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IMPACT OF INTRASPECIFIC TAXIS ON INVASION AND COMPETITION IN TWO-SPECIES MODEL

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Abstract: We study the interplay of two competing species across heterogeneous habitat. The system of reaction-diffusion-advection equations is used to consider the intraspecific taxis and nonuniform distribution of the resource. We analyze the influence of migration coefficients on the forming of stationary distributions and occupying of the environment. Massive computer simulation allowed to describe scenarios of successful and unsuccessful invasion, species coexistence, and the effect of initial distributions.

Keywords: population dynamics, invasion, competition, diffusion, taxis, nonlinear PDEs.

1 Introduction

In theoretical ecology, the problems of species coexistence and invasion are important, because of the different scenarios. The Gause principle [1] states that the coexistence of two populations is impossible with common vital resource. However, there are many examples when closely related species are present in the same ecological niche [2]. To study the dynamics of population

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systems, it is necessary to consider the factor of spatial and temporal heterogeneity [3, 4]. One of the effective techniques here is modeling with partial differential equations, especially reaction-diffusion-advection equations [5]. Usually, in Lotka-Volterra competitive systems, investigation only resource taxis take into account, see Refs. [6]–[16] and references therein.

The investigations [17]–[22] were addressed to the role of directed migration to resource and influence of interspecific taxis. In particular, it was found the multistability of stationary distributions under additional relations on system parameters. The study of relationships between parameters at which multistability occurred in a system helps in analysis of dynamics. The results [18] show that when these relationships are violated, the family is destroyed, but the system "remembers" about multistability. Trajectories from different initial states pass in the vicinity of the disappeared family in the convergence to steady isolated solutions. In [19] we pointed that the taxis to resource yields maximum of species density at the optimal value of the migration parameter. The impact of intraspecific taxis on invasion and competition was not studied yet.

In the present work, the dynamics of two competing species (resident and invader) is modeled, based on a system of partial differential equations. We study a one-dimensional spatial domain, with a heterogeneous resource (carrying capacity). Mobility, controlled by the gradients of population densities and the resources (taxis) is taken into account both for resident and invader. We assume that species are closely related, and they have a comparable need for the common resource. The purpose of this article is to study the effect of intraspecific taxis on invasive scenarios using combined mathematical approach and simulation.

2 Two-species model

We model the distributions of resident $u(x,t)$ and invader $v(x,t)$ on an inhomogeneous habitat $\Omega = [0,a]$ using reaction-diffusion-advection equations [17, 20]. This allows to describe local dynamics, spatial transport by diffusion, and migration due to taxis.

$$\dot{u} = -q_1' + \eta_1 u \left(1 - \frac{u+v}{p}\right), \tag{1}$$

$$\dot{v} = -q_2' + \eta_2 v \left(1 - \frac{u+v}{p}\right). \tag{2}$$

Here dot and prime denote differentiation on t and x respectively. Resource function $p(x)$ depends on x and positive constants η_j are growth parameters. The migration fluxes are given by functions q_j:

$$q_1 = -k_1 u' + u\varphi_1', \quad \varphi_1 = \alpha_1 p + \beta_1 u + \gamma_1 v, \tag{3}$$

$$q_2 = -k_2 v' + v\varphi_2', \quad \varphi_2 = \alpha_2 p + \beta_2 v + \gamma_2 u, \tag{4}$$

where k_j are diffusive coefficients, α_j, β_j and γ_j are coefficients of the resource taxis, intraspecific taxis and interspecific taxis, respectively.

We consider no-flux boundary conditions:

$$q_1(0,t) = q_1(a,t) = q_2(0,t) = q_2(a,t). \tag{5}$$

The model is completed by initial conditions:

$$u(x,0) = u^0(x), \quad v(x,0) = v^0(x)\,, \quad x \in [0,a]\,. \tag{6}$$

3 Analysis of model

The existence of a one-parameter family of stationary distributions in the system of two competing species was established [20, 21]. The analysis was performed for the taxis causing by the heterogeneity of the resource. This multistability is a consequence of the cosymmetry of the problem with additional relations on system parameters. Here we analyze the model taking into account interspecific and intraspecific taxis. We begin by defining the conditions under which cosymmetry is possible, i.e. there is a vector field L orthogonal to the vector field of the problem. If in this case there is an equilibrium (stationary solution) at which L does not vanish, then this equilibrium belongs to the family of stationary solutions [23].

Lemma 1. *The operator*

$$L = exp\left(-\frac{\varphi_1}{k_1}\right)(\kappa v, -u)^T$$

is a cosymmetry of the system (1)–(6), under the following conditions:

$$\{k_2, \alpha_2, \beta_2, \gamma_2, \eta_2\} = \kappa\{k_1, \alpha_1, \beta_1, \gamma_1, \eta_1\}. \tag{7}$$

Proof. Due to the definition of cosymmetry [23, 24], the vector L should be orthogonal to the right-hand side of system (1)–(5) for any arbitrary functions u and v, i.e.

$$\int_0^a \exp(-\varphi_1/k_1)\big([(k_1u' - u\varphi_1')' + \eta_1 u f_0]\kappa v - [(k_2v' - v\varphi_2')' + \eta_2 v f_0]u\big)dx = 0,$$

where φ_j are given (3), (4).

Using integration by parts and taking in account boundary conditions, this equality can be rewritten as $I_1 + I_2 = 0$, where

$$I_1 = \int_0^a \big\{ -[k_1u' - u\varphi_1'][\exp(-\varphi_1/k_1)\kappa v]' + [k_2v' - v\varphi_2'][\exp(-\varphi_1/k_1)u]'\big\}dx,$$

$$I_2 = \int_0^a \big\{ \left(1 - \frac{u+v}{p}\right)\exp(-\varphi_1/k_1)(\eta_1 u\kappa v - \eta_2 vu)\big\}dx.$$

After simplification we rewrite I_1 as

$$I_1 = \int_0^a uv\exp(-\varphi_1/k_1)\left(\frac{-\kappa\varphi_1'\varphi_1'}{k_1} + \frac{\varphi_2'\varphi_2'}{k_2}\right)dx.$$

Since the diffusion and taxis coefficients are restricted by the relation (7), we obtain that $I_1 = 0$. Using relation (7) for the growth parameters η_j we get $I_2 = 0$. This way, the lemma is proved, i.e. the operator L is indeed a cosymmetry of the system (1)–(6). □

Lemma 2. *The system (1)–(6) admits one-parameter family of stationary distributions*

$$u = (1-\theta)w(x), \quad v = \theta w(x), \quad \theta \in [0,1], \tag{8}$$

where $w(x)$ is a solution of boundary–value problem

$$\big(k_1 w' - w(\alpha_1 p' - (1-\theta)\beta_1 w' + \theta\gamma_1 w')\big)' + \eta_1 w\left(1 - \frac{w}{p}\right) = 0, \tag{9}$$

$$\big(k_1 w' - w(\alpha_1 p' - (1-\theta)\beta_1 w' + \theta\gamma_1 w')\big)|_{x=0,a} = 0. \tag{10}$$

Proof. The stationary solution of the system (1)–(6) satisfies the equations:

$$\big(k_1 u' - u(\alpha_1 p' - \beta_1 u' + \gamma_1 v')\big)' + \eta_1 u\left(1 - \frac{u+v}{p}\right) = 0,$$

$$\big(k_2 v' - v(\alpha_2 p' - \beta_2 v' + \gamma_2 u')\big)' + \eta_2 v\left(1 - \frac{u+v}{p}\right) = 0,$$

and boundary conditions (5). After substitution (8) we get:

$$(1-\theta)\left[(k_1 w' - w(\alpha_1 p' + \beta_1(1-\theta)w' + \gamma_1\theta w'))' + \eta_1 w\left(1 - \frac{w}{p}\right)\right] = 0,$$

$$\theta\left[(k_2 w' - w(\alpha_2 p' + \gamma_2(1-\theta)w' + \beta_2\theta w'))' + \eta_2 w\left(1 - \frac{w}{p}\right)\right] = 0.$$

These equations are satisfied for any θ due to (9) and relations (7). The same is valid for the boundary conditions. □

This lemma establishes the existence of a one-parameter family of equilibria or a continuum of stationary states. In a computational experiment, the stability of the members of this family was established, which means the multistability of the system (1)–(6).

Remark 1. *(see Ref. [20]) In the case $\gamma_1 = \gamma_2 = 0$ multistability occurs in the case $\beta_1 = \beta_2 = 0$ and*

$$k_2 = \kappa k_1, \quad \alpha_2 = \kappa\alpha_1, \quad \eta_2 = \kappa\eta_1,$$

as it was shown in [20]. This is a sequence of cosymmetry for (1)–(6) which may written as

$$L = \exp\left(-\frac{\alpha_1 p}{k_1}\right)(\kappa v, -u)^T. \tag{11}$$

Lemma 3. *The system (1)–(6) in the absence of an interspecific taxis ($\gamma_1 = \gamma_2 = 0$) and $\beta_1\beta_2 > 0$ has the following isolated solution:*

$$u = (1-\theta)w, \quad v = \theta w, \quad \theta = \frac{\beta_1\kappa}{\kappa\beta_1 + \beta_2},$$

where w is defined by the boundary value problem (9)–(10).

Proof. Here we employ the technique of cosymmetric defect and selective function [24]. After multiplying the right-hand part (1)–(5) on L (11) and integrating by parts, we obtain the cosymmetric defect D:

$$D = \int_0^a \{\beta_1 u u' \kappa \left[\exp\left(\frac{-\alpha_1 p}{k_1}\right) v\right]' - \beta_2 v v' \left[exp\left(\frac{-\alpha_1 p}{k_1}\right) u\right]' \}dx. \quad (12)$$

Substituting solution (9) to (12) and simplifying, we come to selective function in the form

$$S(\theta) = (1-\theta)\theta \int_0^a w w' \left[w \exp\left(-\frac{\alpha_1 p}{k_1}\right)\right]' \left[\kappa(1-\theta)\beta_1 - \theta\beta_2\right] \, dx\,. \quad (13)$$

So, the destruction of a family takes place. Instead of a continuous family, we have three distinguished solutions:

$$\theta = 0\,, \quad \theta = 1\,, \quad \theta = \frac{\beta_1 \kappa}{\kappa\beta_1 + \beta_2}\,.$$

The cases $\theta = 0$ and $\theta = 1$ correspond semipositive distributions of species and the third solution corresponds to the coexistence of species. □

For example, identical distributions $u = v$ are possible when $\beta_2/\beta_1 = \kappa$. The case of small β_j may be treated as a disturbance of cosymmetric situation. Stationary distribution with two nonzero species is stable when $\beta_j < 0$ and unstable for small $\beta_j > 0$. The case of moderate or large β_j does not allow analytic treating and requires numerical simulation.

4 Resource migration and intraspecific taxis

We employ a numerical scheme described in the Appendix to simulate population dynamics in the range $\Omega = [0, a]$, $a = 2$. Finite-difference mesh was used for spatial discretization. Runge-Kutta integrator of 4th order applied to solve the resulting system of ODEs in MATLAB. The formula for resource function corresponds to the case of an interval with one favorable zone:

$$p(x) = 0.5 \left[\sin\frac{\pi x}{a}\right]^3 + 0.1. \quad (14)$$

First, we consider the role of migration parameters for the single species and fix the growth parameter $\eta_1 = 3$. Fig. 4 shows the dependences of the average population density ($\overline{u} = \int_0^a u dx$) on the α_1 for several values of diffusion coefficient k_1 at $\beta_1 = 0$. One can see a direct correlation between k_1 and the optimal value of the migration parameter α_1 where the maximum of $\overline{u}$ is reached. Increasing k_1 implies growth of α_1. We should mention that variation of $\overline{u}$ is small. Role of growth parameter η_1 was analyzed in [18].

Fig. 4 shows the dependence of average population density on the intraspecific taxis parameter β_1. We presented results for three values of coefficient α_1 at $k_1 = 0.03$ and $\eta_1 = 3$. Calculations show that, optimal value of $\beta_1 = \beta_{opt}$ depends on the α_1. For $\alpha_1 = 0.12$, we found $\beta_{opt} = -0.0478$, and $\beta_{opt} = 0.032$

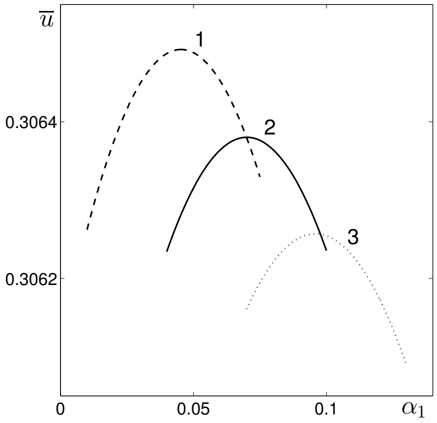


Рис. 1. The dependence of the average density of the population in the range on the migration parameter α_1: $k_1 = 0.02$ (curve 1), $k_1 = 0.03$ (2), $k_1 = 0.04$ (3); $\beta_1 = 0$, $\eta_1 = 3$

for $\alpha_1 = 0.03$. One can see that intraspecific parameter β_1 compensates non-optimal value α_1. At $\alpha_1 = \alpha_{opt}$, the optimal value $\beta_1 = \beta_{opt} \approx -0.0025$ is close to zero.

Now we present the results of a computational experiment for different values of migration parameters and build up maps with various scenarios for species, see Figures 3–7. Diffusion and growth coefficients were fixed: $k_1 = 0.03$, $k_2 = 0.04$, $\eta_1 = 3$, $\eta_2 = 4$. Through a computational experiment, we checked the stability of stationary distributions belonging to the family (8). We found such a convergence for different nonzero reasonable initial data.

For given parameters and resource (14), we found the optimal values of the parameters for both species: $\alpha_1 \approx 0.0701$ and $\alpha_2 \approx 0.0935$. In this case, the maximum filling of the range with each species occurs. Fig. 4 shows maps of α_1 and α_2 parameters which correspond to the coexistence of species (zone III) and the survival of each population (zones I and II). The optimal values of parameters α_1, α_2 respond to a common point for all zones. The following ratio on parameters holds:

$$\frac{k_2}{k_1} = \frac{\eta_2}{\eta_1} = \frac{\alpha_2}{\alpha_1} = \frac{4}{3}. \tag{15}$$

In this case, for $\beta_1{=}\beta_2{=}0$ the system (1)–(6) meets the cosymmetry condition, under which multistability is possible in the form of a family of stationary population distributions [17]. We remark only that point A lay on the solid line (cosymmetry case), in contrast with points B, C, D. We note that the

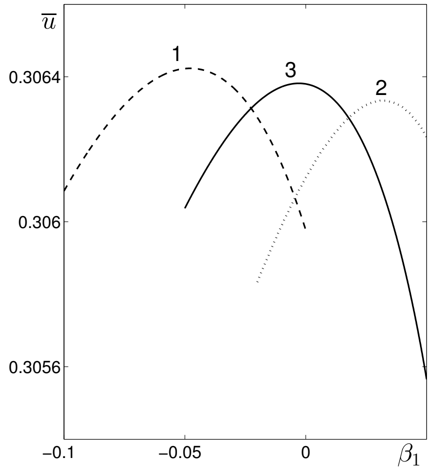


Рис. 2. The dependence of the average density of the population in the range on the migration parameter β_1: $\alpha_1 = 0.12$ (curve 1), $\alpha_1 = 0.03$ (2), α_1=α_{opt}=0.0701 (3)

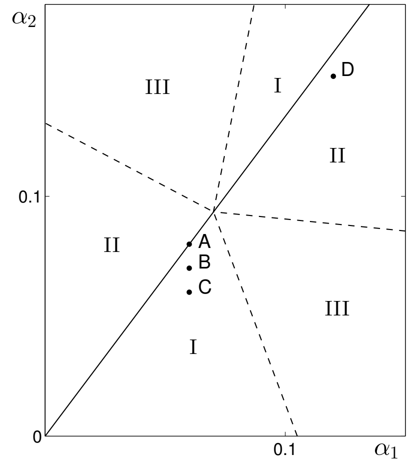
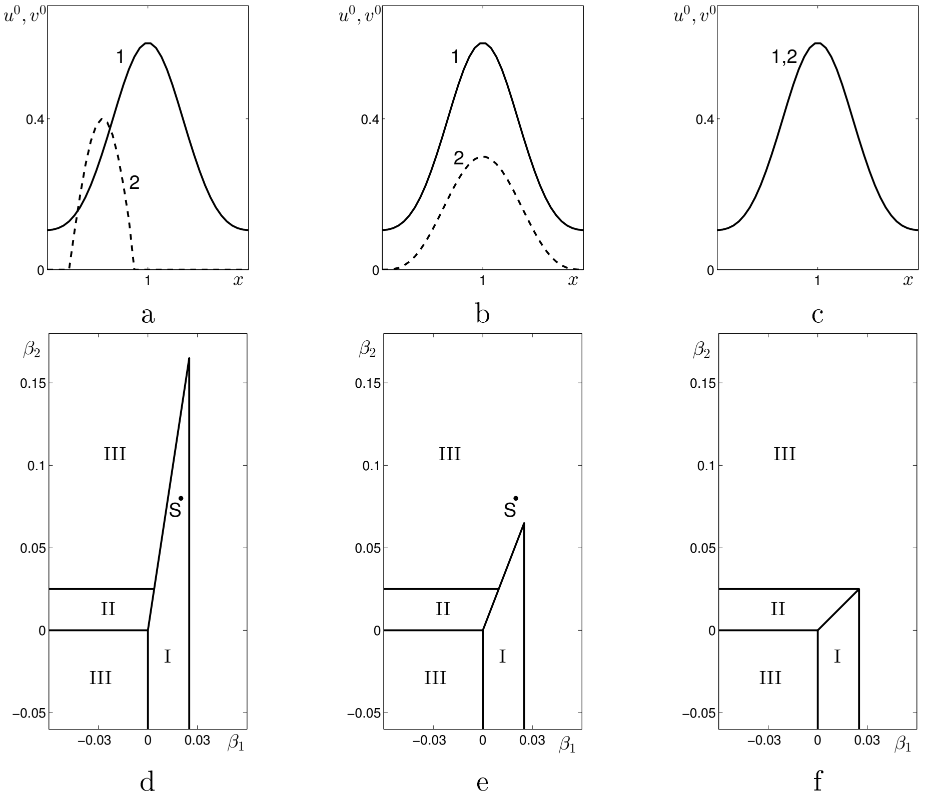


Рис. 3. Map of migration parameters: coexistence of species (III), survival u (I) or v (II); β_1=β_2=0

map in Fig. 4 and subsequent maps, see Figs. 4, 4, 5, have been built as a result of a direct computational experiment for values β_j with step 0.01 for each parameter.

5 Simulation of invasion and competition

We analyse of invasion, when the initial distributions of the resident population $u^0(x)$ corresponded to the complete filling of the ecological niche.



a b c

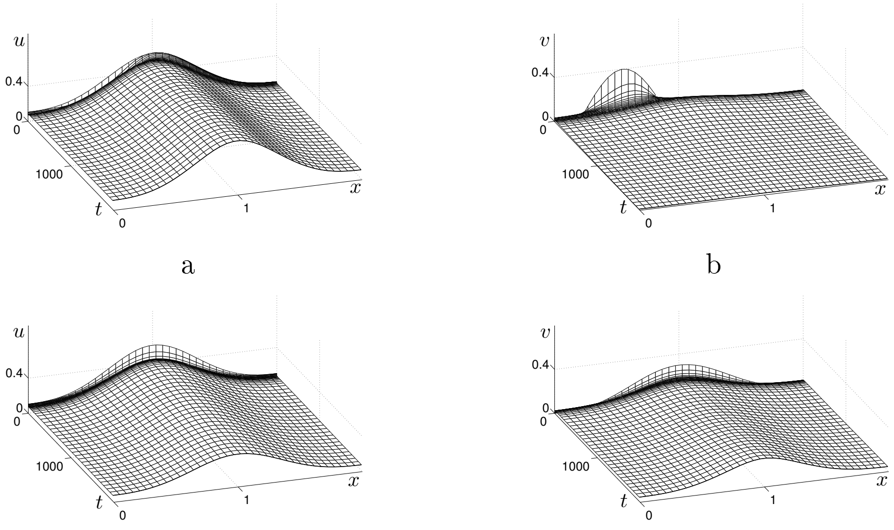
d e f

Рис. 4. Initial distributions u^0 (curve 1) and v^0 (2) – top, maps of migration parameters: coexistence of species (III), survival u (I) or v (II) – bottom: a – formula (16), b – $v^0(x) = 0.3\left[\sin\frac{\pi x}{a}\right]^3$, c – $v^0 = u^0$; α_1=0.06, α_2=0.08 (point A in Fig. 4)

Density $u^0(x)$ was found as a result of the numerical solution of the system (1)–(6) for $v = 0$. The initial distributions of invader are shown in Fig. 4. Distribution of invader for Fig. 4a is given by

$$v^0(x) = \begin{cases} 0.4\sin\frac{\pi x}{a}, & x \in l_v = [0.22, 0.81], \\ 0, & x \in \Omega \setminus l_v. \end{cases} \tag{16}$$

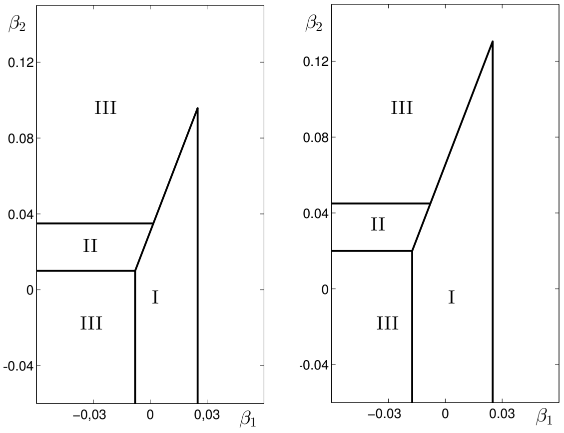
We performed numerical simulation for different values β_j and draw maps of migration parameters, corresponding to coexistence (III) or survival of only one of the species (I and II), see Fig. 4def. The calculations were carried out for the parameters corresponding to the point A in Fig. 4 ($\alpha_1 = 0.06$ and $\alpha_2 = 0.08$). With $\beta_1, \beta_2 < 0$, the coexistence of species is obtained regardless of the initial data. It should be noted that the case β_1=β_2=0 corresponds to the multistability of the system and this point is common for all zones. Unsuccessful invasion (elimination of invader) corresponds to zone I. The area of zone I decreases when density v^0 growing. Thus, the values of the



a b

c d

Рис. 5. Elimination of invader (top) and coexistence of species (bottom) for the initial distributions from Fig. 4a and Fig. 4b respectively; $\alpha_1 = 0.06$, $\alpha = 0.08$, $\beta_1 = 0.02$, $\beta_2 = 0.08$



a b

Рис. 6. Maps of migration parameters, corresponding to coexistence of species (III), survival of u (I) or v (II) for the initial distributions u^0 and v^0 given by curves 1, 2 on Fig. 4b: α_1=0.06; α_2=0.07 (a); α_1=0.06; α_2=0.06 (b)

migration parameters $\beta_1 = 0.02$, $\beta_2 = 0.08$ (point S) belong to the region I in Fig. 4d and the region III in Fig. 4e.

To reveal various invasive scenarios, we carried out calculations for parameters corresponding to point S in Fig. 4 ($\beta_1 = 0.02$, $\beta_2 = 0.08$). Fig. 4 presents the evolution of species densities over time for the initial distributions given in Fig. 4a and Fig. 4b. It shows the impact of initial distributions on the invasion process. Fig. 4ab demonstrates the elimination of the invader (unsuccessful invasion), and Fig. 4cd shows the coexistence of species (successful invasion).

When the coefficients α_1, α_2 do not satisfy the condition (15), the point $\beta_1 = \beta_2 = 0$ ceases to be common to zones I, II, III, as it was stated for the case $\alpha_1 = 0.06$, $\alpha_1 = 0.08$ (point A in Fig. 4), see Fig. 4. Below, we illustrate the situation with another choice of parameters α_j. Figures 4 and 5 respond to the initial distributions given in Fig. 4b. Fig. 4 presents maps of migration parameters β_1, β_2 corresponding to points B and C in Fig. 4. We should note that parameters $\beta_1 = \beta_2 = 0$ belong to the zone I in Fig. 4. The area of unsuccessful invasion (I) in Fig. 4b is larger than in Fig. 4a. This is because the distance to the solid line (cosymmetry case) from point C is greater than from point B, see Fig. 4.

Fig. 5 shows maps of parameters β_1 and β_2 when α_j are greater than the optimal values (point D in Fig. 4). In this case, the situation is opposite to that shown in Fig. 4.

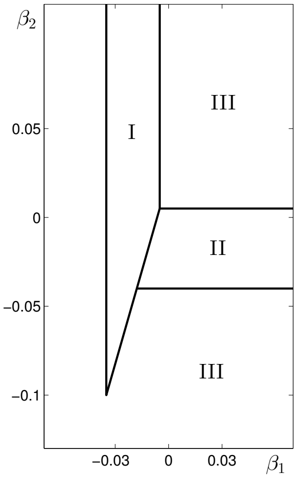


Рис. 7. Map of migration parameters: coexistence of species (III), survival u (I) or v (II) for the initial distributions u^0 and v^0 corresponding to curves 1, 2 in Fig. 4b; α_1=0.12; α_2=0.15

6 Conclusion

The impact of migration effects on the formation of population distributions has been studied. We considered the model of invasion describing the interplay of two species (resident and invader). The analysis concerned the case with migration fluxes depend on the intraspecific taxis and nonuniform distribution of the resource. We constructed, through simulation, the maps of migration parameters describing various scenarios of invasion and competition. Thus, we have pointed that intraspecific taxis may compensates non-optimal migration to resource and therefore influences on invasion.

Finally, we conclude that the cosymmetric approach allow to analyze the role of intraspecific taxis coefficients.

1) Negative values of intraspecific taxis coefficients stimulate diffusion for both species and prevent excessive concentration. This aids the coexistence of species.
2) Different sign coefficients imply the implementation of corresponding stable semi-positive solutions. A species in the case of a positive coefficient captures the resource and squeezes out a competitor with a negative coefficient of intraspecific taxis.
3) Direct numerical experiments show that the coexistence of species occurs at large positive coefficients of intraspecific taxis.
4) To predict invasion, the values of migration coefficients responsible for taxis per resource are important. Depending on the ratio of migration coefficient on resource to the optimal values, opposite scenarios are realized, see Fig. 4e and Fig. 5.
5) The dependence of the scenario on the initial distributions has been established.

A Discretization on spatial coordinates

For the numerical solution of the problem (1)–(6) the Method of Lines is applied, basing on a spatial discretization with staggered grids. The space variable x is handled by equidistant partitions $x_r = rh$, $r = 0, \dots, n$, $h = a/n$. Further, by u_r and v_r we denote the values of the population densities at the node x_r. For the calculation of the fluxes q_i in (1)–(2) we introduce the auxiliary grid $x_{r-1/2} = -h/2 + rh$, $r = 0, \dots, n+1$.

Further we use the following notion for the first order differential operator and the averaging operator respectively

$$(dw)_{r+\frac{1}{2}} = \frac{w_{r+1} - w_r}{h}, \quad (\delta w)_{r+\frac{1}{2}} = \frac{w_{r+1} + w_r}{2}.$$

Eventually, we come to the system of ordinary differential equations

$$\dot{u}_r = \left[-dq_1 + \eta_1 u \left(1 - \frac{u+v}{p}\right)\right]_r, \tag{17}$$

$$\dot{v}_r = \left[-dq_2 + \eta_2 v \left(1 - \frac{u+v}{p}\right)\right]_r, \tag{18}$$

$$p_r = \left[\frac{1}{h}\int_{x_{r-1/2}}^{x_{r+1/2}} \frac{dx}{p(x)}\right]^{-1}, \quad r = 0, \dots, n. \tag{19}$$

Here the fluxes $q_{i,r+1/2}$ $(r = 0, \ldots, n-1)$ are calculated from the formulas:

$$\begin{aligned} (q_1)_{r+1/2} &= -\left[k_1 du - \alpha_1 dp\delta u - \beta_1 du\delta u - \gamma_1 dv\delta u\right]_{r+1/2}, \qquad (20) \\ (q_2)_{r+1/2} &= -\left[k_2 dv - \alpha_2 dp\delta v - \beta_2 dv\delta v - \gamma_2 du\delta v\right]_{r+1/2}. \end{aligned}$$

Discrete versions of the boundary conditions are formulated using fictive nodes:

$$q_{i,-1/2} = -q_{i,1/2}, \quad q_{i,n+1/2} = -q_{i,n-1/2}, \quad i = 1, 2. \tag{21}$$

From (6) one obtains the initial conditions for (17)–(21):

$$u_r = u^0(x_r), \quad v_r = v^0(x_r), \quad r = 0, \ldots, n. \tag{22}$$

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