ABOUT A COMPETITION-COLONIZATION MATHEMATICAL MODEL

MODELUL MATEMATIC DE TIP COMPETIȚIE - COLONIZARE

BURDUJAN I.
University of Agricultural Sciences and Veterinary Medicine Iaşi

Abstract. *The well known competition-colonization mathematical model, ob-tainned by extending Levins' model, is analyzed. It is a two-parameter model for which some results on dynamics and bifurcation are deduced. The nature of the equilibria is found. Finally, a biological interpretation for the results is given.*

Rezumat. *Se analizează modelul bine-cunoscut al interacțiunii de tip competiție-colonizare obținut extinzând modelul lui Levins. Acesta este un model cu doi parametri pentru care se deduc rezultate de dinamică şi biburcație. Se stabileşte natura punctelor de echilibru. În sfârşit, se dă interpretarea biologică a rezulta-telor obținute.*

A BRIEF HYSTORY

This paper deals with a particular family of planar vector fields which models the dynamics of two populations which are in a competition-colonization interaction.

The study of population change has a very long history. It begins, probably, with the book by Leonardo Pisano (1202), continues with the papers by A. J. Lotka and V. Volterra, and it is even today of a great actuality. Maybe, the first important model, which had intrigued the whole scientific world, was the population model due to T. R. Malthus (1798); unfortunately, it was very soon proved that it is fairly unrealistic. Some defects of Malthus' model were corrected by Pierre-François Verhulst, in 1835, which proposed the following mathematical model:

$$\frac{\mathbf{dN}}{\mathbf{dt}} = \mathbf{rN}\left(\mathbf{1} - \frac{\mathbf{N}}{\mathbf{K}}\right). \tag{1}$$

Here **N(t)** denotes the population volume at time **t**, **r** is the *intrinsic rate of growth* (i.e., it is the maximum per capita growth rate), **K** is the *carrying capacity* of the environment (which is determined by the available sustaining resources and it is the nonzero equilibrium population size); **r** and **K** are positive constants. This model was named, by Verhulst, the *logistic growth* in a population. The easiest way to include space in the logistic model is to use the *metapopulation framework* in which an infinite number of sites are linked by migration. The analogue of the logistic model in the metapopulation framework is the Levins' model. The evolutionary process consisting in the colonization of a territory by a single species is described by the following differential equation

(2) $$\frac{\mathbf{du}}{\mathbf{dt}} = \lambda\mathbf{u}(1-\mathbf{u}) - \mathbf{u}\ ,$$

where **u(t)** denotes the fraction of the occupied sites at time **t**. In this model, the *colonization rate* is equal to the parameter **λ** times the product of the fraction of occupied sites and the fraction of vacant sites. Deterministic models with global dispersal, originated in physics, are usually called *mean-field models*. The idea is to replace complicated local interactions by an "effective field" produced by all other particles and to use the *mass-action law* to describe the dynamics.

Multispecies models can be built from single species models by incorporating interactions between species.

As it is well known, there exist three main types of interaction:

(i) if the growth rate of one population is decreased and the other increased the populations are in a *predator-prey* situation,

(ii) if the growth rate of each population is decreased, then the interaction is a *competition*,

(iii) if each population's growth rate is enhanced then the interaction is called *mutualism* or *symbiosis.*

Recall that the classical two-species Lotka-Volterra competition model, is given by

(3) $$\begin{cases} \dfrac{dN_1}{dt} = r_1N_1\left(1-\dfrac{N_1}{K_1}-\alpha_{12}\dfrac{N_2}{K_1}\right) \\ \dfrac{dN_2}{dt} = r_2N_2\left(1-\dfrac{N_2}{K_2}-\alpha_{21}\dfrac{N_1}{K_2}\right), \end{cases}$$

where $\mathbf{N_i(t)}$ is the abundance of species **i** at time **t**, $\mathbf{r_1}$, $\mathbf{K_1}$, $\mathbf{r_2}$, $\mathbf{K_2}$, α_{12} and α_{21}. are all positive constants; **r**'s are the linear birth rates, **K**'s are the carrying capacities, and α_{12} and α_{21} measure the competitive effect of $\mathbf{N_2}$ on $\mathbf{N_1}$ and of $\mathbf{N_1}$ on $\mathbf{N_2}$, respectively. The three types of interaction are reflected in the specific ranges for the parameters in (3). In the particular case when one of the species is not affected by the presence of the other, i.e., one of the parameters α_{12} and α_{21} is zero, one obtains a *competition-colonization interaction*. This time, the Lotka-Volterra model becomes improper; it will be replaced by a specific model that will be presented in the next section.

MATHEMATICAL MODEL FOR A COMPETITION-COLONIZATION INTERACTION

We shall present and study the mathematical model for competition-colonization interaction described by C. Neuhauser in [7], and Tilman&Kareiva in [9]. The competition-colonization interaction is a mechanism that is frequently invoked to explain plant coexistence in the mountain grasslands. Some grass species allocate more biomass to their roots, which makes them better *competitors* for nitrogen, while others allocate more to seeds, which makes them better *colonizers*. Often, such species coexist. Their interaction can be well illustrated in a model in which the species are hierarchically ordered. This model is usually known as the *grass-bushes-trees* model. In the two-species mean-field version, the mathematical model is given by the following system of ordinary differential equations:

$$(4)\qquad \begin{cases} \dfrac{du_1}{dt} = \lambda_1 u_1(1-u_1) - u_1 \\ \dfrac{du_2}{dt} = \lambda_2 u_2(1-u_1-u_2) - u_2 - \lambda_1 u_1 u_2, \end{cases}$$

where $u_i(t)$ is the density of species i at time t and λ_1, λ_2 is are positive parameters which take parts in the so-called the colonization rates. Biological reasons impose to consider the phase space be the first quadrant in the plane (u_1, u_2) together the positive half-axes. The two populations coexist when (u_1, u_2) is an equilibrium point of (4) laying in the first quadrant of the (u_1, u_2)-plane. The system (4) has the following four equilibrium points:

$$O(0,0),\ A\left(\frac{\lambda_1-1}{\lambda_1}, 0\right), B\left(0, \frac{\lambda_2-1}{\lambda_2}\right), C\left(\frac{\lambda_1-1}{\lambda_1}, \frac{\lambda_2-\lambda_1^2}{\lambda_1\lambda_2}\right).$$

All (together) these equilibrium points have a biological interpretation if and only if $\lambda_1 > 1$, $\lambda_2 > 1$ and $\lambda_2 > \lambda_1^2$. More exactly, both species become extinct in **O**, species 1 survives and species 2 becomes extinct in **A**, species 1 becomes extinct and species 2 survives in **B**, and the two species coexist in **C**. In the particular case when $\lambda_1 = \lambda_2 = 1$ the four equillibria coincide, i.e., the only (geometric) equilibrium point is **O**, i.e., both species extinct in long time. Another particular important case is when $\lambda_1 > 1$ and $\lambda_2 = \lambda_1^2$; this time **A** is a double equilibrium.

In order to study the nature of an equilibrium point $E(u_1, u_2)$ we consider the Jacobian matrix of the right hands in (4), namely

$$J_E(u_1,u_2) = \begin{bmatrix} \lambda_1 - 1 - 2\lambda_1 u_1 & 0 \\ -(\lambda_1+\lambda_2)u_2 & \lambda_2 - 1 - 2\lambda_2 u_2 - (\lambda_1+\lambda_2)u_1 \end{bmatrix}.$$

$J_O(0, 0)$ has the characteristic values $s_1 = \lambda_1 - 1$, $s_2 = \lambda_2 - 1$, and, consequently, when $\lambda_1 > 1$, $\lambda_2 > 1$, **O** is a hyperbolic equilibrium for the system; more exactly **O** is a repulsive (unstable) node. Since $J_A\left((\lambda_1-1)/\lambda_1, 0\right)$ has the eigenvalues $s_1 = 1 - \lambda_1 < 0$ and $s_2 = = \dfrac{\lambda_2-\lambda_1^2}{\lambda_1} > 0$, then **A** is a saddle point. For the equilibrium point **B** the Jacobian matrix is $J_B\left(0, \dfrac{\lambda_2-1}{\lambda_2}\right)$, it has the eigenvalues $s_1 = \lambda_1 - 1 > 0$ and $s_2 = 1 - \lambda_2 < 0$, so that it results **B** is also a saddle point. Finally, $J_C\left(\dfrac{\lambda_1-1}{\lambda_1}, \dfrac{\lambda_2-\lambda_1^2}{\lambda_2}\right)$ has the eigenvalues $s_1 = 1 - \lambda_1 < 0$ and $s_2 = -\dfrac{\lambda_2-\lambda_1^2}{\lambda_1} < 0$, i.e., **C** is an attractive (stable) node. Consequently, if $\boldsymbol{\lambda_1 > 1}$ and $\boldsymbol{\lambda_2 > \lambda_1^2}$ the two species coexist in long time.

SKETCHING A QUANTITATIVE ANALYSIS

Obviously, the equation (4_1) can be solved and, for $\boldsymbol{\lambda_1 \neq 1}$, one gets

$$\mathbf{u_1(t) = \frac{\lambda_1 - 1}{\lambda_1 + C_1(\lambda_1 - 1)e^{-(\lambda_1 - 1)t}}}\,; \tag{5}$$

in case $\boldsymbol{\lambda_1 = 1}$ it results

$$\mathbf{u_1(t) = \frac{1}{t + C}}\,. \tag{6}$$

Consequently, if $\boldsymbol{\lambda_1 > 1}$ for $\mathbf{t \to \infty}$ it results

$$\mathbf{u_1(\infty) = \lim_{t \to \infty} u_1(t) = \frac{\lambda_1 - 1}{\lambda_1}}$$

while, if $\boldsymbol{\lambda_1 \leq 1}$ then $\mathbf{u_1(\infty) = \lim_{t \to \infty} u_1(t) = 0}$. This means that the species 1 can survive only in the case $\boldsymbol{\lambda_1 > 1}$. That is why, in the followings, we are interested in the case $\boldsymbol{\lambda_1>1}$, only. This time, if the initial state of species 1 is $\mathbf{u_1(0) = a}$, then $\mathbf{C_1 = \frac{\lambda_1 - 1 - a\lambda_1}{a(\lambda_1 - 1)}}$ what implies that $\mathbf{C_1 > 0}$ whenever $\boldsymbol{\lambda_1 > 1}$ and $\mathbf{0 < a < \frac{\lambda_1 - 1}{\lambda_1}}$. In Fig.1 is represented the function $\mathbf{u_1}$ corresponding to $\boldsymbol{\lambda_1 = 2}$ and $\mathbf{C_1 \in \{-0.8, -0.6, -0.4, -0.2, 0, 0.2, 0.4, 0.6, 0.8\}}$ (i.e., for the initial values $\mathbf{a \in \{0.83, 0.71, 0.63, 0.55, 0.5, 0.45, 0.41, 0.38, 0.36\}}$, respectively).

For any $\boldsymbol{\lambda_1 > 1}$ the graphic representations of $\mathbf{u_1(t)}$ in dependence with the values of the parameter $\mathbf{C_1}$ look like in the Fig. 1, except the fact that the separatrix $\mathbf{u_1(t) = 0.5}$ is replaced by the separatrix $\mathbf{u_1(t)=(\lambda_1-1)/\lambda_1}$.

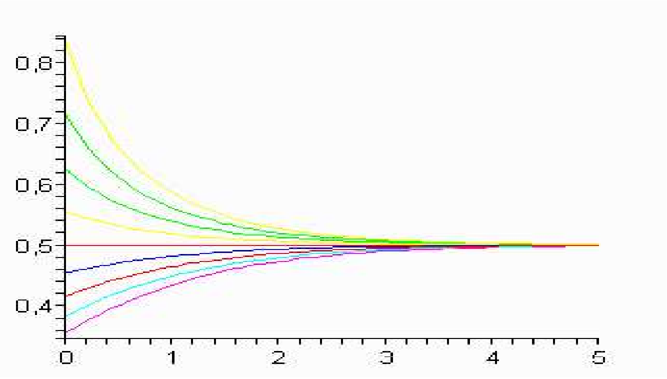

Fig. 1 - The graph of $\mathbf{u_1}$ for $\boldsymbol{\lambda_1 = 2}$ and $\mathbf{a \in \{0.83, 0.71, 0.63, 0.55, 0.5, 0.45, 0.41, 0.38, 0.36\}}$

If $\lambda_1 < 1$ the graphic representation of $u_1(t)$ is similar to that in Fig.2.

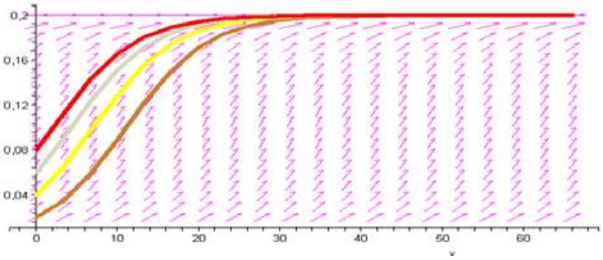

Figure 2 - The phase portrait for (4_1) and the graph of u_1 for $\lambda_1 = 0.2$ and $a \in \{0.02, 0.04, 0.08\}$

$$u_2(t) = \frac{e^{(\lambda_2-1)t}\left(\lambda_1 e^{(\lambda_1-1)t} + C_1(\lambda_1-1)\right)^{-\frac{\lambda_1+\lambda_2}{\lambda_1}}}{\lambda_2 \int e^{(\lambda_2-1)t}\left(\lambda_1 e^{(\lambda_1-1)t} + C_1(\lambda_1-1)\right)^{-\frac{\lambda_1+\lambda_2}{\lambda_1}} dt + C_2}$$

In order to determine the value of the integral

$$I = \int e^{(\lambda_2-1)t}\left(\lambda_1 e^{(\lambda_1-1)t} + C_1(\lambda_1-1)\right)^{-\frac{\lambda_1+\lambda_2}{\lambda_1}} dt$$

we denote $a = \lambda_2 - 1$, $b = \lambda_1 - 1$, $p = 1 + \lambda_2/\lambda_1$, $q = C_1(\lambda_1 - 1)$. After using the substitution $t = \ln x$ I becomes $I_1 = \int x^{a-1}(\lambda_1 x^b + q)^{-\frac{\lambda_1+\lambda_2}{\lambda_1}} dx$. According with the well known Tchebychev result the indefinite integral in u_2 is a linear combination of elementary functions if and only if λ_1, λ_2 are rational numbers and satisfy to one (at least) of the following three conditions:

$$1°.\ \lambda_2/\lambda_1 \in N^*, \qquad 2°.\ \frac{\lambda_2-1}{\lambda_1-1} \in N^*, \qquad 3°.\ \frac{\lambda_2-1}{\lambda_1-1} + \frac{\lambda_2}{\lambda_1} \in N^*.$$

CONCLUDING REMARKS

In the first quadrant of the (λ_1, λ_2) – plan, we have to distinguish nine zones (corresponding to topologically equivalent dynamical systems), namely:

I. $\lambda_1 < 1, \lambda_2 < 1, \lambda_2 < \lambda_1^2$,
II. $\lambda_1 > 1, \lambda_2 < 1, \lambda_2 < \lambda_1^2$,
III. $\lambda_1 > 1, \lambda_2 > 1, \lambda_2 < \lambda_1^2$,
IV. $\lambda_1 > 1, \lambda_2 > 1, \lambda_2 > \lambda_1^2$,
V. $\lambda_1 < 1, \lambda_2 > 1, \lambda_2 > \lambda_1^2$.
VI. $\lambda_1 < 1, \lambda_2 < 1, \lambda_2 > \lambda_1^2$,
VII. $\lambda_1 = 1$,
VIII. $\lambda_2 = 1$,
IX. $\lambda_2 = \lambda_1^2$.

According with the position of (λ_1, λ_2) in the one or other zone, we get:

I. O is the only equilibrium point**,** which is a stable node; this time both species extinct in long time,

II. the dynamical system has two equilibria: **O** - a saddle point and **A** - a stable node; this time, corresponding to **A**, species 1 survives while the species 2 becomes extinct,

III. the dynamical system has three equilibria: **O** - an unstable node, **A** - a stable node and **B** - a saddle point,

IV. the dynamical system has four equilibria: **O** - an unstable node, **A** - a saddle point, **B** a saddle point and **C** a stable node, i.e., the two species can coexist (the inferior competitor- species 2- can coexists with the superior competitor – species 1 – if and only if its birth rate exceeds the square of the birth rate of species 1),

V. the dynamical system has two equilibria: **O** an unstable node and **B** a stable node,

VI. the dynamical system has two equilibria: **O** an unstable node and **C** a saddle point.

The cases VII, VIII, IX imply one-parameter models which can be easily studied one by one.

All these assertions are confirmed by the corresponding phase portrait. For example, the case I has the phase portrait presented in Fig. 3.

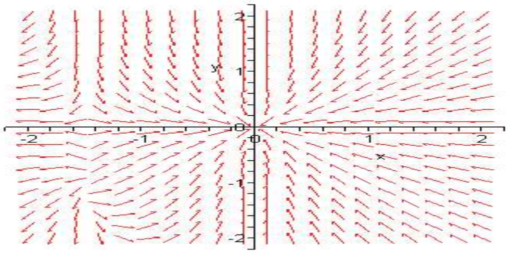

Figure 3 -The phase portrait of (4) for **$\lambda_1 = 0.4$, $\lambda_2 = 0.2$**

In this case, it must be remarked that even if the equilibria **A, B, C** have no biological interpretation they necessarily have an important contribution in the structure of the phase portrait.

The cases **$\lambda_1 = 1$, $\lambda_2 = 1$** or $\lambda_2 = \lambda_1^2$ can be analyzed one by one; they lead to one-parameter dynamical systems.

REFERENCES

1. **Barbu V.**, 1985 - *Differential Equations* (Romanian). Ed. Junimea, Iaşi.
2. **Brauer F., Castillo-Chavez C.,** 2001 - *Mathematical Models in Population Biology and Epidemiology,* Texts in Applied Mathematics, **40**, Springer-Verlag, New-York.
3. **Burdujan I.,** 2005 **-** *On a Criss-cross Model for the Dynamics of Infectious Diseases*, Ann. of USAMV Iaşi, Hort., tom XLVIII, v.2, seria Hortic. Proc. Ann. Symposium “Mathematics applied in Biology &Biophysics”, U:A.S.V.M.-Iaşi, p. 85-94.
4. **Burdujan I.,** 2003 **-** *Dynamical systems as epidemic models*, Ann. USAMV Iaşi, T. XLVI, v.2, Hortic., Proc. Ann. Symposium “Mathematics applied in Biology &Biophysics”, U:S.A.M.V.-Iaşi, p.63-86.
5. **Dumitriu N., Burdujan I., Dimitriu G.,** 2005 **-** *Mathematical Models in Biology and Environmental Sciences,* Ed. Cermi.
6. **Keshet L.**, 2004 **-** *Mathematical Models in Population Biology*, SIAM *Classics in Applied Mathematics,* **46**, SIAM.
7. **Neuhauser C.,** 2001 **-** *Mathematical Challenges in Spatial Ecology*, Amer. Math. Soc. Notices, v. 48, n. 11, p.1304-1314.
8. **Perko L.,** 2001 **-** *Differential Equations and Dynamical Systems,*Texts in Applied Mathematics, 7, Springer-Verlag.
9. **Tilman D., Kareiva P.,** 1997 **-** *Spatial Ecology,* Princeton University Press.