is not strength" theorem

Our main result follows.

Theorem 2.1 $\left(d \mapsto c_{k,d}\right)_{k>1}$ *converges locally uniformly in* $(0, +\infty)$ *to a continuous function* $d \mapsto c_{\infty,d}$ *which satisfies the following:*

(1) $c_{\infty,d} = 0$ *if* $d = \frac{\alpha^2}{r}$;

(2) $c_{\infty,d} \in (0, 2)$ *if* $d \in \left(0, \frac{\alpha^2}{r}\right)$;

(3) $c_{\infty,d} \in \left(-2\sqrt{rd}, 0\right)$ *if* $d > \frac{\alpha^2}{r}$.

Remark 2.2 *This result is profoundly unexpected! It does not suffice to compare d to 1 or α to 1. v can lose even if r is large and u can lose even if α is large, for example. This should yield interesting insight into ecological applications.*

2.3 Well-posedness and regularity of the problem

Theorem 2.3 *For any $k > 1$, there exists a unique c_k such that there exist solutions u_k and v_k of the problem (2.1). It is needed that $c_k \in \left(-2\sqrt{rd}, 2\right)$, $u_k \in \mathscr{C}^\infty(\mathbb{R})$ and $v_k \in \mathscr{C}^\infty(\mathbb{R})$. We can moreover assume exactly one of the following normalization hypotheses:*

- $u_k(0) = v_k(0)$,
- $u_k(0) = \frac{1}{2}$,
- $v_k(0) = \frac{1}{2}$,

and if we do so, u_k and v_k are unique.

Proof The well-posedness and the bounds for c_k are proven by Gardner in [8] and also by Kan-On in [10] (actually, Gardner only showed $c_k \in \left[-2\sqrt{rd}, 2\right]$ but Kan-On showed indeed $c_k \in \left(-2\sqrt{rd}, 2\right)$ which will be important in the end). It is worth mentioning that their papers actually proved that the problem is well-posed without any monotonicity condition and that the monotonicity is indeed needed.

Since $u_k, v_k \in L^\infty(\mathbb{R})$ and $u_k', v_k' \in L^1(\mathbb{R})$, the regularity just follows from $W^{k,p}$-estimates and Sobolev's injections. $\qquad\square$

Remark 2.4 *The extremal speeds* $-2\sqrt{rd}$ *and* 2 *are the invasion speeds of respectively* v_k *when* $u_k = 0$ *and* u_k *when* $v_k = 0$. *This is a well-known result from Fisher, Kolmogorov, Petrovsky and Piscounov [11].*

3 Limit problem

Here we show that (u_k), (v_k) and (c_k) converge when $k \to +\infty$ and formulate the limit problem.

3.1 Existence of limit points

First, (c_k) is relatively compact and therefore, by the Bolzano–Weierstrass theorem, has a limit point $c \in \left[-2\sqrt{rd}, 2\right]$.

If $c \leqslant 0$, we fix for any $k > 1$ the normalization $u_k(0) = \frac{1}{2}$. On the contrary, if $c > 0$, we fix for any $k > 1$ $v_k(0) = \frac{1}{2}$. This choice will be explained later on. In either case, this implies that the functions $k \mapsto u_k$ and $k \mapsto v_k$ are well-defined.

Proposition 3.1 *For any* $i \geqslant 1$, *let* $K_i = [-i, i]$. (u_k) *and* (v_k) *are relatively compact in* $\mathscr{C}(K_i)$.

Proof Our aim here is to use Ascoli's theorem. To that end, let us show that each u_k is Hölder-continuous with a constant independent of k.

There exists a positive function $\chi \in \mathscr{D}(\mathbb{R})$ such that $\chi(x) = 0$ if $x \notin [-i-1, i+1]$ and $\chi(x) = 1$ if $x \in [-i, i]$.

For any $k > 1$, if we multiply the equation defining u_k by $u_k \chi$ and then integrate, we get

$$\int \left(-u_k'' u_k \chi - c_k u_k' u_k \chi\right) = \int u_k^2 \chi - \int u_k^2 (u_k + k v_k) \chi.$$

The third term is obviously negative. An integration by parts yields

$$\int u_k'^2 \chi - \int \frac{u_k^2}{2} \chi'' + c_k \int \frac{u_k^2}{2} \chi' \leqslant \int u_k^2 \chi.$$

Finally, since $\int u_k'^2 \chi \geqslant \int_{-i}^{i} u_k'^2$ and $\|u_k\|_{L^\infty} \leqslant 1$, we have

$$\|u_k'\|_{L^2(K_i)}^2 \leqslant \int \left(\chi + \frac{|c_k|}{2} |\chi'| + \frac{1}{2} |\chi''|\right).$$

Then we use Ascoli's theorem: the family (u_k) is bounded in $L^\infty(K_i)$ and uniformly equicontinuous in K_i therefore it is relatively compact in $\mathscr{C}(K_i)$. The exact same proof works for (v_k). $\qquad\square$

It is now clear, by a standard diagonal extraction argument, that there exists a subsequence of (u_k) (resp. (v_k)) which converges locally uniformly to a limit point u (resp. v).

3.2 Properties of the limit points

c, u and v are actually unique and true limits as will be proven later on. For the moment, let us just consider extracted convergent subsequences, still denoted by (c_k), (u_k) and (v_k).

Lemma 3.2 $uv = 0$.

Proof Multiplying by a test function $\varphi \in \mathscr{D}(\mathbb{R})$ and integrating the equation for u_k yields

$$k \left| \int u_k v_k \varphi \right| \leqslant \int u_k (1 - u_k) |\varphi| + |c_k| \int u_k |\varphi'| + \int u_k |\varphi''|$$
$$\leqslant C \|\varphi\|_{W^{2,1}(\mathbb{R})}.$$

Hence $u_k v_k \to 0$ in $\mathscr{D}'(\mathbb{R})$.

Since $u_k v_k \to uv$ locally uniformly, we get indeed $uv = 0$. $\qquad\square$

Remark 3.3 *This kind of result is usually referred to as a segregation property. There is a lot of similar results in the literature.*

Lemma 3.4 *We have*

$$-\alpha u'' + dv'' - \alpha c u' + c v' = \alpha u (1 - u) - r v (1 - v)$$

in $\mathscr{D}'(\mathbb{R})$.

Proof Multiply the equation for u_k by α and subtract from it the one for v_k. The left-hand side converges trivially in $\mathscr{D}'(\mathbb{R})$. The right-hand side converges by dominated convergence. $\qquad\square$

Lemma 3.5 $u, v \in \mathscr{C}(\mathbb{R})$ *and* $\alpha u - dv \in \mathscr{C}^1(\mathbb{R})$.

Proof The continuity of u and v is immediate thanks to the continuity of each u_k and v_k and the locally uniform convergence.

Let $a, b \in \mathbb{R}$ such that $a < b$ and $I_a : C([a,b]) \to C([a,b])$ defined by $I_a(f) : x \mapsto \int_a^x f$. By continuity of u and v, it is quite obvious that the function

$$\alpha c u - c v + I_a (\alpha u (1 - u) - r v (1 - v)) - (\alpha c u (a) - c v (a)),$$

is continuous. But, thanks to the previous lemma, it is also equal in $\mathscr{D}'((a,b))$ to $-\alpha u' + dv'$ up to an additive constant. Therefore $-\alpha u' + dv'$ is a well-defined function of $\mathscr{C}([a,b])$. $\quad\square$

Lemma 3.6 u *and* v *have finite limits at* $\pm\infty$. *Also*

$$0 \leqslant \lim_{+\infty} u \leqslant \lim_{-\infty} u \leqslant 1,$$

and

$$0 \leqslant \lim_{-\infty} v \leqslant \lim_{+\infty} v \leqslant 1.$$

Proof By locally uniform convergence, u and v are monotone, respectively non-increasing and non-decreasing, and satisfy $0 \leqslant u, v \leqslant 1$. ☐

Lemma 3.7 *u and v cannot vanish simultaneously on a compact set with non-empty interior.*

Proof Once again, we consider a compact set with non-empty interior $[a, b]$. By monotonicity, if $u_{|[a,b]} = 0$, then $u_{|[a,+\infty)} = 0$. Similarly, $v_{|(-\infty,b]} = 0$. Thus, in $\mathscr{D}'((-\infty, a))$, $-u'' - cu' = u(1-u)$ and $\alpha u' - dv' = \alpha u'$. Therefore u' is continuous and, using $-u'' - cu' = u(1-u)$, u'' is also continuous and the previous differential equation is satisfied pointwise.

Now, we get by induction that u is $\mathscr{C}^\infty$ in $(-\infty, a)$. Since it does not explode on the left of a, it is the restriction of a solution on a strictly larger interval. Since u is regular, $u'(a) = 0$ and by Cauchy–Lipschitz's theorem, u is identically null. By the same reasoning, v is also identically null.

To prevent u and v from being both null on the whole real line, either one of the two normalization sequences $(u_k(0))_{k>1} = \left(\frac{1}{2}\right)$ and $(v_k(0)) = \left(\frac{1}{2}\right)$ combined with locally uniform convergence suffices. ☐

Remark 3.8 *We already knew that $uv = 0$ everywhere. Thus the previous lemma ensures that, for any $a < b$, $u_{|[a,b]} = v_{|[a,b]} = 0$ is not possible; one of the two densities has to be positive whereas the other has to be null.*

Lemma 3.9 *Neither u nor v can be positive everywhere.*

Proof If $c \leqslant 0$, the normalization sequence is $(u_k(0)) = \left(\frac{1}{2}\right)$. It ensures that u is not null. We define $\xi_u = \sup\{\xi \in \mathbb{R} \mid u(\xi) > 0\} \in (-\infty, +\infty]$.

If $\xi_u = +\infty$ (that is, u positive everywhere), v is null.

In such a case, we have u decreasing, bounded between 0 and 1, with limits at infinity, non-constant by normalization, and $-u'' - cu' = u(1-u)$ everywhere with $u \in \mathscr{C}^\infty(\mathbb{R})$.

This yields that $\lim_{-\infty} u = 1$ and $\lim_{+\infty} u = 0$. To that end, we use L'Hospital's rule.

Let $l = u(-\infty)$, $G : \xi \mapsto \exp(c\xi)$ and $F = Gu'$ so that $F' = G(u'' + cu') = -Gu(1-u)$. F and G are differentiable in $\mathbb{R}$, $G' \neq 0$ and $G \to +\infty$ as $\xi \to -\infty$; moreover, $\frac{F'}{G'} \to -\frac{l(1-l)}{c}$. By L'Hospital's rule, $\frac{F}{G} \to -\frac{l(1-l)}{c}$, that is $u'(-\infty) = -\frac{l(1-l)}{c}$. In the end, necessarily, $l \in \{0, 1\}$.

At $+\infty$, we use the other version of L'Hospital's rule, noticing that u' is bounded in $\mathbb{R}_+$ (easy to prove) and checking that F and G go to 0. Eventually, by monotonicity, the limits are 1 at $-\infty$ and 0 at $+\infty$.

Thus u is a travelling wave for the Fisher–KPP equation with speed $c \leqslant 0 < \sqrt{2}$, hence the contradiction [11].

If $c > 0$, we just apply this reasoning to v with normalization $(v_k(0)) = \left(\frac{1}{2}\right)$. ☐

Corollary 3.10 *The two quantities $\sup\{\xi \in \mathbb{R} \mid u(\xi) > 0\}$ and $\inf\{\xi \in \mathbb{R} \mid v(\xi) > 0\}$ are real and equal. Up to translation, we can assume it to be 0. By continuity of u and v, $u(0) = v(0) = 0$.*

Lemma 3.11 *We have*

- $u \in \mathscr{C}^{\infty} \left((-\infty, 0) \cup (0, +\infty) \right)$,
- $v \in \mathscr{C}^{\infty} \left((-\infty, 0) \cup (0, +\infty) \right)$.

Moreover, we can extend u' and v' by continuity on the left and on the right respectively and obtain $u'(0) = \lim_{\xi \to 0, \xi < 0} u'(\xi)$ and $v'(\xi_v) = \lim_{\xi \to 0, \xi > 0} v'(\xi)$ which are finite and satisfy $-\alpha u'(0) = d v'(0) > 0$.

Proof u is identically zero on $(0, \infty)$ so $u_{|(0, +\infty)}$ is trivially $\mathscr{C}^{\infty}$. In $(-\infty, 0)$, it is a weak, and then regular (same routine), solution of $u'' + c u' + u(1 - u) = 0$.

Eventually, just recall that $\alpha u - d v \in \mathscr{C}^1 (\mathbb{R})$. If its derivative at 0 is zero, by the same kind of Cauchy–Lipschitz reasoning, $u = v = 0$ everywhere. $\qquad \square$

Remark 3.12 *The relation $\alpha u'(0) + d v'(0) = 0$ is essentially the free boundary condition obtained by Nakashima and Wakasa in [13].*

Lemma 3.13 $\lim_{-\infty} u = 1$ *and* $\lim_{+\infty} v = 1$.

Proof Same as before. $\qquad \square$

Lemma 3.14 $c \in \left(-2\sqrt{rd}, 2 \right)$, *that is* $c \notin \left\{ -2\sqrt{rd}, 2 \right\}$.

Proof Let us assume, for example, $c = -2\sqrt{rd}$. Let $\xi^{\star} > 0$ such that $v(\xi^{\star}) = \frac{1}{2}$.

We know from Fisher and KPP [11] that $c = -2\sqrt{rd}$ is the maximal speed for which there exists a travelling wave v_{KPP} positive, going from 0 at $-\infty$ to 1 at $+\infty$, which satisfies

$$-d v''_{\mathrm{KPP}} - c v'_{\mathrm{KPP}} = r v_{\mathrm{KPP}} (1 - v_{\mathrm{KPP}}).$$

We normalize by fixing $v_{\mathrm{KPP}}(\xi^{\star}) = \frac{1}{2}$. Let $f = v_{\mathrm{KPP}} - v$.

First, we can easily check that f is in $\mathscr{C}(\mathbb{R}) \cap \mathscr{C}^{\infty} ((-\infty, 0) \cup (0, +\infty))$ and satisfies

$$-d f'' - c f' = r f(1 - f) - 2 r v f,$$

in $(0, +\infty)$.

For any $\xi > \xi^{\star}$, $1 - f(\xi) - 2 v(\xi) = 1 - v_{\mathrm{KPP}}(\xi) - v(\xi) < 0$, with $f(\xi^{\star}) = 0$. We can therefore apply the maximum principle to the operator

$$d \bullet'' + c \bullet' + r(1 - f - 2v) \bullet,$$

in any interval $(\xi^{\star}, b)$, $b > \xi^{\star}$. Since $\lim_{+\infty} f = 0$, it gives us that $f(\xi) \leqslant 0$ for any $\xi \in (\xi^{\star}, +\infty)$. But we can also apply the minimum principle to the same operator, and we eventually get that f is identically zero in $(\xi^{\star}, +\infty)$. This way, $f'(\xi^{\star}) = 0$, hence f is identically zero in $(0, +\infty)$, which is impossible since $f(0) > 0$ and f is continuous in $\mathbb{R}$. $\qquad \square$
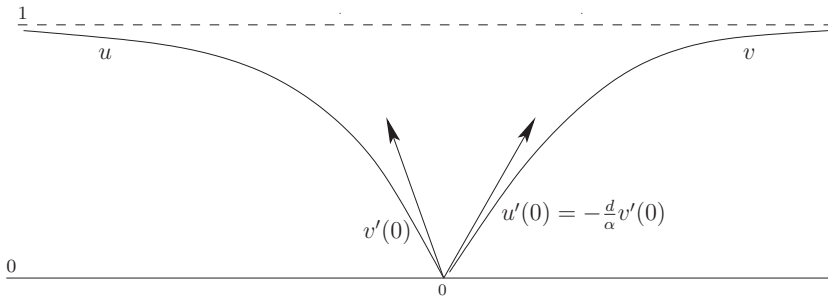
3.3 Limit problem

Let us sum up all these results in the following theorem.

Theorem 3.15 *There exist locally uniform limits u and v of (u_k) and (v_k) respectively. They satisfy*

(1) $u, v \in \mathscr{C}(\mathbb{R}) \cap \mathscr{C}^{\infty}((-\infty, 0) \cup (0, +\infty))$;

(2) $\lim_{\xi \to -\infty} u(\xi) = 1$;

(3) $\lim_{\xi \to +\infty} v(\xi) = 1$;

(4) $u_{|\mathbb{R}_+} = 0$;

(5) $v_{|\mathbb{R}_-} = 0$;

(6) $u' \leqslant 0$ *in* $\mathbb{R}_-$ *with* $u'(0)$ *defined by left-continuity*;

(7) $v' \geqslant 0$ *in* $\mathbb{R}_+$ *with* $v'(0)$ *defined by right-continuity*;

(8) $-u'' - cu' = u(1 - u)$ *in* $(-\infty, 0)$;

(9) $-dv'' - cv' = rv(1 - v)$ *in* $(0, +\infty)$;

(10) $\alpha u'(0) = -dv'(0)$.

The behaviour of these limits is illustrated with the following figure.

3.4 Uniqueness of the limit points

Theorem 3.16 *For any $c > -2$, the problem*

$$\begin{cases} -y_c'' - cy_c' = y_c(1 - y_c) & in \quad (0, +\infty) \\ \quad\quad\quad y_c(0) = 0, \end{cases}$$

admits a unique positive solution.

It satisfies $y_c' > 0$ in $\mathbb{R}_+$ and $\lim_{\xi \to +\infty} y(\xi) = 1$. Besides, $\gamma : c \mapsto y_c'(0)$ is increasing and continuous.

Proof This result was proved by Du and Lin in [7] (Proposition 4.1) but wrongly stated. Indeed, the requirement in their theorem should be $c < 2$, not $c \geqslant 0$ as stated in [7]. (Moreover, be aware that our statement is written with $-cy_c'$ whereas their statement is

written with $+cy'_c$; so the requirement $c < 2$ becomes here $c > -2$; this also changes the monotonicity of γ.)

Let us remove all doubts by filling the gap in their proof, that is at the beginning where they construct their subsolution.

- Case $|c| < 2$: For all $\ell > 0$, let y^ℓ the positive solution of

$$\begin{cases} -y'' - cy' = y(1-y) & \text{in } (0, \ell), \\ y(0) = y(\ell) = 0. \end{cases}$$

According to Berestycki [1] (Theorem 4), such a solution exists if and only if the Dirichlet principal eigenvalue of the operator $-L$ on $(0, \ell)$ is negative: $\lambda_1(-L, (0, \ell)) < 0$, where L is the operator associated with the linearized equation near $y = 0$: $L\phi := \phi'' + c\phi' + \phi$. It is easy to compute

$$\lambda_1(-L, (0, \ell)) = -1 + \frac{c^2}{4} + \frac{\pi^2}{\ell^2}.$$

Hence, when $|c| < 2$, one has $\lambda_1(-L, (0, \ell)) < 0$ when ℓ is large enough and thus we can construct y^ℓ. Vice-versa, if $|c| \geqslant 2$, $\lambda_1(-L, (0, \ell)) > 0$ and the solution does not exist (whereas Du and Lin claim it does for all $c \leqslant 0$).

- Case $c \geqslant 2$: It suffices to remark that, for example, if y_1 is a solution of the previous Dirichlet problem for some $c_1 \in (-2, 2)$, then y_1 is a subsolution for the Dirichlet problem with any speed $c > c_1$.

In either case, the subsolution is now properly constructed and we can continue the proof as in [7] and conclude the proof. $\qquad\square$

Remark 3.17 *We need to change u and v before pursuing this direction. Let us consider $\tilde{u} : \xi \mapsto u(-\xi)$ and $\tilde{v} : \xi \mapsto v\left(\sqrt{\frac{d}{r}}\xi\right)$. $\tilde{u}$ is a solution of the problem*

$$\begin{cases} -\tilde{u}'' + c\tilde{u}' = \tilde{u}(1 - \tilde{u}) & \text{in} \quad (0, +\infty) \\ \tilde{u}(0) = 0. \end{cases}$$

$\tilde{v}$ is a solution of the problem

$$\begin{cases} -\tilde{v}'' - \frac{c}{\sqrt{rd}}\tilde{v}' = \tilde{v}(1 - \tilde{v}) & \text{in} \quad (0, +\infty) \\ \tilde{v}(0) = 0. \end{cases}$$

Also, $c \in \left(-2\sqrt{rd}, 2\right)$ so $-c > -2$ and $\frac{c}{\sqrt{rd}} > -2$, therefore we can apply the theorem.

Corollary 3.18 *For any $d > 0$, there exists a unique (u, v, c) satisfying the limit problem (and may thereafter be called $\left(u_{\infty,d}, v_{\infty,d}, c_{\infty,d}\right)$).*

Proof The equality $-\alpha u'(0) = dv'(0)$ can be written as $\alpha\gamma(-c) = \sqrt{rd}\gamma\left(\frac{c}{\sqrt{rd}}\right)$. Now we consider the two functions $x \mapsto \alpha\gamma(-x)$ and $x \mapsto \sqrt{rd}\gamma\left(\frac{x}{\sqrt{rd}}\right)$. They necessarily have an

intersection point since c exists. But as they are respectively decreasing and increasing, this intersection point is unique.

The uniqueness of c implies by the previous theorem the uniqueness of u and v. □

Corollary 3.19 *The sequences (c_k), (u_k) and (v_k) each have a unique limit point. Hence the pointwise convergence of (c_k) and locally uniform convergence of (u_k) and (v_k) are fully proved and there is no need to consider extracted subsequences anymore.*

Proof Recall that, in any metric space, a sequence whose image is relatively compact and which has a unique limit point converges to this limit point. □

Remark 3.20 *It is now clear that the sum up theorem of the previous section gives sufficient but far from necessary conditions for uniqueness. For any c, u and v are unique iff they are positive and satisfy points 4, 5, 8 and 9 and then the uniqueness of c is just a consequence of point 10.*

Proposition 3.21 *The convergence of $\left(d \mapsto c_{k,d}\right)_{k>1}$ to $d \mapsto c_{\infty,d}$ is locally uniform.*

Proof Actually, one can see easily that the whole proof of pointwise convergence of $\left(d \mapsto c_{k,d}\right)_{k>1}$ holds if we do not fix *a priori* d. It suffices to have $d \in [D_1, D_2]$, with $D_2 > D_1 > 0$ fixed, so that we can replace bounds like $-2\sqrt{rd}$ by $-2\sqrt{rD_2}$. □

4 Dependency of the invasion speed on the diffusion rates

This last section is where we derive from the limit problem the result: how does the invasion speed c depend on the diffusion rate d? Thanks to the convergence of (c_k) to c, we will then be able to extend it to c_k (for k large enough).

Theorem 4.1 *We have*

- *if $d = \frac{\alpha^2}{r}$, $c_{\infty,d} = 0$;*
- *if $d > \frac{\alpha^2}{r}$, $c_{\infty,d} \in \left(-2\sqrt{rd}, 0\right)$;*
- *if $d < \frac{\alpha^2}{r}$, $c_{\infty,d} \in (0, 2)$.*

Proof The sign of $c_{\infty,d}$ is actually a simple consequence of the relation $\alpha\gamma(-c) = \sqrt{rd}\gamma\left(\frac{c}{\sqrt{rd}}\right)$. Indeed, let us prove that $rd < \alpha^2$ implies $c_{\infty,d} > 0$. Indeed, if $rd < \alpha^2$, then $\frac{\sqrt{rd}}{\alpha} < 1$ and as $\gamma\left(\frac{c}{\sqrt{rd}}\right) > 0$, we get $\frac{\sqrt{rd}}{\alpha}\gamma\left(\frac{c}{\sqrt{rd}}\right) < \gamma\left(\frac{c}{\sqrt{rd}}\right)$. Since γ is increasing, $\frac{c}{\sqrt{rd}} > -c$, which clearly implies that $c > 0$. The case $rd > \alpha^2$ is similar.

If $rd = \alpha^2$, the relation becomes $\gamma(-c) = \gamma\left(\frac{c}{\sqrt{rd}}\right)$. An obvious zero of $x \mapsto \gamma(-x) - \gamma\left(\frac{x}{\sqrt{rd}}\right)$ is 0, and by monotonicity it is unique, hence $c = 0$. □

Proposition 4.2 *The function $d \mapsto c_{\infty,d}$ is continuous in $(0, +\infty)$.*

Proof This could follow from the continuity of each $d \mapsto c_{k,d}$ and the locally uniform convergence, but the continuity of $d \mapsto c_{k,d}$ is actually a more difficult problem (and is not solved by Kan-On [10]). Therefore, we prove the continuity of $d \mapsto c_{\infty,d}$ directly. Our proof being basically a repetition of the whole previous section of this article, we give only a sketch of it.

First, let $0 < D_1 < D_2$. We have

$$\{c_{\infty,d} \mid d \in [D_1, D_2]\} \subset \left\{c_{\infty,d} \mid d \in [D_1, D_2] \cap \left(\frac{\alpha^2}{r}, +\infty\right)\right\} \cup \{0\} \cup \left\{c_{\infty,d} \mid d \in \cap \left(0, \frac{\alpha^2}{r}\right)\right\}$$

$$\subset \left(\bigcup_{d \in [D_1, D_2] \cap \left(\frac{\alpha^2}{r}, +\infty\right)} \left[-2\sqrt{rd}, 0\right]\right) \cup [0, 2]$$

$$\subset \left[-2\sqrt{rD_2}, 2\right].$$

Thus, $\{c_{\infty,d} \mid d \in [D_1, D_2]\}$ is a relatively compact subset of $\mathbb{R}$.

Now, let $\delta \in [D_1, D_2]$ and $(\delta_n)_{n \in \mathbb{N}} \in [D_1, D_2]^{\mathbb{N}}$ a positive sequence which converges to δ. Up to extraction, (c_{∞,δ_n}) converges to a limit point C.

If $C \leqslant 0$, we translate each couple $(u_{\infty,\delta_n}, v_{\infty,\delta_n})$ so that $(u_{\infty,\delta_n}(0)) = (\frac{1}{2})$. If $C > 0$, we translate each couple $(u_{\infty,\delta_n}, v_{\infty,\delta_n})$ so that $(v_{\infty,\delta_n}(0)) = (\frac{1}{2})$. In either case, $\{u_{\infty,d} \mid d \in [D_1, D_2]\}$ and $\{v_{\infty,d} \mid d \in [D_1, D_2]\}$ are relatively compact in each $C(K_i)$ by Ascoli's theorem, and, up to extraction, (u_{∞,δ_n}) and (v_{∞,δ_n}) converge locally uniformly. Let U and V be their limits.

- We have $-\alpha U'' + \delta V'' - \alpha C U' + C V' = \alpha U (1 - U) - r V (1 - V)$ in $\mathscr{D}'(\mathbb{R})$.
- U and V are continuous, $\alpha U - \delta V$ is C^1.
- U and V are positive and have finite limits at infinity.
- $UV = 0$.
- If $C \leqslant 0$, U is not identically null by normalization and V cannot be identically null since if it was, U would be a travelling wave for the Fisher–KPP equation with a speed smaller than 2. The same reasoning applies for $C > 0$ and finally, neither U nor V can be identically null.
- U and V cannot be both null on a compact subset by continuity of $(\alpha U - \delta V)'$ and a Cauchy–Lipschitz's argument.

Now we translate back so that

$$\sup \{\xi \in \mathbb{R} \mid U(\xi) > 0\} = \inf \{\xi \in \mathbb{R} \mid V(\xi) > 0\} = 0.$$

This yields $U_{|\mathbb{R}_+} = 0$, $V_{|\mathbb{R}_-} = 0$, $-U'' - C U' = U(1 - U)$ in $(-\infty, 0)$, $-\delta V'' - C V' = r V(1 - V)$ in $(0, +\infty)$ and $\alpha U'(0) = -\delta V'(0)$. Basically, C, U and V satisfy the exact same problem as $c_{\infty,\delta}$, $u_{\infty,\delta}$ and $v_{\infty,\delta}$. By uniqueness, $C = c_{\infty,\delta}$, that is $c_{\infty,\delta}$ is the unique limit point of (c_{∞,δ_n}) and eventually $c_{\infty,\delta_n} \to c_{\infty,\delta}$. Therefore, $d \mapsto c_{\infty,d}$ is indeed continuous.

$\square$

5 Conclusion

We have proved our "Unity is not strength" theorem. Some remaining questions concern the shape of the asymptotic speed: What are the limits when $d \to 0$ or $d \to +\infty$? Are there optimal diffusion rates so that the invasion of one species or the other is the fastest? And eventually, how fast is the convergence to this asymptotic limit and, for example, is it monotone?

These could be addressed with the knowledge of the derivatives of the speed as a function of k or d. These might be determined analytically thanks to Kan-On formulas [10]. However, we did not manage to compute the sign of these derivatives, that is, the monotonicity of the speed with respect to k or d. We leave it as an open problem.

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