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Spreading speeds for a two-species competition-diffusion system

Cécile Carrère*

October 4, 2017

Abstract

In this paper, spreading properties of a competition-diffusion system of two equations are studied. This system models the invasion of an empty favorable habitat, by two competing species, each obeying a logistic growth equation, such that any coexistence state is unstable. If the two species are initially absent from the right half-line $x > 0$, and the slowest one dominates the fastest one on $x < 0$, then the latter will invade the right space at its Fisher-KPP speed, and will be replaced by or will invade the former, depending on the parameters, at a slower speed. Thus, the system forms a propagating terrace, linking an unstable state to two consecutive stable states.

1 Introduction

This paper is devoted to the study of the spreading of the following competition-diffusion system between two species s and r :

$$\begin{cases} \partial_t s - \delta_0 \partial_{xx}^2 s = s(\alpha_0 - s - \gamma_0 r), \\ \partial_t r - \partial_{xx}^2 r = r(1 - \beta_0 s - r) \end{cases} \quad (1)$$

with positive parameters $\alpha_0, \beta_0, \gamma_0, \delta_0$ satisfying $1/\beta_0 < \alpha_0 < \gamma_0$, which ensures that equilibria $(\alpha_0, 0)$ and $(0, 1)$ are both stable for the corresponding ODE system. More precisely, for initial conditions where both species are absent from the right half-line $x > 0$, and s dominates r around $x = -\infty$ initially, if s spreads in absence of r slower than r in absence of s , then solutions of (1) will approach a propagating terrace, which connects the unstable equilibrium $(0, 0)$ to the stable equilibrium $(0, 1)$, and then the stable equilibrium $(0, 1)$ to the other stable equilibrium $(\alpha_0, 0)$.

Propagating terraces arise when two phenomena spread successively with two different speeds. Two types of speeds are used in the system (1): one is linked to a monostable scalar equation, the Fisher-KPP equation, and the second derives from a bistable system of differential equation, which was studied by Y.Kan-On [19]. Spreading results for reaction-diffusion equations often use a comparison principle, which derives from a maximum principle on elliptic equations. In the case of systems of competition-diffusion equations, maximum principles are rarely applicable directly. Moreover, the appearance of two different propagating speeds forming a propagating terrace prevents the direct application of most classical methods of scalar reaction-diffusion equations.

System (1) arises from a biological problematic: it describes the propagation of two competing species in a favorable environment. More specifically, it derives from a study on heterogeneous

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tumours, composed of cancerous cells that are sensitive or resistant to a certain drug. But this result can be applied to several other biological systems, for example invading species in ecology, or also to chemical reactions.

Definition and properties of Fisher-KPP and bistable competition-diffusion travelling waves, alongside with developments linked to these equations, are recalled in the following. This will allow us to define some notations that will be used in the rest of the article.

Fisher-KPP equation In the model (1), if $r(x, t) \equiv 0$ or $s(x, t) \equiv 0$, the other function obeys a Fisher-KPP equation, which is a classical model for species growth and propagation [20, 12]. It models the evolution of a population $n = n(x, t)$ depending on both position $x \in \mathbb{R}$ and time $t \geq 0$. Individuals move randomly in space, divide at a certain maximal rate ρ and compete over nutrients:

$$\partial_t u(x, t) - D\Delta_x u(x, t) = u(x, t)(\rho - u(x, t)). \quad (2)$$

When system (2) is considered on $x \in \mathbb{R}$, it admits travelling fronts solutions, *i.e.* solutions of the form $u(x, t) = U(x - ct)$ where c is a constant. For sake of notations, the following well-known result from [20] is recalled:

Let (D, ρ) be two positive parameters. For any $c \geq c^ = 2\sqrt{D\rho}$, there exist a unique (up to translation) solution $U \in C^2(\mathbb{R})$ of the equation:*

$$\begin{cases} DU'' + cU' + U(\rho - U) = 0, \\ \lim_{\xi \rightarrow -\infty} U(\xi) = \rho \text{ and } \lim_{\xi \rightarrow +\infty} U(\xi) = 0. \end{cases} \quad (3)$$

If U is a solution of (3), then $u : (x, t) \mapsto U(x - ct)$ is a solution to (2). Moreover, a solution u of (2) with Heavyside initial data $u(\cdot, 0) = \mathbf{1}_{x < 0}$ spreads with speed c^ in the following sense: for any $c < c^*$, it satisfies $\lim_{t \rightarrow +\infty} \sup_{x < ct} |u(x, t) - 1| = 0$ and for any $c > c^*$, $\lim_{t \rightarrow +\infty} \sup_{x > ct} u(x, t) = 0$.*

In the rest of this article, c_S (resp. c_R) will denote the minimal speed associated with parameters $(D, \rho) = (\delta_0, \alpha_0)$ (resp. $(D, \rho) = (1, 1)$) for system (3). Since all solutions are invariant up to translation, U_S (resp. U_R) will denote one fixed solution of (3) for parameters $(D, \rho) = (\delta_0, \alpha_0)$ (resp. $(D, \rho) = (1, 1)$) and speed c_S (resp. c_R).

The articles of Fisher [12] and Kolmogorov-Petrovskii-Piscounoff [20] have been a milestone for the field of reaction diffusion equations. In general, we refer to [25] for results on travelling waves in physics and biology, and to [26] for a review of this field of research. In [5], the speed of convergence of solutions u of (2) with Heavyside initial data is investigated with more details: the authors show that level sets of u travel at a speed slower than c^* . On an other hand, [18] exhibited a family of initial conditions for (2) such that the solution spreads with accelerated speed.

System of competition-diffusion equations System (1) is a model of two different species competing and dispersing in the same habitat. They both follow a Fisher-KPP model for growth and interaction, but the parameters might differ from one species to another. After a change of variables and states, the system can be reduced to (1), where $\alpha_0, \beta_0, \gamma_0$ and δ_0 are positive constants. Results on the behaviour of (1) depend on the values of the parameters, and on the behaviour of the corresponding ODE system:

$$\begin{cases} \partial_t s = s(\alpha_0 - s - \gamma_0 r), \\ \partial_t r = r(1 - \beta_0 s - r). \end{cases} \quad (4)$$

The asymptotic behaviour of this system depends on parameters $(\alpha_0, \beta_0, \gamma_0)$. If $\alpha_0 \leq \min(\gamma_0, 1/\beta_0)$, then $\lim_{t \rightarrow +\infty} (s, r)(t) = (0, 1)$: the r population is the only one stable. If $\gamma_0 < \alpha_0 < 1/\beta_0$, then

$$\lim_{t \rightarrow +\infty} (s, r)(t) = \left(\frac{1 - \alpha_0 \beta_0}{1 - \beta_0 \gamma_0}, \frac{\alpha_0 - \gamma_0}{1 - \beta_0 \gamma_0} \right)$$

which means that a mixed population is stable. If $1/\beta_0 < \alpha_0 < \gamma_0$, then both $(\alpha_0, 0)$ and $(0, 1)$ are stable: almost every solution converges to one of them as $t \rightarrow +\infty$. Finally, if $\alpha_0 \geq \max(1/\beta_0, \gamma_0)$, then $\lim_{t \rightarrow +\infty} (s, r)(t) = (\alpha_0, 0)$: the s population is the only one stable. In this paper, the bistable case is considered: $1/\beta_0 < \alpha_0 < \gamma_0$.

This range of parameters defines a set of competition-diffusion bistable PDE systems. There exists diverse results on such systems, especially in ecology modelling. In [19], Y. Kan-On demonstrates the following result:

Let $(\alpha, \beta, \gamma, \delta)$ be four positive parameters, such that $1/\beta < \alpha < \gamma$. Then there exists a unique speed $c \in (-2, 2\sqrt{\alpha\delta})$ such that the system

$$\begin{cases} \delta U'' + cU' + U(\alpha - U - \gamma V) = 0, \\ V'' + cV' + V(1 - \beta U - V) = 0, \\ \lim_{\xi \rightarrow -\infty} U(\xi) = \alpha \text{ and } \lim_{\xi \rightarrow +\infty} U(\xi) = 0, \\ \lim_{\xi \rightarrow -\infty} V(\xi) = 0 \text{ and } \lim_{\xi \rightarrow +\infty} V(\xi) = 1 \end{cases} \quad (5)$$

admits a solution $(U, V) \in C^2(\mathbb{R})$. This solution is furthermore unique up to translation, positive, U is decreasing and V is increasing. The speed c depends continuously on the parameters (α, β, γ) , is increasing with respect to α and β and decreasing with respect to γ .

Since solutions of (5) are unique up to translation, in the rest of this article, (S, R) will denote a fixed pair of solutions and c_{SR} the speed solution of (5) for parameters $(\alpha, \beta, \gamma, \delta) = (\alpha_0, \beta_0, \gamma_0, \delta_0)$.

In relation to this result, [13] showed with a degree theoretic approach that such travelling waves are C^0 stable. Recently [16] shows that travelling waves still exist if the competition becomes strong, which is to be expected for very aggressive species. In the setting of this article, it corresponds to fixing $\gamma = \beta k$, and letting $k \rightarrow +\infty$. Finally, [3] demonstrated the existence and stability of pulsating waves if the parameters $\alpha_0, \beta_0, \gamma_0$ and δ_0 are all periodic in time with the same period: this would, for example, model a periodic external action on the environment.

Propagating terraces Bearing in mind that travelling waves exist between the two stable states, a spreading result will here be demonstrated, *i.e.* the long-time behaviour of the system for a class of initial conditions. Suppose species s and r are present on the left side of the plane, with r smaller than a certain exponential function at $t = 0$:

$$\begin{cases} s(x, 0) = \phi(x) \text{ for } x < 0 \text{ with } 0 < \phi_m \leq \phi(x) \leq \phi_M < \alpha_0, \\ s(x, 0) = 0 \text{ for } x \geq 0, \\ 1 > r(x, 0) > 0 \text{ for } x < 0 \text{ and } r(x, 0) = O_{x \rightarrow -\infty}(-xe^{\frac{1}{2}x}), \\ r(x, 0) = 0 \text{ for } x \geq 0. \end{cases} \quad (6)$$

Numerical experiments suggest that the long-time behaviour of this system is organized in a propagating terrace, which means that several speeds of invasion can be observed, depending on the parameters. Propagating terraces have been first exhibited by [11] for a scalar equation $\partial_t u - \Delta u = f(u)$, with f bistable on range $[0, a]$ with speed c_1 , and bistable on range $[a, 1]$ with speed $c_2 > c_1$.

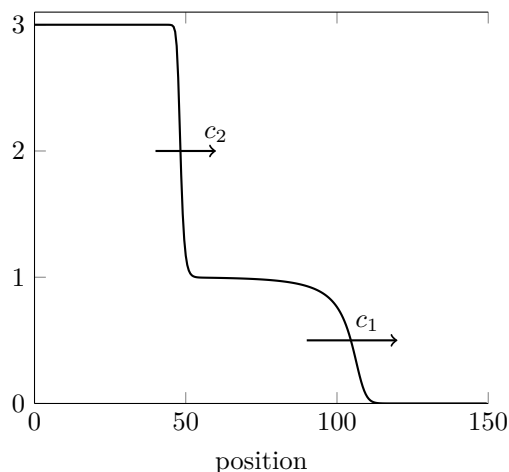


Figure 1: Numerical simulation of a propagating terrace for $f(u) = u(u - 1)(u - 1.2)(u - 3)$

Figure 1 shows a numerical example of propagating terrace, performed on Scilab.

In recent developments, [10] proved that such propagating terraces exist and are stable in a sense for periodic in space medium. The proof of theorem 1 will develop technics to show the existence of a propagating terrace for a system of coupled differential equations. In [9], the authors show that a prey-predator system will develop such propagating terraces. If the prey is faster than its predator, it will develop out of the predator's reach, at its natural speed (*i.e.* the speed at which it would propagate if there was no predators), then it is preyed on at a lower speed. The proof of invasion of the empty space relies on properties of the growth function of preys similar to Fisher-KPP. As growth functions in (1) are of Fisher-KPP type, the invasion of empty space will rely on a similar proof. On another hand, competition will intervene in the proof of replacement of one species by the other in (1): this competition is not symmetrical in [9], thus their results do not apply in the present paper case.

Statement of the theorem and outline of the paper The aim of this paper is to demonstrate the following theorem:

Theorem 1. *Let (s, r) be a bounded solution of (1) with initial conditions (6) where the parameters $(\alpha_0, \beta_0, \gamma_0)$ satisfy the bistability criterium:*

$$\frac{1}{\beta_0} < \alpha_0 < \gamma_0 \quad (7)$$

Then the following spreading results hold:

$$\forall c > \max(c_S, c_R), \lim_{t \rightarrow +\infty} \sup_{x > ct} |s(x, t)| + |r(x, t)| = 0, \quad (8)$$

$$\forall c < c_{SR}, \lim_{t \rightarrow +\infty} \sup_{x < ct} |s(x, t) - \alpha_0| + |r(x, t)| = 0. \quad (9)$$

Suppose furthermore that $c_S < c_R$, then

$$\forall c_{SR} < c_1 < c_2 < c_R, \lim_{t \rightarrow +\infty} \sup_{c_1 t < x < c_2 t} |s(x, t)| + |r(x, t) - 1| = 0. \quad (10)$$

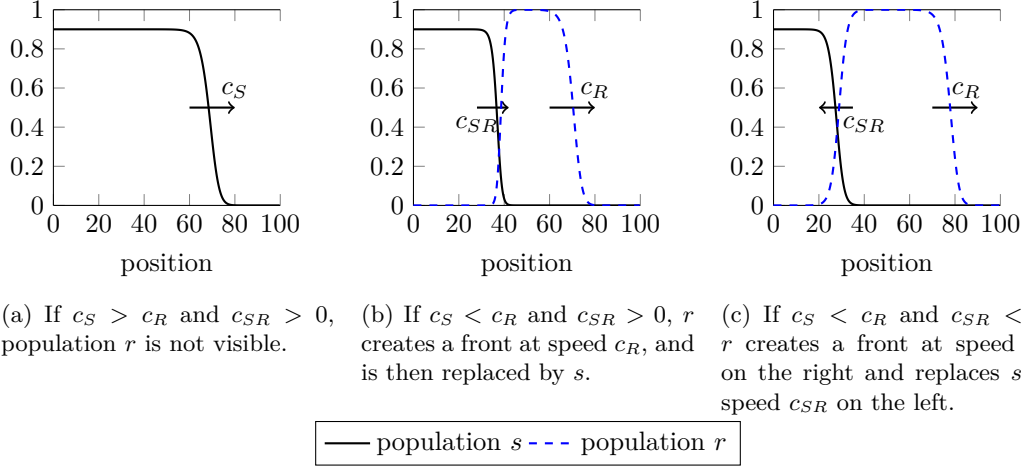


Figure 2: Numerical simulations of the system for different values of the parameters: the global behaviour depends on the comparison between c_S and c_R , and on the sign of c_{SR} .

In the case $c_S > c_R$, the behaviour of the system depends on the sign of c_{SR} and on the initial conditions. Indeed, if $c_{SR} > 0$, one can adapt the proof to show that

$$\forall c > c_S, \lim_{t \rightarrow +\infty} \sup_{x > ct} |s(x, t)| + |r(x, t)| = 0, \quad (11)$$

$$\forall c < c_S, \lim_{t \rightarrow +\infty} \sup_{x < ct} |s(x, t) - \alpha_0| + |r(x, t)| = 0. \quad (12)$$

The system thus almost eliminates species r : it does not appear in the long time behaviour. If $c_{SR} < 0$, the global behaviour depends on the initial repartition of s and r , this case is not treated in this paper.

Figure 2 shows numerical simulations of the evolution of (1), performed on Scilab for different values of the parameters.

A partial result for (10) can be extended to a more general type of growth functions. More specifically, the limit result:

$$\forall c_S < c_1 < c_2 < c_R, \lim_{t \rightarrow +\infty} \sup_{c_1 t < x < c_2 t} |s(x, t)| + |r(x, t) - 1| = 0$$

still holds if instead of system (1) we consider:

$$\begin{cases} \partial_t s - \partial_{xx}^2 s = sF(s, r), \\ \partial_t r - \delta \partial_{xx}^2 r = rG(s, r) \end{cases}$$

where F, G are \mathcal{C}^1 functions satisfying:

- $\forall s > 0$ (resp. $r > 0$), $r \mapsto F(s, r)$ (resp. $s \mapsto G(s, r)$) is strictly decreasing,
- there exists $a, b > 0$ such that $F(a, 0) = 0$ and $G(0, b) = 0$,
- $\forall s \in [0, a)$ (resp. $r \in [0, b)$, $F(s, 0) > 0$ (resp. $G(0, v) > 0$),

- $\forall s, r \geq 0, F(s, r) \leq F(0, r)$ and $G(s, r) \leq G(s, 0)$.

The first hypothesis ensures that there is competition between the two species. The second and third ones give us a hair-trigger effect: when only one of the species is present, it will grow until it reaches its maximum capacity, a or b . The last hypothesis, finally, states that the species attain their maximal growth rates for small densities ; this suggests that their propagation speeds can be determined by the leading edge, as in the Fisher-KPP framework. For more details on this proof, see [9].

However, the proofs of (9) and (10) heavily rely on the existence of a travelling wave connecting the two stable states $(\alpha_0, 0)$ and $(0, 1)$, and on the dependance of the speed c_{SR} on α_0 and other parameters. These results all are present in [19], but as far as the author knows, they have not been generalized to other types of growth functions. Theorem 1 is thus stated only under the Fisher-KPP hypothesis.

This paper is organized as follows. The first part will present the biological problem which called for the study of system (1), and an interpretation of Theorem 1. In the second part, a lemma that will be useful for the whole study is stated ; the system behaviour far from competition is then studied, showing that the fastest species can grow out of reach of the slowest one. The third part is concerned with what happens in the competition zone, and will show that the replacement of one species by the other will in fact occur at the speed defined by Kan-On [19].

2 Biological interpretation: a model of cancer growth

Model (1) has been used to study heterogeneous tumour growth. Solid tumours are subject to non uniform phenomena, and as such, can develop heterogeneous behaviours. Especially, the use of chemotherapy to cure cancers often triggers the emergence of resistant lineages, that will not be affected by the drug, by selecting them against more sensitive cells. When the tumour does not reply to the treatment any more, medical doctors then have to find a different drug, if it exists, to tackle this new kind of cancerous cells, which can be more harmful for the patient. In any case, appearance of a resistance to the chemotherapy is a cause of treatment failure, and should be avoided. Moreover, cytotoxic drugs, which are widely used in classical protocols, cause unwanted toxic side effects, thus their dosage should be carefully designed.

These problems can be addressed by *in vivo* or *in vitro* experimentation, and also by mathematical modelling of the different phenomena inside tumours. Therapy optimization in the case of heterogeneous tumours, for example, has been studied among others with the use of cellular automata [24, 15], with the construction of complex systems and their numerical studies [1], and also with the construction of simple models and their analytical studies, using, for example, Pontryagin Maximum Principle [8, 21]. We refer to [7] for a review of mathematical modelling of resistance apparition in solid tumours.

In a previous article [6], the author studied the effect of chemotherapy on heterogeneous tumours. A series of biological experimentations on *in vitro* tumours, composed of sensitive and resistant cells, showed that large doses of chemotherapy would kill all sensitive cells and let resistant cells grow to a maximum population. A mathematical ODE model adapted to these experimentations was designed, and different adaptive treatment protocols to reduce risks of resistance to chemotherapy were constructed, notably with optimal control theory. The main idea is to choose the maximal drug dosage such that, in the model (4), a population with only sensitive cells is stable and locally attractive, and to bring the system in this bassin of attraction. In order to better understand the experiments, it appeared crucial that spatial diffusion should be taken into account, which is why system (1) was constructed.

Spatial heterogeneity has a great influence on cancer virulence and evolution, as illustrated in [14]. In [22], the authors construct a model of solid tumours taking into account spatial diffusion of nutrients, treatment and cells, as well as the resistance of cells as a continuous trait. Diverse treatment protocols can be tested and compared in this framework, like combination of constant infusion and alternative maximum-minimum delivery of cytotoxic drugs. Game theory is used in [4] to explain how a more invasive lineage can be selected against a proliferative one. It uses cellular automata, and support the use of therapies that would increase the cost of motility, in order to maintain the tumour at a benign state. We are developing in our article a PDE model that enhances this idea, that cytotoxic drugs will be efficient as long as it does not favour a more motile lineage.

In model (1), s represents the population of cells that are sensitive to a certain drug, and r a lineage of resistant cells. They divide, spread and compete at different rates. We do not investigate how the resistant trait emerge, but only how they spread with the tumour once they have appeared. Thus, we do not take into account mutations of sensitive cells into resistant cells, or resistant cells into sensitive cells. Using the hypothesis of mutations, [17] showed the existence of a travelling wave connecting $(0, 0)$ to a coexistence state. Finally, the action of chemotherapy is taken into account through parameter α_0 , the growth rate of s . If no treatment is applied, α_0 is at a maximal value, and as treatment dosage increases, α_0 decreases. The bistability criterium (7) states that if $\alpha_0 < 1/\beta_0$, then the sensitive population $(s, r) = (\alpha_0, 0)$ is no longer stable: this property gives us a limit value for treatment dosage. Since we are interested in biological coherent solutions, we only consider bounded solutions of (1).

Theorem 1 states that the fastest species will escape the region where the slowest one is present, and act as if there was no competition. Let us rephrase these results in the framework of cancer modelling. If $\alpha_0 > 1/\delta_0$, then the overall growth speed of the tumour is $2\sqrt{\delta_0\alpha_0}$, this speed decreases as we augment the drug dosage. But as soon as $\alpha_0 < 1/\delta_0$, resistant cells are selected by the treatment, and form a growing ring around the sensitive core ; the global growth speed becomes 2 and does not depend on the treatment any more. Even worse, as α_0 decreases, c_{SR} may become negative: resistant cells will replace sensitive cells in already invaded environments. In a previous paper [6] where no spatial effects were taken into account, we stated that treatment protocols could be designed for the ODE system (4), such that the steady state with only sensitive cells is always stable, and that reduce the number of cancerous cells to a minimum. We thus proposed $\alpha_0 > 1/\beta_0$ as a limiting value for the treatment. With spatial effects, we see that the motility of cells – that is, their ability to move – should also be taken into account when designing a treatment protocol, as explained also in [4].

With results from [3], we could extent our theorem to time periodic coefficients. This would model, for example, periodic chemotherapy dosages, or periodic growth cycles for cells. As the overall behaviour of solutions from [3] only depends on the means and extrema of the parameters, our results would not be drastically modified ; we thus decided not to take this phenomenon into account.

3 Outside of competition

3.1 Comparison lemma

The following comparison lemma for competitive systems will be crucial in the demonstration of Theorem 1.

Lemma 1 (Comparison principle). *Let (s_1, r_1) and (s_2, r_2) be such that for all $(x, t) \in D \times \mathbb{R}^+$*

with $D \subseteq \mathbb{R}$, we have $0 \leq s_i(x, t) \leq \alpha_0$, $0 \leq r_i(x, t) \leq 1$ for $i = 1, 2$, and such that

$$\begin{cases} \partial_t s_1 - \delta_0 \partial_{xx}^2 s_1 - s_1(\alpha_0 - s_1 - \gamma_0 r_1) \leq 0, \\ \partial_t r_1 - \partial_{xx}^2 r_1 - r_1(1 - \beta_0 s_1 - r_1) \geq 0 \end{cases} \quad \text{and} \quad \begin{cases} \partial_t s_2 - \delta_0 \partial_{xx}^2 s_2 - s_2(\alpha_0 - s_2 - \gamma_0 r_2) \geq 0, \\ \partial_t r_2 - \partial_{xx}^2 r_2 - r_2(1 - \beta_0 s_2 - r_2) \leq 0 \end{cases}$$

and such that for all $x \in D$,

$$s_1(x, 0) \leq s_2(x, 0) \quad \text{and} \quad r_1(x, 0) \geq r_2(x, 0),$$

and for all $x \in \partial D$ and $t \geq 0$,

$$s_1(x, t) \leq s_2(x, t) \quad \text{and} \quad r_1(x, t) \geq r_2(x, t).$$

Then for all $t \geq 0$ and for all $x \in D$,

$$s_1(x, t) \leq s_2(x, t) \quad \text{and} \quad r_1(x, t) \geq r_2(x, t).$$

This lemma is a consequence of both a comparison theorem for cooperative systems (applied here to $(s, -r)$), which can be found in [23], and the Phragmén-Lindelöf principle, also demonstrated in [23].

In order to simplify notations, in the rest of the article the functionals N_1 and N_2 are defined on functions $(u, v) : \mathbb{R} \times \mathbb{R}^+ \rightarrow \mathbb{R}$ by:

$$N_1[u, v](x, t) = \partial_t u(x, t) - \delta_0 \partial_{xx}^2 u(x, t) - u(\alpha_0 - u - \gamma_0 v), \quad (13)$$

$$N_2[u, v](x, t) = \partial_t v(x, t) - \partial_{xx}^2 v(x, t) - v(1 - \beta_0 u - v). \quad (14)$$

We will also note $(s_1, r_1) \preceq (s_2, r_2)$ if $s_1 \leq s_2$ and $r_1 \geq r_2$.

3.2 Limitation of speeds in both directions

This first part will show that the species s and r do not develop faster than if they were without competition.

Recall U_S is a solution of

$$\begin{cases} \delta_0 U_S'' + c U_S' + U_S(\alpha_0 - U_S) = 0, \\ U_S(-\infty) = \alpha_0 \quad \text{and} \quad U_S(+\infty) = 0 \end{cases} \quad (15)$$

with $c = c_S$: it is the KPP front defined in (3). There exists $x_0 \in \mathbb{R}$ such that for all $x \in \mathbb{R}$, $\phi(x) \leq U_S(x - x_0)$. Then $(\bar{s}, \underline{r}) : (x, t) \mapsto (U_S(x - x_0 - cst), 0)$ satisfies:

$$\begin{aligned} N_1[\bar{s}, \underline{r}](x, t) &= \partial_t \bar{s}(x, t) - \delta_0 \partial_{xx}^2 \bar{s}(x, t) - \bar{s}(x, t)(\alpha_0 - \bar{s}(x, t)) \\ &= -c_S U_S'(x - x_0 - cst) - \delta_0 U_S''(x - x_0 - cst) - U_S(x - x_0 - cst)(\alpha_0 - U_S(x - x_0 - cst)) \\ &= 0 \end{aligned}$$

and $N_2[\bar{s}, \underline{r}](x, t) = 0$. Thus, according to the comparison lemma 1, $(s, r) \preceq (\bar{s}, \underline{r})$.

Then, let $c > c_S$: the first population s satisfies for every $t \geq 0$ and every $x > ct$:

$$s(x, t) \leq U_S(x - x_0 - cst) \leq U_S((c - c_S)t - x_0)$$

because U_S is decreasing. Using that $\lim_{\xi \rightarrow +\infty} U_S(\xi) = 0$, we conclude that:

$$\lim_{t \rightarrow +\infty} \sup_{x > ct} s(x, t) = 0. \quad (16)$$

Reasonning similarly on r we show that, for every $c > c_R$,

$$\lim_{t \rightarrow +\infty} \sup_{x > ct} r(x, t) = 0.$$

Moreover, [20] gives an asymptotic estimation on U_R around $+\infty$: there exists $C > 0$ such that

$$U_R(\xi) = C\xi e^{-\frac{c_R}{2}\xi} (1 + o_{\xi \rightarrow +\infty}(1)). \quad (17)$$

Thus, we can deduce a similar result around $-\infty$: for any $c > c_R$,

$$\lim_{t \rightarrow +\infty} \sup_{x < -ct} r(x, t) = 0$$

in the other direction.

These results conclude the demonstration of (8).

3.3 Invasion of the empty space by the fastest species

In this section, we will show that the fastest species invades the right empty space at its Fisher-KPP speed. Let us suppose that, for example, $c_R > c_S$.

Lemma 2. *Let c_1, c_2 be two speeds such that $c_S < c_1 < c_2 < c_R$. Then*

$$\lim_{t \rightarrow +\infty} \sup_{c_1 t < x < c_2 t} |s(x, t)| + |r(x, t) - 1| = 0.$$

It is a partial proof of (10). We already know because of 3.2 that

$$\lim_{t \rightarrow +\infty} \sup_{c_1 t < x < c_2 t} |s(x, t)| = 0$$

for any $c_S < c_1 < c_2 < c_R$. The idea of this lemma is that because r moves faster than s , it does not see any competition ahead of $c_S t$, and thus acts as a Fisher-KPP front.

To prove this, we will need an intermediate lemma:

Lemma 3. *For any c such that $c_S < c < c_R$, for any $x \in \mathbb{R}$, we have*

$$\lim_{t \rightarrow +\infty} r(x + ct, t) = 1$$

where the convergence is uniform on every compact for x .

Proof. This proof will be divided into three steps. Let c be such that $c_S < c < c_R$.

Step 1: Let c' be such that $c < c' < c_R$. We claim that there exists $a > 0$, $x_2 \in \mathbb{R}$ and $\eta_1 > 0$ such that:

$$\liminf_{t \rightarrow +\infty} \inf_{x \in (-a, a)} r(x + ct + x_2, \frac{ct}{c'}) \geq \eta_1. \quad (18)$$

In other words, the solution r is greater than a small bump travelling at the speed c' .

To prove this, let $\epsilon > 0$ be such that:

$$c' < 2\sqrt{1 - \epsilon\beta_0} < c_R. \quad (19)$$

For any $a > 0$, we define $\psi_a : \mathbb{R} \rightarrow \mathbb{R}$ the principal eigenfunction of the Laplace operator on a ball $[-a, a]$ with Dirichlet boundary conditions, normalized with $\|\psi_a\|_\infty = 1$, *i.e.*:

$$\begin{cases} \partial_{xx}^2 \psi_a = \lambda_a \psi_a \text{ on } (-a, a), \\ \psi_a(-a) = \psi_a(a) = 0, \\ \psi_a > 0 \text{ on } (-a, a), \\ \|\psi_a\|_\infty = 1. \end{cases} \quad (20)$$

Here, λ_a is the principle eigenvalue and satisfies $\lambda_a < 0$ for any $a > 0$, and tends to 0 as a tends to $+\infty$. In the following, we extend the definition of ψ_a on the whole space by setting $\psi_a(x) = 0$ if $|x| \geq a$.

We now define:

$$\underline{r}(x, t) := \eta e^{-\frac{c'}{2}(x - c't)} \psi_{2a}(x - c't - x_2)$$

where a , x_2 and η will be characterized later. Let $\bar{s}(x, t) := U_S(x - x_0 - c_S t)$, where x_0 is such that $(s, r) \preceq (\bar{s}, 0)$. There exists $x_1 \in \mathbb{R}$ such that for any $x > x_1 + x_0 + c_S t$, we have $\bar{s}(x, t) < \epsilon$. We will choose a , x_2 and η such that $(s, r) \preceq (\bar{s}, \underline{r})$. First,

$$\begin{aligned} N_1[\bar{s}, \underline{r}](x, t) &= \partial_t \bar{s}(x, t) - \delta_0 \partial_{xx}^2 \bar{s}(x, t) - \bar{s}(x, t)(\alpha_0 - \bar{s}(x, t) - \gamma_0 \underline{r}(x, t)) \\ &= \gamma_0 U_S(x - c_S t - x_0) \underline{r}(x, t) \\ &\geq 0. \end{aligned}$$

Moreover, by taking $x_2 \geq x_1 + 2a$, we ensure that for $-2a < x - c't - x_2 < 2a$, we have $\underline{r}(x, t) > 0$ and $\bar{s}(x, t) = U_S(x - c_S t - x_0) \leq U_S(x - c't - x_0) \leq U_S(-2a + x_2 - x_0) \leq \epsilon$. Thus:

$$\begin{aligned} N_2[\bar{s}, \underline{r}](x, t) &= \partial_t \underline{r}(x, t) - \partial_{xx}^2 \underline{r}(x, t) - \underline{r}(x, t)(1 - \beta_0 \bar{s}(x, t) - \underline{r}(x, t)) \\ &\leq \left(\frac{c'^2}{4} - \lambda_{2a} \right) \underline{r}(x, t) - \underline{r}(x, t)(1 - \beta_0 \epsilon - \underline{r}(x, t)) \\ &\leq \underline{r}(x, t) \left(\frac{c'^2}{4} - \lambda_{2a} - (1 - \beta_0 \epsilon - \underline{r}(x, t)) \right). \end{aligned}$$

We can then choose a large enough such that $\frac{c'^2}{4} - \lambda_{2a} - (1 - \beta_0 \epsilon) < 0$ because of (19), and η small enough such that $\frac{c'^2}{4} - \lambda_{2a} - (1 - \beta_0 \epsilon - \eta e^{-\frac{c'}{2}(x_2 - 2a)}) < 0$. Then $N_2[\bar{s}, \underline{r}](x, t) \leq 0$ for all $(x, t) \in \mathbb{R} \times \mathbb{R}^+$.

Finally, for any fixed $t_0 > 0$, we can further reduce η such that $r(x, t_0) \geq \underline{r}(x, t_0)$. Then, by the comparison lemma 1, $(s, r) \preceq (\bar{s}, \underline{r})$. By setting

$$\eta_1 := \eta e^{-\frac{c'}{2}(x_2 + a)} \min_{x \in (-a, a)} \psi_{2a}(x),$$

we get that, since $r(x, \frac{ct}{c'}) \geq \underline{r}(x, \frac{ct}{c'}) = \underline{r}(x - ct, 0)$, the limit (18) is satisfied.

Step 2: We now claim that there exists $b > 0$, $\eta_2 > 0$ and $x_3 \in \mathbb{R}$ such that

$$\liminf_{t \rightarrow +\infty} \inf_{\substack{x \in (-b, b) \\ t' \in (\frac{ct}{c'}, t)}} r(x + ct + x_3, t') > \eta_2. \quad (21)$$

In other words, the bump does in fact persist under r for time t' between $\frac{ct}{c'}$ and t .

For that, let us fix $t > 0$, and define:

$$\underline{r}(x, t') := \eta' \psi_a(x - ct - x_2)$$

where η' will be characterized later. For any $t' < t$, the pair (\bar{s}, \underline{r}) satisfies $N_1[\bar{s}, \underline{r}](x, t') \geq 0$, and:

$$\begin{aligned} N_2[\bar{s}, \underline{r}](x, t') &= \partial_t \underline{r}(x, t') - \partial_{xx}^2 \underline{r}(x, t') - \underline{r}(x, t')(1 - \beta_0 \bar{s}(x, t') - \underline{r}(x, t')) \\ &\leq -\underline{r}(x, t')(1 + \lambda_a - \underline{r}(x, t') - \beta_0 \epsilon). \end{aligned}$$

By increasing a if necessary, we can suppose $1 + \lambda_a - \beta_0 \epsilon > 0$. Then, by taking $\eta' < 1 + \lambda_a - \beta_0 \epsilon$, we get that $N_2[\bar{s}, \underline{r}](x, t') \leq 0$ for any $t' < t$. We can further reduce η' such that $r(x + ct + x_2, \frac{ct}{c'}) \geq \underline{r}(x, \frac{ct}{c'})$. Because of (18), for t large enough, η' does not depend on t . Then, by the comparison lemma 1, we have $(s, r) \preceq (\bar{s}, \underline{r})$ for any $x \in \mathbb{R}$ and any t' such that $\frac{ct}{c'} < t' < t$. By setting $b = \frac{a}{2}$ and $\eta_2 = \eta' \min_{x \in (-b, b)} \psi_a(x)$, we get (21).

Step 3: Now we demonstrate the convergence towards 1 of $r(x + ct, t)$ when $t \rightarrow +\infty$, uniformly on compact subsets. Let $(t_n)_n$ be such that $t_n \rightarrow +\infty$. We define the following sequence of functions:

$$r_n(x, t) = r(x + ct_n, t + t_n) \quad \forall (x, t) \in \mathbb{R} \times [-t_n, +\infty).$$

Standard parabolic estimates allow us to use Arzela theorem: we can extract a subsequence still denoted t_n such that r_n converges locally uniformly to r_∞ , which satisfies:

$$\partial_t r_\infty - \partial_{xx}^2 r_\infty - r_\infty(1 - \beta_0 \epsilon - r_\infty) \geq 0 \quad \forall (x, t) \in \mathbb{R}^2$$

Moreover, because of (21), we know that for any $t \leq 0$, $\inf_{x \in (-b, b)} r_\infty(x + x_3, t) \geq \eta_2$. Let r_ϵ be the solution of

$$\begin{cases} \partial_t r_\epsilon - \partial_{xx}^2 r_\epsilon - r_\epsilon(1 - \beta_0 \epsilon - r_\epsilon) = 0, \\ r_\epsilon(x, 0) = \eta_2 \mathbf{1}_{(-b, b)}(x - x_3). \end{cases}$$

Then for any $x \in \mathbb{R}$ and any $t \geq 0$, by the classical comparison principle, $r_\infty(x, 0) \geq r_\epsilon(x, t)$. But r_ϵ converges locally uniformly to $1 - \beta_0 \epsilon$ [20], thus for any $x \in \mathbb{R}$ we have $r_\infty(x, 0) \geq 1 - \beta_0 \epsilon$.

Looking back at the definition of r_∞ , we deduce that for all $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ we have

$$\liminf_{t \rightarrow +\infty} r(x + ct, t) \geq 1 - \beta_0 \epsilon$$

locally uniformly with respect to x . This is true for any $\epsilon > 0$ small enough, so we have

$$\lim_{t \rightarrow +\infty} r(x + ct, t) = 1$$

which concludes the proof of lemma 3. □

We are now equipped to prove lemma 2.

Proof. Let c_1 and c_2 be two speeds such that $c_S < c_1 < c_2 < c_R$. Let $\epsilon > 0$ be such that $c^* = 2\sqrt{1 - \beta_0\epsilon}$ satisfies $c_2 < c^* < c_R$. For any $\theta < 1 - \beta_0\epsilon$ close enough to $1 - \beta_0\epsilon$, the following system:

$$\begin{cases} \hat{R}'' + c^* \hat{R}' + \hat{R}(1 - \beta_0\epsilon - \hat{R}) = 0, \\ \hat{R}(0) = \theta \text{ and } \hat{R}'(0) = 0 \end{cases}$$

admits a solution \hat{R} that satisfies $\hat{R}(b) = 0$ for a certain $b > 0$, and $\hat{R}'(\xi) < 0$ for any $\xi \in (0, b]$. We refer for example to [2] for a proof of existence of such a solution ; it relies mostly on phase plane analysis. We then define $\underline{r} : \mathbb{R} \times \mathbb{R}^+ \rightarrow \mathbb{R}$ by:

$$\underline{r}(x, t) = \begin{cases} \theta & \text{if } x - c^*t < \rho, \\ \hat{R}(x - c^*t - \rho) & \text{if } \rho \leq x - c^*t < \rho + b, \\ 0 & \text{if } x - c^*t \geq \rho + b \end{cases}$$

where ρ is to be chosen later.

Consider now (\bar{s}, \underline{r}) where $\bar{s}(x, t) = U_S(x - c_S t - x_0)$ is a Fisher-KPP front satisfying $\bar{s}(x, 0) \geq s(x, 0)$ for any $x \in \mathbb{R}$. There exists $x_1 \in \mathbb{R}$ such that for any $x > x_1$, we have $U_S(x) \leq \epsilon$. Then, for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$:

$$N_1[\bar{s}, \underline{r}](x, t) = \gamma_0 U_S(x - c_S t - x_0) \underline{r}(x, t) \geq 0$$

and for any (x, t) such that $x \geq x_1 + c_S t$:

$$\begin{aligned} N_2[\bar{s}, \underline{r}](x, t) &= \begin{cases} \theta(\beta_0 U_S(x - c_S t - x_0) - 1 + \theta) & \text{if } x - c^*t < \rho \\ \beta_0 \hat{R}(x - c^*t - \rho)(U_S(x - c_S t - x_0) - \epsilon) & \text{if } \rho \leq x - c^*t < \rho + b \\ 0 & \text{if } x - c^*t \geq \rho + b \end{cases} \\ &\leq 0. \end{aligned}$$

Moreover, we know that $\lim_{t \rightarrow +\infty} r(c_1 t, t) = 1$ because of lemma 3, thus there exists $T > 0$ such that for any $t > T$, $r(c_1 t, t) \geq \theta$.

Finally, consider the situation at time $t = T$. By setting $\rho \leq -b + (c_1 - c^*)T$, we have $\underline{r}(x, T) = 0$ for any $x \geq c_1 T$. Thus, by using the comparison lemma 1, for any $t \geq T$ and $x \geq c_1 t$,

$$r(x, t) \geq \underline{r}(x, t). \quad (22)$$

For t large enough, $\rho + c^*t > c_2 t$, thus

$$\liminf_{\substack{t \rightarrow +\infty \\ c_1 t < x < c_2 t}} r(x, t) \geq \theta.$$

This is true for any $\theta < 1 - \beta_0\epsilon$ close enough to $1 - \beta_0\epsilon$ and for any $\epsilon > 0$ small enough, so we can pass to the limit as $\epsilon \rightarrow 0$ and $\theta \rightarrow 1$, and deduce that

$$\liminf_{\substack{t \rightarrow +\infty \\ c_1 t < x < c_2 t}} r(x, t) \geq 1 \quad (23)$$

which concludes the proof of lemma 2. □

This proof uses loosely the Fisher-KPP hypothesis: we could have taken more general growth functions for sensitive and resistant cells, and still have this result of invasion, as stated in 1.

With a similar reasoning, we can prove the following lemma:

Lemma 4. For all $c < -c_R$,

$$\lim_{t \rightarrow +\infty} \sup_{x < ct} |s(x, t) - \alpha_0| + |r(x, t)| = 0.$$

This lemma is an intermediate proof of (9).

4 Competition between species

We are now interested in an intermediate zone, where competition between species can have an influence on their behaviour. We will first prove (9). In a second part, we will complete the proof of (10) by studying the zone of interaction of s and r .

4.1 Left side of the interaction zone

We know that $\lim_{t \rightarrow +\infty} \sup_{x < ct} |s(x, t) - \alpha_0| + |r(x, t)| = 0$ for any $c < -c_R$ because of Lemma 4. Let us now prove that it is the case for any $c < c_{SR}$. The method we use here is developed for a scalar equation in [11].

Let c be such that $c < c_{SR}$. We recall that as stated in the introduction 5 and in [19], c_{SR} depends continuously on the parameters and is increasing with respect to α_0 . Thus, there exists $\underline{\alpha} < \alpha_0$ such that $1/\beta_0 < \underline{\alpha} < \gamma_0$ and the Kan-On speed \underline{c}_{SR} corresponding to parameters $(\underline{\alpha}, \beta_0, \gamma_0, \delta_0)$ satisfies $c < \underline{c}_{SR} < c_{SR}$. We define (\underline{S}, \bar{R}) the corresponding Kan-On front; it satisfies:

$$\begin{cases} \delta_0 \underline{S}'' + \underline{c}_{SR} \underline{S}' + \underline{S}(\underline{\alpha} - \underline{S} - \gamma_0 \bar{R}) = 0, \\ \bar{R}'' + \underline{c}_{SR} \bar{R}' + \bar{R}(1 - \beta_0 \underline{S} - \bar{R}) = 0, \\ \lim_{\xi \rightarrow -\infty} \underline{S}(\xi) = \underline{\alpha} \text{ and } \lim_{\xi \rightarrow +\infty} \underline{S}(\xi) = 0, \\ \lim_{\xi \rightarrow -\infty} \bar{R}(\xi) = 0 \text{ and } \lim_{\xi \rightarrow +\infty} \bar{R}(\xi) = 1. \end{cases}$$

We now define (\underline{s}, \bar{r}) on $\mathbb{R} \times \mathbb{R}^+$ by:

$$\begin{cases} \underline{s}(x, t) = \max(0, \underline{S}(x - \underline{c}_{SR}t - \xi(t)) - q(t)), \\ \bar{r}(x, t) = \min(1, \bar{R}(x - \underline{c}_{SR}t - \xi(t)) + p(t)) \end{cases}$$

where ξ , p and q will be characterized later.

Let $\epsilon > 0$ be such that $\epsilon < \min(\underline{\alpha}, \underline{\alpha} - \frac{1}{\beta_0}, \frac{\gamma_0 - \alpha_0}{\gamma_0}, \frac{1}{3})$ (this is possible because of (7) and the definition of $\underline{\alpha}$). Because \underline{S} is strictly decreasing and \bar{R} is strictly increasing, there exists $\eta > 0$ such that, for any ζ satisfying either $\epsilon < \underline{S}(\zeta) < \underline{\alpha} - \epsilon$ or $\epsilon < \bar{R}(\zeta) < 1 - \epsilon$, we have $\underline{S}'(\zeta) < -\eta$ and $\bar{R}'(\zeta) > \eta$. We then state the following lemma, that will impose conditions on p , q and ξ .

Lemma 5. We choose ξ , p and q of the form

$$\begin{cases} \xi(t) = \xi_1 + \xi_0 e^{-\mu t}, \\ p(t) = p_0 e^{-\mu t}, \\ q(t) = q_0 e^{-\mu t} \end{cases}$$

where p_0 , q_0 and $\mu > 0$, p_0 satisfies

$$p_0 < \frac{\alpha_0 - \underline{\alpha}}{2\gamma_0}, \tag{24}$$

q_0 and μ satisfy

$$q_0 < \frac{\epsilon p_0}{2\beta_0}, \quad (25)$$

$$q_0 + \mu < \gamma_0(1 - \epsilon) - \alpha_0, \quad (26)$$

$$\beta_0 q_0 + \mu < \beta_0(\underline{\alpha} - \epsilon) - 1, \quad (27)$$

$$q_0(\alpha_0 + \mu + q_0) < (\underline{\alpha} - \epsilon) \frac{\alpha_0 - \underline{\alpha}}{2}, \quad (28)$$

$$\mu < \frac{1 - 3\epsilon}{2}, \quad (29)$$

$$\mu < \gamma_0 - \alpha_0, \quad (30)$$

and ξ_0 satisfies

$$\xi_0 > \frac{q_0 \gamma_0 (1 - \epsilon)}{\mu \eta}, \quad (31)$$

$$\xi_0 > \frac{p_0 \beta_0 (\underline{\alpha} - \epsilon)}{\mu \eta}. \quad (32)$$

Then we have for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ that:

$$N_1[\underline{s}, \bar{r}](x, t) \leq 0,$$

$$N_2[\underline{s}, \bar{r}](x, t) \geq 0.$$

Proof. For any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$, we have with $\zeta = x - \underline{c}_{SR}t - \xi(t)$ and if $\underline{s}(x, t) > 0$ and $\bar{r}(x, t) < 1$:

$$\begin{aligned} N_1[\underline{s}, \bar{r}](x, t) &= \partial_t \underline{s}(x, t) - \delta_0 \partial_{xx}^2 \underline{s}(x, t) - \underline{s}(x, t)(\alpha_0 - \underline{s}(x, t) - \gamma_0 \bar{r}(x, t)) \\ &= -\xi'(t) \underline{S}'(\zeta) - q'(t) + \underline{S}(\zeta)(\underline{\alpha} - \alpha_0 + \gamma_0 p(t) - q(t)) \\ &\quad + q(t)(\alpha_0 - \underline{S}(\zeta) - \gamma_0 \bar{R}(\zeta) + q(t) - \gamma_0 p(t)) \end{aligned}$$

and

$$\begin{aligned} N_2[\underline{s}, \bar{r}](x, t) &= \partial_t \bar{r}(x, t) - \partial_{xx}^2 \bar{r}(x, t) - \bar{r}(x, t)(1 - \beta_0 \underline{s}(x, t) - \bar{r}(x, t)) \\ &= -\xi'(t) \bar{R}'(\zeta) + p'(t) + \bar{R}(\zeta)(p(t) - \beta_0 q(t)) - p(t)(1 - \bar{R}(\zeta) - \beta_0 \underline{S}(\zeta) - p(t) + \beta_0 q(t)) \end{aligned}$$

Around $\pm\infty$ Let (x, t) be such that $\underline{S}(x - \underline{c}_{SR}t - \xi(t)) > \underline{\alpha} - \epsilon$ and $\bar{R}(x - \underline{c}_{SR}t - \xi(t)) < \epsilon$. Then:

$$\begin{aligned} N_1[\underline{s}, \bar{r}](x, t) &= -\xi'(t) \underline{S}' - q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 + \gamma_0 p(t) - q(t)) + q(t)(\alpha_0 - \underline{S} - \gamma_0 \bar{R} + q(t) - \gamma_0 p(t)) \\ &\leq -q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 + \gamma_0 p_0) + q(t)(\alpha_0 + q_0) \\ &\quad \text{if we take } \xi_0 > 0 \\ &\leq q_0 e^{-\mu t}(\mu + \alpha_0 + q_0) + (\underline{\alpha} - \epsilon) \frac{\alpha_0 - \underline{\alpha}}{2} \text{ because of (24)} \\ &\leq 0 \end{aligned}$$

because of (28). Furthermore,

$$N_2[\underline{s}, \bar{r}](x, t) = -\xi'(t) \bar{R}' + p'(t) + \bar{R}(p(t) - \beta_0 q(t)) - p(t)(1 - \bar{R} - \beta_0 \underline{S} - p(t) + \beta_0 q(t)) \quad (33)$$

$$\geq p'(t) + p(t)(\beta_0(\underline{\alpha} - \epsilon) - 1 - \beta_0 q(t)) \text{ because of (25)} \quad (34)$$

$$\geq p(t)(\beta_0(\underline{\alpha} - \epsilon) - 1 - \beta_0 q_0 - \mu) \quad (35)$$

$$\geq 0 \quad (36)$$

because of (27).

Now, let (x, t) be such that $\underline{S}(x - \underline{c}_{SR}t - \xi(t)) < \epsilon$ and $\overline{R}(x - \underline{c}_{SR}t - \xi(t)) > 1 - \epsilon$. Then:

$$N_1[\underline{s}, \bar{r}](x, t) = -\xi'(t)\underline{S}' - q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 + \gamma_0 p(t) - q(t)) + q(t)(\alpha_0 - \underline{S} - \gamma_0 \overline{R} + q(t) - \gamma_0 p(t)) \quad (37)$$

$$\leq -q'(t) + q(t)(\alpha_0 - \gamma_0(1 - \epsilon) + q(t)) \quad (38)$$

$$\leq q(t)(\alpha_0 - \gamma_0(1 - \epsilon) + q_0 + \mu) \quad (39)$$

$$\leq 0 \quad (40)$$

because of (26). Furthermore,

$$N_2[\underline{s}, \bar{r}](x, t) = -\xi'(t)\overline{R}' + p'(t) + \overline{R}(p(t) - \beta_0 q(t)) - p(t)(1 - \overline{R} - \beta_0 \underline{S} - p(t) + \beta_0 q(t))$$

$$\geq p'(t) + (1 - \epsilon)(p_0 - \beta_0 q_0) - \epsilon p(t)$$

$$\geq p'(t) + (1 - \epsilon)\frac{p(t)}{2} - \epsilon p(t) \text{ because of (25)}$$

$$\geq \frac{p(t)}{2}(1 - 3\epsilon - 2\mu)$$

$$\geq 0$$

because of (29).

In the intermediary zone Let (x, t) be such that $\epsilon < \underline{S}(x - \underline{c}_{SR}t - \xi(t)) < \underline{\alpha} - \epsilon$ or $\epsilon < \overline{R}(x - \underline{c}_{SR}t - \xi(t)) < 1 - \epsilon$. Then because \underline{S} is strictly decreasing, and \overline{R} is strictly increasing, there exists $\eta > 0$ such that $\underline{S}'(x - \underline{c}_{SR}t - \xi(t)) < -\eta$ and $\overline{R}'(x - \underline{c}_{SR}t - \xi(t)) > \eta$. Then:

$$N_1[\underline{s}, \bar{r}](x, t) = -\xi'(t)\underline{S}' - q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 + \gamma_0 p(t) - q(t)) + q(t)(\alpha_0 - \underline{S} - \gamma_0 \overline{R} + q(t) - \gamma_0 p(t))$$

$$\leq \xi'(t)\eta - q(t)(\alpha_0 - \gamma_0(1 - \epsilon) + q(t)) + q(t)(\alpha_0 + q(t))$$

because of (40)

$$\leq (-\xi_0 \mu \eta + q_0 \gamma_0 (1 - \epsilon))e^{-\mu t}$$

$$\leq 0$$

because of (31). Furthermore,

$$N_2[\underline{s}, \bar{r}](x, t) = -\xi'(t)\overline{R}' + p'(t) + \overline{R}(p(t) - \beta_0 q(t)) - p(t)(1 - \overline{R} - \beta_0 \underline{S} - p(t) + \beta_0 q(t))$$

$$\geq -\xi'(t)\eta - p(t)(\beta_0(\underline{\alpha} - \epsilon) - 1 - \beta_0 q(t)) - p(t)(1 + \beta_0 q(t))$$

because of (36)

$$\geq (\xi_0 \mu \eta - p_0 \beta_0 (\underline{\alpha} - \epsilon))e^{-\mu t}$$

$$\geq 0$$

because of (32).

In flat zones We now want to check that $N_1[\underline{s}, \bar{r}](x, t) \leq 0$ and $N_2[\underline{s}, \bar{r}](x, t) \geq 0$ even if $\underline{s}(x, t) = 0$ or $\bar{r}(x, t) = 1$.

Let $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ be such that $\underline{s}(x, t) = 0$, *i.e.* $\underline{S}(x - \underline{c}_{SR}t - \xi(t)) < q(t)$, and $\bar{r}(x, t) < 1$. Then $N_1[\underline{s}, \bar{r}](x, t) = 0$ and up to further reducing q_0 , we can suppose $\overline{R}(x - \underline{c}_{SR}t - \xi(t)) > 3/4$,

thus:

$$\begin{aligned}
N_2[\underline{s}, \bar{r}](x, t) &= \partial_t \bar{r} - \partial_{xx}^2 \bar{r} - \bar{r}(1 - \bar{r}) \\
&= -\xi'(t) \bar{R}' + p'(t) + \bar{R}(1 - \beta_0 \underline{s} - \bar{R}) - (\bar{R} + p(t))(1 - \bar{R} - p(t)) \\
&\geq p'(t) + \bar{R}(p(t) - \beta_0 q(t)) - p(t)(1 - \bar{R}) \\
&\geq p'(t) + \frac{1}{2} p(t) - \frac{3}{4} \beta_0 q(t) \\
&\geq (-\mu p_0 + \frac{1}{2} p_0 - \frac{3}{4} \beta_0 q_0) e^{-\mu t} \\
&\geq 0
\end{aligned}$$

because of (29) and (25).

Now, let $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ be such that $\underline{s}(x, t) > 0$ and $\bar{r}(x, t) = 1$, i.e. $\bar{R}(x - c_{SR}t - \xi(t)) > 1 - p(t)$. Then $N_2[\underline{s}, \bar{r}](x, t) = \beta_0 \underline{s} \geq 0$ and

$$\begin{aligned}
N_1[\underline{s}, \bar{r}](x, t) &= \partial_t \underline{s}(x, t) - \delta_0 \partial_{xx}^2 \underline{s}(x, t) - \underline{s}(x, t)(\alpha_0 - \underline{s}(x, t) - \gamma_0) \\
&= -\xi'(t) \underline{S}' - q'(t) + \underline{S}(\underline{\alpha} - \underline{S} - \gamma_0 \bar{R}) - (\underline{S} - q(t))(\alpha_0 - \underline{S} - \gamma_0 + q(t)) \\
&\leq -q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 - \gamma_0 \bar{R} + \gamma_0 - q(t)) + q(t)(\alpha_0 - \gamma_0 - (\underline{S} - q(t))) \\
&\leq -q'(t) + \underline{S}(\underline{\alpha} - \alpha_0 + \gamma_0 p(t) - q(t)) + q(t)(\alpha_0 - \gamma_0) \\
&\leq q(t)(\mu + \alpha_0 - \gamma_0) \\
&\leq 0
\end{aligned}$$

because of (30).

Finally, if (x, t) is such that $\underline{s}(x, t) = 0$ and $\bar{r}(x, t) = 1$, then $N_1[\underline{s}, \bar{r}](x, t) = N_2[\underline{s}, \bar{r}](x, t) = 0$. \square

We have constructed a "sub-super solution" (\underline{s}, \bar{r}) of (1). We now want to compare it to the solution (s, r) with initial condition (6). To demonstrate the following lemma, we will finally characterize the constant ξ_1 :

Lemma 6. *There exists $T > 0$ and $c_* < c$ such that for every $t \geq T$:*

$$s(c_*t, t) \geq \underline{s}(c_*t, t) \text{ and } r(c_*t, t) \leq \bar{r}(c_*t, t),$$

and for every $x \geq c_*T$:

$$s(x, T) \geq \underline{s}(x, T) \text{ and } r(x, T) \leq \bar{r}(x, T).$$

Proof. Let $c_* < c$ be such that $c_* < -c_R$. Because of Lemma 4, we know that

$$\lim_{t \rightarrow +\infty} |s(c_*t, t) - \alpha_0| + |r(c_*t, t)| = 0.$$

Thus, there exists $T_1 > 0$ such that for every $t \geq T_1$, $s(c_*t, t) > \underline{\alpha}$ and $r(c_*t, t) < p_0$. Then, we already have that $s(c_*t, t) \geq \underline{s}(c_*t, t)$ for every $t \geq T_1$.

Furthermore, we know that there exists $X \in \mathbb{R}$ such that $r(x, t) \leq \tilde{U}_R(x - c_Rt - X)$ for all $(x, t) \in \mathbb{R} \times \mathbb{R}^+$, where \tilde{U}_R is the Fisher-KPP front satisfying:

$$\begin{cases} \tilde{U}_R'' + c_R \tilde{U}_R' + \tilde{U}_R(1 - \tilde{U}_R) = 0, \\ \tilde{U}_R(-\infty) = 0 \text{ and } \tilde{U}_R(+\infty) = 1. \end{cases}$$

We also know from [20] that \tilde{U}_R satisfies for a certain constant $C > 0$ and any $\zeta \in \mathbb{R}$:

$$\tilde{U}_R(\zeta) \leq C\zeta e^{\frac{c_R}{2}\zeta}.$$

Thus for all $t > 0$, we have

$$r(c_*t, t) \leq \tilde{U}_R((c_* - c_R)t - X) \leq C((c_* - c_R)t - X)e^{\frac{c_R}{2}((c_* - c_R)t - X)}.$$

If we further reduce μ such that $\mu < \frac{c_R}{2}(c_R - c_*)$, there exists $T_2 > 0$ such that for all $t > T_2$,

$$C((c_* - c_R)t - X)e^{\frac{c_R}{2}((c_* - c_R)t - X)} \leq p_0 e^{-\mu t}.$$

Then, by taking $T = \max(T_1, T_2)$, we get that for all $t > T$,

$$s(c_*t, t) \geq \underline{s}(c_*t, t) \text{ and } r(c_*t, t) \leq \bar{r}(c_*t, t).$$

Now consider (\underline{s}, \bar{r}) at time T and for $x \geq c_*T$, and recall that \underline{S} is decreasing and \bar{R} increasing:

$$\begin{aligned} \underline{s}(x, T) &= \max(0, \underline{S}(x - \underline{c}_{SR}T - \xi(T)) - q(T)) \\ &\leq \max(0, \underline{S}(c_*T - \underline{c}_{SR}T - x_1 - x_0 e^{-\mu T}) - q(T)) \\ &= 0 \end{aligned}$$

if we take $\xi_1 < 0$ small enough. In the same way:

$$\begin{aligned} \bar{r}(x, T) &= \min(1, \bar{R}(x - \underline{c}_{SR}T - \xi(T)) + p(T)) \\ &\geq \min(1, \bar{R}(c_*T - \underline{c}_{SR}T - x_1 - x_0 e^{-\mu T}) + p(T)) \\ &= 1 \end{aligned}$$

by possibly taking ξ_1 smaller. We then get the second part of the lemma. \square

Lemmas 5 and 6 allow us to conclude that, because of the comparison lemma 1,

$$\forall t \geq T, \quad \forall x \geq ct, \quad (\underline{s}, \bar{r})(x, t) \preceq (s, r)(x, t).$$

We thus have the following spreading result:

$$\lim_{t \rightarrow +\infty} \inf_{x \geq ct} s(x, t) \geq \underline{\alpha} \text{ and } \lim_{t \rightarrow +\infty} \inf_{x \geq ct} r(x, t) \leq 0. \quad (41)$$

This is true for any $\underline{\alpha} < \alpha_0$ close enough to α_0 , and for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ we have $s(x, t) < \alpha_0$, so in conclusion:

$$\lim_{t \rightarrow +\infty} \sup_{x \geq ct} |s(x, t) - \alpha_0| + |r(x, t)| = 0,$$

which concludes the proof of (9).

4.2 Right side of the interaction zone

This section is devoted to the demonstration of (10). We already proved in Subsection 3.3 that if $c_S < c_R$, for any c_1, c_2 satisfying $c_S < c_1 < c_2 < c_R$, we have:

$$\lim_{t \rightarrow +\infty} \sup_{c_1 t < x < c_2 t} |s(x, t)| + |r(x, t) - 1| = 0.$$

We will now prove that it is in fact true for $c_{SR} < c_1 < c_2 < c_R$.

Let c_1 and c_2 be such that $c_{SR} < c_1 < c_2 < c_R$. In a proof similar to what we did in 4.1, we define a pair $(\bar{s}, \underline{r}) : \mathbb{R} \times \mathbb{R}^+ \rightarrow \mathbb{R}$ that will satisfy $(s, r) \preceq (\bar{s}, \underline{r})$ on an appropriate domain, with (\bar{s}, \underline{r}) almost travelling at a speed faster than c_{SR} and slower than c_1 .

Let $1 > \theta > 0$ and $\bar{\alpha} > 0$ to be characterized later, and consider the following system for $c \in \mathbb{R}$ and (\bar{S}, \underline{R}) :

$$\begin{cases} \delta_0 \bar{S}''(\xi) + c \bar{S}'(\xi) + \bar{S}(\xi)(\bar{\alpha} - \bar{S}(\xi) - \gamma_0 \underline{R}(\xi)) = 0, \\ \underline{R}''(\xi) + c \underline{R}'(\xi) + \underline{R}(\xi)(\theta - \beta_0 \bar{S}(\xi) - \underline{R}(\xi)) = 0, \\ \bar{S}(-\infty) = \bar{\alpha} \text{ and } \bar{S}(+\infty) = 0, \\ \underline{R}(-\infty) = 0 \text{ and } \underline{R}(+\infty) = \theta. \end{cases} \quad (42)$$

After the change of variable $\tilde{\xi} = \sqrt{\theta} \xi$ and of states $\bar{S} = \theta \tilde{S}$, $\underline{R} = \theta \tilde{R}$, we find that it is equivalent to the following system:

$$\begin{cases} \delta_0 \tilde{S}''(\tilde{\xi}) + \sqrt{\theta} c \tilde{S}'(\tilde{\xi}) + \tilde{S}(\tilde{\xi})(\frac{\bar{\alpha}}{\theta} - \tilde{S}(\tilde{\xi}) - \gamma_0 \tilde{R}(\tilde{\xi})) = 0, \\ \tilde{R}''(\tilde{\xi}) + \sqrt{\theta} c \tilde{R}'(\tilde{\xi}) + \tilde{R}(\tilde{\xi})(1 - \beta_0 \tilde{S}(\tilde{\xi}) - \tilde{R}(\tilde{\xi})) = 0, \\ \tilde{S}(-\infty) = \frac{\bar{\alpha}}{\theta} \text{ and } \tilde{S}(+\infty) = 0, \\ \tilde{R}(-\infty) = 0 \text{ and } \tilde{R}(+\infty) = 1. \end{cases} \quad (43)$$

This corresponds to the Kan-On system of equations: we know because of [19] that it admits a solution (\tilde{S}, \tilde{R}) when $\tilde{c} = \frac{c}{\sqrt{\theta}}$ is the Kan-On speed of propagation associated to parameters $(\frac{\bar{\alpha}}{\theta}, \beta_0, \gamma_0, \delta_0)$. We deduce that (42) has a unique solution (\bar{S}, \underline{R}) up to translation if $c = \sqrt{\theta} \tilde{c}$. Note that for this result to hold, we need that $\gamma_0 > \frac{\bar{\alpha}}{\theta} > \frac{1}{\beta_0}$.

If $\bar{\alpha} = \alpha_0$, we have that $c = \sqrt{\theta} \tilde{c} > \sqrt{\theta} c_{SR}$. Numerical tests suggest that in fact, if $\bar{\alpha} = \alpha_0$, we have $c > c_{SR}$: this seems reasonable, since in (42), we reduce the growth rate of the right-side placed species. But we do not need this inequality to prove our spreading result. As a matter of fact, for any $\bar{\alpha} > \alpha_0$ close enough to α_0 , there exists $\theta < 1$ such that, if \tilde{c} is the Kan-On speed associated to parameters $(\frac{\bar{\alpha}}{\theta}, \beta_0, \gamma_0, \delta_0)$, then $\tilde{c} > \frac{c_{SR}}{\sqrt{\theta}}$.

We choose such $\bar{\alpha}$, θ , and the corresponding speed c , that we will now note \bar{c}_{SR} and that satisfies $\bar{c}_{SR} > c_{SR}$. By possibly taking a bigger θ and a smaller $\bar{\alpha}$, we can suppose $c_{SR} < \bar{c}_{SR} < c_1$ by continuity of the Kan-On speed with respect to the parameters. We can now state the following lemma:

Lemma 7. *Let (\bar{S}, \underline{R}) be a solution of (42) with $c = \bar{c}_{SR}$. We define $(\bar{s}, \underline{r}) : \mathbb{R} \times \mathbb{R}^+ \rightarrow \mathbb{R}^2$ by*

$$\begin{cases} \bar{s}(x, t) = \min(\alpha_0, \bar{S}(x - \bar{c}_{SR}t - \xi(t)) + q(t)), \\ \underline{r}(x, t) = \max(0, \underline{R}(x - \bar{c}_{SR}t - \xi(t)) - p(t)). \end{cases}$$

Then for p, q and ξ well-chosen functions of t , (\bar{s}, \underline{r}) satisfies for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$, $N_1[\bar{s}, \underline{r}](x, t) \geq 0$ and $N_2[\bar{s}, \underline{r}](x, t) \leq 0$.

Proof. The proof of lemma 7 is very similar to the proof of lemma 5. We impose $p(t) = p_0 e^{-\mu t}$, $q(t) = q_0 e^{-\mu t}$ and $\xi(t) = \xi_1 + \xi_0 e^{-\mu t}$. Recall $\bar{\alpha}$ satisfies $\gamma_0 > \frac{\bar{\alpha}}{\theta} > \frac{1}{\beta}$. Let $\epsilon > 0$ be such that $\gamma_0(\theta - \epsilon) - \alpha_0 > 0$, $\theta > \epsilon$, $\bar{\alpha} - \alpha_0 > \epsilon$ and $\beta_0(\bar{\alpha} - \epsilon) > 1$. There exists η such that, if $\epsilon < \bar{S}(\zeta) < \alpha_0 - \epsilon$ or $\epsilon < \underline{R}(\zeta) < \theta - \epsilon$, then $\bar{S}'(\zeta) < -\eta$ and $\underline{R}'(\zeta) > \eta$. Then, the choice of

parameters $p_0 > 0$, $q_0 > 0$, $\mu > 0$ and $\xi_0 < 0$ satisfying:

$$\gamma_0 p_0 < \bar{\alpha} - \alpha_0, \quad (44)$$

$$\gamma_0 p_0 + \mu < \gamma_0(\theta - \epsilon) - \alpha_0, \quad (45)$$

$$p_0(\mu + 2) < \frac{1 - \theta}{2}(\theta - \epsilon), \quad (46)$$

$$\beta_0 q_0 < \frac{1 - \theta}{2}, \quad (47)$$

$$\gamma_0 p_0 < \frac{\bar{\alpha} - \alpha_0 - \epsilon}{2}, \quad (48)$$

$$\mu < \frac{\bar{\alpha} - \alpha_0 - \epsilon}{2}, \quad (49)$$

$$p_0 + \mu < \beta_0(\bar{\alpha} - \epsilon) - 1, \quad (50)$$

$$\xi_0 < -\frac{q_0 \gamma_0 (\theta - \epsilon)}{\eta \mu}, \quad (51)$$

$$\xi_0 < -\frac{p_0 \beta_0 (\bar{\alpha} - \epsilon)}{\eta \mu}, \quad (52)$$

is enough to ensure that, for every $(x, t) \in \mathbb{R} \times \mathbb{R}^+$, we have $N_1[\bar{s}, \underline{r}](x, t) \geq 0$ and $N_2[\bar{s}, \underline{r}](x, t) \leq 0$. \square

As in 4.1, we now want to choose ξ_1 and maybe further reduce μ such that (\bar{s}, \underline{r}) and (s, r) are well-ordered at some time T and on a well-chosen border.

Recall that $c_2 < c_R$. We state the following lemma:

Lemma 8. *There exists $T > 0$ and $c^* > c_2$ such that for every $t \geq T$:*

and for every $x \leq c^* T$:

$$s(x, T) \leq \bar{s}(x, T) \text{ and } r(x, T) \geq \underline{r}(x, T).$$

Proof. We take $c^* > c_2$ such that $c_S < c^* < c_R$. Just as in the proof of lemma 6, we know that

$$\lim_{t \rightarrow +\infty} |s(c^* t, t)| + |r(c^* t, t) - 1| = 0.$$

Thus, there exists $T_1 > 0$ such that for any $t > T_1$, $s(c^* t, t) \leq q_0$ and $r(c^* t, t) \geq \theta$.

We also know that there exists $X \in \mathbb{R}$ such that for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$, $s(x, t) \leq U_S(x - c_S t - X)$ where U_S is a Fisher-KPP front defined in (3). We also know from [20] that U_S satisfies for a certain constant $C > 0$ and any $\zeta \in \mathbb{R}$:

$$U_S(\zeta) \leq C \zeta e^{-\frac{c_S}{2} \zeta}.$$

Thus for all $t > 0$, we have

$$s(c^* t, t) \leq U_S((c^* - c_S)t - X) \leq C((c^* - c_S)t - X) e^{-\frac{c_S}{2}((c^* - c_S)t - X)}.$$

If we further reduce μ such that $\mu < \frac{c_S}{2}(c^* - c_S)$, there exists $T_2 > 0$ such that for all $t > T_2$,

$$C((c^* - c_S)t - X) e^{-\frac{c_S}{2}((c^* - c_S)t - X)} \leq q_0 e^{-\mu t}.$$

Then, by taking $T = \max(T_1, T_2)$, we get that for all $t > T$,

$$s(c^*t, t) \leq \bar{s}(c^*t, t) \text{ and } r(c^*t, t) \geq \underline{r}(c^*t, t).$$

The parameter ξ_1 remains to be chosen. We can take it large enough that for any $x \leq c^*T$,

$$\bar{s}(x, T) = \bar{\alpha} \text{ and } \underline{r}(x, T) = 0,$$

which concludes the second part of the lemma. □

We can then apply the comparison lemma 1 with lemmas 7 and 8 to conclude that:

$$\forall t \geq T, \quad \forall x \in [c_1t, c_2t], (s, r)(x, t) \preceq (\bar{s}, \underline{r})(x, t).$$

We thus have the following spreading result:

$$\lim_{t \rightarrow +\infty} \inf_{c_1t \leq x \leq c_2t} s(x, t) \leq 0 \text{ and } \lim_{t \rightarrow +\infty} \inf_{c_1t \leq x \leq c_2t} r(x, t) \geq \theta. \quad (53)$$

This is true for any $\theta < 1$ close enough to 1, and for any $(x, t) \in \mathbb{R} \times \mathbb{R}^+$ we have $r(x, t) < 1$, so in conclusion:

$$\lim_{t \rightarrow +\infty} \sup_{c_1t \leq x \leq c_2t} |s(x, t)| + |r(x, t) - 1| = 0,$$

which concludes the proof of Theorem 1.

As stated in 1, the proof of these results relies heavily on the Fisher-KPP hypothesis and theorems from [19].

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