ENERGY AND INFORMATION ASPECTS OF SELF-ORGANISATION OF ECOLOGICAL SYSTEMS: MATHEMATICAL MODELS AND INTERPRETATIONS

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ABSTRACT

Models of the long-term ecological successions are considered. The model of open Eigen's hypercycle has been used to model the process. It is shown that ecological succession is a complex process with ability for self-organisation. It is distinguished two type of self-organisation: by adjusting system control parameters or by change of quantity of its components. The first type is determined by bifurcation properties of the system. In both cases the process is under essential influence of a level of flows of matter and information through the system.

INTRODUCTION

Majority of natural, economic, are social systems are complex, i.e. it consists of a large number of elements, each of which is also quite complex. A large number of links between elements of such systems and their complexity determine their essentially nonlinear behaviour. Usage of nonlinear models and relevant research methods allows to describe different types of structures, ways to their stabilization or transition to instability.
Basics of the theory of nonlinear systems were formed by such classics as J.W. Rayleigh, J.L d'Alembert, J.H. Poincare. Their ideas were developed in the works of O.L. Lyapunov (Lyapunov 1950), A.A. Andronov (Andronov et al. 1966), V.I. Arnold (Arnold et al. 1986) within the qualitative theory of differential equations. One of stages of of the theory was synergetics, developed by H. Haken (Haken 1980) and I. Prigogine (Prigogine and Nicolis 1979).
The first "customer" of the nonlinear theory was physics. However, with the development of systems approach and cybernetic theory the use of the nonlinear ideas was extended and covered the processes of a different nature, including ecological ones. Thus, in the paper (Samarskiy and Mihailov 2001) A.P. Mikhailov showed a spatial self-organization of populations basing on a diffusion-reaction equation. The mosaic structure of ecological macrosystems was studied in the article (Riitters K.H. et al. 2009). Interesting results on the self-organization in spatially distributed plant communities were obtained in (Kolobov and Frisman 2008). Mainly, the researches were focused on analysis of spatial and spatial-temporal processes of self-organization.
In the current paper self-organisation is considered for systems with lumped parameters. The model of open Eigen's hypercycle (Chernyshenko 2005) is used to describe such ecological processes of self-organisation as primary succession.

GENERALIZED MODEL

Let's consider the model

$$\frac{dx_i}{dt} = \left(f_i(X) - S_0^{-1} \sum_{j=1}^{n} x_j f_j(X) \right) x_i,\ i = \overline{1,n}. \qquad (1)$$

Here $x_i(t),\ i = \overline{1,n}$ are variables, which reflect size of associations; $f_i(X),\ i = \overline{1,n}$ are functions of interaction between the associations; S_0 is capacity of environment; $X = [x_1,...,x_n]^T$.

Summing up all equations of the system (1), one can get:

$$\frac{d\sum_{i=1}^{n} x_i}{dt} = \left(1 - S_0^{-1} \sum_{i=1}^{n} x_i \right) \sum_{i=1}^{n} x_i f_i(X).$$

Let's analyse this expression. It is evident, that some of equilibrium points of the model (1) have the property, that the sum of their coordinates equals S_0, and there is the stationary point with all zero coordinates.
Let's consider only the positive region of the phase space $\{x_1,...,x_n\}$. If $f_i(X) > 0,\ i = \overline{1,n}$, then the system state tends to the equilibrium point with the total size of the associations equals to S_0. If $f_i(X) < 0,\ i = \overline{1,n}$ and the sum of initial coordinates less than S_0, then all the coordinates will tend to zero. If one of the coordinates is larger than S_0, the sum of coordinates grows.

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SELF-ORGANIZATION BY ADJUSTING CONTROL PARAMETERS

Let interaction between the associations will be described by Allen's functions

$$F_1(X)=N-x_1,\quad F_i(X)=a_{i-1}x_{i-1}-x_i,\ i=\overline{2,n}, \tag{2}$$

where a_i, $i=\overline{1,n-1}$, $a_i>0$ are coefficients, which reflect a level of dependence of association i from the previous one i-1; $N>0$ is a coefficient, which determine equilibrium size of the first association, when it develops alone. These functions describe an interaction between associations, when the first stage of succession is characterised by logistic rise, and growth rate of each further stage depends linearly on association size on previous stage.

As it was shown in (Ruzich 2011), the two-dimensional model of open Eigen's hypercycle has 6 equilibrium points: $(0,0)$, $(0,S_0)$, $(N,0)$, $(S_0,0)$, $\left(\frac{S_0+N}{a_1+2},\frac{S_0(a_1+1)-N}{a_1+2}\right)$, (N,a_1N). Characteristics of stability of these points are represented in Table 1.

Using standard methodology (Andronov et al. 1966), behaviour of trajectories near degenerate equilibrium points can be found. Thus, the point $(0,0)$ is an equilibrium points of the "saddle-node" type for any positive values of the model parameters; point $(N,0)$ is the same, if $S_0/N=1$; point $(S_0,0)$ is the same, if $S_0/N=(a_1+1)^{-1}$; point (N,a_1N) is the same, if $S_0/N=a_1+1$.

For any set of positive parameters, there is only one attractor, namely stable node, in the two-dimensional case of the model (1)-(2).

If size of ecological niche is small ($S_0/N<(a_1+1)^{-1}$), only one association is able to exist in the ecosystem. When $S_0/N=(a_1+1)^{-1}$, the point $\left(\frac{S_0+N}{a_1+2},\frac{S_0(a_1+1)-N}{a_1+2}\right)$ appears in the first quarter of the phase portrait (which is interesting from practical point of view). In this bifurcation point the appearance of second association in the ecosystem takes place. If $S_0/N>a_1+1$, there is surplus of resources in the system, two associations cannot utilise all of them. In the two-dimension system, naturally, we cannot expect origin of a third association, but it is really a case in the three-dimension model.

In the article (Chernyshenko and Ruzich 2013a) it was shown that 11 equilibrium points of the 3-D model of open Eigen's hypercycle (1)-(2) exist:

P_1: $(0,0,0)$; P_2: $(N,0,0)$; P_3: $(N,a_1N,0)$; P_4: (N,a_1N,a_1a_2N); P_5: $(S_0,0,0)$; P_6: $(0,S_0,0)$; P_7: $(0,0,S_0)$; P_8: $\left(\frac{N+S_0}{a_1+2},\frac{S_0(a_1+1)-N}{a_1+2},0\right)$; P_9: $\left(\frac{S_0+N}{2},0,\frac{S_0-N}{2}\right)$; P_{10}: $\left(0,\frac{S_0}{a_2+2},\frac{S_0(a_2+1)}{a_2+2}\right)$;

P_{11}: $\left(\frac{S_0+N(a_2+2)}{a_1a_2+a_1+a_2+3},\frac{(a_1+1)S_0+N(a_1-1)}{a_1a_2+a_1+a_2+3},\frac{(a_1a_2+a_2+1)S_0-N(a_1+a_2+1)}{a_1a_2+a_1+a_2+3}\right)$.

It was proved that:

P_1 and P_2 are unstable complicated equilibrium points;

P_3 is a saddle with two-dimension unstable subspace, if $S_0/N\in(0,\ a_1+1)$, or two-dimension stable subspace, if $S_0/N\in(a_1+1,\ +\infty)$;

P_4 is a saddle with two-dimension stable subspace, if $S_0/N\in(0,1+a_1+a_1a_2)$, or stable equilibrium point (node or spiral point) if $S_0/N\in(1+a_1+a_1a_2,+\infty)$;

P_5 is a stable node, if $S_0/N\in\left(0,\ (a_1+1)^{-1}\right)$, a saddle with two-dimension stable subspace, if $S_0/N\in\left((a_1+1)^{-1},\ 1\right)$, and an unstable node, if $S_0/N\in(1,\ +\infty)$;

P_6 and P_7 are unstable nodes;

P_8 is a saddle with two-dimension stable subspace, if $\frac{S_0}{N}\in\left(0,\frac{1}{a_1+1}\right)\cup\left(\frac{1+a_1+a_2}{1+a_2+a_1a_2},\ 1+a_1\right)$, a stable node, if $\frac{S_0}{N}\in\left(\frac{1}{a_1+1},\frac{1+a_1+a_2}{1+a_2+a_1a_2}\right)$, and a saddle with two-dimension unstable subspace, if $S_0/N\in(1+a_1,\ +\infty)$;

P_9 is a saddle with two-dimension unstable subspace, if

$$\begin{cases}\frac{S_0}{N}\in\left(\frac{1-a_1}{1+a_1},1\right)\cup(1,+\infty),\\ a_1\in(0,1),\end{cases}\cup\begin{cases}\frac{S_0}{N}\in(0,1)\cup(1,+\infty),\\ a_1\in[1,+\infty),\end{cases}$$

and with two-dimension stable subspace, if

$$S_0/N\in\left(0,\ (1-a_1)/(1+a_1)\right),\qquad a_1\in(0,\ 1),$$

P_{10} is a saddle with two-dimension unstable subspace;

P_{11} is a saddle with two-dimension unstable subspace, if

$$S_0/N\in\left(0,\ (1-a_1)/(1+a_1)\right),\qquad a_1\in(0,\ 1),$$

or a stable equilibrium point (node or spiral point) if

$$\frac{S_0}{N}\in\left(\frac{a_1+a_2+1}{1+a_2+a_1a_2},1+a_1+a_1a_2\right),$$

Table 1: Stability of Equilibrium Points

Points \ Intervals	$\frac{S_0}{N} \in$			
	$\left(0;\frac{1}{a_1+1}\right)$	$\left(\frac{1}{a_1+1};1\right)$	$(1;a_1+1)$	$(a_1+1;+\infty)$
$(0,0)$	Saddle-node	Saddle-node	Saddle-node	Saddle-node
$(0,S_0)$	Unstable node	Unstable node	Unstable node	Unstable node
$(N,0)$	Unstable node	Unstable node	Saddle	Saddle
$(S_0,0)$	Stable node	Saddle	Unstable node	Unstable node
$\left(\frac{S_0+N}{a_1+2},\frac{S_0(a_1+1)-N}{a_1+2}\right)$	Saddle	Stable node	Stable node	Saddle
(N,a_1N)	Saddle	Saddle	Saddle	Stable node

or a saddle with two-dimension unstable subspace, if

$$\left\{\frac{S_0}{N}\in\left(\frac{1-a_1}{a_2+1},\ \frac{a_1+a_2+1}{a_2+a_1a_2+1}\right];\ a_1\in(0,1)\right\}\cup$$
$$\cup\left\{\begin{array}{l} a_1\in[1,+\infty), \\ \frac{S_0}{N}\in\left(0,\ \frac{a_1+a_2+1}{a_2+a_1a_2+1}\right],\end{array}\right.\cup$$
$$\cup\frac{S_0}{N}\in(a_1+a_1a_2+1,\ +\infty).$$

So, the system of three associations has several equilibrium points, which are equivalent to ones of the system with two associations: if $S_0/N<(a_1+1)^{-1}$ size of ecological niche is so small, that only one association is able to exist in the ecosystem; then the second association appears ($\frac{N}{a_1+1}<S_0<\frac{1+a_1+a_2}{1+a_2+a_1a_2}N$). But the third association appears in this system earlier than surplus of resources in system with two associations takes place. It occurs, when $\frac{1+a_1+a_2}{1+a_2+a_1a_2}N<S_0<(1+a_1+a_1a_2)N$. And, at last, if $S_0>(1+a_1+a_1a_2)N$, there is surplus of resources for all three associations.

The same situation was described for ecosystems of higher dimension (Chernyshenko and Ruzich 2013b). It was shown that all stages of ecological succession are accompanied by bifurcations in the positive region of the phase space. Also it was shown that the process of stages' change (in the course of continuous increasing of S_0) is linear.

The process is even more complex. It can be considered as self-organization by adjusting control parameters. The size of ecological niche S_0 can play role of such parameter. It is adjusted by flows of matter and energy through the ecosystems. Total size of associations, which are inherent for each stage of succession, is equal to the size of ecological niche. And in the case of surplus of resources only, the adjusting does not work.

SELF-ORGANIZATION BY SELECTION OF QUANTITY OF COMPONENTS

What is a way of the system dynamics, when some external impact changes essentially sizes of some associations? Let's consider the 3-D model (1)-(2). Use ideas of method of inner bifurcations (Chernyshenko 2005) for analysis of size dynamics of an association depending on size of others. Let's define the stationary values of x_2, considering all the other variables as parameters:

$$x_2^{(1)}=0, \tag{3}$$

$$x_2^{(2)}=\frac{S_0+a_1x_1+a_2x_3}{2}-\frac{\sqrt{(S_0+a_1x_1+a_2x_3)^2+4(Nx_1-x_1^2-Sa_1x_1-x_3^2)}}{2}, \tag{4}$$

$$x_2^{(3)}=\frac{S_0+a_1x_1+a_2x_3}{2}+\frac{\sqrt{(S_0+a_1x_1+a_2x_3)^2+4(Nx_1-x_1^2-Sa_1x_1-x_3^2)}}{2}. \tag{5}$$

Similar procedure can be done for x_3:

$$x_3^{(1)}=0, \tag{6}$$

$$x_3^{(2)} = \frac{S_0 + a_2 x_2}{2} - \frac{\sqrt{(S_0 - a_2 x_2)^2 + 4(Nx_1 + a_1 x_1 x_2 - x_1^2 - x_2^2)}}{2}, \quad (7)$$

$$x_3^{(3)} = \frac{S_0 + a_2 x_2}{2} + \frac{\sqrt{(S_0 - a_2 x_2)^2 + 4(Nx_1 + a_1 x_1 x_2 - x_1^2 - x_2^2)}}{2}. \quad (8)$$

Let $x_2 = x_2^{(1)}$ (the second association is absent). Then the equilibrium sizes x_3 of the third association equal:

$$x_3^{(1)} = 0\,,\ x_1 > \frac{N + \sqrt{N^2 + S_0^2}}{2}; \quad (9)$$

$$x_3^{(2)} = \frac{S_0}{2} - \frac{\sqrt{S^2 + 4x_1(N - x_1)}}{2}, \quad 0 < x_1 < \frac{N + \sqrt{N^2 + S_0^2}}{2}, \quad (10)$$

or

$$x_3^{(3)} = \frac{S_0}{2} + \frac{\sqrt{S_0{}^2 + 4x_1(N - x_1)}}{2}, \quad 0 < x_1 < \frac{N + \sqrt{N^2 + S_0^2}}{2}. \quad (11)$$

State (3) is stable if

$$\frac{x_1^2 - Nx_1 + x_3^2}{S} + a_1 x_1 < 0\,. \quad (12)$$

If the size of the first association is sufficiently big (the case 9), than the third association will disappear ($x_3 = 0$), and inequality (12) is right if

$$0 < x_1 < N - S_0 a_1\,,\ S_0 < N / a_1\,.$$

But it means that the condition in (9) cannot be satisfied, so this state of the system is unstable. The system will try to restore its structure.

In the case, when the size of the first association is sufficiently small, the size of the third association is determined by (10). The inequality (12) is right if

$$0 < x_1 < \frac{N - S_0 a_1}{a_1^2 + 1}\,,\ S_0 < N / a_1\,. \quad (13)$$

But the state (10) is stable if

$$N < x_1 < \left(N + \sqrt{N^2 + S_0^2}\right)/2\,,$$

and it does not satisfy the condition (13). So, the mechanism of homeostasis is triggered in this case.

If the size x_3 of the third association is determined by (11), then state (3) is unstable too.

Let's define the stationary value of x_1, considering all the other variables as parameters:

$$x_1^{(1)} = 0\,, \quad (14)$$

$$x_1^{(2)} = \frac{N + S_0 + a_1 x_2}{2} - \frac{\sqrt{(N + S_0 + a_1 x_2)^2 + 4(NS_0 - x_2^2 - a_2 x_2 x_3 - x_3^2)}}{2}, \quad (15)$$

$$x_1^{(3)} = \frac{N + S_0 + a_1 x_2}{2} + \frac{\sqrt{(N + S_0 + a_1 x_2)^2 + 4(NS_0 - x_2^2 - a_2 x_2 x_3 - x_3^2)}}{2}. \quad (16)$$

Let the first association is excluded from the system ($x_1 = x_1^{(1)}$). The state (14) is stable if

$$N + \frac{x_2^2 - a_2 x_2 x_3 + x_3^2}{S_0} < 0\,. \quad (17)$$

Then size of the second association x_2, depending on the initial values, is:

$$x_2^{(1)} = 0\,,\ \begin{cases} 0 < a_2 < 2, \\ 0 < x_3 < \dfrac{S_0}{2 - a_2}, \end{cases} \quad (18)$$

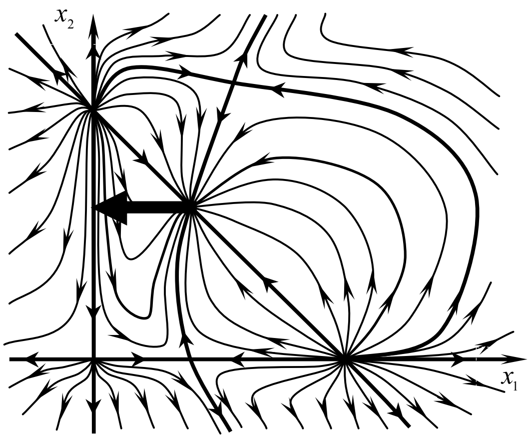
$$x_2^{(2)} = \frac{S_0 + a_2 x_3}{2} - \frac{\sqrt{(S_0 + a_2 x_3)^2 - 4x_3^2}}{2}, \quad \begin{cases} a_2 \ge 2, \\ x_3 \ge 0, \end{cases} \cup \begin{cases} 0 < a_2 < 2, \\ x_3 > \dfrac{S_0}{2 - a_2}, \end{cases} \quad (19)$$

$$x_2^{(3)} = \frac{S_0 + a_2 x_3}{2} + \frac{\sqrt{(S_0 + a_2 x_3)^2 - 4x_3^2}}{2}, \quad \begin{cases} a_2 \ge 2, \\ x_3 \ge 0, \end{cases} \cup \begin{cases} 0 < a_2 < 2, \\ x_3 > \dfrac{S_0}{2 - a_2}. \end{cases} \quad (20)$$

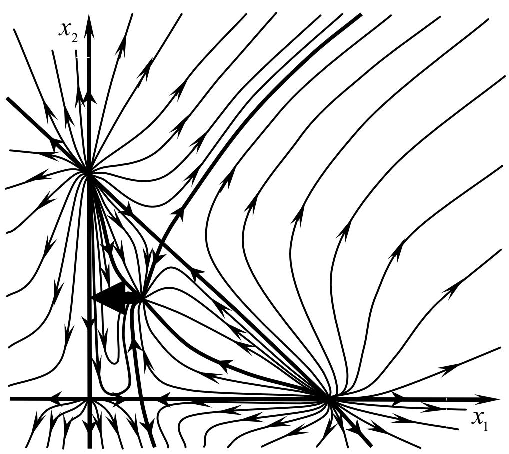
If the size of the second association x_2 equals zero (18), then inequality (17) cannot be true, and the state (14) is unstable.

If size of the second association x_2 is determined by (19), then condition (17) is not satisfied. The state (20) is unstable, and the system tends to the state (19). Correspondingly, the state (14) is unstable, and the situation can be interpreted as restoring by the system its structure.

The situation has been considered from practical point of view in the article (Ruzich 2012). Any association in the ecosystem is based of previous associations and their elimination is a reason of system's destabilization. Exclusion of the first association leads to full degradation of system in the both cases: of total sharing of limited resources (Fig.1, a) and of surplus of resources (Fig.1, b). The origin of coordinates is always unstable point; therefore even low-level introduction of the first association's representatives activates mechanism of system restoration.



a)



b)

Figure 1: Removal of the First Association in Case of:
a) Limited Resources; b) Excess of Resources.

So, self-organization of an ecosystem can take place in the form of changing quantity of its components. Sometimes such process can be degenerative: elimination of an element can provoke simplification of the system. Though, as it was shown above, the new state is usually unstable, and the system has homeostatic mechanisms of restoring initial structure.

CONCLUSION

The model of open Eigen's hypercycle (1)-(2) was considered as a model of successions in an ecosystem. Two types of self-organisation in ecological macrosystems, closely connected with successions, were illustrated: self-organisation by adjusting parameters and self-organisation by change of quantity of components.

The size of ecological niche S_0 is an adjusting parameter in the first case. Value of this parameter determines number of associations, which can exist in the ecosystem. Total size of all associations is usually equals to size of corresponding ecological niche, and only in the case of surplus it is smaller. According to "the fourth law of the thermodynamics" ecosystem tends to take form, allowing to maximise use of energy potential of environment. This result is consistent with theoretical studies (Harper and Clatworthy 1963; Ovsjanikov and Pasekov 1990). Flows of energy through the system determine this type of self-organisation.

Mechanism of the second type of self-organisation can be described by the following statement: new association, originated during successions, oppresses, but keeps associations-predecessors (associations, which are inherent to the system with smaller size of ecological niche). If some association-predecessor is eliminated from the system, all its successors are under danger to be eliminated also. Successions do not change associations, but make layers of them. In the same time, "the fourth law of the thermodynamics" still works: when association-predecessor is reintroduced to the ecosystem, it restores its structure, which is determined by energy potential of the environment.

The considered processes can take pace not only in ecological systems, but also in social and economic ones. For example, scientific and technological progress have all the properties of successions, innovations do not destroy previous technologies, but create new layers on them. So, the model can find not only ecological applications.

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