Can climate change lead to gap formation ?

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Abstract

Consider a situation where spatial heterogeneity leads to a cline, a gradual transition in dominance of two competing species. We first prove, in the context of a simplified competition-diffusion model, that there exists a stationary solution showing that the two species coexist in a transition zone. What happens then if, owing to climate change, the environmental profile moves with constant speed in space? We show here that, when the speed with which the environmental condition shifts exceeds the Fisher invasion speed of the advancing species, an expanding gap will form. We raise the question of whether such a phenomenon has been or can be observed.

1 Introduction

In this note we consider two competing species in a one-dimensional domain characterized by an environmental gradient such that species 1 is favoured far to the left (corresponding, say, to the South) and species 2 is favoured far to the right (corresponding to the North). One expects that a cline will form as a result, with species 1 being replaced gradually by species 2 when one moves from South to North. We indeed establish this property in the context of a simple reaction-diffusion model for such a situation. We prove the existence of a stationary solution of the system showing that the two species coexist in a transition region.

But what do we expect to see when the environmental conditions themselves are "on the move"? In particular, what if due to climate change the species-specific indicators of local suitability are not fixed for a given spatial position x but are in fact a function of $x - ct$ where t denotes time and c is the speed at which isolines of environmental quality move up North?

In this short note we show that, in this context of the simple reaction-diffusion system modelling such a situation, gap formation can occur. By this we mean the following. The speed at which species 2 is forced to retreat towards the North is exactly c. An upper bound for the speed with which species 1 can occupy the region from which species 2 has withdrawn is the Fisher invasion

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speed c_0. We show here that whenever $c_0 < c$ an ever increasing gap will form in which species 2 is already brought down to a very low density while species 1 is yet to attain a substantial density. Thus, in particular, we will see in this case a phase separation such that, in the limit, the two species do not interact.

The underlying reason is an asymmetry in the effect of a moving climate depending on whether suitable habitat expands or retracts. In the first case, the invasion speed sets an upper bound for the ability to follow, while in the second case the speed of retreat is forced by the climate and hence is independent of dispersal. Our aim is to substantiate this statement in terms of simple estimates for solutions of a system of two reaction-diffusion equations.

By formulating explicitly the theoretical possibility of gap formation we hope to trigger ecological awareness such that, perhaps, the phenomenon can be related to actual observations of shift in competitive balance. Clearly, ecological reality is far more complex than our simplified description does capture. Here we focus on the single aspect of a moving competition framework. But many other phenomena can come into play and deserve to be studied. For instance, one can imagine that, in addition to climatic conditions, competition involves food and that the food population will grow to higher than usual levels in the gap. Thus the phenomenon may take the form of a moving succession of patterns involving two speeds, c and c_0 and possibly other parameters.

In this paper we report a precise theoretical result and ask whether it can be related to field observations. The aim here is not to survey the manifold aspects of modelling the impact of climate change on population dynamics. The recent references [6], [14] provide an entrance to the rapidly growing literature. The modelling approach of the present paper overlaps with the approach in the references [3, 7, 8, 11, 15, 16].

In a subsequent work we plan to study the case when $c < c_0$ for which we prove that coexistence occurs in the form of a joint travelling wave solution. Here, we already study the existence of stationary solutions for the case $c = 0$. More precisely, for $0 \leq c < c_0$, we intend to establish in [2] the existence, uniqueness and global stability of a traveling wave solution $u(x-ct), v(x-ct)$ of speed c for the system (1)– (2) below. This behavior is illustrated by numerical simulation in section 5 below (compare Figure **??**). Here, we prove the case $c = 0$. Thus, this case gives rise to a different behavior from the one we derive here.

2 Cline formation

We consider the system of two equations:

$$\partial_t u(t,x) - d_1\,\partial_{xx} u(t,x) = u(t,x)\Big(r_1(x - c\,t) - u(t,x) - v(t,x)\Big), \qquad (1)$$

$$\partial_t v(t,x) - d_2\,\partial_{xx} v(t,x) = v(t,x)\Big(r_2(x - c\,t) - u(t,x) - v(t,x)\Big). \qquad (2)$$

Here, $t \in \mathbb{R}_+$, $x \in \mathbb{R}$, $u := u(t,x)$ and $v := v(t,x)$ are the number densities of two different species, d_1, $d_2 > 0$ are their respective diffusion rates. The per capita growth rates (when $u = v = 0$) $r_1, r_2 : \mathbb{R} \to \mathbb{R}$ satisfy the following conditions: r_1, r_2 are continuous, monotone, with values in $[-L, K]$, and have the following limits

$$r_1(-\infty) = K > 0,\ r_1(+\infty) = -L < 0, \quad r_2(-\infty) = -L,\ r_2(+\infty) = K. \tag{3}$$

Here K, $-L$ represent the asymptotic (when $x \to \pm\infty$) low density growth rates of the species.

We begin with a result concerning the situation when $c = 0$. We show that in that case, there exists a nontrivial steady state for system (1)–(2), in which the first species (u) is dominant when $x \to -\infty$, and the second species (v) is dominant when $x \to +\infty$.

More precisely, we show the following result.

Theorem 1. *We consider the system (1), (2), when* $c = 0$, *that is*

$$\partial_t u(t,x) - d_1\,\partial_{xx} u(t,x) = u(t,x)\Big(r_1(x) - u(t,x) - v(t,x)\Big), \tag{4}$$

$$\partial_t v(t,x) - d_2\,\partial_{xx} v(t,x) = v(t,x)\Big(r_2(x) - u(t,x) - v(t,x)\Big). \tag{5}$$

Then, there exists a stationary solution to system (4) – (5), denoted by $(U(x), V(x))$, *such that* $0 \le U(x), V(x) \le K$. *Moreover,* U *is decreasing on* $\mathbb{R}$, V *is increasing on* $\mathbb{R}$, *and* $\lim_{x\to-\infty} U(x) = K$, $\lim_{x\to-\infty} V(x) = 0$, $\lim_{x\to+\infty} U(x) = 0$, $\lim_{x\to+\infty} V(x) = K$.

This theorem is proven in section 4.

In the forthcoming paper (cf. [2]), we shall study the issues related to uniqueness and global stability for system (4)– (5), and make more precise the asymptotic behavior of U and V.

3 Gap formation

We now consider $c > 0$ a given constant. For the initial value problem we complement the system (1)– (2) with some suitable initial data

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x), \qquad \text{for all} \quad x \in \mathbb{R}. \tag{6}$$

In the absence of species 2, and if r_1 were the constant given by $r_1(x) \equiv K$, then the classical Fisher – KPP invasion speed of u would be given by

$$c_0 := 2\sqrt{d_1 K}.$$

In the present note we focus on the case $c > c_0$, that is, when there is a fast change of climate. The aim is to provide estimates that characterize the large time behaviour. Our main result states that in a region of asymptotic size $(c - c_0)\,t$ the density of individuals of *both* species decreases exponentially. Accordingly we call this region a gap. Thus, there is a phase separation with widening gap. We now state precisely the result.

Theorem 2. *Assume* $c > c_0$*. Let* $u_0, v_0 \in L^\infty(\mathbb{R})$ *(that is,* u_0 *and* v_0 *are bounded) be initial data such that for all* $x \in \mathbb{R}$*,* $u_0(x) \geq 0$*,* $v_0(x) \geq 0$*,* $u_0(x), v_0(x) \leq K$ *and the support of* u_0 *is bounded from above, that is, there exists* $R \in \mathbb{R}$ *such that* $u_0(x) = 0$ *for all* $x \geq R$*.*

Then the unique bounded solution of equations (1) – (2) *with the initial condition* (6) *satisfies for all* $t \geq 0$*,* $x \in \mathbb{R}$*:* $u(t,x) \geq 0$*,* $v(t,x) \geq 0$*,* $u(t,x), v(t,x) \leq K$*. Furthermore, for all* c_1, c_2 *satisfying* $c_0 < c_1 < c_2 < c$*, and for all constants* $b_1, b_2 \in \mathbb{R}$

$$\forall t \geq 0, \qquad \sup_{x \geq c_1\,t + b_1} u(t,x) \leq A_1\, e^{-\alpha_1\, t}, \tag{7}$$

$$\forall t \geq 0, \qquad \sup_{x \leq c_2\,t + b_2} v(t,x) \leq A_2\, e^{-\alpha_2\, t}, \tag{8}$$

where the positive constants $A_2, \alpha_2 > 0$ *only depend upon* $K, L, r_2^{-1}(-L/2), d_2, c, c_2, b_2$ *and* $A_1, \alpha_1 > 0$ *only depend upon* K, d_1, c_1, b_1, R*.*

This theorem is proved in section 4.

Remarks.– (i) Actually, the assumption $u_0(x), v_0(x) \leq K$ is used only for presentation convenience, the proof below can be adapted to the more general case of merely bounded nonnegative initial data.

(ii) The condition that the support of u_0 be bounded from above by some R could also be replaced by the hypothesis of a sufficiently fast exponential decay for the right tail of u_0.

(iii) Lastly, the assumption that $-L \leq r_1, r_2 \leq K$ is not needed, and the same is true for the assumption that r_1, r_2 are monotone. We assume it here to somewhat simplify the argument. However, the result holds only under the requirement of the limiting conditions (3). This will be further detailed in [2].

(iv) In that paper, we also intend to show that in the present case $c_0 < c$, then, c_0 and c are sharp in the following sense. First for all u_0, v_0 with $u_0 \not\equiv 0$, let γ_1 be any real such that $\gamma_1 < c_0 < c$, then,

$$\underline{lim}_{\{t \to \infty;\, -\gamma_1 t \leq x \leq \gamma_1 t\}} u(t,x) = K\,,$$

Likewise, for all u_0, v_0 with $\underline{lim}_{\{x \to \infty\}} v_0 > 0$, let γ_2 be any real such that $c_0 < c < \gamma_2$, then,

$$\underline{lim}_{\{t \to \infty;\, x \geq \gamma_2 t\}} v(t,x) = K.$$

Thus, c is the exact asymptotic speed of retreat of v and c_0 is the exact asymptotic speed of advance of u.

4 Proof of the theorems

Proof of Theorem 1: We start with a lemma in which we summarize the results of existence, uniqueness and qualitative behavior for one reaction-diffusion equation with inhomogeneous coefficients. This type of equations, in higher dimension and cylindrical domains, for more general non-linear terms (but that in the present case would involve some restriction on the parameters), was studied by F. Hamel in [4, 5].

Lemma 3. *Let* $R := R(x)$ *be a decreasing function from* $\mathbb{R}$ *to* $\mathbb{R}$ *such that* $\lim_{x\to-\infty} R(x) = K > 0$ *and* $\lim_{x\to+\infty} R(x) = -L < 0$ *and let* $d > 0$ *be given. We consider the equation*

$$-\, d\,\partial_{xx} w(x) = w(x)\,(R(x) - w(x)). \tag{9}$$

Then, there exists a unique C^2 *nonnegative solution (denoted by* $G(R,d)$*) of eq. (9) such that* $G(R,d)(x) > 0$ *for some* $x \in \mathbb{R}$*. Moreover* $x \mapsto G(R,d)(x)$ *is decreasing, and* $lim_{x\to-\infty} G(R,d)(x) = K$*,* $lim_{x\to+\infty} G(R,d)(x) = 0$*. Finally,* $R \mapsto G(R,d)$ *is order preserving.*

A symmetric result is obtained for the case of an increasing R by using the transformation $x \mapsto -x$.

Proof of Lemma 3: We first note that $\bar\Psi := K$ is a supersolution. Then, we build a nontrivial subsolution thanks to the following procedure: we consider some $\varepsilon \in (0, K/2)$, and $\bar x \in \mathbb{R}$, such that $R(\bar x) = \frac{K}{2} + \varepsilon$. For any $x_0 \le \bar x - \sqrt{\frac{2d}{K}}\,\frac{\pi}{2}$, the function χ_{ε,x_0} defined by

$$\chi_{\varepsilon,x_0}(x) = \varepsilon\,\cos\left(\sqrt{\frac{K}{2d}}\,(x - x_0)\right)\,1_{\{\sqrt{\frac{K}{2d}}\,|x-x_0|\le\pi/2\}}$$

satisfies, for $|x - x_0| \le \sqrt{\frac{2d}{K}}\,\frac{\pi}{2}$,

$$-d\,\frac{d^2\chi_{\varepsilon,x_0}}{dx^2}(x) - \chi_{\varepsilon,x_0}(x)\,(R(x) - \chi_{\varepsilon,x_0}(x))$$

$$\le \chi_{\varepsilon,x_0}(x)\left[-\,\varepsilon + \varepsilon\,\cos\left(\sqrt{\frac{K}{2d}}\,(x - x_0)\right)\right] \le 0.$$

As a consequence, χ_{ε,x_0} is a (generalized) subsolution, and so is

$$\chi^{\varepsilon} := \sup_{x_0 \le \bar x - \sqrt{\frac{2d}{K}}\,\pi/2} \chi_{\varepsilon,x_0},$$

which is in fact defined by

$$\chi^{\varepsilon}(x) = \varepsilon\,1_{\{x\le\bar x - \sqrt{\frac{2d}{K}}\,\pi/2\}} + \varepsilon\,\cos\left(\sqrt{\frac{K}{2d}}\left(x - \bar x + \sqrt{\frac{2d}{K}}\,\frac{\pi}{2}\right)\right)\,1_{\{\bar x - \sqrt{\frac{2d}{K}}\,\pi/2 \le x \le \bar x\}}.$$

Then there exists at least one steady solution w to eq. (9) satisfying $\chi^\varepsilon \le w \le \bar{\Psi} = K$ for any $\varepsilon \in (0, K/2)$. For results related to the comparison principle for elliptic equations and cooperative systems (and their variants), we refer to [1] ,[10], [12] and [13].

We now show that any nontrivial (nonnegative, and bounded) solution w to eq. (9) is decreasing. Indeed, we first observe that if $x_1 < x_2$ are a resp. minimum and maximum of w, such that w increases between x_1 and x_2, and $w(x_2) > w(x_1)$, then $0 \le -\frac{d^2w}{dx^2}(x_2) = w(x_2)\,(R(x_2) - w(x_2))$. We get therefore the estimates $w(x_2) \le R(x_2)$, and, by a similar study, $w(x_1) \ge R(x_1)$, so that $R(x_2) > R(x_1)$, which is impossible since R is decreasing. Note then that if w is minimal at some point x_0 and then increases (on $[x_0, +\infty)$), it admits a strictly positive limit, and so does $\frac{d^2w}{dx^2}$, which is impossible. Finally, if w admits a unique maximum at some point x_0, then $w(x_0) < K$, and w admits a limit in $[0, K)$ at point $-\infty$. The quantity $\frac{d^2w}{dx^2}$ also admits a limit, which can only be 0. This ensures that w is concave close to $-\infty$, which is impossible. As a consequence, w is decreasing on $\mathbb{R}$, and necessarily converges to K at point $-\infty$, and to 0 at point $+\infty$.

In order to prove uniqueness, we consider an interval $[a, b]$ ($b > a$) on which two (C^2) solutions $w_1, w_2 \ge 0$ of eq. (9) are such that $w_1 \ge w_2$, and $w_1(a) = w_2(a)$, $w_1(b) = w_2(b)$. Then, we multiply by w_1 the equation satisfied by w_2, and by w_2 the equation satisfied by w_1. Substracting those two equations, we end up with (for all $x \in [a, b]$),

$$d\left(w_1(x)\,\frac{\partial^2 w_2}{\partial x^2}(x) - w_2(x)\,\frac{\partial^2 w_1}{\partial x^2}(x)\right) + w_1(x)\,w_2(x)\,(w_1(x) - w_2(x)) = 0.$$

Integrating on $[a, b]$, we get the identity

$$d\,w_1(b)\,\left[\frac{\partial w_1}{\partial x}(b) - \frac{\partial w_2}{\partial x}(b)\right] + d\,w_1(a)\,\left[\frac{\partial w_2}{\partial x}(a) - \frac{\partial w_1}{\partial x}(a)\right]$$

$$= \int_a^b w_1(x)\,w_2(x)\,(w_1(x) - w_2(x))\,dx.$$

In the above identity, the right-hand side is nonnegative, while the left-hand side is nonpositive. As a consequence, $w_1 = w_2$ on $[a, b]$.

Note that the same proof holds when a or b is $\pm\infty$, as soon as both w_1 and w_2 admit limits at those points, as proven above (together with their derivatives).

We can therefore define $G(R, d)$, the unique nontrivial solution of eq. (9).

We now consider two functions R_1 and R_2 (satisfying the assumptions of the lemma) such that $R_1 \ge R_2$. Then

$$d\,\frac{\partial^2 G(R_1, d)}{\partial x^2}(x) + G(R_1, d)\,(R_1 - G(R_1, d)) = 0,$$

$$d\,\frac{\partial^2 G(R_2,d)}{\partial x^2}(x)+G(R_2,d)\,(R_2-G(R_2,d))=0,$$

so that

$$d\,\frac{\partial^2 G(R_2,d)}{\partial x^2}(x)+G(R_2,d)\,(R_1-G(R_2,d))=G(R_2,d)\,(R_1-R_2)\geq 0.$$

Then, $G(R_2,d)$ is a subsolution to the equation with R_1, and (remembering that K is a supersolution to the same equation) there exists a solution $W \geq G(R_2,d)$. By uniqueness, this solution W is $G(R_1,d)$. Finally $G(R_1,d)\geq G(R_2,d)$.

Using the argument above for $R_1 = R$, $R_2 = R(x+\cdot)$, and using the monotonicity of R, we recover the monotonicity of $x \mapsto G(R,d)(x)$.

This concludes the proof of Lemma 1.

We now return to the proof of Theorem 1. We define sequences of functions by the following inductive procedure:

$$v_0 := 0, \qquad u_0 := G(r_1,d_1),$$

$$v_1 := G(r_2-u_0,d_2), \qquad u_1 := G(r_1-v_1,d_1),$$

$$\dots$$

$$\forall n\geq 1, \qquad v_{n+1} := G(r_2-u_n,d_2), \qquad u_{n+1} := G(r_1-v_{n+1},d_1).$$

In the definition above, the maximal negative value of the r coefficient is $-L-K$ instead of $-L$. The properties of G however remain the same as in Lemma 1.

The monotonicity properties of G show by induction that for all $n\in\mathbb{N}$, u_n is decreasing and v_n is increasing. They also show that for all $n\geq 0$, $v_{n+1}\geq v_n$, $u_{n+1}\leq u_n$.

Then, pointwise, $u_n \to U := \inf_{p\in\mathbb{N}} u_p$, and $v_n \to V := \sup_{p\in\mathbb{N}} v_p$.

The definition of G shows that for all $n\geq 0$, $u_n, v_n \in C^2(\mathbb{R})$, and

$$-d_1\,\frac{d^2 u_{n+1}}{dx^2} = u_{n+1}\,(r_1-u_{n+1}-v_{n+1}),$$

$$-d_2\,\frac{d^2 v_{n+1}}{dx^2} = v_{n+1}\,(r_2-u_n-v_{n+1}).$$

Then, the sequences $(u_n)_{n\in\mathbb{N}}$ and $(v_n)_{n\in\mathbb{N}}$ are bounded in $W^{2,\infty}(\mathbb{R})$. As a consequence, the convergences $u_n\to U$ and $v_n\to V$ hold locally uniformly, U and V are continuous on $\mathbb{R}$, and eq. (4), (5) are satisfied by (U,V) in the sense of distributions. Remembering that r_1, r_2 are continuous on $\mathbb{R}$, we see that in fact, (U,V) is a C^2 solution to system (4), (5).

It remains to show that the limits as $x \to \pm\infty$ of a solution (U, V) to the system built as above can be computed. Since U and V are monotone, they admit limits (denoted by $u_\pm$ and $v_\pm$ as $x \to \pm\infty$). These limits satisfy

$$u_- \,(K - u_- - v_-) = 0, \qquad v_- \,(-L - u_- - v_-) = 0,$$

$$u_+ \,(-L - u_+ - v_+) = 0, \qquad v_+ \,(K - u_+ - v_+) = 0.$$

Remembering that U is decreasing and V is increasing, $u_- \neq 0$ and $v_+ \neq 0$. Then

$$u_- + v_- = u_+ + v_+ = K.$$

Finally,

$$u_+ = v_- = 0, \qquad u_- = v_+ = K.$$

This concludes the proof of Theorem 1.

We now turn to the

Proof of Theorem 2: Let us start with the estimate on the invasion speed of u. It is a fairly straightforward consequence of the fact that, because of competition, the invasion speed cannot exceed the Fisher-KPP speed. More precisely, since $r_1 \leq K$ and $u, v \geq 0$, using the comparison principle for parabolic equations, we first observe that $u \leq u_1$ where $u_1 = u_1(t, x)$ is the solution of the equation

$$\partial_t u_1 - d_1 \,\partial_{xx} u_1 = \, K u_1, \tag{10}$$

with

$$u_1(0, x) = u_0(x).$$

Let

$$0 < \rho = \frac{c_0}{2d_1} = \sqrt{\frac{K}{d_1}}.$$

Thus, $\rho c_0 - \rho^2 d_1 - K = 0$ and it follows that

$$z_1(t, x) = K e^{-\rho(x - c_0 t - R)}$$

is a solution of equation (10). In addition, since $u_0 \leq K$ and $u_0(x) = 0$ for all $x \geq R$, we see that $u_0(x) \leq z_1(0, x)$ for all $x \in \mathbb{R}$. It is then a consequence of the comparison principle that $u(t, x) \leq u_1(t, x) \leq z_1(t, x)$ from which we derive that

$$\sup_{x \geq c_1 t + b_1} u(t, x) \leq K e^{\rho(R - b_1)} e^{-\rho(c_1 - c_0)t}.$$

We have thus proved (7) with $\alpha_1 = \rho(c_1 - c_0)$ and $A_1 = K e^{\rho(R - b_1)}$.

Let us turn next to the estimate on the speed of retraction to the North for v. Recall that v satisfies equation (2):

$$\partial_t v(t, x) - d_2 \,\partial_{xx} v(t, x) = v(t, x) \Big(r_2(x - c\,t) - u(t, x) - v(t, x) \Big).$$

From the maximum principle we know that $v(t,x) \leq K$ for all $t \geq 0$ and $x \in \mathbb{R}$. Choose some γ such that $0 < \gamma < L$ (e.g. pick $\gamma = L/2$). Since $r_2(-\infty) = -L$ there exists some $\xi_0 \in \mathbb{R}$ such that $r_2(\xi) \leq -\gamma$ for all $\xi \leq \xi_0$. Therefore, we get

$$\begin{cases} \partial_t v - d_2\, \partial_{xx} v + \gamma v \leq 0, \quad \text{for all} \quad t, x \quad \text{such that} \quad x \leq ct + \xi_0, \\ v \leq K, \quad \text{for all} \quad t \geq 0,\ x \in \mathbb{R}. \end{cases} \tag{11}$$

We can get a super solution of the first equation in (11) in the following manner. Define

$$w(t,x) = K\left(e^{\rho(x-ct-\xi_0)} + e^{-mt}\right),$$

where ρ and m are positive constants chosen such that

$$0 < m \leq \gamma\,, \quad \rho > 0, \quad -c\rho - d_2\rho^2 + \gamma \geq 0.$$

With this choice, we get

$$\partial_t w - d_2\, \partial_{xx} w + \gamma w \geq 0, \quad \text{for all} \quad t, x.$$

Note that on the right end boundary points of the set $\{(t,x)\,;\ x \leq ct + \xi_0\}$, namely $x = ct + \xi_0$, we have

$$v(t, ct + \xi_0) \leq K < w(t, ct + \xi_0)$$

for all $t \geq 0$. Gathering these properties, we obtain:

$$\begin{cases} \partial_t(w - v) - d_2\, \partial_{xx}(w - v) + \gamma(w - v) \geq 0, \quad \text{for all } t, x \text{ such that } x \leq ct + \xi_0, \\ v(t, ct + \xi_0) \leq K < w(t, ct + \xi_0), \quad \text{for all} \quad t \geq 0, \\ v(0,x) = v_0(x) \leq K < w(0,x) \quad \text{for all} \quad x \in (-\infty, \xi_0]. \end{cases}$$

Then, we can apply the maximum principle to the parabolic equation in the domain $\{(t,x)\,;\ x \leq ct+\xi_0\}$. Indeed, for instance, a change of variable $(t,x) \to (t, \xi = x - ct - \xi_0)$ transforms the problem into one with a fixed domain and does not change the equation apart from adding a first order term. Therefore, by the maximum principle, from the above system of inequalities we infer that $v \leq w$ on this set $\{(t,x)\,;\ x \leq ct + \xi_0\}$. Choosing $t_0 \geq 0$ such that $c_2\, t + b_2 \leq ct + \xi_0$ for all $t \geq t_0$, we get

$$\forall t \geq t_0, \qquad \sup_{x \leq c_2\, t + b_2} v(t,x) \leq \sup_{x \leq c_2\, t + b_2} K\left(e^{\rho(x-ct-\xi_0)} + e^{-mt}\right) \leq A_2\, e^{-\alpha_2\, t}.$$

Here, $\alpha_2 = \min\{m, \rho(c - c_2)\}$ and A_2 is explicitly computed. Then, increasing, if need be, the constant A_2 so that $A_2 e^{-\alpha_2 t_0} \geq K$, we now get the last estimate to hold for all $t \geq 0$, that is we get formula (8). The proof of Theorem 2 is thereby complete.

5 Numerical simulations

We show in this section some numerical simulations that illustrate the movement and expansion of a gap.

We considered the equations (1), (2) with the following data:

$$d_1 = d_2 = 0.01,$$

$$r_2(z) = 0.25 + 0.75 * (z/(1 + |z|)),$$

$$r_1(z) = r_2(-z).$$

Note that the (asymptotic) classical invasion speed which is also the velocity of the traveling wave associated with u (in absence of individuals of the species 2, and without forcing) is $c_0 = 0.2$.

The system (1), (2) is discretized by first replacing the infinite interval $\mathbb{R}$ (for the variable x) by the interval $[-L_0, L_0]$, with $L_0 = 50.0$, and by imposing homogeneous Neumann boundary conditions at points $-L_0$ and L_0. We then used a finite differences centered explicit scheme for the parabolic equations with time step $dt = 0.05$ and space step $dx = 0.05$ (that is, 2000 cells are used and the CFL constant is strictly smaller than 1).

For the simulations, we used the spatially homogeneous initial data $u = 0.1$, $v = 0.1$ and we chose the forcing velocities $c = 0.16$, $c = 0.24$, and $c = 0.32$.

In Fig. 1, we consider the case $c = 0.16$, and we show the curves for $u(t, \cdot)$ (in blue) and $v(t, \cdot)$ (in red) as a function of the space variable x at times $t = 2$, $t = 6$, $t = 10$, $t = 14$. The figure shows that no gap appears between the domains occupied by the two species, which both travel at velocity $c = 0.16$. The numerical evidence supports the existence of a joint traveling wave solution $u(x - ct), v(x - ct)$ which we intend to prove in [2].

The case $c = 0.24$ is the object of Fig. 2, and we display again the curves for $u(t, \cdot)$ (in blue) and $v(t, \cdot)$ (in red) as a function of the space variable x at times $t = 2$, $t = 6$, $t = 10$, $t = 14$. The picture now exhibits a gap appearing between the domains occupied by the two species. The advancing one is traveling at its own velocity $c_0 = 0.2$, while the retreating one travels at the higher velocity $c = 0.24 > c_0 = 0.2$.

Lastly, we present the case $c = 0.32$ in Fig. 3. The curves which are represented are still $u(t, \cdot)$ (in blue) and $v(t, \cdot)$ (in red), as a function of the space variable x at times $t = 2$, $t = 6$, $t = 10$, $t = 14$. The gap which appears is now much easier to detect. We recall that the advancing species is traveling at its own velocity $c_0 = 0.2$, while the retreating one travels at the (much) higher velocity $c = 0.32 > c_0 = 0.2$.

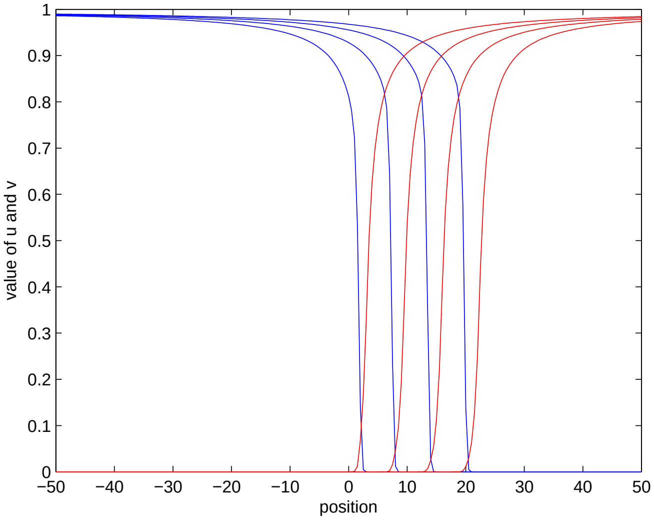

Figure 1: Densities of u (blue) and v (red) in function of x when $c = 0.16$, at times $t = 2$, $t = 6$, $t = 10$ and $t = 14$

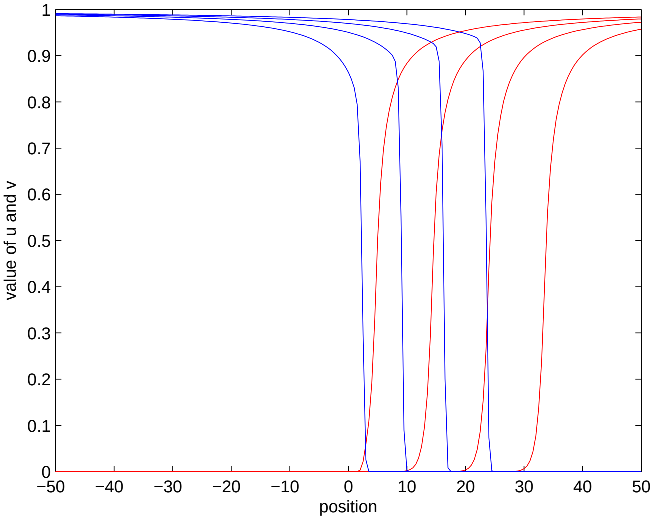

Figure 2: Densities of u (blue) and v (red) in function of x when $c = 0.24$, at times $t = 2$, $t = 6$, $t = 10$ and $t = 14$

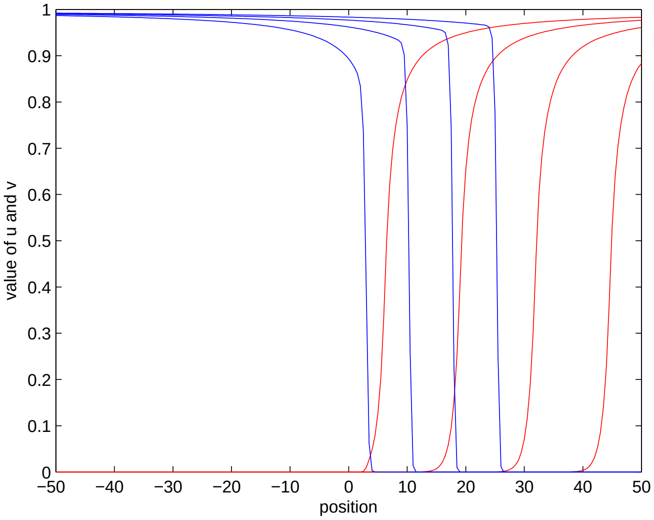

Figure 3: Densities of u (blue) and v (red) in function of x when $c = 0.32$, at times $t = 2$, $t = 6$, $t = 10$ and $t = 14$

We now show a figure obtained from the same simulations, in which $u(100, \cdot)$ and $v(100, \cdot)$ are presented in terms of c (between 0 and 0.4) and x. The red color corresponds to high values of u (on the left) and v (on the right), while the blue color corresponds to lesser values of u and v.

The figure illustrates the fact that when $c < 0.2$, no gap appears between the two species, whereas a gap exists when $c > 0.2$ (with a width proportional to $c - 0.2$). The exact value $c = 0.2$ is of course only approximately observed on the figure because of the discretization error, and the asymptotic character of the formation of the gap.

Note that when $c > 0.2$, the retraction wave (corresponding to v, on the right-hand side of the figure) closely follows the forced velocity (c), but the "free" traveling wave (corresponding to u, on the left-hand side of the figure) slightly deviates from its theoretical asymptotic velocity ($c_0 = 0.2$).

6 A different geometry

We believe that the appearance of a gap, in which two species that are competing both disappear because of a fast climate change, is a phenomenon which is robust with respect to the form that the spatial heterogeneity takes. In order to test this idea, we present a few numerical simulations which correspond to a

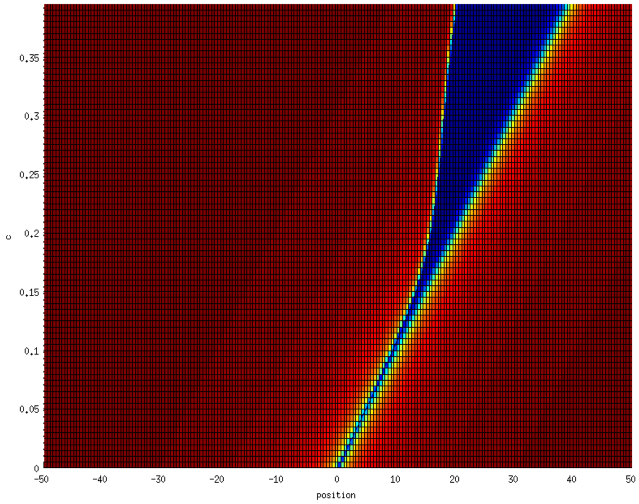

Figure 4: Densities u and v in terms of x and c (ranging from 0 to 0.4)

different geometry.

We consider a situation in which initially (before the climate change) the temperature T is a function of the space variable x (for example because to each point x corresponds an altitude). We also assume that two species (represented by their number density $u := u(t,x)$ and $v := v(t,x)$) are in competition and have a growth rate (denoted by ϕ_1 and ϕ_2) which is temperature-dependent. Typically, each species is adapted to a certain range of temperatures.

We assume that $T(x)$ becomes $T(x) + c\,t$ because of the climate change (the implicit modeling assumption being that the increase of temperature is homogeneous in space), and we numerically compute the solution of the system:

$$\frac{\partial u}{\partial t} - d_1 \frac{\partial^2 u}{\partial x^2} = u\,(\phi_1(T(x) + c\,t) - u - v),$$

$$\frac{\partial v}{\partial t} - d_2 \frac{\partial^2 v}{\partial x^2} = v\,(\phi_2(T(x) + c\,t) - u - v).$$

We use the following data in order to produce the figures:

$$\phi_1(T) = \begin{cases} 1.0 & \text{for} \quad T > 0.0, \\ 1.0 + 4.0\,T & \text{for} \quad -0.375 \le T \le 0.0, \\ -0.5 & \text{for} \quad T < -0.375, \end{cases}$$

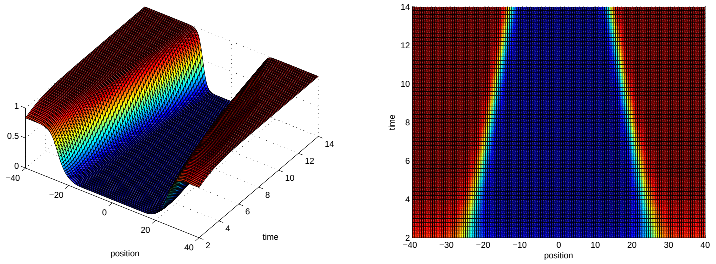

Figure 5: Density of u as a function of t and x

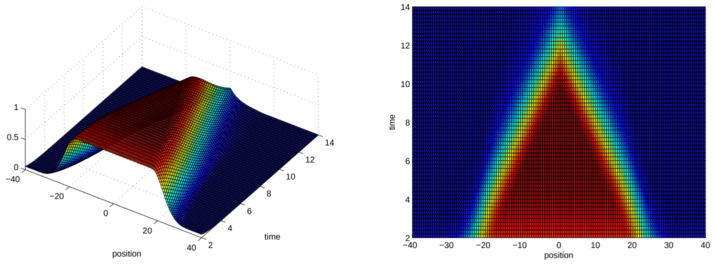

Figure 6: Density of v as a function of t and x

$$\phi_2(T) = \begin{cases} -0.5 & \text{for} \quad T > 0.125, \\ 1.0 - 4.0\,|T + 0.25| & \text{for} \quad -0.25 \leq T \leq 0.125, \\ 1.0 & \text{for} \quad T < -0.25, \end{cases}$$

$$T(x) = \frac{10}{3l}\left(|x - \frac{l}{2}| - \frac{3l}{10}\right) 1_{\{|x-\frac{l}{2}| \leq \frac{3l}{10}\}},$$

where $l = 100$ and $c = 0.8$. Here, the multiplication by $1_{\{|x-\frac{l}{2}|\leq\frac{3l}{10}\}}$ means that $T(x) = 0$ when $|x - \frac{l}{2}| \geq \frac{3l}{10}$.

The panels of Figure 5 represent the same surfaces seen from a different angle, and show the value of u as a function of t and x. The red color corresponds to higher values of the function, while the blue color corresponds to lesser values. The same is shown on Figure 6, but for the value of v. Finally, we show on the same figure (Figure 7) the values of u and v.

We still observe (especially on Figure 7) the widening of the gap but now extinction of the species adapted to the coldest region (that is, species 2 with number density v) occurs at the end of the simulation (which is most clearly seen in Figure 6). The extension of the gap, in this complex geometry, does not seem to follow a linear law with respect to time.

It would also be interesting to take into account other effects such as trans-

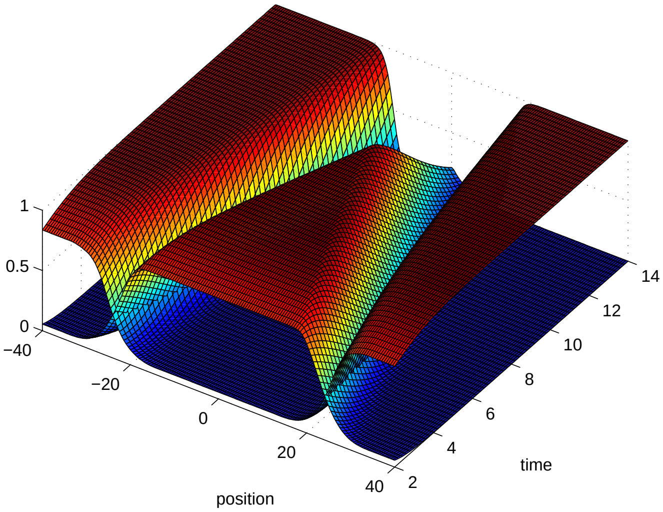

Figure 7: Densities of u and v as a function of t and x

port terms by an underlying flow. A system having a certain analogy with (1)–(2) but with different functions r_i from the one studied here and without shift, is studied in [7]. The model in that paper is about competing populations in a river and the effect of flow is analyzed.

7 Conclusion

When climatic conditions shape the spatial abundance pattern of closely related competing species, it is to be expected that climate change will be reflected in changes of such patterns, as indeed shown in [11]. For a survey of closely related issues and many references, with the focus on ecosystems in streaming rivers, we refer the reader to [9]. In [3], it was shown (in a single species context) that the sign of $c - c_0$, where c is the speed at which the climate moves and c_0 is the invasion speed into virgin habitat, is of crucial importance if the suitable habitat consists of a finite patch.

Here we showed the theoretical possibility that a systematic movement of climatic conditions leads to a moving and widening gap in between regions of dominance of one and the other competitor. One should expect such gap formation whenever the speed at which a habitat type shifts as a result of climate change exceeds the speed at which a species can expand its range by dispersal. We demonstrated gap formation in the context of a special and somewhat simple model example, but we think that the presence of a widening gap is a rather general phenomenon when the forcing speed of climate change is large.

This belief is sustained by numerical computations. We wonder whether the phenomenon has been (or will be) observed in the field.

Acknowledgments

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References

[1] H. Berestycki, F. Hamel, *Reaction-diffusion equations and propagation phenomena*, To appear.

[2] H. Berestycki, L. Desvillettes and O. Diekmann, *On gap formation between competing species induced by climate shift*, In Preparation.

[3] H. Berestycki, O. Diekmann, C.J. Nagelkerke and P.A. Zegeling, *Can a species keep pace with a shifting climate?*, Bull. Math. Biol., **71** (2009), 399–429.

[4] F. Hamel, *Reaction-diffusion problems in cylinders with no invariance by translation, Part I: Small perturbations*, Ann. Inst. H. Poincaré, Anal. Non Linéaire **14** (1997), 457–498.

[5] F. Hamel, *Reaction-diffusion problems in cylinders with no invariance by translation, Part II: Monotone perturbations*, Ann. Inst. H. Poincaré, Anal. Non Linéaire **14** (1997), 555–596.

[6] S. J. Leroux, M. Larrivé, V. Boucher-Lalonde, A. Hurford, J. Zuloaga, J. T. Kerr, and F. Lutscher, *Mechanistic models for the spatial spread of species under climate change*, Ecological Applications, **23** n.4 (2013), 815–828.

[7] F. Lutscher, E. McCauley, M.A. Lewis, *Spatial patterns and coexistence mechanisms in systems with unidirectional flow*, Theoretical Population Biology, **71** 267-277 (2007).

[8] F. Lutscher, R. M. Nisbet, and E. Pachepsky, *Population persistence in the face of advection*, Theoretical Ecology, **3** n.4 (2010), 271–284.

[9] R.M. Nisbet, K.E. Anderson, E. McCauley and U. Feudel, *Spatial Scale and Population Dynamics in Advective Media*, In: Spatial Ecology, 129–144, Stephen Cantrell, Chris Cosner, Shigui Ruan (eds.) 2009, Chapman and Hall/CRC.

[10] C.V. Pao *Nonlinear parabolic and elliptic equations* Plenum Press, New York, 1992

[11] A.B. Potapov and M.A. Lewis *Climate and competition : the effect of moving range boundaries on habitat invasibility*, Bull. Math. Biol., **66** (2004), 975–1008.

[12] M.H. Protter and H.F. Weinberger *Maximum principles in differential equations*, Springer, New York, 1999 (Prentice Hall, N.J., 1967)

[13] H.L. Smith *Dynamics of competition*, In: Mathematics inspired by biology, 191–240, V. Capasso, O. Diekmann (eds.) 1999, Springer LNiM 1714,

[14] C.J. Sorte. *Predicting persistence in a changing climate: flow direction and limitations to redistribution*, Oikos, **122** n.2 (2013), 161–170.

[15] O. Vasilyeva and F. Lutscher. *How flow speed alters competitive outcome in advective environments*, Bulletin of Mathematical Biology, **74** n.12 (2012), 2935–2958.

[16] Y. Zhou and M. Kot. *Discrete-time growth-dispersal models with shifting species ranges*, Theoretical Ecology, **4** n.1 (2011) 13–25.