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Climate and competition: the effect of moving range boundaries on habitat invasibility

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Abstract

Predictions for climate change include movement of temperature isoclines up to 1000 meters per 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 decribe 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.

Key words: Invasion, competition, climate change, critical domain size

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 has 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 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 isoterms 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 analyze 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 (Shigesada and Kawasaki, 1997; Okubo, 1980).

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

$$u_{1t} = D_1 u_{1xx} + (r_1 - \alpha_{11}u_1 - \alpha_{12}u_2)\, u_1, \tag{1}$$
$$u_{2t} = D_2 u_{2xx} + (r_2 - \alpha_{21}u_1 - \alpha_{22}u_2)\, u_2 \tag{2}$$

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

$$u_{1t} = D_1 u_{1xx} - \kappa_1 u_1, \tag{3}$$
$$u_{2t} = D_2 u_{2xx} - \kappa_2 u_2 \tag{4}$$

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, α_{ij} are the interspecies competition coefficients, and κ_i characterize the degree of outside environment hostility. For the simplicity we set the same diffusion coefficients within and outside the patch. We use the natural boundary condition $u_i \to 0$ as $x \to \pm\infty$.

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; 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 analyzing competition is in terms of invasibility (Durrett, 2002). Suppose that the 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 analyze the influence of climate change on interspecies competition within the framework of the model (1), (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 analyzed 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 $x \to x - ct$ allows us to analyze this as a problem on a fixed spatial domain $0 \le x \le L$ 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

$$u_{1t} = D_1 u_{1xx} + c u_{1x} + (r_1 - \alpha_{11} u_1 - \alpha_{12} u_2) u_1, \tag{5}$$
$$u_{2t} = D_2 u_{2xx} + c u_{2x} + (r_2 - \alpha_{21} u_1 - \alpha_{22} u_2) u_2 \tag{6}$$

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

$$u_{1t} = D_1 u_{1xx} + c u_{1x} - \kappa_1 u_1, \tag{7}$$
$$u_{2t} = D_2 u_{2xx} + c u_{2x} - \kappa_1 u_2, \tag{8}$$

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 twelve parameters: 2 D_i, 2 r_i, 4 α_{ij}, c, L, and 2 κ_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 κ_i which are used in the equations outside the patch.

Let $x \to x_0 x$, $t \to t_0 t$, $u_i \to u_{0i} u_i$, then

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

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

The choice of

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

and denoting

$$c' = \frac{c}{\sqrt{D_1 r_1}}, \quad D = \frac{D_2}{D_1}, \quad r = \frac{r_2}{r_1}, \quad L' = \frac{L}{x_0}, \quad \alpha_{ij}' = \frac{\alpha_{ij}}{\alpha_{jj}}, \quad \kappa_i' = \frac{\kappa_i}{r_1}, \tag{12}$$

yields

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

$$u_{2t} = D u_{2xx} + c u_{2x} + (r - \alpha_{21} u_1 - u_2) u_2 \tag{14}$$

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

$$u_{1t} = u_{1xx} + c u_{1x} - \kappa_1 u_1, \tag{15}$$

$$u_{2t} = D u_{2xx} + c u_{2x} - \kappa_2 u_2 \tag{16}$$

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

$$\begin{aligned} k_1^2 + ck_1 - \kappa = 0, \\ Dk_2^2 + ck_2 - \kappa = 0. \end{aligned}$$

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 $x > L$,

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

These roots satisfy the constraint that u_i approaches zero as $|x| \to \infty$. 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 stationary problem only inside the patch with the following Robin's boundary conditions

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

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

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

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

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 κ 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

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

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

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

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

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

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

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

Here the dominant eigenvalue $\lambda = \lambda(l)$ depends on l. According to (Smoller, 1994; Cantrell et al., 1998) λ is a continuous and decreasing function of $\left|k_i^{\pm}\right|$, 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 σ 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 case $|c| > 0$ the equations (18), (19) has a nonselfadjoint operator, and we cannot directly apply the proof above. Nonetheless, it is possible to use the change of variables $u_1(x,t) = \tilde{u}_1(x,t)\exp\left(-\frac{cx}{2}\right)$, $u_2(x,t) = \tilde{u}_2(x,t)\exp\left(-\frac{cx}{2D}\right)$ (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. □

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 the (13)–(16) by change of variables:

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

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

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

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

within the patch and

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

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

outside the patch, where

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

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

Here

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

are the well known asymptotic rate of population spread for the single-species models (equations (13), (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 allow us to draw two important conclusions. Let us turn to the equations without the advection term (31), (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_* (Okubo, 1980; Ludwig et al., 1979; Shigesada and Kawasaki, 1997). The value of L_* depends on the boundary conditions. In case of Dirichlet boundary condition ($\kappa = \infty$ for our model (13), (14) with $c = \alpha_{12} = \alpha_{21} = 0$) the critical patch sizes are

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

In case of general κ 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 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), (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 transformating (31) — (34) to a problem on the finite domain: equations (31), (32) and boundary conditions

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

where

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

Here, the terms with explicit dependence on x in (31), (32) are nonlinear terms of higher order which do not affect the linear stability. Each linearized equation decouples from the other. For 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

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

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

When the hostility of the exterior κ is finite, the single species critical domain lengths become

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

One can see that for $\kappa \to \infty$ 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 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 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 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 α, the asymptotic behavior can belong to one of the four kinds, listed in Table 5.2.1.

Table 5.2.1. Outcomes of competition in Volterra model (43)

name	u_1, u_2	outcome	conditions
A	$u_1 \to 0$, $u_2 \to u_{02} > 0$	2 wins	$\alpha_{21} < r$, $1/\alpha_{12} < r$
B	$u_1 \to u_{01} > 0$, $u_2 \to u_{02} > 0$	coexistence	$\alpha_{21} < r$, $1/\alpha_{12} > r$
C	$u_1 \to u_{01} > 0, u_2 \to 0$	1 wins	$\alpha_{21} > r$, $1/\alpha_{12} > r$
D	A or C, depending on $u_i(0)$	1 or 2 wins	$\alpha_{21} > r$, $1/\alpha_{12} < r$

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 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 analyze, what will happen in 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 $0 \le c < \min\{c_{1*}, c_{2*}\}$, 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 5.2.1. As we change c, R may pass through the values α_{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 5.2.1, 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 swithching 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 α_{21} and $1/\alpha_{12}$. This determines which of the inequalities in Table 5.2.1 changes first, and hence the details of the mode swithing.

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 through S4.

S1: $c_{1*} > c_{2*}$, $\alpha_{21} > 1/\alpha_{12}$, r corresponds to case A. For $0 \le c < c_{2*}$ $R(c)$ decreases from r to 0 giving the sequence of competition modes A $\to$ D $\to$ C or "2"$\to$"1/2"$\to$"1".

S2: $c_{1*} < c_{2*}$, $\alpha_{21} > 1/\alpha_{12}$, r corresponds to case C. For $0 \le c < c_{1*}$ $R(c)$ increases from r to ∞ through C $\to$ D $\to$ A or "1"$\to$"1/2"$\to$"2".

S3: $c_{1*} > c_{2*}$, $\alpha_{21} < 1/\alpha_{12}$, r corresponds to case A. For $0 \le c < c_{2*}$ $R(c)$ decreases from r to 0 through A $\to$ B $\to$ C or "2"$\to$"1+2"$\to$"1".

S4: $c_{1*} < c_{2*}$, $\alpha_{21} < 1/\alpha_{12}$ r corresponds to case C. For $0 \le c < c_{1*}$ $R(c)$ increases from r to ∞ through C $\to$ B $\to$ A or "1"$\to$"1+2"$\to$"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 α_{ij} of the equations we have chosen 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 analyzed the resulting stationary profiles. This procedure has been performed for c from 0 to $\max\{c_{1*}, c_{2*}\}$. Some results are presented in Fig. 2, 3, 4. The values of $u_i(x)$ for every c are shown by the shades of gray: from 0 (white) to maximal $u_{i\max}$ (black).

We cannot physically present all the results, instead we shall describe 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.

- For $L_{2*}/L_{1*} > 1$ usually the numerical results correspond 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, Fig. 3, 4.

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, Fig. 3a-c, 4d. 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 the species 1, Fig. 3d, 4a-c. We observed this effect only for nonzero patch speed.

6 Invasion analysis and basic effects

Let us suppose that the 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 $\delta u_1 e^{\lambda t} = u_1 - u(x)$, $\delta u_2 e^{\lambda t} = u_2$, $|\delta u_i| \ll 1$ leads to the linearized problem

$$\begin{aligned} D\delta u_{2xx} + c\delta u_{2x} + (r - \alpha_{21}u)\delta u_2 &= \lambda \delta u_2 \\ \delta u_{2x} - k_2^+ \delta u_2 &= 0, \quad x = 0, \\ \delta u_{2x} - k_2^- \delta u_2 &= 0, \quad x = L. \end{aligned} \tag{46}$$

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

$$\begin{aligned} Dv_{xx} + (r - \frac{c^2}{4D} - \alpha_{21}u)v &= \lambda v \\ v_x - \tilde{k}_2^+ v &= 0, \quad x = 0, \\ v_x - \tilde{k}_2^- v &= 0, \quad x = L. \end{aligned} \tag{47}$$

where $u(x)$ is the solution of

$$\begin{aligned} u_{xx} + cu_x + (1-u)u &= 0. \\ u_x - k_1^+ u &= 0, \quad x = 0, \\ u_x - k_1^- u &= 0, \quad x = L. \end{aligned}$$

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

$$\begin{aligned} v_{xx} + (1 - \frac{c^2}{4} - \alpha_{12}u)v &= \lambda v \\ v_x - \tilde{k}_1^+ v &= 0, \quad x = 0, \\ v_x - \tilde{k}_1^- v &= 0, \quad x = L. \\ Du_{xx} + cu_x + (r-u)u &= 0 \\ u_x - k_2^+ u &= 0, \quad x = 0, \\ u_x - k_2^- u &= 0, \quad x = L. \end{aligned} \tag{48}$$

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 ($c = 0$, $\kappa \to \infty$)

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 analyze 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

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

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

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

and

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

In the proofs of the theorems we shall use the following theorems from (Smoller, 1994; 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 Ω 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 Ω 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 (1-st species wins), and $L_{2*} > L_{1*}$. Suppose that the species 1 has established and reached its stationary distribution $u_1(x)$, then the species 2 cannot invade.*

Proof. Let us consider stationary distributions of both species in 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

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

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 population of the second species cannot grow in presence of the established population of the first one. □

Note 1. The theorem can be extended to the case of more general boundary conditions if the "hostility parameters" κ outside the patch are proportional to the diffusion coefficients, that is $\kappa_1/\kappa_2 = D_1/D_2$. In 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 κ_i/D_i. For the same κ 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 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 the interchanging the species $1 \leftrightarrow 2$ the theorem states that the first species cannot invade if there exists 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 presence of the established population

of the first one. Now suppose there is another situation: both species can grow in 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 the (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, the species 1 can grow in presence of the 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 $k = \infty$

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

Substitution of u_A into (50) gives a Mathieu equation, for which there are no good estimates of λ. 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

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

Let us consider the eigenvalue problem

$$\begin{aligned} Dv_{xx} + (r - \alpha_{21}x)v &= \mu v, \\ v(0) &= v(L) = 0. \end{aligned} \tag{61}$$

According to (60) and (T2), $\lambda_{\max} > \mu_{\max}$. If, for certain D, r, and α_{21}, this problem has $\mu_{\max} = 0$, then $\lambda_{\max} > 0$ and the second species can invade. It is convenient to fix D and α_{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

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

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

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

A general solution to this equation can be expressed through the Airy functions, $\mathrm{Ai}(z)$ and $\mathrm{Bi}(z)$ (Abramowitz and Stegun, 1965), $v(z) = a\mathrm{Ai}(z) - b\mathrm{Bi}(z)$. For $z < 0$ both of these functions behave like trigonometric ones; in particular they have infinite number of zeroes and $|\mathrm{Ai}(z)| < 1$, $|\mathrm{Bi}(z)| < 1$ (Fig. 5). For $z > 0$ they behave like exponential functions, and for z large there are asymptotic formulas

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

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

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

The solution to (62)–(63) satisfies

$$\Gamma(z_1) = \Gamma(z_2) = A \tag{66}$$

where $\Gamma(z) = \mathrm{Bi}(z)/\mathrm{Ai}(z)$ 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 $z_b \approx 2.34$ (Figure 6). This gives a critical growth rate for the cecond species, r, which satisfies $z_1 = z_{1c}$ so when

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

$\mu_{\max} = 0$ and hence $\lambda_{\max} > 0$ and the second species can invade. As can be seen from Figure 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 u is an increasing function of r. Hence the second species can invade for any

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

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* $L > \max\left\{\pi, \pi\sqrt{D/r}\right\}$. *If (69) holds, the species 2 can grow in the presence of the 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 $\mathrm{Ai}(z)$ looks qualitatively similar to 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 the size $\sim L_{2*}$, where $\mathrm{Ai}(z)$ 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 the 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 individual densities. This model has been analyzed 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 neighboring 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 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 has 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 the species 1 is disturbed by the edge while that of the species 2 almost does not feel it. If the ratio of intrinsic growth rates $r = r_2/r_1$ is big enough, then the species 2 has a good chance to survive in this domain. Instead of extinction the species 2 retreats to a ring surrounding the habitat of the species 1. If on the other hand, $L_{1*} < L_{2*}$, then spatial inhomogeneity is not of any help for the species 2, and the outcome of competition can be predicted by the Volterra model.

6.4 Edge effects and competition in 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 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 then 1, even if in case $c = 0$ there were no coexistence.

However, for $c > 0$ numerics showed one more effect, which has no analog in 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 disappear, and after some relatively short transition time a wave of species replacement will form. Species 1 propagates to the right and replaces the 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,

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

then the speed of the invasion front is equal to

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

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 the speed $c_{F1} = c_F - c$. But if $c > c_F$, in the moving system we shall see qualitatively different situation: the front moving on the left, that is the 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 the species 2 has been created at the in-flow boundary (right for $c > 0$), then the species 2 can successfully propagate to the left and make the species 1 extinct, Fig. 8. If on the other hand the population of the species 2 is created at the out-flow end, it will quickly become extinct itself, Fig. 9.

Now suppose that the 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 the 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, 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, 9. A small perturbation at the in-flow edge grows and occupies all the domain, while the preexisting species extincts. At the same time a much bigger perturbation at the other edge quickly dies out.

7 Summary and Conclusions

7.1 Mathematical conclusions

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

7.2 Ecological conclusions

The model described in the 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

3. Habitat motion may result in reversal of 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 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 $c \approx 600\,\mathrm{m/year}$ (Parmesan and Yohe, 2003). On the other hand it is known that for some species $c_* \approx 1 - 3\,\mathrm{km/year}$. 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 isotherms 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 spatiotemporal 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 a large number 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.

7.5 Acknowledgments

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A 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 Sect. 6.2.1. It gives a rather simple criterion for obtaining upper and lower bound 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

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

¿From the boundary conditions it follows that

$$\begin{aligned} \Omega \cos\theta - k \sin\theta &= 0, \\ \Omega(\cos \Omega L \cos\theta - \sin \Omega L \sin\theta) + k(\sin \Omega L \cos\theta + \cos \Omega L \sin\theta) &= 0. \end{aligned}$$

¿From the first equation it follows that

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

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 Ω, 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 ψ into the right hand side of (42) and taking into account that

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

we have

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

provided $A \le \tilde{r} - \Omega^2$. Therefore

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

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

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

$$\phi_{xx} - \omega^2 \phi = 0, \qquad \omega^2 = 1 + \frac{c^2}{4},$$

$$\phi = a e^{\omega x} + b e^{-\omega x}.$$

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

$$\begin{aligned} (k-\omega)\, a + (k+\omega)\, b &= k, \\ (k+\omega)\, a e^{\omega L} + (k-\omega)\, b e^{-\omega L} &= k e^{\frac{cL}{2}}. \end{aligned}$$

Solving the system for a and b yeilds

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

and hence

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

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 the equation (41). This result is used in Sect. 6.2.3 for the proof of coexistence theorem and in the next section to obtain estimates for the approach described in Sect. 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

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

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

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

for big enough L. Since u_A is an increasing function of L, therefore this estimate still is 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 $x = 0$

$$u(x) \le \frac{\omega}{\omega+k} + \frac{\left(\omega+\frac{c}{2}\right)kx}{\omega+k}, \qquad x \ge 0,$$

and near to $x = L$

$$u(x) \le \frac{\omega}{\omega+k} + \frac{\left(\omega-\frac{c}{2}\right)k\,(L-x)}{\omega+k}, \qquad x \le L,$$

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 — the equation (A.1) for Ω cannot be solved analytically. So to get an estimate we shall use the estimates for Ω^+ from above and Ω^- 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 $f_1(x) \ge f_2(x)$, then $f_1^{-1}(k) \le f_2^{-1}(k)$. Since $\sin x \le x \le \tan x$, then to get Ω^- we can multiply (A.1) by $L/2$ and replace $\frac{\Omega L}{2}$ by $\tan\frac{\Omega L}{2}$, so

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

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

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

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 $k\to\infty$ (Dirichlet boundary conditions) both Ω^- and Ω^+ tend to π/L.

Now let us get the estimates of the solution $u(x)$.

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

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

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

Leaving only terms linear in x we have

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

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

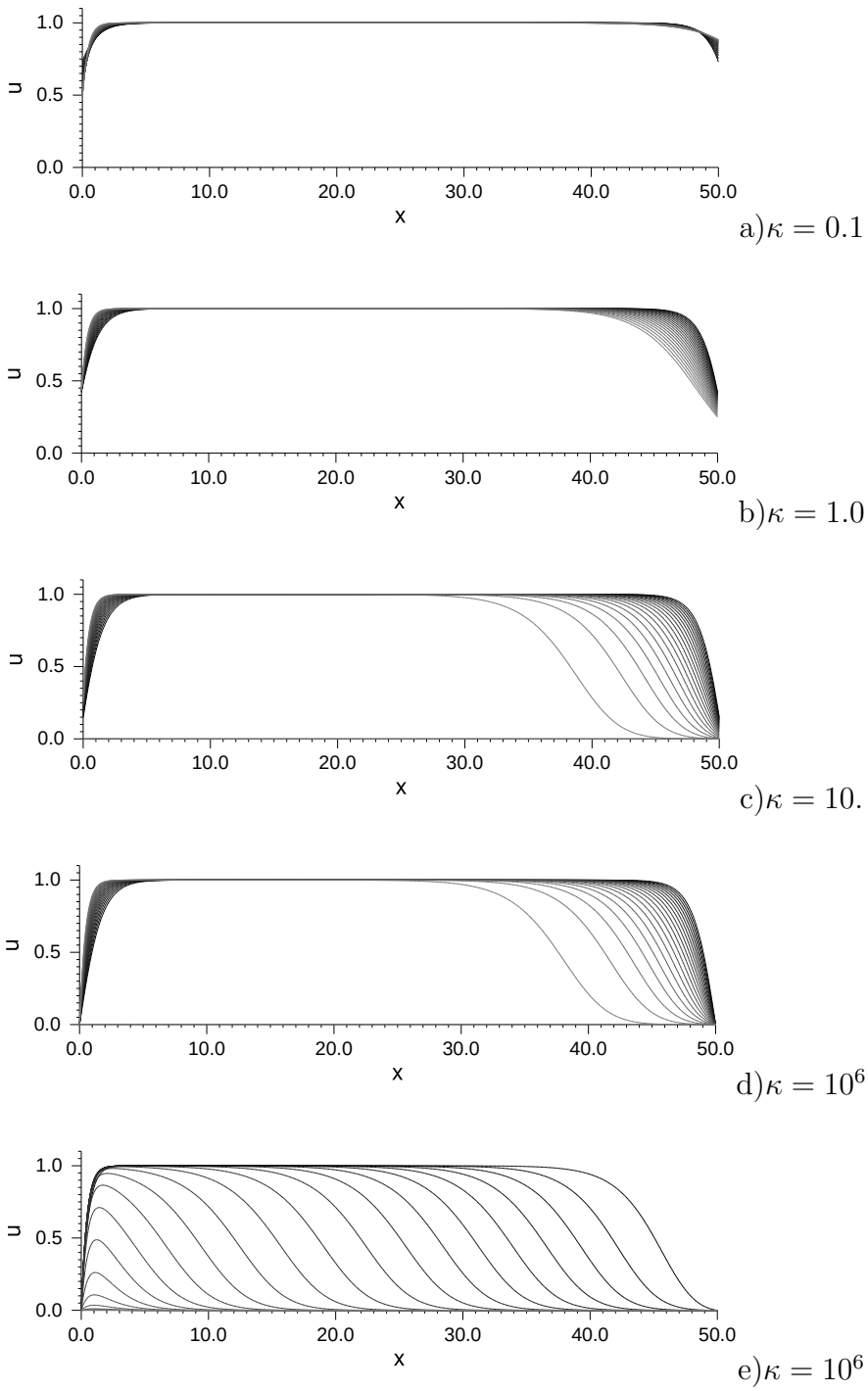
$$\begin{aligned} &\sin\left(\Omega x+\theta\right) = \sin(\Omega L+\theta-\Omega y) = \sin\left(\pi-\theta-\Omega y\right) = \sin\left(\Omega y+\theta\right), \\ &\exp\left(-\frac{cx}{2}\right) = \exp\left(-\frac{cL}{2}\right)\exp\left(\frac{cy}{2}\right), \end{aligned}$$

and hence up to linear terms in y

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

Due to the factor $e^{-\frac{cL}{2}}$, this estimate may be not 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 case $|c|>0$, when the coexistence theorem does not apply. The technique is the same as in the proof of the coexistence theorem in Sect. 6.2.3 — see Sect. 6.4.1 for more comments.



a)$\kappa = 0.1$

b)$\kappa = 1.0$

c)$\kappa = 10.$

d)$\kappa = 10^6$

e)$\kappa = 10^6$

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

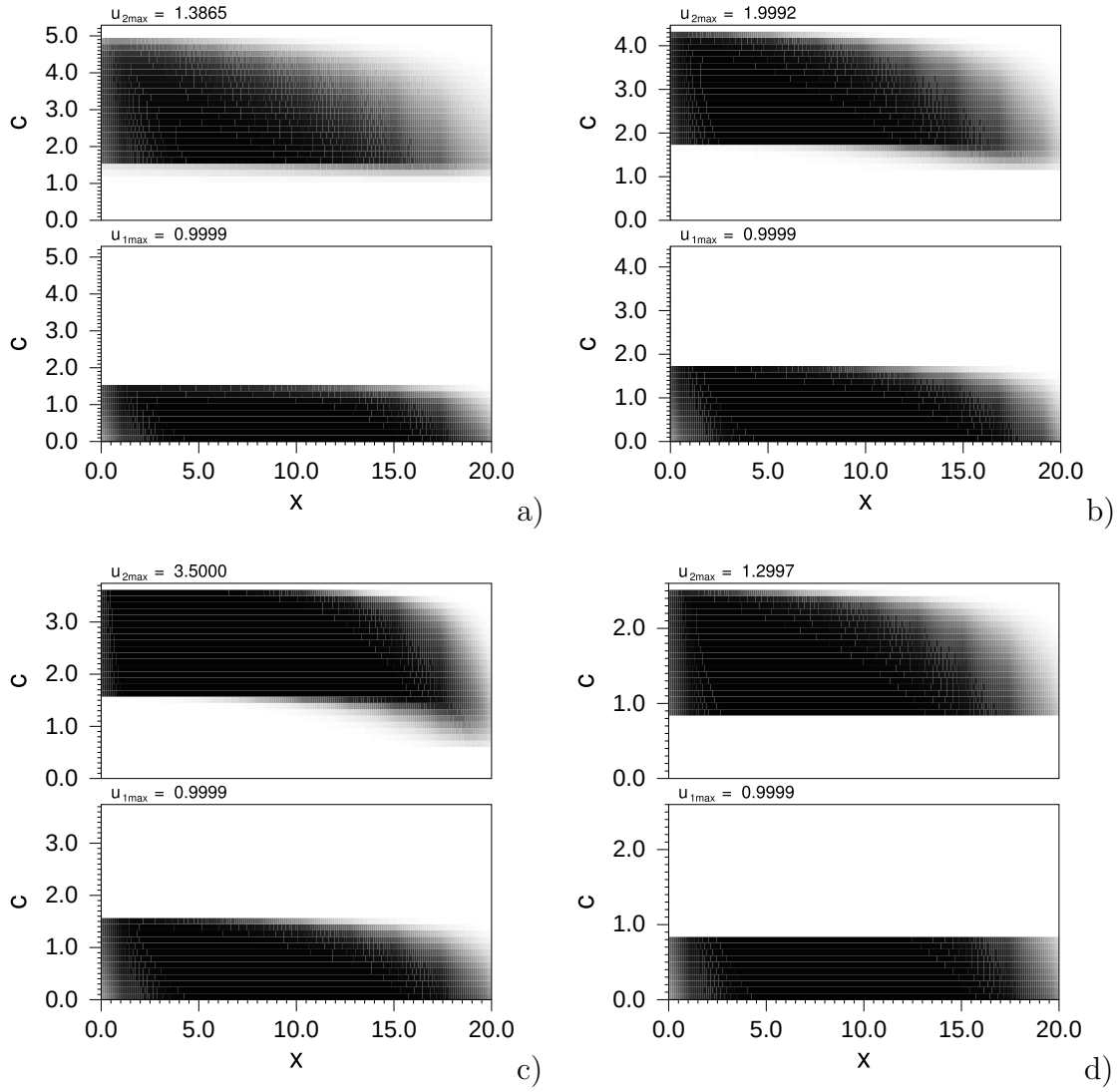


Fig. 2. Dependence of stationary profiles $u_i(x)$ on the patch speed c. Gray shade shows the value of u from 0 (white) to $u_{\max}$ (black, the value shown above the plot). Shown are examples of good agreement with predictions of S1–S4 scenarios. Note that in all cases $L_{2*}/L_{1*} > 1$. Parameters $\kappa = 1$, $L = 20.00$, (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: $1 \to 1{+}2 \to 2$; (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:$1 \to 1{+}2 \to 2$; (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:$1 \to 1{+}2 \to 2$; (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:$1 \to 1/2 \to 2$.

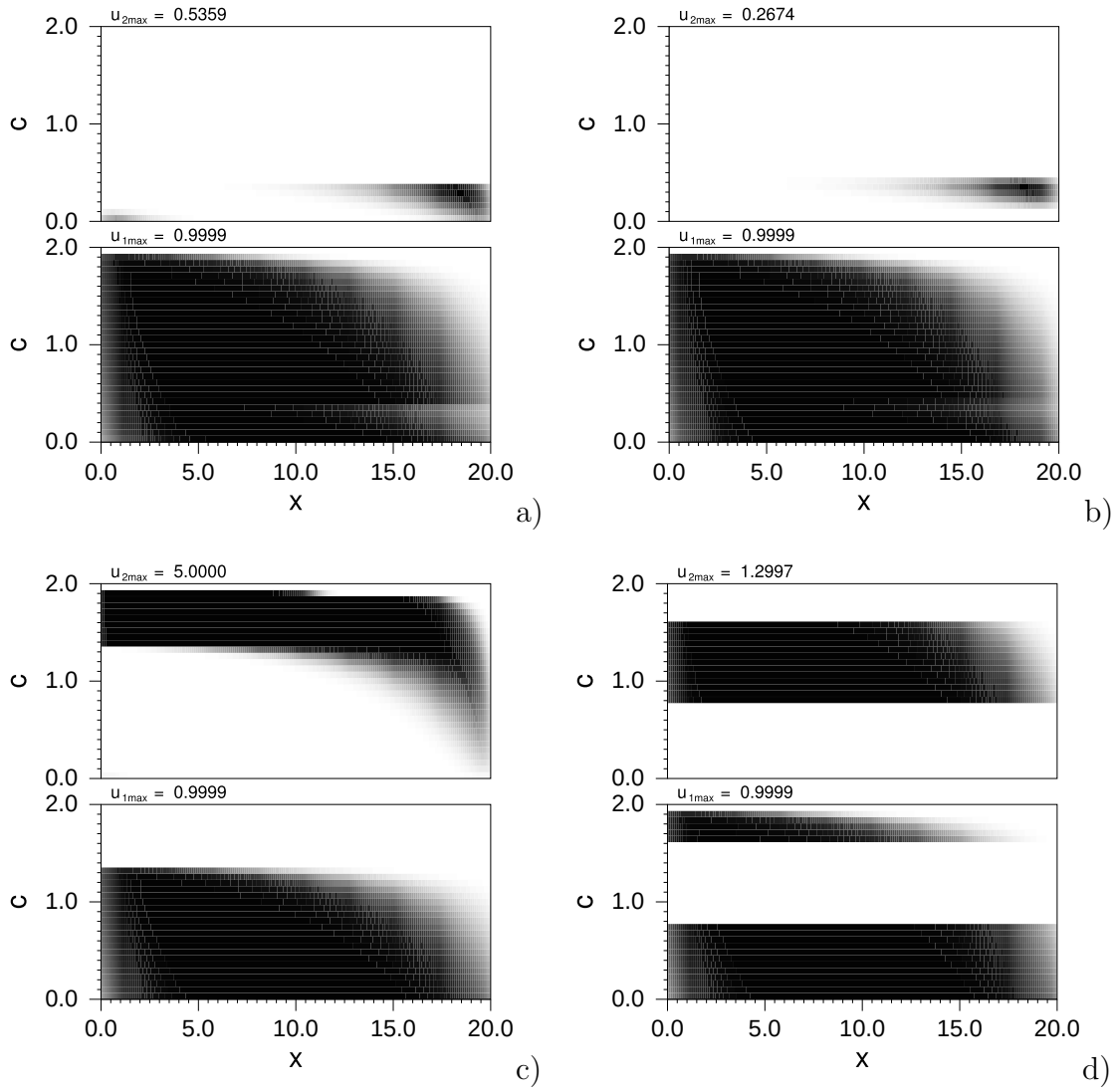


Fig. 3. Examples of bad agreement with predicted scenarios — in all cases predicted is extinction of species 2 and existence of species 1 for the shown range of c values. Instead the species 2 sometimes appear at the boundary (Panels a–c) and in some cases even out-competes species 1 and occupies the whole patch (Panels c, 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) $D = 0.70$, $r = 1.30$, $\alpha_{12} = 0.70$, $\alpha_{21} = 1.50$, $c_2/c_1 = 0.95$, $L_{2*}/L_{1*} = 0.73$.

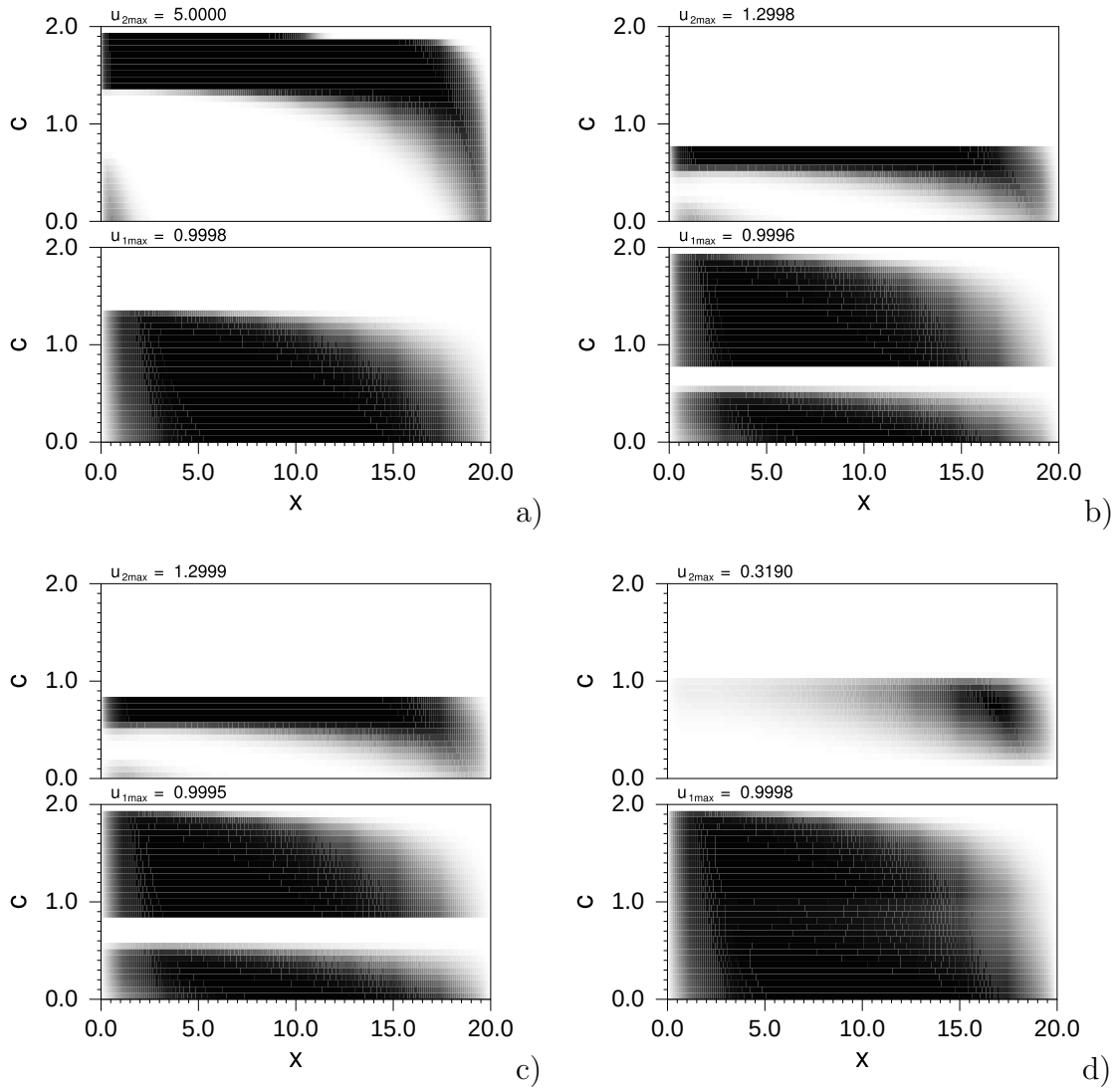


Fig. 4. Examples of bad agreement with predicted scenarios — in all cases predicted is extinction of species 2 and existence of species 1 for the shown range of c values. Instead the species 2 sometimes appear at the boundary (all panels) and in some cases even out-competes species 1 and occupies the whole patch (Panels b, 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) $D = 0.50$, $r = 1.30$, $\alpha_{12} = 0.50$, $\alpha_{21} = 1.50$, $c_2/c_1 = 0.81$, $L_{2*}/L_{1*} = 0.62$.

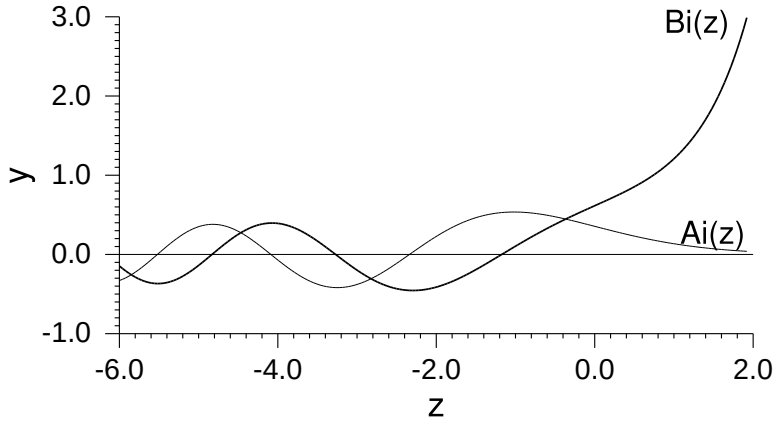


Fig. 5. Appearance of the Airy functions.

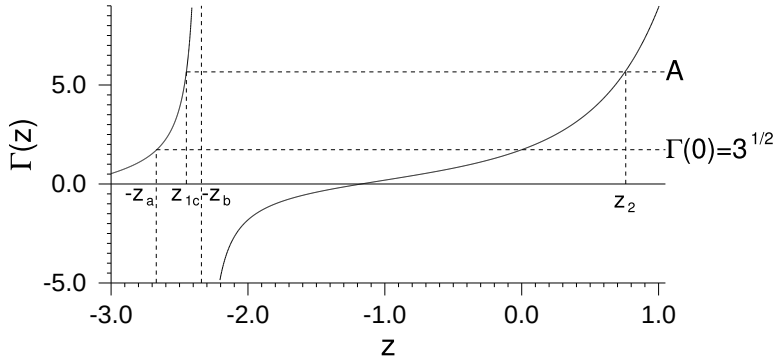


Fig. 6. For every $z_2 > 0$ there is a value of $z_1 \in (-z_a, -z_b)$ satisfying $\Gamma(z_1) = \Gamma(z_2)$ where $\Gamma(z) = \mathrm{Bi}(z)/\mathrm{Ai}(z)$. The number $-z_b$ satisfies $\Gamma(-z_a) = \Gamma(0) = \sqrt{3}$ and the number $-z_b$ is a vertical asimptote for Γ ($\mathrm{Ai}(-z_b) =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

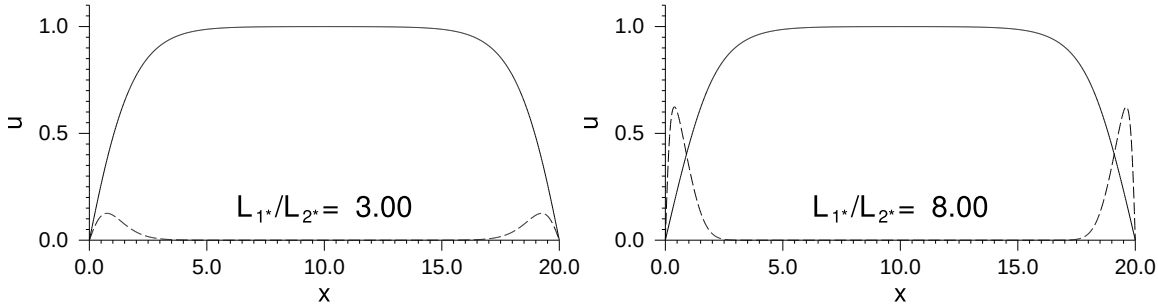


Fig. 7. Examples of boundary coexistence for $L_{2*} < L_{1*}$. Solid line — species 1, dashed — species 2.

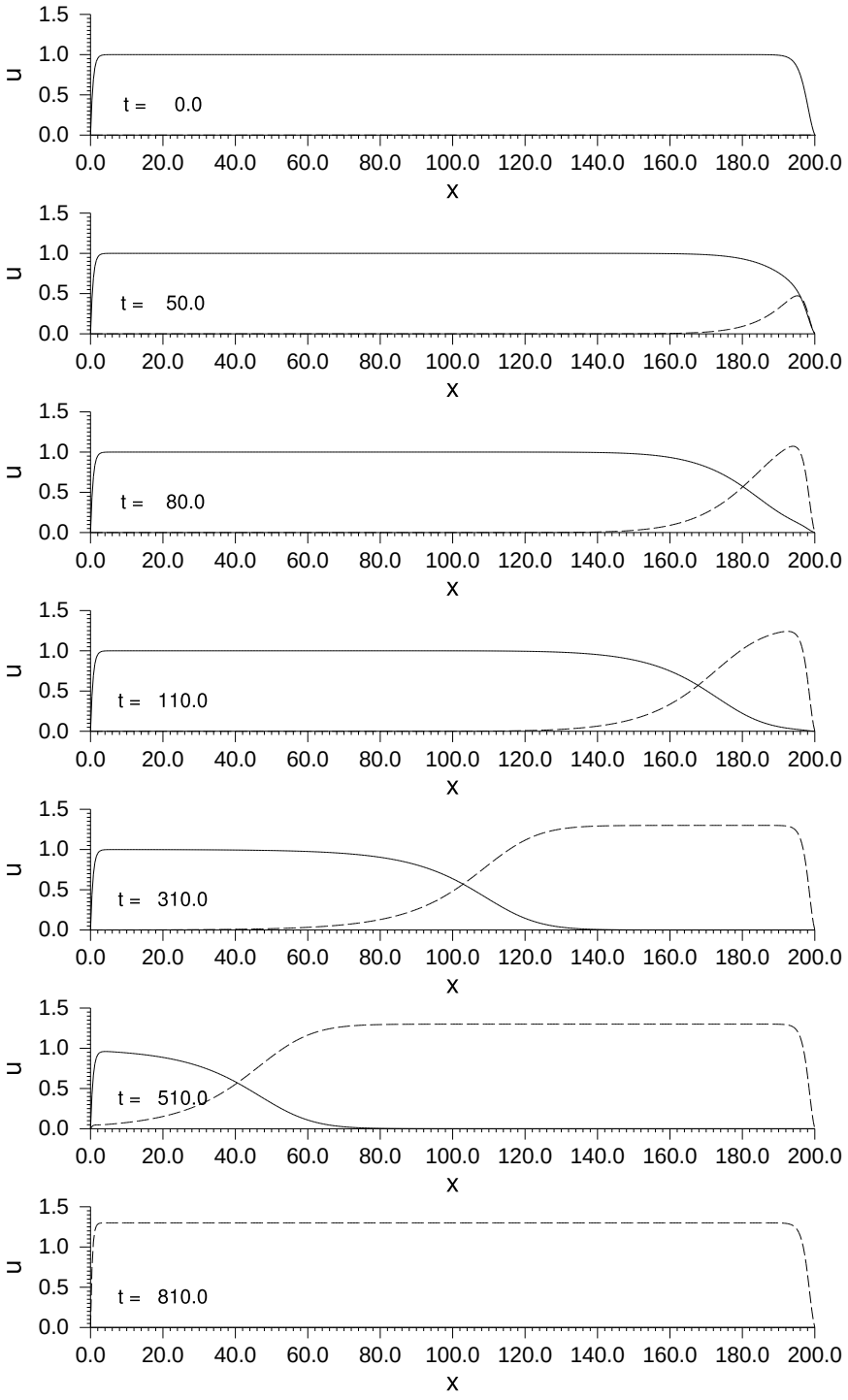


Fig. 8. Invasion of a very small amount of the species 2 (dashed line) at the propagating (in-flow) boundary leads first to boundary coexistence, then turns into a moving front and then replacement of the dominant species 1 (solid line). Parameters $\kappa = 10^6$, $D = 0.7$, $r = 1.3$, $\alpha_{12}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

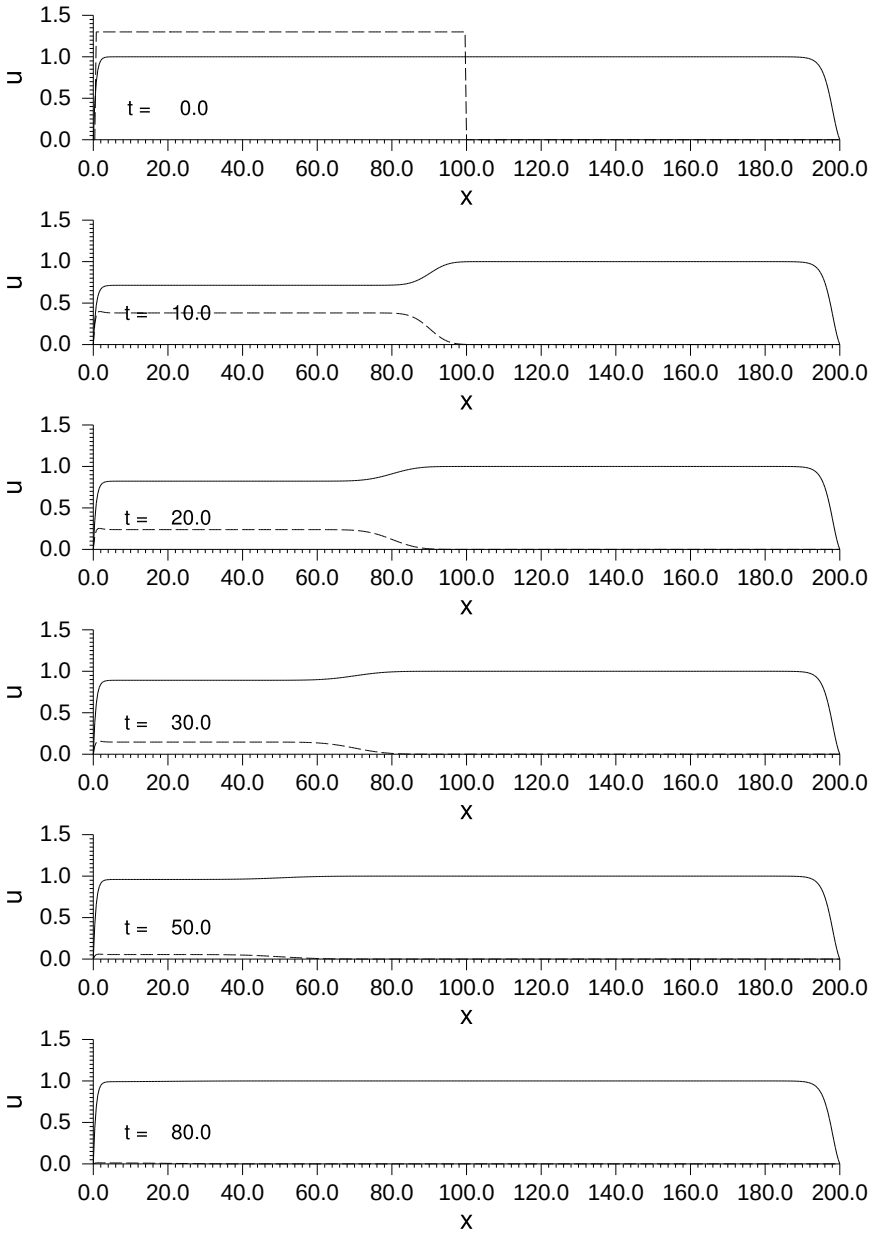


Fig. 9. Resonant character of the speed-induced invasion. Compared to the previous figure, much bigger initial invasion of the species 2 at the other edge dies out very quickly to zero.