Mathematical Models of Ecological Niches Search

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Abstract

This work develops mathematical models of two communities escaping the competition. Models are represented by the Cauchy problem for the system of ordinary differential equations and boundary value problems for systems of partial differential equations.

Keywords: population, modeling, differential equations, stability, competition

1 Introduction

First mathematical models of competition designed for biological populations belong apparently to Volterra [1]. Within the framework of these models in a competitive environment, only that species “survives” which, ceteris paribus, breeds faster than others. However, in an environment of biological populations, there are many examples [2] of “peacefully” co-existence of species with different reproduction speeds in the same trophic resource. Constant competitive suppression of one community by another would significantly reduce the number of species. However, the fact of existence in the nature of a variety of animals and plants does not comply in general with this hypothesis [2]. The abundance of species can be explained by the fact that competition was in the past, and eventually species found its environmental niche in the form of other trophic re-
sources and habitats [2]. In today’s system of economic relations between the vast majority of small businesses compared to the number of large enterprises also requires an explanation [3-5]. Modern mathematical models describing the individual elements of a competitive relationship in the economic environment offer a variety of options for reducing the level of competition [6-8].

It is very difficult to compare the theoretical results with the experimental ones. Dynamics of population growth depends on many factors: weather conditions, the emergence of new trophic resources, accidents and many other reasons. The change of the habitat of the population leads to a change in the existing population system [2, 9-13]. The formation of spatial structure of population leads to the similar effect [14-16]. Under the influence of anthropogenous factors a redistribution of the territory takes place, which happens between populations and between groups of the same population. Emergence of toxins in the territory creates prerequisites for the changes in the metabolism of individuals, as well as for birth and death rates variations [17, 18]. Anthropogenous mechanical pressure on habitat [19, 20] and the human competition for resources and territories [2] lead to physical destruction of trophic resources and shelters [6, 21-25]. All these factors do not allow individuals of population and population as a whole to adapt to new conditions of life. Therefore theoretical results do not coincide well with the experimental data on a long-term investigation [2].

Volterra’s followers developed models admitting simultaneous stable existence of two competing species in a variety of biological communities [26-30] (medicine), [31, 32] (plant), [33, 34] (microbiology), [35, 36] (sport). In other words, they proposed the description options for “survival of the weakest species” among “strong,” which from the point of view of Volterra’s competition model would have to perish. The paper offers a model of avoiding competition or, in other words, the population’s escape to another ecological niche. The models take into account different strategies of population’s survival [2]. The models are represented by the boundary value problem for a system of nonlinear differential equations in partial derivatives. Homogeneous solutions were analyzed for stability. To build solutions of nonlinear equations, numerical methods are used, grid method and Bubnov — Galerkin method.

2 Mathematical model of competition (Volterra—Bigon)

For a description of the population dynamics of two competing species, the “modified” Volterra mathematical model is used that takes into account both interspecific and intraspecific competition

\[
\frac{du_1}{dt} = u_1(1 - u_1 - \gamma_1 u_2),
\]

\[
\frac{du_2}{dt} = \gamma_2 u_2(1 - u_2 - \gamma_2 u_1).
\]

(1)
In these equations, $u_1$ and $u_2$ are the quantities of two competing populations, $\gamma$, $\gamma_1$, $\gamma_2$ are positive constants.

The system of equations (1) has four stationary points

1. $u_1 = 0, \ u_2 = 0$.
2. $u_1 = 1, \ u_2 = 0$.
3. $u_1 = 0, \ u_2 = 1$.
4. $u_1 = (1-\gamma_1)/(1-\gamma_1\gamma_2), \ u_2 = (1-\gamma_2)/(1-\gamma_1\gamma_2)$ if $\gamma_1 > 1$ and $\gamma_2 > 1$, or $\gamma_1 < 1$ and $\gamma_2 < 1$.

The first stationary point is an unstable, the second will be stable if $\gamma_1 < 1$ and $\gamma_2 > 1$, and the third one - if $\gamma_1 > 1$ and $\gamma_2 < 1$. The forth stationary point is implemented and is stable if $\gamma_1 < 1$ and $\gamma_2 < 1$.

Thus, the model of competition (1) allows the simultaneous stable existence of two competing populations.

3 “Active” escape from the competition

Evolution of the species occurred in such a way that under the influence of external factors and internal changes in the organisms of individual species the internal metabolism was changing, and they gradually began to use the new trophic resources [2]. At that, the species continued to exist together. This can be accommodated by assuming that in the model (1) $\gamma_1$ and $\gamma_2$ are time functions. Then the model of the “escape” from the competition takes the form of

$$
\frac{du_1}{dt} = u_1(1-u_1-\gamma_1u_2),
\frac{du_2}{dt} = \gamma u_2(1-u_2-\gamma_2u_1),
\frac{d\gamma_1}{dt} = -\alpha_1\gamma_1\varphi_1(u_1,u_2,t),
\frac{d\gamma_2}{dt} = -\alpha_2\gamma_2\varphi_2(u_1,u_2,t).
$$

(2)

In this model, it is assumed that $\varphi_1(u_1,u_2,t) \geq 0$ and $\varphi_2(u_1,u_2,t) \geq 0$. That is, it is considered that the functions $\gamma_1(t)$ and $\gamma_2(t)$ are not increasing time function. This enables a gradual escape from the competitive relationship. Adoption as functions of $\varphi_1(t)$ and $\varphi_2(t)$

$$
\varphi_1(t) = 0 \text{ if } \frac{du_1}{dt} > 0, \text{ and } \varphi_1(t) = 1 \text{ if } \frac{du_1}{dt} \leq 0,
\varphi_2(t) = 0 \text{ if } \frac{du_2}{dt} > 0, \text{ and } \varphi_2(t) = 1 \text{ if } \frac{du_2}{dt} \leq 0
$$

Thus, the model of competition (1) allows the simultaneous stable existence of two competing populations.
means that the populations “feel” reducing their numbers and immediately “react” to it. This model assumes that each population is trying to reduce the impact on them by a competing population.

4 “Passive” avoidance of competition

This model assumes that the avoidance of competition occurs “naturally.”

\[
\begin{align*}
\frac{du_1}{dt} &= u_1 (1 - u_1 - \gamma_1 e^{-\alpha_1 u_2}), \\
\frac{du_2}{dt} &= \gamma_2 u_2 (1 - u_2 - \gamma_2 e^{-\alpha_2 u_1}).
\end{align*}
\]

Here it is assumed, that the functions \( f_1(u_2) \) and \( f_2(u_1) \) are positive and decreasing functions its arguments, and \( \lim_{u_2 \to \infty} f_1(u_2) = 0, \lim_{u_1 \to \infty} f_2(u_1) = 0 \). For instance, such conditions satisfy the function \( f_1(u_2) = e^{-\alpha_1 u_2} \) and \( f_2(u_1) = e^{-\alpha_2 u_1} \).

A non-trivial stationary point of the system of equations (3), wherein \( 0 < u_1 < 1 \) and \( 0 < u_2 < 1 \), is the solution of the system of equations

\[
\begin{align*}
1 - u_1 - \gamma_1 e^{-\alpha_1 u_2} &= 0, \\
1 - u_2 - \gamma_2 e^{-\alpha_2 u_1} &= 0.
\end{align*}
\]

The function \( f(z) = 1 - \alpha e^{-\beta z} \) in the point \( z = 0 \) is positive (\( f(0) = 1 \)) and decreasing (\( f'(0) = -\alpha \)); and in the point \( z = 1 \), it will take positive values if the inequality is \( \alpha e^{-\beta} < 1 \). When the inequality is \( \beta < 1 \) in the interval of \([0,1] \), \( f(z) \) will be monotonically decreasing function. If both of the inequalities are \( \gamma_1 e^{-\alpha_1} < 1 \), \( \gamma_2 e^{-\alpha_2} < 1 \), \( \alpha_1 < 1 \), and \( \alpha_2 < 1 \), the system of equations (4) has a unique solution satisfying \( 0 < u_1 < 1 \) and \( 0 < u_2 < 1 \). When the inequality is \( \beta > 1 \), the function \( f(z) \) will be minimal \([0,1] \) in the point \( z = 1/\beta \). Therefore, when the inequality is \( \alpha_1 > 1 \) or \( \alpha_2 > 1 \), the system of equations (4), depending on the values of the constants in the equation (3) can have two solutions satisfying the conditions \( 0 < u_1 < 1 \) and \( 0 < u_2 < 1 \). Thus, this model may have three stationary points.

The eigenvalues of the Jacobi matrix of the right side of the equations (3) are the roots of the polynomial

\[
\lambda^2 + (u_1 + \gamma_2 u_2) \lambda + \gamma_1 u_2 (1 - \gamma_1 \gamma_2 e^{-\alpha_1 \alpha_2} (1 - \alpha_1 u_2)(1 - \alpha_2 u_1)) = 0.
\]

If both of the inequalities are \( \gamma_1 e^{-\alpha_1} < 1 \), \( \gamma_2 e^{-\alpha_2} < 1 \), \( \alpha_1 < 1 \), and \( \alpha_2 < 1 \), the constant term of this polynomial is positive, its roots have negative real parts, and the non-trivial stationary point is therefore stable.
5 Change of the habitat

In competition, one of the species can gradually avoid the competitive relationship by moving to another trophic resource. Suppose there are two competing populations in a common area or a trophic resource, and one of them can move to a trophic resource not available to the other populations. Let \( v_i \) be the number of the first population in a new trophic resource. Then the model (1) goes into the model

\[
\begin{align*}
\frac{du_1}{dt} &= u_1(1-u_1-\gamma u_2) - bu_1, \\
\frac{du_2}{dt} &= \gamma u_2(1-u_2-\gamma u_1), \\
\frac{dv_1}{dt} &= \gamma v_1(1-v_1) + bu_1,
\end{align*}
\]

(5)

where \( \gamma_v \) is the constant, and \( b \) is the rate of transition of the first population species to a new trophic resource.

As follows from the analysis of equations (1), when \( \gamma_1 > 1 \) and \( \gamma_2 < 1 \), the first population in the model (1) dies. With \( \gamma_1 \) and \( \gamma_2 \) satisfying these inequalities, the stationary point of the system (5)

\[
u_1 = 0, \quad v_1 = 1, \quad u_2 = 1
\]

will be stable since all the eigenvalues

\[
\lambda_1 = -(\gamma_1 + b - 1), \quad \lambda_2 = -\gamma, \quad \lambda_3 = -\gamma_v
\]

of the Jacobi matrix of the right hand side of equation (5) in the fixed point will be negative. This corresponds to a complete transition of the first population to a new trophic resource.

If both of the inequalities are \( \gamma_1 < 1 \) and \( \gamma_2 < 1 \), the system of equations may have a non-trivial stationary point

\[
u_1 = \frac{1-b-\gamma_1}{1-\gamma_1\gamma_2}, \quad u_2 = \frac{1-\gamma_2(1-b)}{1-\gamma_1\gamma_2}, \quad v_1 = \frac{1}{2} \left(1 + \sqrt{1+4bu_1/\gamma_v}\right),
\]

if the inequality is \( b + \gamma_1 < 1 \). At that, the eigenvalues of the Jacobi matrix of the right side of the equation (5) being the roots of the equation

\[
\left(\lambda + \gamma_v \sqrt{1+4bu_1/\gamma_v}\right)\left(\lambda^2 + (u_1 + \gamma u_2) + \gamma u_2 u_1(1-\gamma_1\gamma_2)\right) = 0,
\]

will have negative real parts. That is, in case of implementation, this stationary point is stable.
6 Heterogeneous areal

Populations live in areas with different trophic functions in different parts of it. Moving species within areas occurs randomly. The intensity of the competitive relationship may depend on what part of the area it takes place. When building models of interacting populations in the territory, the mathematical apparatus of continuum mechanics is used [28, 37-40]. The competition model in the interval [0,l] in this case is a system of differential equations in partial derivatives

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= D_1 \frac{\partial^2 u_1}{\partial x^2} + u_1(1-u_1 - \gamma_1(x)u_2), \\
\frac{\partial u_2}{\partial t} &= D_2 \frac{\partial^2 u_2}{\partial x^2} + \gamma u_2(1-u_2 - \gamma_2(x)u_1).
\end{align*}
\]

(6)

In these the equations parameters \(D_1\) and \(D_2\) characterize mobility of individuals of populations. Functions \(\gamma_1(x)\) and \(\gamma_2(x)\) determine the intensity of the competitive relationship.

The system of equations is added by the boundary conditions

at \(x = 0\): \(u_1 = 0\), \(u_2 = 0\) \hspace{1cm} (7)

at \(x = l\): \(\frac{\partial u_1}{\partial x} = 0\), \(\frac{\partial u_2}{\partial x} = 0\). \hspace{1cm} (8)

If the functions \(\gamma_1(x)\) and \(\gamma_2(x)\) in some points of the interval are greater than one and in some points are less than one, the system of equations (6) may have heterogeneous solutions.

The number of populations \(M_1(t)\) and \(M_2(t)\) on the time cell \(t\) are calculated by the following formula

\[
M_1 = \int_0^t u_1(t,x) \, dx, \quad M_2 = \int_0^t u_2(t,x) \, dx.
\]

To assess the influence of parameters \(D_1\) and \(D_2\), we assume that the solution of the equations (6) with boundary conditions (7)-(8) as a first approximation is described by the functions

\[
\begin{align*}
u_1(t,x) &= A(t) \sin \frac{\pi x}{2l}, \\
u_2(t,x) &= B(t) \sin \frac{\pi x}{2l}.
\end{align*}
\]

Then with the application of the variational method Bubnov-Galerkin equations (10)-(11) [38] followed by the equations for the coefficients \(A(t)\) and \(B(t)\)

\[
\begin{align*}
dA &= -\frac{\pi^2}{4} D_1 A + A - \frac{8}{3\pi} A(A + \gamma_1 B), \\
dB &= -\frac{\pi^2}{4} D_2 B + \gamma B - \frac{8}{3\pi} \gamma B(\gamma_2 A + B).
\end{align*}
\]

(9)
The system of equations (9) has four stationary points.

1. $A = 0$, $B = 0$.

2. $A = 0$, $B = \frac{3\pi}{8} \left(1 - \frac{\pi^2}{4\gamma} D_2\right)$.

3. $A = \frac{3\pi}{8} \left(1 - \frac{\pi^2}{4} D_1\right)$, $B = 0$.

4. $A = \frac{1}{1 - \gamma_1\gamma_2} \frac{3\pi}{8} \left(1 - \gamma_1 - \frac{\pi^2}{4} D_1 + \frac{\pi^2}{4\gamma} D_2\right)$,

$$B = \frac{1}{1 - \gamma_1\gamma_2} \frac{3\pi}{8} \left(1 - \gamma_2 - \frac{\pi^2}{4\gamma} D_2 + \frac{\pi^2}{4} D_1\right).$$

The number of populations on the time cell are calculated by the formulae $M_1 = 2A/\pi$ and $M_2 = 2B/\pi$. Therefore, only positive values of $A$ and $B$ have the physical meaning. Unlike model (1), the coordinates of stationary points depend not only on the parameters $\gamma_1$ and $\gamma_2$, and parameters $D_1$ and $D_2$. Taking values of $D_2 > 4\gamma / \pi^2$ the second stationary point doesn’t make sense, and taking values of $D_1 > 4/ \pi^2$ the third doesn’t make sense.

In the performance of inequalities $\gamma_1 < 1$ and $\gamma_2 < 1$ unlike model (2) the existence region of positive values $A$ and $B$ for the fourth fixed point in the coordinate system $(D_1, D_2)$ is determined by a system of inequalities.

$$\frac{\pi^2}{4} D_1 < 1, \quad \frac{\pi^2}{4\gamma} D_2 < 1, \quad 0 < \frac{4}{\pi^2} \left(1 - \gamma_1\right) - D_1 + \frac{1}{\gamma} D_2, \quad 0 < \frac{4}{\pi^2} \left(1 - \gamma_2\right) - \frac{1}{\gamma} D_2 + D_1.$$ 

In performance of inequality $\gamma_1\gamma_2 < 1$ the second and third stationary points will be unstable. Eigenvalues of the Jacobian matrix in the fourth stationary point are the roots of the quadratic equation

$$\lambda^2 + \frac{8}{3\pi} (A + \gamma B) \lambda + \left(\frac{8}{3\pi}\right)^2 \gamma (1 - \gamma_1\gamma_2) AB = 0,$$

that has complex conjugated roots. Therefore the fourth stationary point will be steady if it is realized. Thus in model (6)-(8) the escape from the competitive relationship could be executed due to the change of mobility of individuals of one of the populations.

7 Numerical experiment

Assume that the two populations do not compete throughout their areal, but only in one part and $\gamma_1$ and $\gamma_2$ depend on coordinate $x$. 

\[ \gamma_1 = \begin{cases} 0, & \text{if } x < l - b, \\ c_1, & \text{if } x \geq l - b. \end{cases} \]

\[ \gamma_2 = \begin{cases} 0, & \text{if } x < l - b, \\ c_2, & \text{if } x \geq l - b. \end{cases} \]

The solution for the system of equations (6) for these functions are is obtained by applying numerical methods.

These algorithms have been developed to solution for non-linear equations in partial derivatives. In one case the discretization of differential operators by finite differences has been done. The obtaining system of non-linear algebraic equations has been solved by simple iteration method. Numerical solution of equations (6) for the case \( D_1 = 0.001, \ D_2 = 0.01, \ c_1 = 1.2 \) and \( c_2 = 0.9, \ l = 1, \ b = l/2 \) on the time cell \( t = 100 \) is given at Figure 1 - 2. Figure 1 shows the dependence \( u_1 = u_1(x) \) and \( u_2 = u_2(x) \) on the time cell \( t = 100 \). In Figure 2 shows the dependence of the stationary values \( M_1, M_2 \) and the parameter \( b \).

![Figure 1: the dependence of the functions \( u_1 = u_1(x) \) and \( u_2 = u_2(x) \) in the time of \( t = \infty \).](image1)

![Figure 2: the dependence \( M_1(t = \infty) \) and \( M_2(t = \infty) \) on \( b \).](image2)
8 Travelling wave

The solution of equations (6) are looking for in the form of a travelling wave propagating with \( v \) the velocity from \(-\infty\) to \(+\infty\).

That is, we believe that the solution depends only on one argument \( z = x - vt \). Under this assumption equation (6) is converted to the form

\[
\frac{du_1}{dz} = w_1, \\
D_1 \frac{dw_1}{dz} = -vw_1 - u_1(1-u_1 - \gamma_1 u_2), \\
\frac{du_2}{dz} = w_2, \\
D_2 \frac{dw_2}{dz} = -vw_2 - \gamma u_2(1-u_2 - \gamma u_1).
\]  
(10)

These equations are added conditions imposed on the functions \( u_1 \) and \( u_2 \) [1],

at \( x = -\infty \): \( u_1 = (1-\gamma_1)/(1-\gamma_1 \gamma_2) \), \( u_2 = (1-\gamma_2)/(1-\gamma_1 \gamma_2) \);

at \( x = +\infty \): \( u_1 = 1 \), \( u_2 = 0 \).

These conditions correspond to the case where the area on which there is only one population with a linear density of population \( u_1 = 1 \), the second population moves into. In this case, under the coexistence equilibration is observed at the point \( x = -\infty \). Supposed that \( \gamma_1 < 1 \) and \( \gamma_2 < 1 \).

Eigenvalues of the Jacobian matrix of the right part of the equations (10)

\[
J = \begin{pmatrix}
0 & 1 & 0 & 0 \\
\frac{-1}{D_1} (1-2u_1 - \gamma_1 u_2) & \frac{-v}{D_1} & \frac{1}{D_1} \gamma_1 u_1 & 0 \\
0 & 0 & 0 & 1 \\
\frac{\gamma_2}{D_2} u_2 & 0 & -\frac{\gamma}{D_2} (1-2u_2 - \gamma_2 u_1) & -\frac{v}{D_2}
\end{pmatrix}
\]

at \( u_1 = (1-\gamma_1)/(1-\gamma_1 \gamma_2) \), \( u_2 = (1-\gamma_2)/(1-\gamma_1 \gamma_2) \) are roots of the equation

\[
\lambda^2 + \frac{v}{D_1} \lambda - \frac{1}{D_1} u_1 \left( \lambda^2 + \frac{v}{D_2} \lambda - \frac{\gamma}{D_2} u_2 \right) = 0. 
\]  
(11)

At the point \( x = -\infty \) the function \( u_1 = u_1(z) \) must be increasing, but the function \( u_2 = u_2(z) \) -decreasing. Equation (11) has two positive and two negative roots. Therefore, we can get a decision on which the function \( u_1 = u_1(z) \) increases and the function \( u_2 = u_2(z) \) decreases.

Under \( u_1 = 1 \) and \( u_2 = 0 \) eigenvalues of the Jacobian matrix satisfy the equations
\[ \lambda^2 + \frac{v}{D_1} \lambda - \frac{u_1}{D_1} = 0, \quad \lambda^2 + \frac{v}{D_2} \lambda + \gamma \frac{u_2}{D_2} = 0. \]

The first equation has roots of opposite signs, and the second may have complex-conjugate roots. In this case, the function \( u_2 = u_2(z) \) can take negative values. Under such condition \( v > 2\sqrt{\gamma D_2/(1-\gamma_2)/(1-\gamma_1\gamma_2)} \) the second equation will have negative roots. In this case we can obtain a such solution that at \( x = +\infty \) the function is decreasing and \( u_1 = u_1(z) \) - increasing. This decision will represent a travelling wave for \( u_2 = u_2(x-\nu t) \), propagating from \( x = +\infty \) to \( x = \infty \), and for the function \( u_1 = u_1(x-\nu t) \) is "running" at a velocity no less than \( \nu = 2\sqrt{\gamma D_2/(1-\gamma_2)/(1-\gamma_1\gamma_2)} \).

The solution of equations (6) with boundary conditions at \( x = 0 \) and at \( x = l \)
\[ \frac{\partial u_1}{\partial x} = \frac{\partial u_2}{\partial x} = 0 \]
and initial conditions
\[ u_1 = 1, \quad u_2 = u_2^0 \delta(0), \]
where \( \delta(x) \) is delta-function, and \( u_2^0 \) is a small positive value. This was calculated by applying numerical methods. Over time, in the neighborhood of \( x = 0 \) the values \( u_1(x) \) tended to value \( (1-\gamma_1)/(1-\gamma_1\gamma_2) \), and \( u_2(x) \) - to \( (1-\gamma_2)/(1-\gamma_1\gamma_2) \). Figure 3 shows the dependence \( u_1 = u_1(x) \) and \( u_2 = u_2(x) \) at \( \gamma=1, \quad \gamma_1=0.8, \quad \gamma_2=0.5, \quad D_1=0.00001, \quad D_2=0.00001 \) on the time cell \( t = 100 \) and \( t=200 \). The velocity of wave propagation was close to the value \( \nu = 2\sqrt{\gamma D_2/(1-\gamma_2)/(1-\gamma_1\gamma_2)} \).

![Figure 3](image-url) The shape of the travelling wave in the time \( t=100 \) and \( t=200 \).
9 Conclusion

The above models of two competing populations allow us to describe the mechanisms of search of ecological niches by different populations in the course of their evolution.

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