

BIFURCATION MODEL OF SUCCESSIONS IN ECOSYSTEMS

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ABSTRACT

Models of the long-term ecological successions are considered. Succession process is considered as step-by-step changing of dominant association. The model of open Eigen's hypercycle has been used for modeling of the process. Qualitative analysis for three-dimension case has been carried out, and local bifurcations have been investigated. The process of succession can be interpreted as system's choosing a proper level of complexity (or dimension) depending on the capacity of environment (the size of ecological niche). Connections between changing a state of the system and bifurcations in phase space is shown.

INTRODUCTION

Processes, which take place in ecosystems, are extremely complex; their theoretical investigation should be based on abstract concepts, which describe some general properties of the systems on the global level. One of such theoretical simplifications is the concept of succession. The succession is considered as consecutive change of one ecosystem (phitocoenose, biogeocoenose, etc.) by other in a certain area of environment. It is not a simple transformation, but a process of simplification of the structure of the ecosystem. Any state of a system can be characterised by dominate association of species (usually phototrophic), which are "amalgamated" by other satellite species by trophic relations. Such associations appear as the key elements of biogeocoenose.

Stochastic models (Culver 1981; Lippe et al. 1985; Logofet 1997; Lourival 2011) are often used for description of succession processes. The transition probability is basic parameter which determinate the dynamics of the system in such models. Such approach can be useful for simulation the system dynamics of the system, but does not reflect moving forces of the process.

Concerning long-term successions, many researches (Sukachev 1972; Kogan 1977; Tilman 1990; Rabotnov 1992) emphasized essential role of competition for this processes. Use of models of competition of the Volterra type (Lepš and Prach 1981; Chakrabarti et al. 1995;

Chernyshenko 1995; Weis et al. 2007) for description of succession process looks as very reasonable.

Additionally to competition, there is evident positive influence of previous stages for next ones. Similar relationships between elements are described by the well-known model of hypercycle (Eigen and Schuster 1979). In the same time, relations between associations during succession have not cyclic character; the hypercycle should be open (Chernyshenko 2005). The model of open hypercycle is similar, but not equivalent to Lotka-Volterra models of the competition or "predator-prey" type. The model reflects a connection between final stage of succession (and corresponding level of complexity of the system) and the size of ecological niche. In the contribution a three-dimension case of the open hypercycle model is considered; change of the ecosystem state is interpreted mathematically as a consequence of bifurcations.

OPEN EIGEN'S HYPERCYCLE

Let's consider dynamics of ecosystem, which is described by the three-dimension open hypercycle model:

$$\begin{cases} \frac{dx_1}{dt} = \left(F_1(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_1, \\ \frac{dx_2}{dt} = \left(F_2(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_2, \\ \frac{dx_3}{dt} = \left(F_3(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_3, \end{cases} \quad (1)$$

here $F_1(x) = N - x_1$, $F_2(x) = a_1 x_1 - x_2$, $F_3(x) = a_2 x_2 - x_3$ are known as Allen's functions (Allen 1976); $a_1 > 0$, $a_2 > 0$, $N > 0$, $S_0 > 0$, $x_1(t)$, $x_2(t)$, $x_3(t)$ are sizes (biomasses) of the associations, S_0 is capacity of environment, N is a coefficient which determine equilibrium size of the first association, when it develops alone; a_1 is a coefficient which describes a level of dependence of the second association from the first one, a_2 is the same for the third and second associations.

THE EQUILIBRIUM POINTS OF THE SYSTEM (1)

The system equilibrium points can be found as roots of the system of algebraic equations of the third order:

$$\begin{cases} \left(F_1(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_1 = 0, \\ \left(F_2(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_2 = 0, \\ \left(F_3(x) - \frac{1}{S_0}(x_1 F_1(x) + x_2 F_2(x) + x_3 F_3(x)) \right) x_3 = 0. \end{cases}$$

$$J = \begin{bmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & m_{23} \\ m_{31} & m_{32} & m_{33} \end{bmatrix}, \quad (2)$$

The solution is trivial; there are 11 equilibrium points:

$$\begin{aligned} P_1: (0,0,0); \quad P_2: (N,0,0); \quad P_3: (N, a_1 N, 0); \\ P_4: (N, a_1 N, a_1 a_2 N); \quad P_5: (S_0, 0, 0); \quad P_6: (0, S_0, 0); \\ P_7: (0, 0, S_0); \quad P_8: \left(\frac{N + S_0}{a_1 + 2}, \frac{S_0(a_1 + 1) - N}{a_1 + 2}, 0 \right); \\ P_9: \left(\frac{S_0 + N}{2}, 0, \frac{S_0 - N}{2} \right); \quad P_{10}: \left(0, \frac{S_0}{a_2 + 2}, \frac{S_0(a_2 + 1)}{a_2 + 2} \right); \\ P_{11}: \left(\frac{S_0 + N(a_2 + 2)}{a_1 a_2 + a_1 + a_2 + 3}, \frac{(a_1 + 1)S_0 + N(a_1 - 1)}{a_1 a_2 + a_1 + a_2 + 3}, \right. \\ \left. \frac{(a_1 a_2 + a_2 + 1)S_0 - N(a_1 + a_2 + 1)}{a_1 a_2 + a_1 + a_2 + 3} \right). \end{aligned}$$

One of the signs of system bifurcations is merging of equilibrium points. It is easily possible to find conditions for merging of couples of the points:

$$P_5 \text{ and } P_8, \text{ if } \frac{S_0}{N} = \frac{1}{a_1 + 1};$$

$$P_8 \text{ and } P_{11}, \text{ if } \frac{S_0}{N} = \frac{a_1 + a_2 + 1}{a_1 a_2 + a_2 + 1};$$

$$P_9 \text{ and } P_{11}, \text{ if } \begin{cases} \frac{S_0}{N} = \frac{1 - a_1}{a_1 + 1}, \\ a_1 \in (0, 1); \end{cases}$$

$$P_2, P_5 \text{ and } P_9, \text{ if } \frac{S_0}{N} = 1;$$

$$P_3 \text{ and } P_8, \text{ if } \frac{S_0}{N} = a_1 + 1;$$

$$P_4 \text{ and } P_{11}, \text{ if } \frac{S_0}{N} = a_1 a_2 + a_1 + 1.$$

Hypothesis 1. In the system (1) the bifurcation values of parameters are following:

$$\frac{S_0}{N} = \frac{1 - a_1}{a_1 + 1}, \text{ when } a_1 \in (0, 1); \quad \frac{S_0}{N} = \frac{1}{a_1 + 1};$$

$$\frac{S_0}{N} = \frac{a_1 + a_2 + 1}{a_1 a_2 + a_2 + 1}; \quad \frac{S_0}{N} = 1; \quad \frac{S_0}{N} = a_1 + 1;$$

$$\frac{S_0}{N} = a_1 a_2 + a_1 + 1.$$

ANALYSIS OF THE EQUILIBRIUM POINTS

Let's consider the Jacobi matrix of the system (1):

$$m_{11} = \frac{3}{S_0} x_1^2 - 2 \frac{N + S_0 + a_1 x_2}{S_0} x_1 + \frac{N S_0 + x_2^2}{S_0} + \frac{x_3^2 - a_2 x_3 x_2}{S_0}$$

$$m_{12} = \frac{2x_2 - a_2 x_3}{S_0} x_1 - \frac{a_1}{S_0} x_1^2, \quad m_{13} = \frac{2x_3 - a_2 x_2}{S_0} x_1,$$

$$m_{21} = \frac{a_1 S_0 - N + 2x_1}{S_0} x_2 - \frac{a_1}{S_0} x_2^2,$$

$$m_{22} = \frac{a_1 S_0 - N - 2a_1 x_2}{S_0} x_1 + \frac{1}{S_0} x_1^2 - \frac{2S_0 + 2a_2 x_3}{S_0} x_2 + \frac{x_3^2 + 3x_2^2}{S_0}$$

$$m_{23} = \frac{2x_3 - a_2 x_2}{S_0} x_2, \quad m_{31} = \frac{2x_1 - a_1 x_2 - N}{S_0} x_3,$$

$$m_{32} = \frac{2x_2 + a_2 S_0 - a_1 x_1}{S_0} x_3 - \frac{a_2}{S_0} x_3^2,$$

$$m_{33} = -\frac{N + a_1 x_2}{S_0} x_1 + \frac{a_2 S_0 - 2a_2 x_3}{S_0} x_2 + \frac{1}{S_0} x_1^2 + \frac{1}{S_0} x_2^2 - 2x_3 + \frac{3}{S_0} x_3^2.$$

Eigenvalues of the matrix (2) in the stationary points:

for P_1 they are $\lambda_1 = N$, $\lambda_2 = 0$, $\lambda_3 = 0$;

for P_2 they are $\lambda_1 = \frac{N^2}{S_0} - N$, $\lambda_2 = N a_1$, $\lambda_3 = 0$;

for P_3 they are $\lambda_1 = a_1 a_2 N$, $\lambda_{2,3} = \frac{N}{2S_0} (N - S_0(a_1 + 1) \pm \sqrt{N^2 + 2NS_0(2a_1^2 + a_1 - 1) + S_0^2(a_1 - 1)^2})$;

for P_4 an analytical form of the eigenvalues was not found. (The Descartes method (Berezin and Zitkov 1959) is used for determination of the stress intervals of the eigenvalues. Three eigenvalues are negative, when $S_0 / N \in (1 + a_1 + a_1 a_2; +\infty)$; two negative and one positive when $S_0 / N \in (0; 1 + a_1 + a_1 a_2)$);

for P_5 they are $\lambda_1, \lambda_3 = S_0 - N$, $\lambda_2 = S_0(1 + a_1) - N$;

for P_6 they are $\lambda_1 = N + S_0$, $\lambda_2 = S_0(a_2 + 1)$, $\lambda_3 = S_0$;

for P_7 they are $\lambda_1 = N + S_0$, $\lambda_{2,3} = S_0$;

for P_8 they are

$$\lambda_1 = -\frac{N(a_1 + 1) - S_0}{a_1 + 2}, \quad \lambda_2 = -\frac{(N + S_0)(S_0(a_1 + 1) - N)}{S_0(a_1 + 2)},$$

$$\lambda_3 = -\frac{N(1 + a_1 + a_2) - S_0(1 + a_2 + a_1 a_2)}{a_1 + 2};$$

for P_9 they are $\lambda_1 = \frac{N^2 - S_0^2}{2S_0}$, $\lambda_2 = \frac{S_0 - N}{2}$,

$$\lambda_3 = \frac{S_0(a_1 + 1) + N(a_1 - 1)}{2};$$

for P_{10} they are $\lambda_1 = -\frac{S_0(a_2+1)}{a_2+2}$, $\lambda_2 = \frac{S_0}{s_2+2}$,
 $\lambda_3 = \frac{S_0 + N(a_2+2)}{a_2+2}$;

for P_{11} one eigenvalue is $\lambda_1 = \frac{S_0 - N(1+a_1+a_1a_2)}{a_1+a_2+a_1a_2+3}$, the others are roots of a quadratic equation. The analysis of the equation shown that there is a pair of eigenvalues of different sign, if

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

a pair of positive eigenvalues, if

$$\left\{ \begin{array}{l} a_1 \in (0;1), \\ \frac{S_0}{N} \in \left(0, \frac{1-a_1}{a_1+1} \right) \end{array} \right\},$$

a pair of negative eigenvalues, if

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

On the base of these results one can prove 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 $S_0/N \in (0, (a_1+1)^{-1})$, a saddle with two-dimension stable subspace, if $S_0/N \in ((a_1+1)^{-1}, 1)$, 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

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

and with two-dimension stable subspace, if

$$S_0/N \in (0, (1-a_1)/(1+a_1)), \quad a_1 \in (0, 1),$$

- P_{10} is a saddle with two-dimension unstable subspace;
- P_{11} is a saddle with two-dimension unstable subspace, if

$$S_0/N \in (0, (1-a_1)/(1+a_1)), \quad a_1 \in (0, 1),$$

or a saddle with two-dimension unstable subspace, if

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

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

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

BIFURCATION POINTS

Let's determinate bifurcation values of parameters on the base of analysis of equilibrium points. The bifurcation diagram is presented in Fig.1.

For values of the parameters from the regions I, II, III, IV, there are two complicated equilibrium points, two unstable nodes, three saddles with two-dimension unstable subspace, three saddles with two-dimension stable subspace and one stable node.

For values of the parameters from the regions V, VI, VII, VIII, there are two complicated equilibrium points, three unstable node, three saddles with two-dimension unstable subspace, two saddles with two-dimension stable subspace and one stable node in phase space.

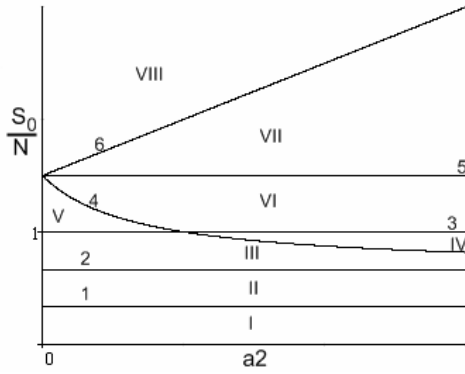
When quotient of the parameters S_0 and N pass through value 1, one saddle disappears and unstable node appears.

Let's consider the phase portrait in the first octant, because of its importance for practical applications. Let's note that there are not equilibrium points, which belongs the first octant for any values of the parameters. Thus, the point P_8 belongs to the first octant, when

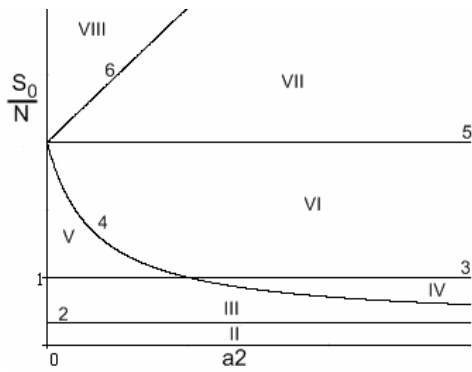
$$\frac{S_0}{N} \geq \frac{1}{1+a_1}, \text{ point } P_9 - \text{ when } \frac{S_0}{N} \geq 1, \text{ point } P_{11} -$$

when $\frac{S_0}{N} \geq \frac{1+a_1+a_2}{1+a_2+a_1a_2}$. One can see that when $\frac{S_0}{N}$ pass through these tree values, topology of the first

octant change. It is possible to summarise the obtained results by a theorem.



a) $a_1 \in (0,1)$



b) $a_1 \in [1, +\infty)$

Figure 1: Sections of the parametric surfaces

$$\left(\begin{array}{l} 1. \frac{S_0}{N} = \frac{1-a_1}{a_1+1}, \quad 2. \frac{S_0}{N} = \frac{1}{1+a_1}, \quad 3. \frac{S_0}{N} = 1, \\ 4. \frac{S_0}{N} = \frac{1+a_1+a_2}{1+a_2+a_1a_2}, \quad 5. \frac{S_0}{N} = a_1+1, \quad 6. \frac{S_0}{N} = 1+a_1+a_1a_2 \end{array} \right)$$

Theorem 1. There are following bifurcation values of parameters for the system (1):

- 1) $S_0 / N = 1$ (for the all phase space);
- 2) $\frac{S_0}{N} = \frac{1}{1+a_1}$, $\frac{S_0}{N} = 1$, $\frac{S_0}{N} = \frac{1+a_1+a_2}{1+a_2+a_1a_2}$ (for the first octant).

Now it is clear, that the Hypothesis 1 is partly wrong. Thus, the equation $\frac{S_0}{N} = \frac{1-a_1}{a_1+1}$ (when $a_1 \in (0,1)$) does

not correspond to a bifurcation. When the quotient of the parameters exceeds this value, two-dimension stable subspace of the point P_9 becomes one-dimension and, contra versa, one-dimension stable subspace of the point P_{11} becomes two-dimension.

The similar situation takes place for the equation $S_0 / N = 1 + a_1 + a_1a_2$: the point P_4 becomes a stable

node (spiral point), whereas the point P_{11} changes type from a stable node (spiral point) to a saddle. The topology of the phase space does not change; therefore, there is not a bifurcation for these values of parameters. A special situation is connected with the equation $S_0 / N = 1$. In this case three equilibrium points (P_2 , P_5 , P_9) merge into one. When parameters pass through this point, stability (and type) of the equilibrium point P_9 does not change, whereas the point P_5 becomes unstable node and two-dimension unstable subspace of the point P_2 becomes one-dimension. It can be shown that the bifurcation takes place in the first octant. Let's consider the set of equilibrium points which have two nonzero components: the first and the j -th ($j > 2$). One can find coordinates of such equilibrium points from the system of algebraic equations:

$$\begin{cases} (N - x_1 - ((N - x_1)x_1 - x_1^2) / S_0)x_1 = 0, \\ (-x_j - ((N - x_1)x_1 - x_j^2) / S_0)x_j = 0, \\ x_1 \neq 0, x_j \neq 0, (j > 2). \end{cases}$$

From here $x_1 = (S_0 + N) / 2$ and $x_j = (S_0 - N) / 2$. Such points form a subset of the set of equilibrium points of the n -dimensional open Eigen's hypercycle model. Every point of this subset appears in nonnegative region of phase space, when $S_0 / N \geq 1$. So, $S_0 / N = 1$ is a bifurcation value. The fact, that at least $n-2$ equilibrium points take part in the above-mentioned bifurcation.

ECOLOGICAL INTERPRETATION

Bifurcations, connected with change of stability of equilibrium points, are especially interesting from practical point of view. Only two bifurcation correspond to this criteria: $\frac{S_0}{N} = \frac{1}{1+a_1}$, $\frac{S_0}{N} = \frac{1+a_1+a_2}{1+a_2+a_1a_2}$.

From the analysis of equilibrium points it was clear that there are four possible stable equilibrium points; during the bifurcations they can change each other, and in any case only one point are an attractor:

1. When $0 < \frac{S_0}{N} < \frac{1}{1+a_1}$, point P_5 is stable. In this case the size of ecological niche is so small, that only one association is able to exist in the ecosystem.
2. When $\frac{1}{1+a_1} < \frac{S_0}{N} < \frac{1+a_1+a_2}{1+a_2+a_1a_2}$, point P_8 is stable.

With such values of the parameters (capacity of the environment) there are sufficient resources for the second association, which is in competition with the first one.

3. When $\frac{1+a_1+a_2}{1+a_2+a_1a_2} < \frac{S_0}{N} < 1+a_1+a_1a_2$, point P_{11} is stable. In this case size of ecological niche is so big, that three associations are able to coexist in the biogeocoenose. And that they use all the resources.

4. When $1+a_1+a_1a_2 < S_0/N < +\infty$, point P_4 is stable. This case corresponds to an excess of resources. In the ecosystem there are three associations, which reach their maximal possible sizes.

One of natural questions: why $S_0/N = 1+a_1+a_1a_2$ is not bifurcation value? When capacity of the environment S_0 becomes larger than $(1+a_1+a_1a_2)N$, the topology of the system is not changed, although, formally, the new point becomes to be stable. Such situations are quite usual in mathematical investigations of equilibrium points and bifurcation.

Concerning the bifurcation value $S_0/N = 1$, it is difficult to determine its practical role. One can assume that this critical rate delineates various ways to stabilise the system if it is out of its steady state.

CONCLUSION

In the contribution, the three-dimension open Eigen's hypercycle model (1) was considered. In the case of small (nonzero) size of the ecological niche, only one association is able to exist in the system. When capacity of the environment grows, the second and the third association are included in the ecosystem gradually. It is shown, that the process of origin of next associations is accompanied with bifurcations of system (1). When size of niche is $S_0 > (1+a_1+a_1a_2)N$, there is excess of resources in the biogeocoenose. The situation of appearance of excess of resources is not bifurcation, because topology of the ecosystem does not change and development of the system is continuous.

As it clear from the research, the main parameter, which determines the behaviour of the system is the capacity of the environment S_0 . Parameters a_1 and a_2 influence only on relationships between the associations.

Analysis of three-dimension open Eigen's hypercycle model, together with the two-dimension one (Chernyshenko, 1995), allows proposing of the following assumptions for n -dimensional case:

1. In the process of ecosystem successions has n stages. Each of them is characterised by activation of a new association. Number of "activated" associations is determined by size of the environment capacity S_0 . If the size of niche is small ($0 < S_0 < N/(1+a_1)$), only one association is able to exist in the ecosystem.

2. Each "activation" of a new association is accompanied with bifurcations of the system. It is interesting, that the first $n-2$ conditions of the activation are the same as for $(n-1)$ -dimensional system.

3. There is excess of resources in the ecosystem when size of ecological niche is $S_0 > N \sum_{i=0}^n \prod_{j=0}^{n-i} a_j$, $a_0 = 1$. Size of associations in this case is calculated as $x_j = N \prod_{i=0}^{j-1} a_i$, $a_0 = 1$, $j = \overline{1, n}$.

The proof of these assumptions is a matter of future research.

REFERENCES

- Allen, P.M. 1976. "Evolution, population dynamics and stability". *Proceedings of the National Academy of Sciences of the USA*, Vol. 73, No. 3, 665-668.
- Berezich, I.C. and N.P. Zitkov. 1959. *Computing technique*. Physico-mathematical literature main Press, Moscow.
- Chakrabarti, C.G.; Ghosh Sutapa; and Bhadra Syamali. 1995. "Non-equilibrium thermodynamics of Lotka-Volterra ecosystems: Stability and evolution." *Journal of Biological Physics*, Vol. 21, Is. 4, 273-284.
- Chernyshenko, S.V. 1995. "Qualitative analysis of two-dimensional modification of the M. Eigen's hypercycle and internal catastrophes" *Problems of applied mathematics and mathematical modelling*. Dnipropetrovsk University Press, 129-134.
- Chernyshenko, S.V. 2005. *Nonlinear analysis of forest ecosystems dynamics*. Dnipropetrovsk University Press, Dnipropetrovsk.
- Culver, D.C. 1981. "On Using Horn's Markov Succession Model." *The American Naturalist*, Vol. 117, No. 4 (Apr), 572-574.
- Eigen M. and P. Schuster. 1979. *The Hypercycle. A principle of natural self-organization*. Springer-Verlag, Berlin, Heidelberg, New York.
- Kogan, A.B.; N.P. Naumov; B.G. Rezbek; and O.G. Chorajan. 1977. *Biological cybernetics*. Vysshaja shkola, Moscow.
- Lepš Jan and Karel Prach. 1981. "A Simple Mathematical Model of the Secondary Succession of Shrubs." *Folia Geobotanica & Phytotaxonomica*, Vol. 16, No. 1, 61-72.
- Lippe E.; J.T. De Smidt; and D.C. Glenn-Lewin. 1975. "Markov Models and Succession: A Test from a Heathland in the Netherlands." *Journal of Ecology*, Vol. 73, No. 3 (Nov), 775-791.
- Logofet, D.O. 1997. "Inhomogeneous Markov models for succession of plant communities: New perspectives on an old paradigm." *Izvestiya Akademii Nauk. Seriya Biologicheskaya*, 613-622.
- Lourival R.; Martin Drechsler; Matthew E. Watts; Edward T. Game; and Hugh P. Possingham. 2011. "Planning for reserve adequacy in dynamic landscapes; maximizing future representation of vegetation communities under flood disturbance in the Pantanal wetland." *Diversity and Distributions*, Vol. 17, Is. 2 (Mar), 297-310.
- Rabotnov, A.T. 1992. *Phytocenology*. MGU Press, Moscow.
- Sukachev, V.N. 1972. *Selected transactions: in three volumes*. Vol. 1. *Bases of forest typology and biogeocenology*. Nauka, Leningrad.
- Tilman D. 1990. "Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession." *Oikos*, Vol. 58, No. 1 (May), 3-15.
- Weis, J.J.; B.J. Cardinale; K.J. Forshay; and A.R. Ives. 2007. "Effects of species diversity on community biomass production change over the course of succession." *Ecology*, Vol. 88, No 4 (Apr), 929-939.

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