



## Climate and Competition: The Effect of Moving Range Boundaries on Habitat Invasibility

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Predictions for climate change include movement of temperature isoclines up to 1000 m/year, and this is supported by recent empirical studies. This paper considers effects of a rapidly changing environment on competitive outcomes between species. The model is formulated as a system of nonlinear partial differential equations in a moving domain. Terms in the equations describe competition interactions and random movement by individuals. Here the critical patch size and travelling wave speed for each species, calculated in the absence of competition and in a stationary habitat, play a role in determining the outcome of the process with competition and in a moving habitat. We demonstrate how habitat movement, coupled with edge effects, can open up a new niche for invaders that would be otherwise excluded.

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### 1. INTRODUCTION

Investigating the potential impact of climate change on biota is one of the important tasks for quantitative modellers. Whereas detailed studies require large complex models, a lot of information and powerful computers, many basic effects can be studied with the help of rather simple models which take into account only a few important factors.

At present one of the important problems is the impact of climate change on the biosphere, and in particular on the distribution and interaction of biological species. Observations show that during several past decades isotherms of year-average temperatures have moved toward poles (Malcolm and Markham, 2000; Parmesan and Yohe, 2003). While computer models for global warming vary with respect to assumptions and outcomes, they commonly predict that in northern Canada, Fennoscandinavia and Russia the speed of isotherm motion will be

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on the order of 100–1000 meters per year (Malcolm and Markham, 2000), which is near or beyond the observed historical spread rates for species such as trees (Clark *et al.*, 1998). Such species may be unable to catch up with the isotherms and thus it is reasonable to expect changes in the composition and structure of northern biota.

One of the first steps in studying the consequences of global warming is to see what effects can arise in simple models describing growth, dispersal and competition of biological species. In this paper we use reaction-diffusion models to analyse the effect of moving range boundaries on spatial competition. Such models have been successfully applied to modelling spatially distributed populations and can be used to predict the speed of species invasion, or the critical patch size needed for persistence of a species (Okubo, 1980; Shigesada and Kawasaki, 1997).

We consider competition of two species and denote their population densities by  $u_i(x, t)$ . It is assumed that the suitable habitat for both species is a moving domain, inside of which species disperse, grow and compete, and outside of which the species die at a given rate, with no reproduction or competition.

The equations are

$$u_{1t} = D_1 u_{1xx} + (r_1 - \alpha_{11} u_1 - \alpha_{12} u_2) u_1, \quad (1)$$

$$u_{2t} = D_2 u_{2xx} + (r_2 - \alpha_{21} u_1 - \alpha_{22} u_2) u_2 \quad (2)$$

on  $x_1(t) \leq x \leq x_2(t)$  and

$$u_{1t} = D_1 u_{1xx} - \kappa_1 u_1, \quad (3)$$

$$u_{2t} = D_2 u_{2xx} - \kappa_2 u_2 \quad (4)$$

on  $x < x_1(t)$  and  $x > x_2(t)$ . At the points  $x_1(t)$  and  $x_2(t)$  the densities  $u_i$  and the fluxes  $D_i u_{ix}$  are assumed to be continuous. Here  $D_i$  are the diffusion coefficients,  $r_i$  are the intrinsic growth rates for the species,  $\alpha_{ij}$  are the interspecies competition coefficients, and  $\kappa_i$  characterize the degree of outside environment hostility. For simplicity we set the same diffusion coefficients within and outside the patch. We use the natural boundary condition  $u_i \rightarrow 0$  as  $x \rightarrow \pm\infty$ .

For this model we are interested in the problem of conditions for species coexistence. In the absence of diffusion, the condition  $\alpha_{12} < \alpha_{11}$ ,  $\alpha_{21} < \alpha_{22}$  is given by phase plane analysis of the Volterra ordinary differential equations, see e.g., Shigesada and Kawasaki (1997). Spatial dependence and habitat motion, as we shall show, bring new features: (i) boundaries can work as additional sinks, which can change the outcome of competition, see also Cantrell *et al.* (1998) and Fagan *et al.* (1999); (ii) habitat motion also acts as an effective sink for populations; and (iii) spatial dependence creates new opportunities: species that cannot coexist at one point in space can form spatially distinct colonies, each of them containing mainly one of the species [see also Levin (1974)].

One classic approach to analysing competition is in terms of invasibility (Durrett, 2002). Suppose that the patch is occupied by a single species. Will a second, introduced species, survive and grow, or become extinct? This problem has been considered by a number of authors, see e.g., Shigesada and Kawasaki (1997). We consider this problem in the context of the spatial distribution of species in the moving patch.

As far as we know, this is the first attempt to analyse the influence of climate change on interspecies competition within the framework of the models (1) and (2). At the same time we must note that models with advection, which leads to the effects close to patch motion have been used in ecological models for rivers, see e.g., Speirs and Gurney (2001). However, (i) the problem of interspecific competition has not been thoroughly analysed in this context, and (ii) the speed of advection in rivers is many orders of magnitude greater than speed of isotherms due to climate change, hence the basic effects must be essentially different.

## 2. THE MODEL EQUATIONS: TRANSFORMATION TO STANDARD FORM

**2.1. Habitat motion as advection of biota.** When the domain is fixed (say,  $x_1 = 0$ ,  $x_2 = L$ ) persistence of species in this model can be thought of as a critical domain size problem with competition (Fagan *et al.*, 1999). Here we consider the case when the patch size  $x_2(t) - x_1(t) = L$  is fixed, and the rate of the movement of the patch  $[x_1(t), x_2(t)]$  is constant, that is  $\dot{x}_1 = \dot{x}_2 = c$ . A change of variables  $x \rightarrow x - ct$  allows us to analyse this as a problem on a fixed spatial domain  $0 \leq x \leq L$  with advection. The speed of advection is  $c$ , and positive values of  $c$  correspond to the motion from right to left. The model now is

$$u_{1t} = D_1 u_{1xx} + cu_{1x} + (r_1 - \alpha_{11}u_1 - \alpha_{12}u_2)u_1, \quad (5)$$

$$u_{2t} = D_2 u_{2xx} + cu_{2x} + (r_2 - \alpha_{21}u_1 - \alpha_{22}u_2)u_2 \quad (6)$$

for  $0 < x < L$ . Outside the patch the equations are

$$u_{1t} = D_1 u_{1xx} + cu_{1x} - \kappa_1 u_1, \quad (7)$$

$$u_{2t} = D_2 u_{2xx} + cu_{2x} - \kappa_1 u_2, \quad (8)$$

for  $x < 0$  and  $x > L$ . At the patch edges ( $x = 0$  and  $x = L$ )  $u_i$  and the fluxes  $D_i u_{ix}$  are assumed to be continuous.

**2.2. Nondimensionalization.** The problem has 12 parameters:  $2 D_i$ ,  $2 r_i$ ,  $4 \alpha_{ij}$ ,  $c$ ,  $L$ , and  $2 \kappa_i$ . By rescaling  $x$ ,  $t$ ,  $u_1$ ,  $u_2$ , we can exclude four of these leaving 6 free parameters for equations in the patch, and the two  $\kappa_i$  which are used in the equations outside the patch.

Let  $x \rightarrow x_0x$ ,  $t \rightarrow t_0t$ ,  $u_i \rightarrow u_{0i}u_i$ , then

$$u_{1t} = \frac{t_0 D_1}{x_0^2} u_{1xx} + \frac{ct_0}{x_0} u_{1x} + (t_0 r_1 - \alpha_{11} t_0 u_{01} u_1 - \alpha_{12} t_0 u_{02} u_2) u_1, \quad (9)$$

$$u_{2t} = \frac{t_0 D_2}{x_0^2} u_{2xx} + \frac{ct_0}{x_0} u_{2x} + (t_0 r_2 - \alpha_{21} t_0 u_{01} u_1 - \alpha_{22} t_0 u_{02} u_2) u_2. \quad (10)$$

The choice of

$$t_0 = \frac{1}{r_1}, \quad x_0 = \sqrt{\frac{D_1}{r_1}}, \quad u_{01} = \frac{r_1}{\alpha_{11}}, \quad u_{02} = \frac{r_1}{\alpha_{22}}, \quad (11)$$

and denoting

$$c' = \frac{c}{\sqrt{D_1 r_1}}, \quad D = \frac{D_2}{D_1}, \quad r = \frac{r_2}{r_1}, \quad L' = \frac{L}{x_0}, \quad \alpha'_{ij} = \frac{\alpha_{ij}}{\alpha_{jj}}, \quad \kappa'_i = \frac{\kappa_i}{r_1}, \quad (12)$$

yields

$$u_{1t} = u_{1xx} + cu_{1x} + (1 - u_1 - \alpha_{12} u_2) u_1, \quad (13)$$

$$u_{2t} = Du_{2xx} + cu_{2x} + (r - \alpha_{21} u_1 - u_2) u_2 \quad (14)$$

inside the patch ( $x \in [0, L]$ ) and

$$u_{1t} = u_{1xx} + cu_{1x} - \kappa_1 u_1, \quad (15)$$

$$u_{2t} = Du_{2xx} + cu_{2x} - \kappa_2 u_2 \quad (16)$$

outside the patch, where the strokes have been omitted for notational simplicity. For the remainder of this paper we shall focus on the case when the mortality rates outside the patch for each species are identical ( $\kappa_1 = \kappa_2 = \kappa$ ).

### 3. REDUCTION TO BOUNDED DOMAIN FOR STATIONARY SOLUTIONS

In this section we reduce the model (13)–(16) on an infinite domain to a related problem with Robin's boundary conditions on a bounded domain. We show that steady-state solutions to the equations and the stability of these solutions is equivalent on the original and reduced systems.

**3.1. Stationary solutions: reduction to a bounded domain.** We consider stationary solutions for the system (13)–(16); that is  $u_{it} = 0$ . Then, following



Ludwig *et al.* (1979), we can transform the problem on the unbounded domain to a boundary value problem on the domain  $[0, L]$ . Outside the patch, a stationary solution has the form  $u_i(x) \sim \exp(k_i x)$ ,  $i = 1, 2$ , where  $k_1, k_2$  are roots of the characteristic equations

$$k_1^2 + ck_1 - \kappa = 0,$$

$$Dk_2^2 + ck_2 - \kappa = 0.$$

There are two roots for each equation, positive  $k_i^+$ , corresponding to the solution  $u_i$  for  $x < 0$  and negative  $k_i^-$ , corresponding to the solution  $u_i$  for  $x > L$ ,

$$k_1^\pm = \frac{-c \pm \sqrt{c^2 + 4\kappa}}{2}, \quad k_2^\pm = \frac{-c \pm \sqrt{c^2 + 4D\kappa}}{2D}. \tag{17}$$

These roots satisfy the constraint that  $u_i$  approaches zero as  $|x| \rightarrow \infty$ . Note, that  $e^{k_i^\pm x}$  satisfies the first order equation  $u_{ix} - k_i^\pm u_i = 0$ . This equation holds outside the patch with corresponding  $k_i^+$  or  $k_i^-$ , and, due to the continuity of both  $u_i$  and  $u_{ix}$ , at the points  $x = 0$  and  $x = L$  as well. Therefore, it is possible to consider the stationary problem only inside the patch with the following Robin's boundary conditions

$$u_{1xx} + cu_{1x} + (1 - u_1 - \alpha_{12}u_2)u_1 = 0, \quad 0 < x < L, \tag{18}$$

$$Du_{2xx} + cu_{2x} + (r - \alpha_{21}u_1 - u_2)u_2 = 0, \quad 0 < x < L, \tag{19}$$

$$u_{ix} - k_i^+ u_i = 0, \quad x = 0, i = 1, 2, \tag{20}$$

$$u_{ix} - k_i^- u_i = 0, \quad x = L, i = 1, 2. \tag{21}$$

The case  $\kappa = \infty$  (extreme hostility) corresponds to Dirichlet boundary conditions  $u_i = 0$  at  $x = 0, L$ . Note that the case of neutral conditions outside the patch ( $\kappa = 0$ ) does not lead to Neumann boundary conditions unless  $c = 0$  (no poleward shift in habitat due to climate change).

**3.2. Equivalence of the models for unbounded and bounded domains for small perturbations of stationary solutions.** Let us introduce a new dynamical problem, associated with the steady-state one (18)–(21):

$$u_{1t} = u_{1xx} + cu_{1x} + (1 - u_1 - \alpha_{12}u_2)u_1, \tag{22}$$

$$u_{2t} = Du_{2xx} + cu_{2x} + (r - \alpha_{21}u_1 - u_2)u_2, \tag{23}$$

$$u_{ix} - k_i^+ u_i = 0, \quad x = 0, i = 1, 2, \tag{24}$$

$$u_{ix} - k_i^- u_i = 0, \quad x = L, i = 1, 2. \tag{25}$$

Note, that nonstationary solutions of (22)–(25) are not equivalent to those of the original problem in unbounded domain (5)–(8). Nonetheless, this associated system enables us to make conclusions about the dynamics of small perturbations of stationary solutions of both systems.

**THEOREM 3.1 (Stability).** *When at least one of  $\kappa$  or  $|c|$  are positive, stationary solutions of (22)–(25) and (5)–(8) are either both linearly stable or unstable.*

**Proof.** For the sake of simplicity let us consider only the case  $c = 0$ . The case of nonzero advection speed has a similar proof with the help of the change of variables. Stationary solutions  $u_{01}(x)$ ,  $u_{02}(x)$  of both original and associated problems coincide inside the patch, hence linearized equations for  $v_i = u_i - u_{0i}$  also coincide.

(1) Suppose that the eigenvalue problem corresponding to the associated linearized system

$$\begin{aligned} v_{1xx} + g_{11}(x)v_1 + g_{12}(x)v_2 &= \lambda v_1, & 0 < x < L \\ Dv_{2xx} + g_{21}(x)v_1 + g_{22}(x)v_2 &= \lambda v_2, & 0 < x < L \\ v_{ix} - k_i^+ v_i &= 0, & x = 0, i = 1, 2, \\ v_{ix} - k_i^- v_i &= 0, & x = L, i = 1, 2; \end{aligned} \quad (26)$$

where  $k_i^\pm$  are given by equation (17), has its dominant eigenvalue  $\lambda_A > 0$ . For the unbounded domain the corresponding eigenvalue problem has the form

$$\begin{aligned} v_{1xx} + g_{11}(x)v_1 + g_{12}(x)v_2 &= \lambda v_1, & 0 < x < L, \\ Dv_{2xx} + g_{21}(x)v_1 + g_{22}(x)v_2 &= \lambda v_2, & 0 < x < L, \\ v_{1xx} - \kappa v_1 &= \lambda v_1, & x < 0, x > L, \\ Dv_{2xx} - \kappa v_2 &= \lambda v_1, & x < 0, x > L. \end{aligned} \quad (27)$$

Let us show that this problem has at least one positive eigenvalue by constructing the corresponding eigenfunction.

Let us consider an auxiliary quasi-eigenvalue problem

$$\begin{aligned} v_{1xx} + g_{11}(x)v_1 + g_{12}(x)v_2 &= \lambda v_1, & 0 < x < L, \\ Dv_{2xx} + g_{21}(x)v_1 + g_{22}(x)v_2 &= \lambda v_2, & 0 < x < L, \\ v_{1xx} - \kappa v_1 &= l v_1, & x < 0, x > L, \\ Dv_{2xx} - \kappa v_2 &= l v_1, & x < 0, x > L, \end{aligned} \quad (28)$$

with  $l > -\kappa$ . Repeating arguments from Section 3.1, this problem can be reduced to an eigenvalue problem on the bounded domain. Introducing  $k_1^\pm(l) = \pm\sqrt{\kappa+l}$ ,  $k_2^\pm(l) = \pm\sqrt{(\kappa+l)/D}$ , we get

$$\begin{aligned} v_{1xx} + g_{11}(x)v_1 + g_{12}(x)v_2 &= \lambda v_1, & 0 < x < L, \\ Dv_{2xx} + g_{21}(x)v_1 + g_{22}(x)v_2 &= \lambda v_2, & 0 < x < L, \\ v_{ix} - k_i^+(l)v_i &= 0, & x = 0, i = 1, 2, \\ v_{ix} - k_i^-(l)v_i &= 0, & x = L, i = 1, 2. \end{aligned} \quad (29)$$

Here the dominant eigenvalue  $\lambda = \lambda(l)$  depends on  $l$ . According to Smoller (1994) and Cantrell *et al.* (1998)  $\lambda$  is a continuous and decreasing function of  $|k_i^\pm|$ , and hence of  $l$ . Consider  $\sigma(l) = \lambda(l) - l$ , which is a decreasing function of  $l$ . We will show that there exists a  $l_B$ ,  $0 < l_B < \lambda_A$  such that  $\sigma(l_B) = 0$ .

For  $l = 0$  we have system (26), and therefore  $\sigma(0) = \lambda_A > 0$ . For  $l = \lambda_A$  we have  $\sigma(\lambda_A) = \lambda(\lambda_A) - \lambda_A < \lambda(0) - \lambda_A = 0$ . Thus  $\sigma(0) > 0$  and  $\sigma(\lambda_A) < 0$ . Due to continuity of  $\sigma$  there must exist an intermediate value  $l_B$ ,  $0 < l_B < \lambda_A$  such that  $0 = \sigma(l_B) = \lambda(l_B) - l_B$ . This means that for  $l = l_B$  (28) is identical to (27), and hence (27) has at least one positive eigenvalue  $\lambda = l_B$ , and therefore its dominant eigenvalue is also positive.

(2) Suppose that (27) has its dominant eigenvalue  $\lambda = \lambda_B > 0$ . Then for  $l = \lambda_B$  (29) has at least one positive eigenvalue  $\lambda = \lambda_B$ , and hence its dominant eigenvalue  $\lambda(l)$  must be positive too. Now let us decrease  $l$  in (29) from  $l = \lambda_B$  to  $l = 0$ . Since  $\lambda(l)$  is a continuously decreasing function,  $\lambda_A = \lambda(0) > \lambda(l_B) \geq \lambda_B > 0$ . At  $l = 0$  (29) coincides with (26), and hence the latter has a positive dominant eigenvalue.

(3) In the case  $|c| > 0$  equations (18) and (19) have a nonself-adjoint operator, and we cannot directly apply the proof above. Nonetheless, it is possible to use the change of variables  $u_1(x, t) = \tilde{u}_1(x, t) \exp(-\frac{cx}{2})$ ,  $u_2(x, t) = \tilde{u}_2(x, t) \exp(-\frac{cx}{2D})$  (see the details in the next section), which makes the operator self-adjoint and hence the technique of the proof becomes applicable.

Therefore both systems (26) and (27) are simultaneously unstable, and hence simultaneously stable too.  $\square$

We can conclude, that the associated system (26) can be used for testing the problem for invasibility in (27): if the species can invade the patch in the original model, the same is true for the associated model and vice-versa.

#### 4. EXCLUSION OF ADVECTION, INHOMOGENEOUS HABITAT MODEL, AND CHARACTERISTIC SCALES

In this section we consider characteristic spatial and temporal scales for the model, nondimensionalize the model, and deduce the habitat movement speed that yields species extinction.

**4.1. Exclusion of advection and inhomogeneous habitat model.** The advection term can be excluded from (13)–(16) by change of variables:

$$u_1(x, t) = \tilde{u}_1(x, t) \exp\left(-\frac{cx}{2}\right), \quad u_2(x, t) = \tilde{u}_2(x, t) \exp\left(-\frac{cx}{2D}\right). \quad (30)$$

Substituting this into (13)–(16) leads to the spatially inhomogeneous system

$$\tilde{u}_{1t} = \tilde{u}_{1xx} + \left(\tilde{r}_1 - e^{-\frac{cx}{2}}\tilde{u}_1 - \alpha_{12}e^{-\frac{cx}{2D}}\tilde{u}_2\right)\tilde{u}_1, \quad (31)$$

$$\tilde{u}_{2t} = D\tilde{u}_{2xx} + \left(\tilde{r}_2 - \alpha_{21}e^{-\frac{cx}{2}}\tilde{u}_1 - e^{-\frac{cx}{2D}}\tilde{u}_2\right)\tilde{u}_2 \quad (32)$$

within the patch and

$$\tilde{u}_{1t} = \tilde{u}_{1xx} - \left(\kappa + \frac{c^2}{4}\right)\tilde{u}_1, \quad (33)$$

$$\tilde{u}_{2t} = D\tilde{u}_{2xx} - \left(\kappa + \frac{c^2}{4D}\right)\tilde{u}_2 \quad (34)$$

outside the patch, where

$$\tilde{r}_1 = 1 - \frac{c^2}{4} = 1 - \left(\frac{c}{c_{1*}}\right)^2 \quad (35)$$

$$\tilde{r}_2 = r \left(1 - \frac{c^2}{4Dr}\right) = r \left(1 - \left(\frac{c}{c_{2*}}\right)^2\right). \quad (36)$$

Here

$$c_{1*} = 2, \quad c_{2*} = 2\sqrt{Dr} \quad (37)$$

are the well known asymptotic rate of population spread for the single-species models [equations (13) and (14) with  $c = \alpha_{12} = \alpha_{21} = 0$  on the infinite domain  $-\infty < x < \infty$  (Aronson and Weinberger, 1975)].

**4.2. Sufficient speed for species extinction.** This change of variables allows us to draw two important conclusions. Let us turn to the equations without the advection terms (31) and (32).

**PROPOSITION 4.1.** For  $|c| > c_{i*}$  the  $i$ th species cannot survive.

It can be easily seen that in this case  $\tilde{r}_i < 0$ , and the equation for  $u_i$  has no sources, only sinks, and hence  $u_i$  must approach zero (Smoller, 1994). In other words, the  $i$ th species will go extinct if the habitat movement speed exceeds the species asymptotic spread rate in the absence of competition.

Another way to characterize the ability of a single species to survive is through its critical patch size  $L_*$  (Ludwig *et al.*, 1979; Okubo, 1980; Shigesada and Kawasaki, 1997). The value of  $L_*$  depends on the boundary conditions. In the case of the Dirichlet boundary condition [ $\kappa = \infty$  for our model (13) and (14) with  $c = \alpha_{12} = \alpha_{21} = 0$ ] the critical patch sizes are

$$L_{1*} = \pi, \quad L_{2*} = \pi \sqrt{\frac{D}{r}}. \quad (38)$$

In the case of general  $\kappa$  values the values of  $L_{i*}$  are smaller, but are still proportional to (38).

This is interpreted as the smallest possible size of a patch that will allow for persistence of a single species. As  $L$  increases through  $L_*$  the trivial equilibrium solution  $u = 0$  becomes unstable and an introduced population will grow. In the presence of competition and patch motion ( $c$  nonzero), we define the critical patch sizes  $\tilde{L}_i$  as the smallest values of  $L$  for which species  $i$  will grow, under the assumption that both species 1 and 2 are rare, that is nonlinear terms in (13) and (14) are negligible.

**PROPOSITION 4.2.** *With the increase of  $|c|$  the critical patch size for  $i$ th species increases and goes to infinity as  $c$  approaches  $c_{i*}$ .*

The size of critical patch is obtained from the linear stability of zero solution  $\tilde{u}_1(x) = \tilde{u}_2(x) = 0$ . As shown in Section 3, analysis of the stability of this zero solution can be facilitated by transforming (31)–(34) to a problem on the finite domain: equations (31) and (32) and boundary conditions

$$\begin{aligned} \tilde{u}_{ix} - \tilde{k}_i^+ \tilde{u}_i &= 0, & x &= 0, \\ \tilde{u}_{ix} - \tilde{k}_i^- \tilde{u}_i &= 0, & x &= L, \end{aligned}$$

where

$$\tilde{k}_1^\pm = \pm \frac{\sqrt{c^2 + 4\kappa}}{2}, \quad \tilde{k}_2^\pm = \pm \frac{\sqrt{c^2 + 4D\kappa}}{2D}. \quad (39)$$

Here, the terms with explicit dependence on  $x$  in (31) and (32) are nonlinear terms of higher order which do not affect the linear stability. Each linearized equation decouples from the other. For the Dirichlet problem (the case  $\kappa = \infty$ ) the boundary conditions do not depend on  $c$ , hence the estimate for the critical length has the same form (38) with  $\tilde{r}_i$  instead of  $r_i$ . Therefore, the critical patch size is

$$\tilde{L}_{i*} = \frac{L_{i*}}{\sqrt{1 - \left(\frac{c}{c_{i*}}\right)^2}}, \quad (40)$$

which approaches infinity as  $|c|$  approaches  $c_{i*}$ .

When the hostility of the exterior  $\kappa$  is finite, the single species critical domain lengths become

$$\tilde{L}_{i*} = \frac{L_{i*}}{\sqrt{1 - (\frac{c}{c_{i*}})^2}} \frac{2}{\pi} \arctan \left( \frac{k_i^+}{\sqrt{r_i}} \right).$$

One can see that for  $\kappa \rightarrow \infty$  we obtain (40).

Below we shall use the values  $L_{i*}$  regardless of the boundary conditions, as a parameter characterizing properties of species  $i$ . In such a context it may be preferable to use the more general term ‘characteristic length’ for species  $i$  instead of ‘critical domain size’.

### 5. NUMERICAL EXPERIMENTS: BASIC EFFECTS OBSERVED

**5.1. Single species at moving patch: extinction at critical speed.** Let us suppose that the second species is absent, so  $u_2 = 0$ . Then equation (13) for the stationary solution takes the form

$$\begin{aligned} u_{xx} + cu_x + (1 - u)u &= 0, \\ u_x - k^\pm u &= 0, \quad x = 0, L, \end{aligned} \tag{41}$$

or

$$\begin{aligned} \tilde{u}_{xx} + \left( 1 - \frac{c^2}{4} - e^{-\frac{cx}{2}} \tilde{u} \right) \tilde{u} &= 0, \\ \tilde{u}_x - \tilde{k}\tilde{u} &= 0, \quad x = 0, L. \end{aligned} \tag{42}$$

Here the index for  $u$  was omitted for brevity. For the case  $c = 0$  the detailed analysis is presented e.g., in Ludwig *et al.* (1979), including an analytically derived solution. For the case  $c \neq 0$  the equation cannot be solved analytically. Only the bounds for the solution can be obtained analytically (see Appendix). The examples of numerically calculated profiles for  $c > 0$  are shown in Fig. 1. As  $c$  approaches the speed of front propagation  $c_* = 2$ , the profile becomes more and more asymmetric, then at the right boundary there appears a domain where  $u$  almost turns to zero. For greater  $c$  values this domain expands, and finally at  $c \geq 2$  only the zero solution exists.

### 5.2. Two species at moving patch: preliminary analysis and choice of parameters.

**5.2.1. The Volterra competition model.** It is well known that important preliminary information about species competition and invasibility can be obtained from

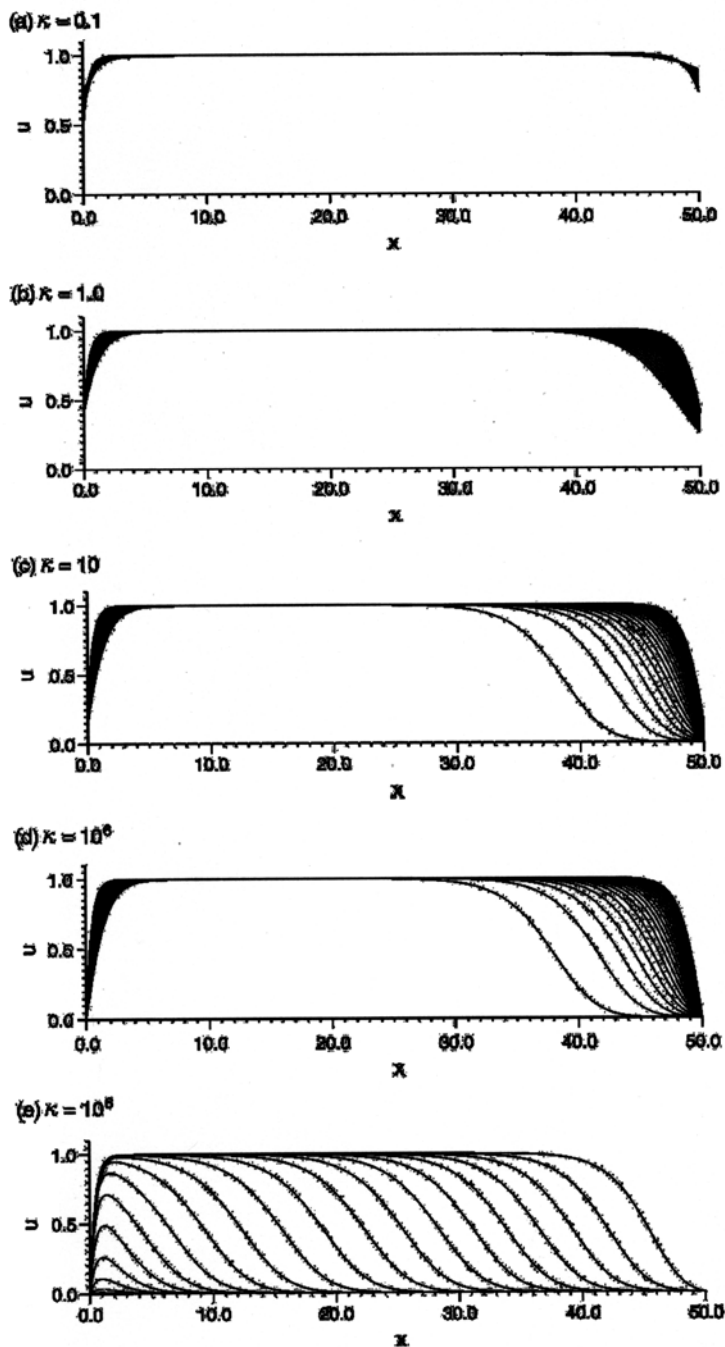


Figure 1. Stationary profiles for a single species for various  $\kappa$  and  $c$ . In panels (a)–(d)  $c = 0, 0.1, 0.2, \dots, 1.8$ . Panel (e) shows shrinking of the profile as  $c$  approaches 2.

Table 1. Outcomes of competition in Volterra model (43).

Name	$u_1, u_2$	Outcome	Conditions
A	$u_1 \rightarrow 0, u_2 \rightarrow u_{02} > 0$	2 wins	$\alpha_{21} < r, 1/\alpha_{12} < r$
B	$u_1 \rightarrow u_{01} > 0, u_2 \rightarrow u_{02} > 0$	Coexistence	$\alpha_{21} < r, 1/\alpha_{12} > r$
C	$u_1 \rightarrow u_{01} > 0, u_2 \rightarrow 0$	1 wins	$\alpha_{21} > r, 1/\alpha_{12} > r$
D	A or C, depending on $u_i(0)$	1 or 2 wins	$\alpha_{21} > r, 1/\alpha_{12} < r$

the model for spatially uniform species distribution, i.e., from equations (13) and (14) without terms containing spatial derivatives

$$\begin{aligned}\dot{u}_1 &= (1 - u_1 - \alpha_{12}u_2)u_1, \\ \dot{u}_2 &= (r - \alpha_{21}u_1 - u_2)u_2.\end{aligned}\tag{43}$$

This is the Volterra competition model, and depending on the coefficients  $\alpha$ , the asymptotic behaviour can belong to one of the four kinds, listed in Table 1. We will focus on the case where the success of invasion of a species depends upon the spatial interaction terms. Specifically, we consider case C, where the nonspatial model denies the possibility of species coexistence, and investigate the possibility of invasion by species 2 in a spatial context.

5.2.2. *The simplest accounting for the speed: the Volterra model with  $\tilde{r}$  instead of  $r$ .* In the case of a single equation with advection we have shown that the effect of advection speed  $c$  can be described by adjusting the species growth rate: using  $\tilde{r}$  instead of  $r$ . It is natural to analyse, what will happen in the Volterra model after similar substitution. Though nonrigorous, such analysis may be helpful for understanding the effects observed in numerical experiments.

Let us consider the following system

$$\begin{aligned}\dot{u}_1 &= (\tilde{r}_1 - u_1 - \alpha_{12}u_2)u_1, \\ \dot{u}_2 &= (\tilde{r}_2 - \alpha_{21}u_1 - u_2)u_2.\end{aligned}\tag{44}$$

Assuming  $0 \leq c < \min\{c_{1*}, c_{2*}\}$ , the outcome of competition in (44) depends now on the ratio

$$R(c) = \frac{r - \frac{c^2}{4D}}{1 - \frac{c^2}{4}} = r \frac{1 - \frac{c^2}{4Dr}}{1 - \frac{c^2}{4}} = r \frac{1 - (c/c_{2*})^2}{1 - (c/c_{1*})^2}\tag{45}$$

which plays the role of  $r$  in (43) and in Table 1. As we change  $c$ ,  $R$  may pass through the values  $\alpha_{21}$  and  $1/\alpha_{12}$ , which results in changing the outcome of competition. For example, for  $c = 0$  we may have case A from Table 1, then case B, and eventually case C. In other words, we may expect *speed-induced mode switching*,



and consequently switches in competitive dominance induced by different rates of climatic change.

Actual sequence of competition modes depends on three factors:

- (1) The value  $R(0) = r$ . In the mentioned example switching from A to B and C means decreasing of  $R$ . To observe the whole sequence we must have big enough  $r$ . On the other hand, if  $r$  is small there is always case C for any speed  $c$  and no mode switching.
- (2) The relation between  $c_{1*}$  and  $c_{2*}$ . For  $c_{1*} > c_{2*}$ ,  $R(c)$  is a decreasing function while for  $c_{1*} < c_{2*}$  it is an increasing one.
- (3) The relation between  $\alpha_{21}$  and  $1/\alpha_{12}$ . This determines which of the inequalities in Table 1 changes first, and hence the details of the mode switching.

Therefore, assuming  $r$  big or small enough to observe the whole sequence of modes, we come to the following four scenarios of mode switching, which we shall denote S1 to S4.

- S1:**  $c_{1*} > c_{2*}$ ,  $\alpha_{21} > 1/\alpha_{12}$ ,  $r$  corresponds to case A. For  $0 \leq c < c_{2*}$ ,  $R(c)$  decreases from  $r$  to 0 giving the sequence of competition modes  $A \rightarrow D \rightarrow C$  or  $'2' \rightarrow '1/2' \rightarrow '1'$ .
- S2:**  $c_{1*} < c_{2*}$ ,  $\alpha_{21} > 1/\alpha_{12}$ ,  $r$  corresponds to case C. For  $0 \leq c < c_{1*}$ ,  $R(c)$  increases from  $r$  to  $\infty$  through  $C \rightarrow D \rightarrow A$  or  $'1' \rightarrow '1/2' \rightarrow '2'$ .
- S3:**  $c_{1*} > c_{2*}$ ,  $\alpha_{21} < 1/\alpha_{12}$ ,  $r$  corresponds to case A. For  $0 \leq c < c_{2*}$ ,  $R(c)$  decreases from  $r$  to 0 through  $A \rightarrow B \rightarrow C$  or  $'2' \rightarrow '1+2' \rightarrow '1'$ .
- S4:**  $c_{1*} < c_{2*}$ ,  $\alpha_{21} < 1/\alpha_{12}$ ,  $r$  corresponds to case C. For  $0 \leq c < c_{1*}$ ,  $R(c)$  increases from  $r$  to  $\infty$  through  $C \rightarrow B \rightarrow A$  or  $'1' \rightarrow '1+2' \rightarrow '2'$ .

Since the model (44) is only an approximation, these scenarios are not by any means rigorous predictions, they may be used only as a guidance helping to understand numerical data, presented below.

**5.3. Numerical data: comparison with conjectures.** Numerical experiments were performed for the system (22)–(25). The parameters  $r$  and  $\alpha_{ij}$  of the equations we have chosen are such that in the Volterra model (43) there is case C: the second species goes extinct and the first one persists for any initial data where the second species is nonzero. This choice allows us to detect new effects that can be related with the patch motion and spatial distribution.

During the calculations we set up nonzero initial data for both species, allowed all transitions to decay and then analysed the resulting stationary profiles. This procedure has been performed for  $c$  from 0 to  $\max\{c_{1*}, c_{2*}\}$ . Some results are presented in Figs. 2–4. The values of  $u_i(x)$  for every  $c$  are shown by the shades of grey: from 0 (white) to maximal  $u_{i \max}$  (black).

We cannot physically present all the results, instead we shall describe the main effects observed. We focus on what seems to be the most important observation, the role of the ratio  $L_{2*}/L_{1*}$  and the four scenarios of the previous section.

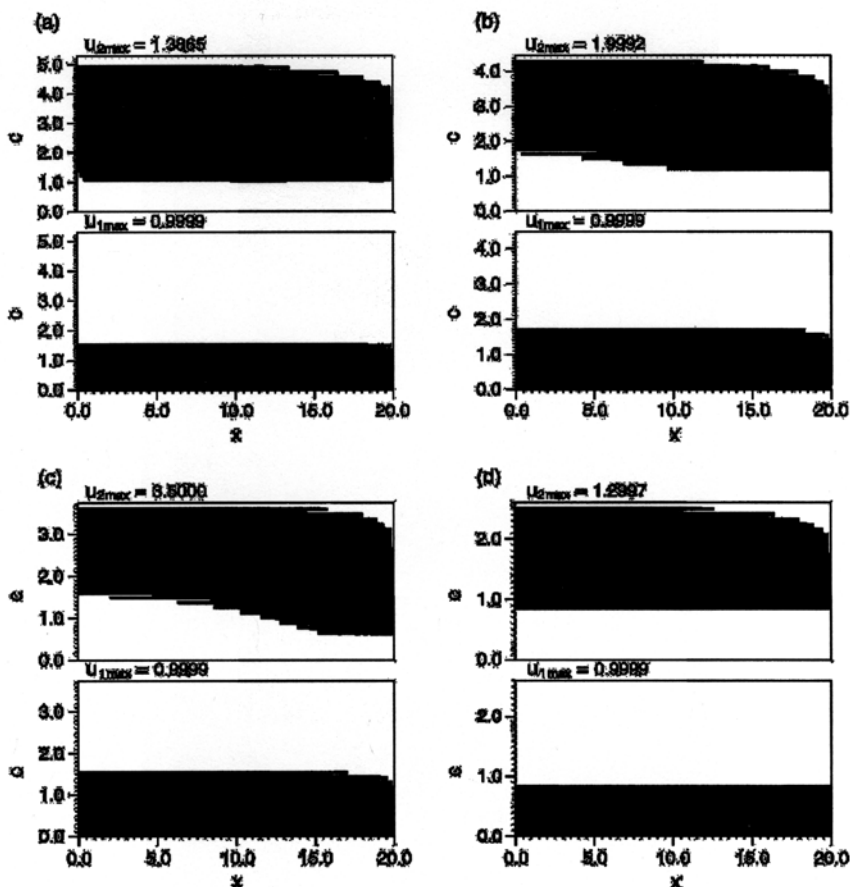


Figure 2. Dependence of stationary profiles  $u_i(x)$  on the patch speed  $c$ . Grey shade shows the value of  $u$  from 0 (white) to  $u_{\max}$  (black, the value shown above the plot). Shown are examples of good agreement with predictions of S1–S4 scenarios. Note that in all cases  $L_{2^*}/L_{1^*} > 1$ . Parameters  $\kappa = 1$ ,  $L = 20.00$ , (a)  $D = 5.00$ ,  $r = 1.40$ ,  $\alpha_{12} = 0.30$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 2.65$ ,  $L_{2^*}/L_{1^*} = 1.89$ , Predicted scenario:  $1 \rightarrow 1 + 2 \rightarrow 2$ ; (b)  $D = 2.50$ ,  $r = 2.00$ ,  $\alpha_{12} = 0.10$ ,  $\alpha_{21} = 3.00$ ,  $c_2/c_1 = 2.24$ ,  $L_{2^*}/L_{1^*} = 1.12$ , Scenario:  $1 \rightarrow 1 + 2 \rightarrow 2$ ; (c)  $D = 1.00$ ,  $r = 3.50$ ,  $\alpha_{12} = 0.10$ ,  $\alpha_{21} = 5.00$ ,  $c_2/c_1 = 1.87$ ,  $L_{2^*}/L_{1^*} = 0.53$ , Scenario:  $1 \rightarrow 1 + 2 \rightarrow 2$ ; (d)  $D = 1.30$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 1.30$ ,  $L_{2^*}/L_{1^*} = 1.00$ , Scenario:  $1 \rightarrow 1/2 \rightarrow 2$ .

- For  $L_{2^*}/L_{1^*} > 1$  usually the numerical results correspond to the predictions of the scenarios S1–S4, Fig. 2.
- Scenarios S1, S2 correspond to abrupt replacement of the species; scenarios S3, S4 give soft replacement—there is a range of  $c$  values for which species coexist.
- For  $L_{2^*}/L_{1^*} < 1$  usually the outcome of the experiments was essentially different from those predictions, Figs. 3 and 4.

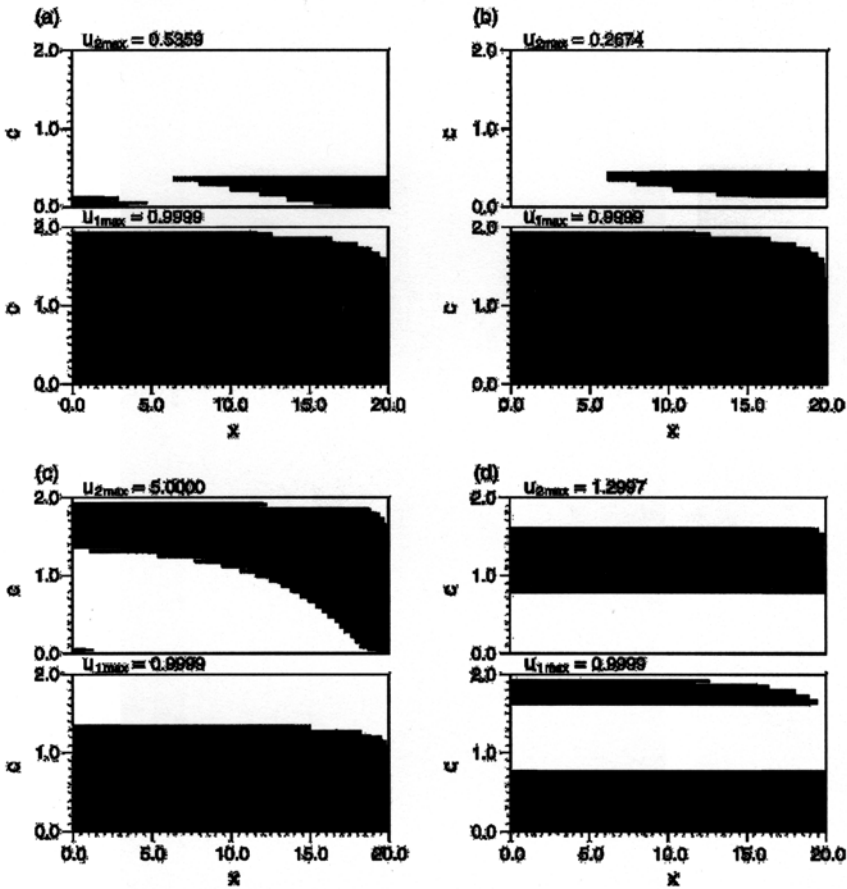


Figure 3. Examples of bad agreement with predicted scenarios—in all cases predicted is extinction of species 2 and existence of species 1 for the shown range of  $c$  values. Instead the species 2 sometimes appear at the boundary [Panels (a)–(c)] and in some cases even out-competes species 1 and occupies the whole patch [Panels (c) and (d)]. Note that in all cases  $L_{2^*}/L_{1^*} < 1$ . Parameters  $\kappa = 1$ ,  $L = 20.00$ , (a)  $D = 0.14$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.43$ ,  $L_{2^*}/L_{1^*} = 0.33$ ; (b)  $D = 0.26$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.58$ ,  $L_{2^*}/L_{1^*} = 0.45$ ; (c)  $D = 0.20$ ,  $r = 5.00$ ,  $\alpha_{12} = 0.10$ ,  $\alpha_{21} = 7.00$ ,  $c_2/c_1 = 1.00$ ,  $L_{2^*}/L_{1^*} = 0.20$ ; (d)  $D = 0.70$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.95$ ,  $L_{2^*}/L_{1^*} = 0.73$ .

There are two basic effects observed mainly for  $L_{2^*}/L_{1^*} < 1$ . (i) Species 2 instead of going extinct, occupies part of the patch near one or both edges, Figs. 3(a)–3(c) and 4(d). Most pronounced this effect is for nonzero  $c$ , though sometimes it can be found for  $c = 0$ . (ii) Species 2 not only survives near the boundary, but occupies the whole domain and replaces species 1, Figs. 3(d) and 4(a)–4(c). We observed this effect only for nonzero patch speed.

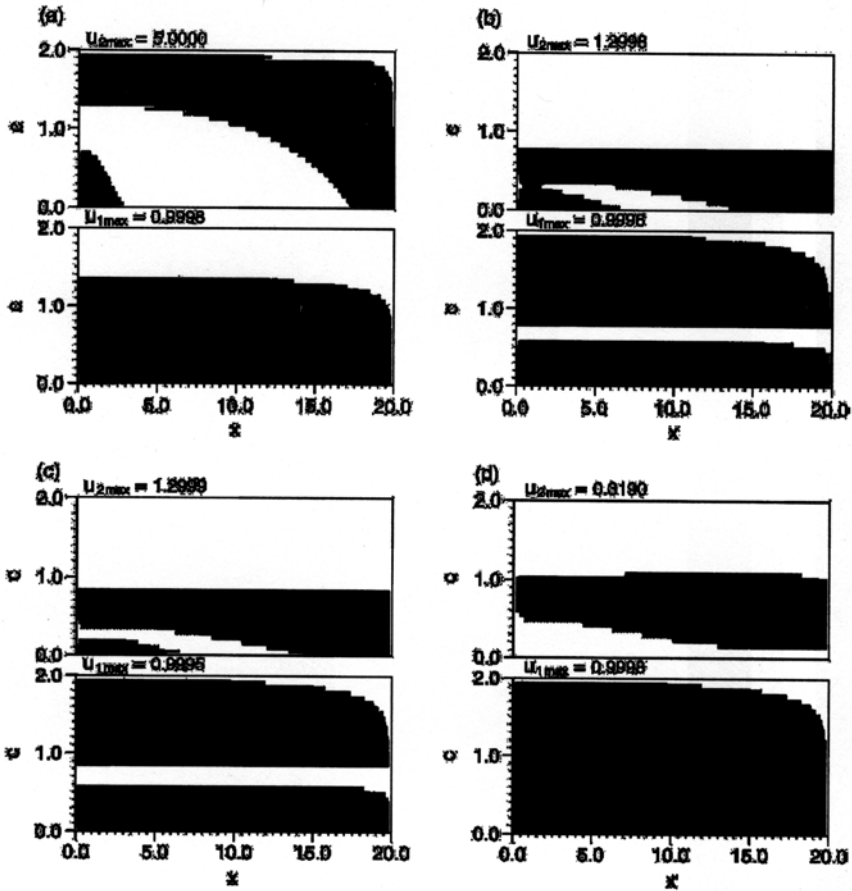


Figure 4. Examples of bad agreement with predicted scenarios—in all cases predicted is extinction of species 2 and existence of species 1 for the shown range of  $c$  values. Instead the species 2 sometimes appear at the boundary (all panels) and in some cases even outcompetes species 1 and occupies the whole patch [Panels (b) and (c)]. Note that in all cases  $L_{2^*}/L_{1^*} < 1$ . Parameters  $\kappa = 10^6$ ,  $L = 20.00$ , (a)  $D = 0.20$ ,  $r = 5.00$ ,  $\alpha_{12} = 0.10$ ,  $\alpha_{21} = 7.00$ ,  $c_2/c_1 = 1.00$ ,  $L_{2^*}/L_{1^*} = 0.20$ ; (b)  $D = 0.26$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.58$ ,  $L_{2^*}/L_{1^*} = 0.45$ ; (c)  $D = 0.30$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.70$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.62$ ,  $L_{2^*}/L_{1^*} = 0.48$ ; (d)  $D = 0.50$ ,  $r = 1.30$ ,  $\alpha_{12} = 0.50$ ,  $\alpha_{21} = 1.50$ ,  $c_2/c_1 = 0.81$ ,  $L_{2^*}/L_{1^*} = 0.62$ .

## 6. INVASION ANALYSIS AND BASIC EFFECTS

Let us suppose that species 1 has established and the corresponding stationary profile  $u_1 = u(x)$  is formed. After that we introduce a small amount of the second species. Will it go extinct or survive and grow? What will be the two-species stationary profile?

**6.1. The problem of invasion.** The invasion problem is well known, and is considered, for example, in Shigesada and Kawasaki (1997). To solve it, one must evaluate the stability of the solution  $u_1 = u(x)$ ,  $u_2 = 0$  for the system (22)–(25). Substitutions of  $\delta u_1 e^{\lambda t} = u_1 - u(x)$ ,  $\delta u_2 e^{\lambda t} = u_2$ ,  $|\delta u_i| \ll 1$  lead to the linearized problem

$$D\delta u_{2xx} + c\delta u_{2x} + (r - \alpha_{21}u)\delta u_2 = \lambda\delta u_2 \tag{46}$$

$$\delta u_{2x} - k_2^+ \delta u_2 = 0, \quad x = 0,$$

$$\delta u_{2x} - k_2^- \delta u_2 = 0, \quad x = L.$$

Applying the change of variables  $\delta u_2 = \exp(-\frac{cx}{2D})v$  transforms this system to

$$Dv_{xx} + \left( r - \frac{c^2}{4D} - \alpha_{21}u \right) v = \lambda v \tag{47}$$

$$v_x - \tilde{k}_2^+ v = 0, \quad x = 0,$$

$$v_x - \tilde{k}_2^- v = 0, \quad x = L,$$

where  $u(x)$  is the solution of

$$u_{xx} + cu_x + (1 - u)u = 0.$$

$$u_x - k_1^+ u = 0, \quad x = 0,$$

$$u_x - k_1^- u = 0, \quad x = L.$$

If the greatest eigenvalue is positive then invasion by the second species is possible, if it is negative, the second species cannot invade.

Similarly, the conditions for the invasion of the first species when the second one has established, are determined by another eigenvalue problem

$$v_{xx} + \left( 1 - \frac{c^2}{4} - \alpha_{12}u \right) v = \lambda v \tag{48}$$

$$v_x - \tilde{k}_1^+ v = 0, \quad x = 0,$$

$$v_x - \tilde{k}_1^- v = 0, \quad x = L.$$

$$Du_{xx} + cu_x + (r - u)u = 0$$

$$u_x - k_2^+ u = 0, \quad x = 0,$$

$$u_x - k_2^- u = 0, \quad x = L.$$

Numerical calculations show that the invasibility essentially depends on the ratio of characteristic lengths of the species  $L_{2*}/L_{1*}$ . The importance of this ratio is shown by the following theorems.

**6.2. Noninvasion and coexistence theorems for the case with a stationary hostile boundary ( $c = 0, \kappa \rightarrow \infty$ ).**

6.2.1. *Equations in stationary case.* This section can be considered as a sequel or complementary to the analysis in Cantrell *et al.* (1998). We shall consider the same questions—which species wins the competition, which is going to be extinct, and which can invade the habitat occupied by the other? However we shall primarily analyse how the situation depends on  $D$  and  $r$  rather than boundary conditions. For the sake of simplicity we shall consider the system with  $c = 0$  and a completely hostile environment

$$\begin{aligned} u_{1t} &= u_{1xx} + (1 - u_1 - \alpha_{12}u_2)u_1, \\ u_{2t} &= Du_{2xx} + (r - \alpha_{21}u_1 - u_2)u_2, \\ u_i &= 0, x = 0, L. \end{aligned} \tag{49}$$

The systems (47) and (48) now take the form

$$\begin{aligned} Dv_{xx} + (r - \alpha_{21}u_1)v &= \lambda v, \\ u_{1xx} + (1 - u_1)u_1 &= 0, \\ u_1, v &= 0, x = 0, L, \end{aligned} \tag{50}$$

and

$$\begin{aligned} v_{xx} + (1 - \alpha_{12}u_2)v &= \lambda v, \\ Du_{2xx} + (r - u_2)u_2 &= 0, \\ u_2, v &= 0, x = 0, L. \end{aligned} \tag{51}$$

In the proofs of the theorems we shall use the following theorems from Smoller (1994) and Cantrell *et al.* (1998):

(T1) Upper and lower solutions. Let  $u$  be a solution of  $Du_{xx} + F(u, x) = 0, x \in \Omega, u|_{\partial\Omega} = h(x)$ . If  $v$  satisfy  $Dv_{xx} + F(v, x) \leq 0, v|_{\partial\Omega} \geq h(x)$ , then  $v \geq u$  in  $\Omega$  and is called an upper solution. If  $v$  satisfy  $Dv_{xx} + F(v, x) \geq 0, v|_{\partial\Omega} \leq h(x)$ , then  $v \leq u$  in  $\Omega$  and is called a lower solution. This is the consequence of maximum principle and comparison theorems for elliptic and parabolic differential equations.

(T2) The dominant eigenvalue  $\lambda_{\max}$  of a problem  $Dv_{xx} - k(x)v = \lambda v, x \in [0, L], v|_{0,L} = 0$  is a continuous and decreasing function of  $k(x)$ , that is if  $k_1 > k_2, \lambda_{\max 1} < \lambda_{\max 2}$ .

The first result is given by the following theorem.

6.2.2. Noninvasion theorem.

**THEOREM 6.1** (Noninvasion of species with longer characteristic length in stationary environment). *Let  $c = 0$ ,  $\kappa = \infty$  (Dirichlet boundary conditions). Consider the case C in the Volterra model (1st species wins), and  $L_{2*} > L_{1*}$ . Suppose that species 1 has established and reached its stationary distribution  $u_1(x)$ , then species 2 cannot invade.*

*Proof.* Let us consider stationary distributions of both species in the absence of the other,  $u_1$  and  $u_2$ . They satisfy the equations

$$u_{1xx} + (1 - u_1)u_1 = 0, \tag{52}$$

$$Du_{2xx} + (r - u_2)u_2 = 0, \tag{53}$$

with the boundary conditions  $u_i = 0, x = 0, L$ . Note that  $0 < u_1 < 1$  for  $0 < x < L$  and hence  $(1 - u_1)u_1 > 0$ . Let us show that  $ru_1 > u_2$  with the help of the theorem (T1). Substituting  $ru_1$  into the second equation we have

$$\begin{aligned} Dru_{1xx} + (r - ru_1)ru_1 &= (r - ru_1)ru_1 - Dr(1 - u_1)u_1 \\ &= -r^2 \left( \frac{D}{r} - 1 \right) (1 - u_1)u_1 < 0 \end{aligned} \tag{54}$$

provided

$$\frac{D}{r} = \left( \frac{L_{2*}}{L_{1*}} \right)^2 > 1. \tag{55}$$

By assumption this condition holds, hence  $ru_1$  is the upper solution for  $u_2$  and hence  $ru_1 \geq u_2$ .

Now let us consider two eigenvalue problems

$$Dv_{xx} + (r - u_2)v = \mu v, \tag{56}$$

$$Dv_{xx} + (r - \alpha_{21}u_1)v = \lambda v, \tag{57}$$

$$v(0) = v(L) = 0, \quad x = 0, L.$$

We are interested in the dominant eigenvalues  $\lambda_{\max}$  and  $\mu_{\max}$  and the corresponding eigenvectors. Since  $\alpha_{21} > r$  (case C),  $\alpha_{21}u_1 \geq u_2$  and hence  $\lambda_{\max} \leq \mu_{\max}$  (Smoller, 1994; Cantrell *et al.*, 1998). In case  $\mu = 0$  we know one of the solutions of (56): if we substitute  $v = u_2$  it turns into (52) for which  $u_2$  is a solution. This means that  $v = u_2$  is an eigenfunction corresponding to the eigenvalue  $\mu = 0$ . Since  $u_2 > 0$ , this is the dominant eigenvalue,  $\mu_{\max} = 0$ , and we can conclude that  $\lambda_{\max} \leq 0$ . Therefore the population of the second species cannot grow in the presence of the established population of the first one.  $\square$

**NOTE 1.** The theorem can be extended to the case of more general boundary conditions if the ‘hostility parameters’  $\kappa$  outside the patch are proportional to the diffusion coefficients, that is  $\kappa_1/\kappa_2 = D_1/D_2$ . In the case  $c = 0$  this implies  $k_1 = k_2$ , that is  $u_{01}$  and  $u_{02}$  satisfy the same boundary conditions. This allows to extend the proof to the case of finite  $\kappa_i/D_i$ . For the same  $\kappa$  for both species the proof encounters problems at the boundary: to ensure that  $u_{01}$  is an upper solution we need to impose condition  $D < 1$  (to make  $k_2 > k_1$ ), and this restricts applicability of the theorem to the not very interesting case of small  $r$ , such that  $D/r$  is still greater than 1.

**NOTE 2.** If parameters correspond to the case *A* of the Volterra model (second species wins) and  $L_{2*} < L_{1*}$  then, after interchanging the species  $1 \leftrightarrow 2$  the theorem states that the first species cannot invade if there exists an established population of the second one.

6.2.3. *Coexistence theorem.* The noninvasion theorem is based upon the observation that under certain conditions the second species cannot grow in the presence of the established population of the first one. Now suppose there is another situation: both species can grow in the presence of the established population of the other, in other words, both 1-species solutions  $u_1 = u_1(x), u_2 = 0$  and  $u_1 = 0, u_2 = u_2(x)$  are unstable. Then we can conclude that the steady state of the system must be a coexistence of both species. This is the idea of the coexistence theorem.

Recall that we are again considering parameter values corresponding to the case C:  $\alpha_{12}r < 1, \alpha_{21} > r$ . Here, invasibility of the first species depends on the principal eigenvalue of the problem (51). It can be shown that  $u_2 \leq r$  (Smoller, 1994), therefore  $\alpha_{12}u_2 < \alpha_{12}r < 1$ . Let us consider the eigenvalue problem

$$v_{xx} + (1 - \alpha_{12}r)v = \mu v, \quad v(0) = v(L) = 0. \tag{58}$$

According to (T2),  $\lambda_{\max} > \mu_{\max}$ , therefore if  $\mu_{\max} > 0$ ,  $\lambda_{\max}$  is also positive. The value of  $\mu_{\max}$  can be found explicitly, this gives the condition

$$\mu_{\max} = 1 - \alpha_{12}r - \left(\frac{\pi}{L}\right)^2 > 0$$

or

$$L > \frac{\pi}{\sqrt{1 - \alpha_{12}r}}. \tag{59}$$

This gives the proof for the following lemma for the invasion of the second species by the first species.

**LEMMA 6.1.** *Consider the case C in the Volterra model. If (59) holds, species 1 can grow in the presence of species 2.*



Invasion of the second species into the first species depends on the principal eigenvalue of the problem (50). Here we cannot just use the estimate  $u_1 < 1$  since it always gives a negative estimate for  $\lambda_{\max}$ .

In the Appendix it is shown that  $u_1(x) \leq u_A(x)$  (A.2), where, for  $c = 0$  and  $k = \infty$

$$u_A(x) = 1 - \frac{1}{1 + e^{-L}} (e^{(x-L)} + e^{-x}) = 1 - \frac{\cosh(x - \frac{L}{2})}{\cosh(\frac{L}{2})}.$$

Substitution of  $u_A$  into (50) gives a Mathieu equation, for which there are no good estimates of  $\lambda$ . For this reason we shall use another estimate which brings more analytical possibilities. Note that  $u_A$  is concave upwards and hence lies below its tangent, in particular the tangent at  $x = 0$ , hence

$$u_1(x) \leq u_A(x) = 1 - \frac{\cosh(\frac{2x-L}{2})}{\cosh(\frac{L}{2})} \leq x \frac{\sinh(\frac{L}{2})}{\cosh(\frac{L}{2})} \leq x. \tag{60}$$

Let us consider the eigenvalue problem

$$Dv_{xx} + (r - \alpha_{21}x)v = \mu v, \tag{61}$$

$$v(0) = v(L) = 0.$$

According to (60) and (T2),  $\lambda_{\max} > \mu_{\max}$ . If, for certain  $D, r$ , and  $\alpha_{21}$ , this problem has  $\mu_{\max} = 0$ , then  $\lambda_{\max} > 0$  and the second species can invade. It is convenient to fix  $D$  and  $\alpha_{21}$  and vary  $r$ . The value of  $\mu_{\max} = 0$  corresponds to some  $r = r_0$ . To find  $r_0$  we need to find conditions under which there is a positive solution of (61) with  $\mu = 0$ . Let us use the change of variable

$$x = \left(\frac{D}{\alpha_{21}}\right)^{1/3} z + \frac{r}{\alpha_{21}},$$

to transform (61) with  $\mu = 0$  to

$$v_{zz} - zv = 0, \tag{62}$$

$$v(z_1) = v(z_2) = 0, \tag{63}$$

$$z_1 = -\frac{r}{\alpha_{21}^{2/3} D^{1/3}}, \quad z_2 = \left(\frac{\alpha_{21}}{D}\right)^{1/3} L + z_1. \tag{64}$$

A general solution to this equation can be expressed through the Airy functions,  $Ai(z)$  and  $Bi(z)$  (Abramowitz and Stegun, 1965),  $v(z) = aAi(z) - bBi(z)$ . For  $z < 0$  both of these functions behave like trigonometric ones; in particular they

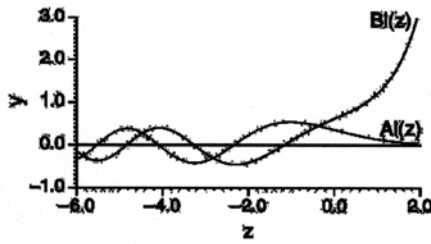


Figure 5. Appearance of the Airy functions.

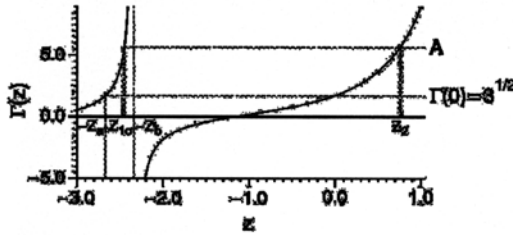


Figure 6. For every  $z_2 > 0$  there is a value of  $z_1 \in (-z_a, -z_b)$  satisfying  $\Gamma(z_1) = \Gamma(z_2)$  where  $\Gamma(z) = \text{Bi}(z)/\text{Ai}(z)$ . The number  $-z_a$  satisfies  $\Gamma(-z_a) = \Gamma(0) = \sqrt{3}$  and the number  $-z_b$  is a vertical asymptote for  $\Gamma$  ( $\text{Ai}(-z_b) = 0$ ). Their values are  $-z_a \approx -2.67$  and  $-z_b \approx -2.34$ .

have an infinite number of zeros and  $|\text{Ai}(z)| < 1, |\text{Bi}(z)| < 1$  (Fig. 5). For  $z > 0$  they behave like exponential functions, and for  $z$  large there are asymptotic formulas

$$\text{Ai}(z) \approx \frac{1}{2\sqrt{\pi z^{1/4}}} e^{-\zeta}, \quad \text{Bi}(z) \approx \frac{1}{\sqrt{\pi z^{1/4}}} e^{\zeta}, \quad \zeta = \frac{2}{3}z^{3/2}.$$

We consider case C in the Volterra model (1st species wins and hence  $r < \alpha_{21}, \alpha_{12}r < 1$ ) and assume that both species can survive in the absence of the other (the domain length exceeds  $L_{1*} = \pi$  and  $L_{2*} = \pi\sqrt{D/r}$ ). Thus

$$z_2 = \left(\frac{\alpha_{21}}{D}\right)^{1/3} L + z_1 = \left(\frac{\alpha_{21}}{D}\right)^{1/3} \left(L - \frac{r}{\alpha_{21}}\right) > \left(\frac{\alpha_{21}}{D}\right)^{1/3} (\pi - 1) > 0. \quad (65)$$

The solution to (62) and (63) satisfies

$$\Gamma(z_1) = \Gamma(z_2) = A \quad (66)$$

where  $\Gamma(z) = \text{Bi}(z)/\text{Ai}(z)$  and  $A = a/b$  constant. It is straightforward to show that for each  $z_2 > 0$  there exists a critical value  $z_{1c}$  of  $z_1 \in (-z_a, -z_b)$  which satisfies (66), where  $z_a \approx 2.67$  and  $z_b \approx 2.34$  (Fig. 6). This gives a critical growth rate for the second species,  $r$ , which satisfies  $z_1 = z_{1c}$  so when

$$r = r_c = z_{1c} \alpha_{21}^{2/3} D^{1/3} \quad (67)$$

$\mu_{\max} = 0$  and hence  $\lambda_{\max} > 0$  and the second species can invade. As can be seen from Fig. 6,  $z_{1c}$  is a decreasing function of  $z_2$  and hence, using (64) and (67) we observe that  $r_c$  is a decreasing function of the domain size  $L$ .

For equation (61) we observe that  $\mu$  is an increasing function of  $r$ . Hence the second species can invade for any

$$r \geq r_a = z_a \alpha_{21}^{2/3} D^{1/3}, \quad z_a = 2.67. \tag{68}$$

Substituting  $D = \left(\frac{L_{2*}}{L_{1*}}\right)^2 r$ , this relation can be rewritten as

$$r^2 \geq z_a^3 \alpha_{21}^2 \left(\frac{L_{2*}}{L_{1*}}\right)^2$$

or

$$\frac{L_{2*}}{L_{1*}} \leq z_a^{-3/2} \frac{r}{\alpha_{21}}, \quad z_a^{-3/2} \approx 0.22, \quad \alpha_{21} > r, \quad \alpha_{12} r < 1. \tag{69}$$

This proves the second lemma.

**LEMMA 6.2.** Consider the case C in the Volterra model and assume  $L > \max\{\pi, \pi\sqrt{D/r}\}$ . If (69) holds, species 2 can grow in the presence of species 1.

Combining both lemmas, we obtain

**THEOREM 6.2 (Coexistence).** Let  $c = 0, \kappa = \infty$ . Consider the case C in the Volterra model. If

$$L > \max\left\{\frac{\pi}{\sqrt{1 - \alpha_{12}r}}, \pi\sqrt{\frac{D}{r}}\right\}, \quad \frac{L_{2*}}{L_{1*}} \leq 0.22 \frac{r}{\alpha_{21}}$$

both species can coexist in the domain.

**NOTE 1.** The appearance of the Airy functions suggests the form of coexistence, Fig. 5. Near the boundary  $Ai(z)$  looks qualitatively similar to the  $xe^{-x}$  function—it goes to zero at the boundary and in the centre of the domain. Therefore the species which is to be extinct according to the Volterra model instead settles near the boundary in the layer of size  $\sim L_{2*}$ , where  $Ai(z)$  is essentially nonzero, while the other species occupies the rest of the patch. Examples of the described coexistence are shown in Fig. 7.

**NOTE 2.** Due to the symmetry of the problem, sufficient conditions for coexistence can be obtained for case A of the Volterra model ( $\alpha_{21} < r, \alpha_{12}r > 1$ ) in the same way.

**6.3. Biological view of edge effects: habitat inhomogeneity as a new opportunity for species.** How biologically important is spatial distribution? The simplest generalization of (43) with accounting for spatial inhomogeneity is a compartment model, where there are several habitats with spatially uniform species distribution, and there is a flow from one habitat into another proportional to the difference in

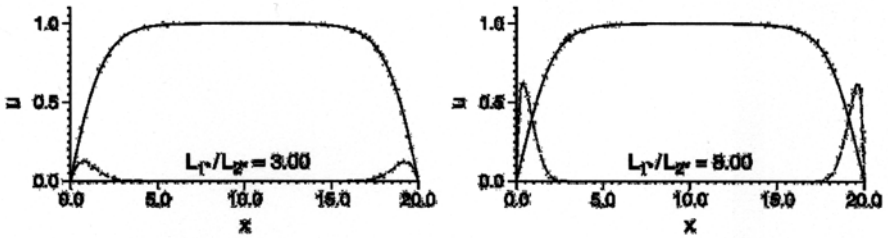


Figure 7. Examples of boundary coexistence for  $L_{2*} < L_{1*}$ . Solid line—species 1, dashed—species 2.

individual densities. This model has been analysed [e.g., in Levin (1974)], and the main conclusion was that the species that cannot share the same homogeneous habitat can use the separation in space: they cannot coexist in the same compartment, but can occupy different neighbouring ones.

The compartmental approach implies spatial inhomogeneity of the habitat, some sort of patchiness, and the patch boundaries cannot be set arbitrarily, they should reflect changes in permeability or local carrying capacity. In other words, inhomogeneity of habitat creates opportunities for species coexistence and invasion. This idea has been stressed in a number of publications [e.g., Fagan *et al.* (1999), Shigesada and Kawasaki (1997), Cantrell *et al.* (1998)]. It has been shown that conditions at the habitat boundary can change and even reverse the outcome of competition compared to the prediction of the homogeneous model.

We would like to stress one feature of habitat edges more clearly: *under certain conditions the habitat edge serves to help the invading species*. The origin of the effect can be explained in rather simple terms as follows. As we have mentioned, each species has a characteristic length  $L_{i*}$ . Besides showing the minimal patch size where the species can exist, it also characterizes the size of the area where the species distribution 'feels' the presence of the edge. If two species have different characteristic lengths, say,  $L_{1*} > L_{2*}$ , and the habitat size is big compared to  $L_{i*}$ , then there is a domain where the population of species 1 is disturbed by the edge while that of species 2 almost does not feel it. If the ratio of intrinsic growth rates  $r = r_2/r_1$  is big enough, then species 2 has a good chance to survive in this domain. Instead of extinction species 2 retreats to a ring surrounding the habitat of species 1. If on the other hand,  $L_{1*} < L_{2*}$ , then spatial inhomogeneity is not of any help for species 2, and the outcome of competition can be predicted by the Volterra model.

#### 6.4. Edge effects and competition in the general case $c \neq 0$ , $\kappa \leq \infty$ . Boundary coexistence and replacement front reversal.

6.4.1. *Boundary coexistence.* In general case where  $c \neq 0$  and  $\kappa < \infty$  the theoretical analysis becomes much harder. It is possible to develop an approximate

analysis for the invasion of the second species assuming the other one  $u(x)$  to be established. Like in the previous section it is possible to approximate  $u(x)$  near the boundary by a linear function  $u(x) \approx u_{B0} + u_{B1}x$ , then to get the eigenvalue problem with the solutions, which again can be expressed through the Airy functions. The estimates for  $u_{Bi}$  from above and below can be obtained (see Appendix), but they are not accurate enough to give practically useful results. For this reason we shall only make some remarks.

As with chemostat flow (Smith and Waltman, 1995), for the moving patch there is the effect of 'washing out' the species, which changes the shape of the profile for the established species near the boundary (Fig. 1). At the in-flow boundary (right for  $c > 0$ , left for  $c < 0$ ) the profile  $u(x)$  becomes less steep and slowly retreats as  $|c|$  increases. This may enhance the opportunity for the second species to invade. At the out-flow boundary the profile of  $u(x)$  becomes more steep, and so invasion becomes harder.

On the other hand, the invading species also suffers from the washing out effects, which may prevent invasion. So we have a combination of a number of different factors, and in different cases they can produce different patterns, see Figs. 2–4. The only general result is that the quotient  $L_{2*}/L_{1*}$  remains an important classifying feature: we observed boundary coexistence for  $c > 0$  only when it was less than 1, even if in the case  $c = 0$  there were no coexistence.

However, for  $c > 0$  numerics showed one more effect, which has no analogue in the case  $c = 0$  — replacement of the dominant species, sometimes with another replacement at greater speed.

**6.4.2. Invasion front reversal.** Let us consider the following problem. Suppose that in the infinite homogeneous domain there is a barrier, and on the left of it there is an established population of species 1, while on the right—that of species 2. Let there be no advection, and the species parameters correspond to the case C of the Volterra model ( $r\alpha_{12} < 1$ ,  $\alpha_{21} > r$ , species 1 wins in the competition). At some moment the barrier between species disappears, and after some relatively short transition time a wave of species replacement will form. Species 1 propagates to the right and replaces species 2, while the latter retreats. This problem has been thoroughly studied in Lewis *et al.* (2002), and it has been shown that if parameters of the model satisfy two inequalities,

$$D < 2, \quad \alpha_{12}\alpha_{21} - 1 < (r^{-1} - \alpha_{12})(2 - D), \quad (70)$$

then the speed of the invasion front is equal to

$$c_F = c_{1*}\sqrt{1 - r\alpha_{12}} = 2\sqrt{1 - r\alpha_{12}}. \quad (71)$$

If the inequalities are not satisfied, the front speed can be greater than this value.

We now return back to the model with advection. If the speed of advection  $c < c_F$ , in the moving system we shall observe the front moving in the same direction with speed  $c_{F1} = c_F - c$ . But if  $c > c_F$ , in the moving system we shall see a qualitatively different situation: the front moving on the left, that is species 2 becomes the winner in the competition!

If the domain is finite, but long enough, this effect can be observed in numerical experiments, when appropriate initial data are set. Note that in this case the problem is not isotropic: if the population of species 2 has been created at the in-flow boundary (right for  $c > 0$ ), then species 2 can successfully propagate to the left and make species 1 extinct, Fig. 8. If on the other hand the population of species 2 is created at the out-flow end, it will quickly become extinct itself, Fig. 9.

Now suppose that species 2 can grow near the boundary up to big enough values. Then the initial conditions for the propagating front may be satisfied, and hence instead of quiet coexistence near the boundary species 2 may become dominant and take over the whole habitat.

In numerical calculations we observed this effect a number of times. Examples can be seen in Figs. 3 and 4. Usually this occurs for the value of  $c$  close to the estimate (71), which suggests that the explanation for the effect is correct.

The profiles for single species (Fig. 1) show that as  $c$  grows, the right (in-flow) edge of the profile becomes less and less steep, which makes invasion simpler. Therefore the possibility of successful invasion should be different for in-flow and out-flow edges.

Numerical experiments confirm this assumption and show the resonant character of such an invasion, Figs. 8 and 9. A small perturbation at the in-flow edge grows and occupies all the domain, while the pre-existing species becomes extinct. At the same time a much bigger perturbation at the other edge quickly dies out.

## 7. SUMMARY AND CONCLUSIONS

**7.1. Mathematical conclusions.** This paper contains a number of rigorous results: (i) proof of equivalence of stationary solutions stability for the problem in unbounded domains and the corresponding boundary value problem; (ii) the noninvasion and coexistence theorems; (iii) the estimates for stationary solutions presented in the Appendix. The first result gives an efficient instrument for numerical studies of stationary solutions and invasibility. The others may be useful for theoretical analysis of invasion problems.

**7.2. Ecological conclusions.** The model described in this paper predicts some new effects:

1. Habitat motion decreases effective growth rates and increases critical length scales for species persistence.
2. Coexistence through edge effects becomes more typical as  $c$  increases.

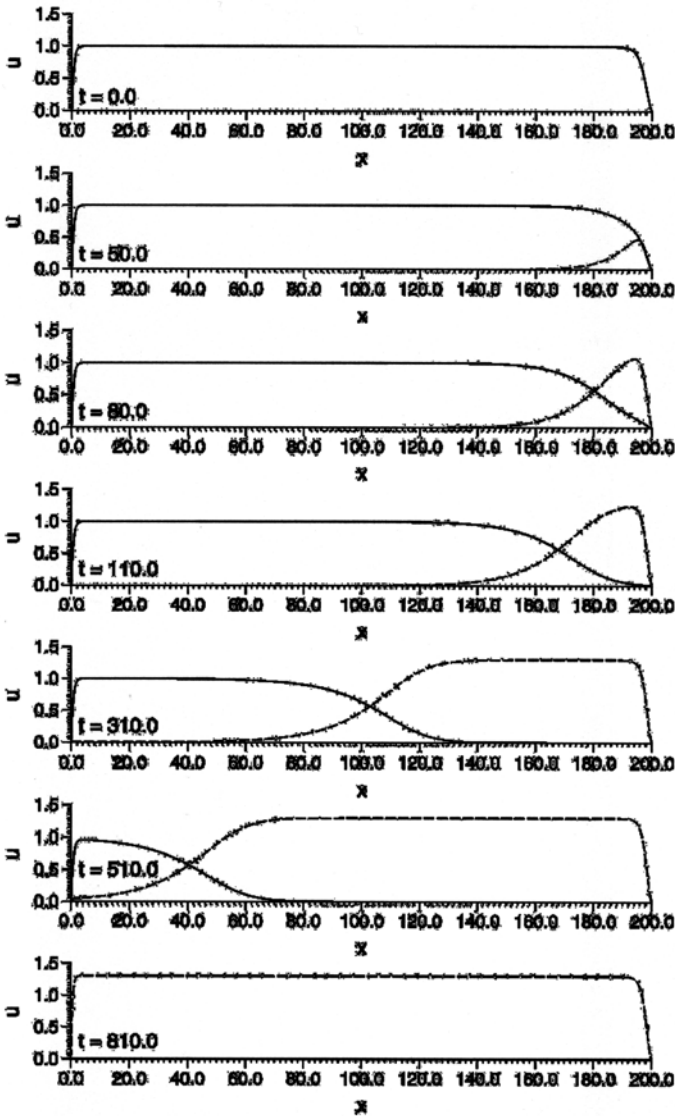


Figure 8. Invasion of a very small amount of the species 2 (dashed line) at the propagating (in-flow) boundary leads first to boundary coexistence, then turns into a moving front and then replacement of the dominant species 1 (solid line). Parameters  $\kappa = 10^6$ ,  $D = 0.7$ ,  $r = 1.3$ ,  $\alpha_{12} = 0.7$ ,  $\alpha_{21} = 1.5$ ,  $L = 20$ ,  $c = 1$ .

- Habitat motion may result in reversal of the invasion process: weaker invaders may become successful if introduced at the in-flow boundary.

From our point of view the most interesting ecological effect described in our work is boundary coexistence. Patch motion enhances it and makes it a primary

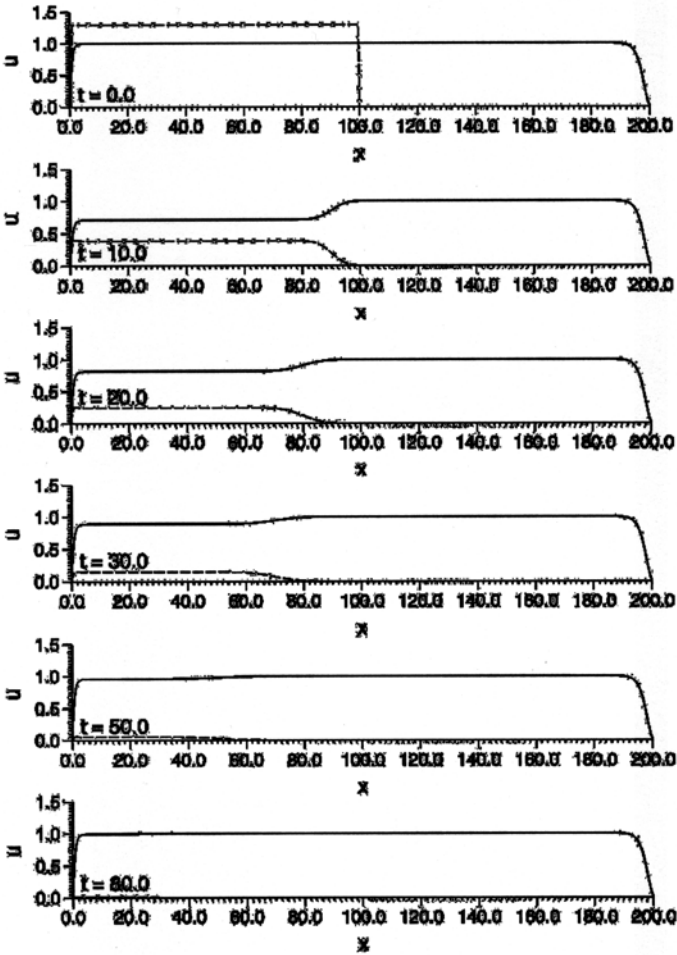


Figure 9. Resonant character of the speed-induced invasion. Compared to the previous figure, much bigger initial invasion of the species 2 at the other edge dies out very quickly to zero.

mechanism for invasion of new species. We would like to note that we present rather simple criteria, when one can expect that the boundary coexistence may take place.

**7.3. Applications to global change.** According to the literature, now the average speed of habitats motion is about  $c \approx 600$  m/year (Parmesan and Yohe, 2003). On the other hand it is known that for some species  $c_* \approx 1\text{--}3$  km/year. Therefore we may expect:

1. Extinction of species with small dispersal speed  $c_*$  (small  $Dr$ ) and big critical domain size (big  $D/r$ ).



2. Invasion of new species, especially at the poleward habitat edges.
3. Replacement of some species by previously unsuccessful competitors if isotherm speed approaches  $c_F$ .

**7.4. Conceptually related questions.** There are conceptually related questions that are interesting from both biological and mathematical perspectives. For example, when species are in alpine habitats, climate change can mean both upwards shifts in habitat zones and shrinkage and fragmentation of those zones because there is less habitat at higher elevations. Although this could be addressed in the reaction-diffusion framework presented here, it would require complex spatio-temporal shifts in the domain boundaries—a nontrivial problem.

Whereas this paper has focused on two species interacting through Lotka–Volterra competition, competitive interactions are undoubtedly more complex, and may involve a large number of species. The effect of climate change on a large number of species with different dispersal and competitive abilities may result in new local mixes of species, which then would have differential effects on any given competitor. Mathematical analysis of this situation would be an important step towards extending the pairwise competition results of this paper to real ecosystems.

#### ACKNOWLEDGEMENTS

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#### APPENDIX: ESTIMATES FOR THE SOLUTION OF (42) AND BOUNDS FOR THE COEFFICIENTS $u_{B1}$ AND $u_{B1}$

We shall apply the method of upper and lower solution of (42), see statement (T1) in Section 6.2.1. It gives a rather simple criterion for obtaining upper and lower bounds for the solution without actually solving the equation.

**A.1: Lower solution.** For the lower solution the recipe is to try a first eigenfunction of the differential operator  $d^2/dx^2$  for the specified domain and the boundary conditions. The solution of the equation

$$\psi_{xx} + \Omega^2\psi = 0$$

is

$$\psi = A \sin(\Omega x + \vartheta) = A(\sin \Omega x \cos \vartheta + \cos \Omega x \sin \vartheta).$$

From the boundary conditions it follows that

$$\Omega \cos \theta - k \sin \theta = 0,$$

$$\Omega (\cos \Omega L \cos \theta - \sin \Omega L \sin \theta) + k (\sin \Omega L \cos \theta + \cos \Omega L \sin \theta) = 0.$$

From the first equation it follows that

$$\cos \theta = \frac{k}{\sqrt{k^2 + \Omega^2}}, \quad \sin \theta = \frac{\Omega}{\sqrt{k^2 + \Omega^2}}, \quad 0 \leq \theta \leq \frac{\pi}{2}.$$

Dividing the second equation by  $\sqrt{k^2 + \Omega^2}$  we obtain

$$\cos \Omega L \sin 2\theta + \sin \Omega L \cos 2\theta = \sin(\Omega L + 2\theta) = 0.$$

The smallest root is  $\Omega L = \pi - 2\theta$ . This gives an equation for  $\Omega$ , but it is more convenient to transform it to

$$\tan \frac{\Omega L}{2} = \tan \left( \frac{\pi}{2} - \theta \right) = \cot \theta = \frac{k}{\Omega}$$

or

$$\Omega \tan \frac{\Omega L}{2} = k. \tag{A.1}$$

Substituting  $\psi$  into the right-hand side of (42) and taking into account that

$$\max_{[0, L]} \left( e^{-\frac{\alpha x}{2}} \sin(\Omega x + \vartheta) \right) \leq \max_{[0, L]} e^{-\frac{\alpha x}{2}} \max_{[0, L]} |\sin(\Omega x + \vartheta)| = 1$$

we have

$$\psi_{xx} + \left( \bar{r} - e^{-\frac{\alpha x}{2}} \psi \right) \psi = A \sin(\Omega x + \vartheta) \left( \bar{r} - \Omega^2 - A e^{-\frac{\alpha x}{2}} \sin(\Omega x + \vartheta) \right) \geq 0$$

provided  $A \leq \bar{r} - \Omega^2$ . Therefore

$$\psi = (\bar{r} - \Omega^2) \sin(\Omega x + \vartheta)$$

is a lower solution for the stationary problem. This result is used below to obtain estimates for the approach described in Section 6.4.1.

**A.2: Upper solution.** To construct an upper solution let us first obtain a solution of an auxiliary problem, and then we shall show that it is the required upper solution. We linearize (42) about the solution  $e^{\frac{cx}{2}}$ ,  $\tilde{u}_A = e^{\frac{cx}{2}} - \phi$ , then

$$\frac{c^2}{4}e^{\frac{cx}{2}} - \phi_{xx} + \left(1 - \frac{c^2}{4} - 1 + e^{-\frac{cx}{2}}\phi\right) \left(e^{\frac{cx}{2}} - \phi\right) = 0,$$

$$\phi_{xx} - \omega^2\phi = 0, \quad \omega^2 = 1 + \frac{c^2}{4}, \phi = ae^{\omega x} + be^{-\omega x}.$$

We require that  $\tilde{u} = e^{\frac{cx}{2}} - \phi$  satisfy the boundary conditions, that is

$$(k - \omega)a + (k + \omega)b = k,$$

$$(k + \omega)ae^{\omega L} + (k - \omega)be^{-\omega L} = ke^{\frac{cL}{2}}.$$

Solving the system for  $a$  and  $b$  yields

$$a = \frac{k}{k + \omega} \frac{e^{-(\omega - \frac{c}{2})L} - Ae^{-2\omega L}}{1 - A^2e^{-2\omega L}}, \quad b = \frac{k}{k + \omega} \frac{1 - Ae^{-(\omega - \frac{c}{2})L}}{1 - A^2e^{-2\omega L}}, \quad A = \frac{k - \omega}{k + \omega}$$

and hence

$$\tilde{u}_A = e^{\frac{cx}{2}} - \frac{k}{k + \omega} \frac{1}{1 - A^2e^{-2\omega L}} \times \left( \left( e^{\frac{cL}{2}} - Ae^{-\omega L} \right) e^{\omega(x-L)} + \left( 1 - Ae^{-(\omega - \frac{c}{2})L} \right) e^{-\omega x} \right). \quad (A.2)$$

Substituting this into (42) we have a function which satisfies the boundary conditions and

$$\tilde{u}_{Axx} + \left( \tilde{r} - e^{-\frac{cx}{2}}\tilde{u}_A \right) \tilde{u}_A = \frac{c^2}{4}e^{\frac{cx}{2}} - \phi_{xx} + \left( -\frac{c^2}{4} + e^{-\frac{cx}{2}}\phi \right) \left( e^{\frac{cx}{2}} - \phi \right) = -e^{-\frac{cx}{2}}\phi^2 < 0,$$

therefore  $\tilde{u}_A$  (A.2) is an upper solution. The same is true for  $u_A = e^{-\frac{cx}{2}}\tilde{u}_A$  for equation (41). This result is used in Section 6.2.3 for the proof of the coexistence theorem and in the next section to obtain estimates for the approach described in Section 6.4.1.

**A.3: Solution near the habitat edge: estimate from above.** For the estimates it is more convenient to use the estimate for  $u_A = e^{-\frac{cx}{2}}\tilde{u}_A$ , where  $\tilde{u}_A$  is given by (A.2) that is

$$u_A = 1 - \frac{k}{k + \omega} \frac{\left( \left( 1 - Ae^{-(\omega + \frac{c}{2})L} \right) e^{(\omega - \frac{c}{2})(x-L)} + \left( 1 - Ae^{-(\omega - \frac{c}{2})L} \right) e^{-(\omega + \frac{c}{2})x} \right)}{1 - A^2e^{-2\omega L}}. \quad (A.3)$$

We are interested in the estimates for  $L$  big enough, when the boundary coexistence effects are possible, so we assume  $e^{-(\omega \pm \frac{\epsilon}{2})L}$  negligible. Then

$$u_A = 1 - \frac{k}{k + \omega} \left( e^{(\omega - \frac{\epsilon}{2})(x-L)} + e^{-(\omega + \frac{\epsilon}{2})x} \right)$$

for big enough  $L$ . Since  $u_A$  is an increasing function of  $L$ , therefore this estimate is still an estimate of  $u$  from above. Since  $u'' < 0$ ,  $u_A$  lies below its tangent at any point, and we shall use tangents at the edges, so near to  $x = 0$

$$u(x) \leq \frac{\omega}{\omega + k} + \frac{(\omega + \frac{\epsilon}{2})kx}{\omega + k}, \quad x \geq 0,$$

and near to  $x = L$

$$u(x) \leq \frac{\omega}{\omega + k} + \frac{(\omega - \frac{\epsilon}{2})k(L-x)}{\omega + k}, \quad x \leq L.$$

**A.4: Solution near the habitat edge: estimate from below.** To get these estimates we can use the lower solution. There is a little problem—equation (A.1) for  $\Omega$  cannot be solved analytically. So to get an estimate we shall use the estimates for  $\Omega^+$  from above and  $\Omega^-$  from below. They can be obtained with the help of the fact that for monotone increasing and continuous functions  $f_1(x)$  and  $f_2(x)$  if  $f_1(x) \geq f_2(x)$ , then  $f_1^{-1}(k) \leq f_2^{-1}(k)$ . Since  $\sin x \leq x \leq \tan x$ , then to get  $\Omega^-$  we can multiply (A.1) by  $L/2$  and replace  $\frac{\Omega L}{2}$  by  $\tan \frac{\Omega L}{2}$ , so

$$\left( \tan \frac{\Omega^- L}{2} \right)^2 = \frac{kL}{2}, \quad \Omega^- = \frac{2}{L} \arctan \sqrt{\frac{kL}{2}}.$$

Similarly, replacing  $\frac{\Omega L}{2}$  by  $\sin \frac{\Omega L}{2}$ , we get the equation for  $\Omega^+$ :

$$\sin \frac{\Omega^+ L}{2} \tan \frac{\Omega^+ L}{2} = \frac{(\sin \frac{\Omega^+ L}{2})^2}{\cos \frac{\Omega^+ L}{2}} = \frac{1 - (\cos \frac{\Omega^+ L}{2})^2}{\cos \frac{\Omega^+ L}{2}} = \frac{kL}{2}, \quad (\text{A.4})$$

hence

$$\cos \frac{\Omega^+ L}{2} = \sqrt{1 + \left(\frac{kL}{4}\right)^2} - \frac{kL}{4} = \frac{1}{\sqrt{1 + \left(\frac{kL}{4}\right)^2 + \frac{kL}{4}}}$$

and, dividing (A.4) by  $\cos \frac{\Omega^+ L}{2}$ ,

$$\left( \tan \frac{\Omega^+ L}{2} \right)^2 = \frac{kL}{2} \left( \sqrt{1 + \left(\frac{kL}{4}\right)^2} + \frac{kL}{4} \right)$$

$$\Omega^+ = \frac{2}{L} \arctan \sqrt{\frac{kL}{2} \left( \sqrt{1 + \left(\frac{kL}{4}\right)^2} + \frac{kL}{4} \right)}.$$

For  $k \rightarrow \infty$  (Dirichlet boundary conditions) both  $\Omega^-$  and  $\Omega^+$  tend to  $\pi/L$ . Now let us get the estimates of the solution  $u(x)$ .

$$u(x) \geq e^{-\frac{cx}{2}} \psi(x) = (\tilde{r} - \Omega^2) e^{-\frac{cx}{2}} \sin(\Omega x + \vartheta).$$

Near  $x = 0$  it is convenient to use the formula of the sine of sum:

$$\begin{aligned} u(x) &\geq \frac{\tilde{r} - \Omega^2}{\sqrt{k^2 + \Omega^2}} e^{-\frac{cx}{2}} (k \sin \Omega x + \Omega \cos \Omega x) \\ &\geq \frac{\tilde{r} - (\Omega^+)^2}{\sqrt{k^2 + (\Omega^+)^2}} e^{-\frac{cx}{2}} (k \sin \Omega^- x + \Omega^- \cos \Omega^+ x). \end{aligned}$$

Leaving only terms linear in  $x$  we have

$$u(x) \geq \frac{\tilde{r} - (\Omega^+)^2}{\sqrt{k^2 + (\Omega^+)^2}} \Omega^- \left( 1 + \left( k - \frac{c}{2} \right) x \right).$$

Near to  $x = L$  it is convenient to make a change  $y = L - x$ , then, taking into account that  $\Omega L = \pi - 2\theta$ ,

$$\begin{aligned} \sin(\Omega x + \theta) &= \sin(\Omega L + \theta - \Omega y) = \sin(\pi - \theta - \Omega y) = \sin(\Omega y + \theta), \\ \exp\left(-\frac{cx}{2}\right) &= \exp\left(-\frac{cL}{2}\right) \exp\left(\frac{cy}{2}\right), \end{aligned}$$

and hence up to linear terms in  $y$

$$u(y) \geq \frac{\tilde{r} - (\Omega^+)^2}{\sqrt{k^2 + (\Omega^+)^2}} \Omega^- e^{-\frac{cL}{2}} \left( 1 + \left( k + \frac{c}{2} \right) y \right).$$

Due to the factor  $e^{-\frac{cL}{2}}$ , this estimate may not be very useful for big values of  $cL$  as it may become very small.

The obtained estimates can be used for approximate theory of boundary coexistence in the case  $|c| > 0$ , when the coexistence theorem does not apply. The technique is the same as in the proof of the coexistence theorem in Section 6.2.3—see Section 6.4.1 for more comments.

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