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Mathematical Analysis in a Model of Primary Succession

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Abstract: This paper is concerned with a long-term ecological primary succession. The model of open Eigen's hypercycle has been used for modeling of the process. The multi-dimension case is analyzed. It is shown that consideration of system's dynamics can be simplified by partial reduction to the cases of lower dimension. The dynamics of ecological system can be considered as a self-organizing process with quasi-discrete characteristic. The quasi-discrete dynamics is explained by bifurcation properties of the system, that produce step-by-step changing of system's structure.

Keywords: *biogeocoenose; primary succession; stability; evolution; bifurcation; self-organization.*

Mathematics Subject Classification (2010): 34A34, 34D20, 37F99, 92D99.

1 Introduction

Since the second half of the 20th century, illusion of happiness with regard to the development of a technocratic society disappears, while the number and severeness of the ecological crises increase. At this time researchers began to pay more attention to the study of ecological processes [2,7,17,25,26,30].

The main object of the study is biogeocoenosis (as a collection of fauna and flora that exist in some area), and in particular a succession that takes place in it. In classical ecological theory there are two main types of succession: primary and secondary succession [26]. Note that a lot of works [5,15,19,21,28] are concerned with the mathematical modeling of the second type of ecological process. As to the first type, the works are mostly descriptive, of non-formalized character [12,24,27]. In this paper we examine the behavior of ecological systems during primary succession.

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Ecological processes (including the succession) are complex and characterized by oscillating processes, processes of self-organization, abrupt change of the mode of a system, the effects of histereses and others. The experience of using linear models showed that they can not adequately describe the behavior of real systems, but only reflect some common trends. Often the stochastic models are used to describe succession processes [1, 12, 20, 22, 23]. The basic parameter that determines the dynamics of biogeocoenosis in such models is the probability of transition. It represents probability of some association to become dominant. Such approach can be useful for simulation of system dynamics, but does not reflect driving forces of the process.

Another tool that is used to describe the succession are differential equations, in particular of the Volltarian type [8, 29]. In such models competition between associations is considered as the basic driving force of ecological process. Note that quite a number of researchers adhere this point of view [16, 25, 26]. However, these models have several weaknesses: they do not reflect the interaction between biotic elements and inert components of the ecosystem; it is possible that associations do not compete, but reach the optimum number. These flaws can be corrected by using a special modification (called an "open hypercycle" [10]) of the famous Eigen hypercycle [14] for description of primary successions. This model is similar,but not equivalent to Lotka-Volterra models of the competition or is of the "predator-prey" type.

2 The Model

Let us consider the behavior of biological associations $x\left(t\right) = \left(x_1\left(t\right), ..., x_n\left(t\right)\right)$ that is described by the model of open Eigen's hypercycle:

$$\frac{dx_i}{dt} = \left(F_i\left(t\right) - \frac{1}{S_0}\sum_{j=0}^{n} x_j F_j\left(t\right)\right) x_i, i = \overline{1,n}, \tag{1}$$

where S_0 is a capacity of environment (size of ecological niche), $S_0 > 0$.

Suppose that the coefficients of propagation and interaction between associations are defined by Allen's functions:

$$F_i\left(t\right) = a_{i-1}x_{i-1}\left(t\right) - x_i\left(t\right), i = \overline{1,n},$$

here $a_1 > 0, i = \overline{1, n-1}, x_0 = 1, a_0 = N$; N is a coefficient which determines the equilibrium size of the first association, when it develops alone; a_1 is a coefficient which describes a level of dependence of the $(i+1)$th association on the previous one, $i = \overline{1, n-1}$. Allen's functions reflect the nature of the relationship between associations where associations are included into a system at certain level of development of stagnant environment.

3 The Jacobi Matrix

The structure of a Jacobi matrix row of system (1) can be represented as

$$\underbrace{f_1 \cdots f_1}_{m}\underbrace{f_2 \cdots f_2}_{l} f_3 \underbrace{f_4 \cdots f_4}_{d}, \tag{2}$$

where $f_1 = -x_i S_0^{-1}\left(a_{k-1}x_{k-1} - 2x_k + a_k x_{k+1}\right)$,

$$f_2 = a_{i-1}x_i - x_i S_0^{-1}\left(a_{i-2}x_{i-2} - 2x_{i-1} + a_{i-1}x_i\right),$$
$$f_3 = \begin{cases} a_{i-1}x_{i-1} - 2x_i - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right) - \\ -x_i S_0^{-1}\left(a_{i-1}x_{i-1} - 2x_i + a_i x_{i+1}\right), k < n; \\ a_{i-1}x_{i-1} - 2x_i - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right) - x_i S_0^{-1}\left(a_{i-1}x_{i-1} - 2x_i\right), \\ k = n; \end{cases}$$
$$f_4 = \begin{cases} -x_i S_0^{-1}\left(a_{k-1}x_{k-1} - 2x_k + a_k x_{k+1}\right), k < n; \\ -x_i S_0^{-1}\left(a_{k-1}x_{k-1} - 2x_k\right), k = n; \end{cases}$$

$m = \varphi(i-2)$, $l = \begin{cases} 1, i > 1; \\ 0, i = 1; \end{cases}$, $d = n - m - l - 1$, $\varphi(x) = \begin{cases} x, x \geq 10; \\ 0, x < 0; \end{cases}$, k, i are a number of column and a row of the Jacobi matrix respectively, $k = \overline{1, n}, i = \overline{1, n}$.

Theorem 3.1 *If the coordinate x_p of a stationary point is zero, then one of eigenvalues of the Jacobi matrix of the system (1) at this stationary point can be calculated as*

$$a_{p-1}x_{p-1} - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right), \tag{3}$$

if x_{p-1} is not zero or $p = 1$. Otherwise the eigenvalue equals

$$- S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right). \tag{4}$$

Proof. If some coordinate x_p of the stationary point is zero, than row p of the Jacobi matrix can be written as (taking into account (2))

$$\underbrace{0\ldots0}_{p-1}a_{p-1}x_{p-1} - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right)\underbrace{0\ldots0}_{n-p}.$$

Write the characteristic equation of this matrix

$$|J - \Lambda I| = 0,$$

here I is an identity matrix, Λ is a matrix of eigenvalues, J is the Jacobi matrix.

Expanding the determinant in algebraic complement to the row p, we find that the eigenvalues are computed as

$$\left[\begin{array}{l} \lambda = a_{p-1}x_{p-1} - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right), \\ A_p = 0, \end{array}\right.$$

here A_p is determinant of minor on diagonal item of row p. Apparently if $x_{p-1} = 0$, then

$$\lambda = -S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right).$$

Thus, the theorem is proved. □

Considering the set of stationary points of the model of open Eigen's hypercycle one can see that there is a subset of points whose first coordinates are equal to the corresponding coordinates of stationary points of lower dimension model and all the other (the last) coordinates are zero. These stationary points are called the "points-descendants".

Theorem 3.2 *$n-1$ eigenvalues of the Jacobi matrix at the "points-descendants" of n-dimensional model of open Eigens hypercycle are the same as at the corresponding stationarity points of $(n-1)$-dimensional model, and the last one is calculated as*

$$a_{n-1}x_{n-1} - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right). \tag{5}$$

Proof. According to Theorem 3.1 one eigenvalue of the Jacobi matrix of system (1) at the "point-descendant" equals

$$a_{n-1}x_{n-1} - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right).$$

Consider the $(n-1)\times(n-1)$ cell of Jacobi matrix (which is the algebraic complement of the matrix). From the analysis of the formula (2) it is obvious that the cell of Jacobi matrix, that contains the first $n-2$ rows and $n-2$ cells, is not different from the general case. The elements of the main diagonal are calculated as

$$a_{i-1}x_{i-1} - 2x_i - S_0^{-1}\textstyle\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right) - x_iS_0^{-1}\left(a_{i-1}x_{i-1} - 2a_i + a_1x_{i+1}\right), \\ i=\overline{1,n-2}.$$

The first $(n-1)$ elements of the $(n-1)$th row of Jacobi matrix are calculated as

$$-x_{n-1}S_0^{-1}\left(a_{k-1}x_{k-1} - 2a_k + a_kx_{k+1}\right), k=\overline{1,n-3}, \\ a_{n-2}x_{n-1} - x_{n-1}S_0^{-1}\left(a_{n-3}x_{n-3} - 2a_{n-2} + a_{n-2}x_{n-1}\right), \\ a_{n-2}x_{n-2} - 2x_{n-1} - S_0^{-1}\textstyle\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right) - x_{n-1}S_0^{-1}\left(a_{n-2}x_{n-2} - 2x_{n-1}\right),$$

and the elements of the $(n-1)$th cell as

$$-x_{n-1}S_0^{-1}\left(a_{n-2}x_{n-2} - 2x_{n-1}\right).$$

Thus $(n-1)\times(n-1)$ cell that is considered, is the Jacobi matrix of $(n-1)$-dimensional model of open Eigen's hypercycle at the point formed by discarding the last coordinates (which are zero) of n-dimensional model's "point-descendant". Hence, $n-1$ eigenvalues of the Jacobi matrix at the "points-descendant" of n-dimensional model are determined from this cell. Thus, the theorem is proved. □

Corollary 3.1 *$n-k$ eigenvalues of the Jacobi matrix at the "points-descendants" where the last k coordinates are zero, are the same as for $(n-k)$-dimensional model, $(k-1)$ of the rest k ones are determined by the formula (4), and the last one can be calculated as*

$$a_{n-k}x_{n-k} - S_0^{-1}\sum_{j=1}^{n-k}\left(a_{j-1}x_{j-1}x_j - x_j^2\right). \tag{6}$$

Proof of Corollary 3.1 is similar to the proof of Theorem 3.2.

Theorem 3.3 *If a stationary point with the last zero coordinate of n-dimensional model of open Eigen's hypercycle is stable, then the "point-descendant" of higher dimension model is stable too and the intervals of parameters, for which the points are stable, are the same. Otherwise, the "point-descendant" is unstable.*

Proof. Consider the stationary point of n-dimensional model where the last $k (k \geq 2)$ coordinates are zero. According to Corollary 3.1 $n-k$ eigenvalues of the Jacobi matrix at this point are the same as for $(n-k)$-dimensional model at the corresponding point. Thus, if the stationary point of $(n-k)$-dimensional model is stable, then $(n-k)$ eigenvalues are negative. According to formulas (4) and (5) other k ones are calculated as

$$\lambda_1 = a_{n-k}x_{n-k} - S_0^{-1}\textstyle\sum_{j=1}^{n-k}\left(a_{j-1}x_{j-1}x_j - x_j^2\right),$$

$$\lambda_i = -S_0^{-1}\textstyle\sum_{j=1}^{n-k}\left(a_{j-1}x_{j-1}x_j - x_j^2\right), i = \overline{2,k}.$$

As only nonnegative sector of phase space is considered, then the difference $\lambda_1 - \lambda_i = a_{n-k}x_{n-k}, i = \overline{1,k-1}$ is positive. Thus the inequality $\lambda_1 \geq \lambda_i$ is correct. Thus, if the eigenvalue λ_1 is negative, then all the other eigenvalues $\lambda_i (i = \overline{2,k})$ are negative too. It means that if the stationary point with the last zero coordinates of $(n-k+1)$-dimensional model is stable, then the "point-descendant" of n-dimensional model is stable too. Moreover, the interval of parameters, for which the point is stable, is not changed. Thus, the theorem is proved. □

Theorem 3.4 *If the stationary point of* $(n-1)$*-dimensional model of open Eigen's hypercycle is stable, then the coresponding "point-descendant" of* n*-dimensional model is stable when the inequality is correct:*

$$\frac{x_{n-2}}{x_{n-1}} > \frac{a_{n-1}+1}{a_{n-2}}.$$

Proof. Consider the stationary "point-descendant" of (n)-dimensional model with only one (the last) zero coordinate. Then according to Theorem 3.2 $n-1$ eigenvalues of Jacobi matrix at this point are defined as the eigenvalues of Jacobi matrix at the corresponding point of $(n-1)$-dimensional system, and one eigenvalue is $\lambda = a_{n-1}x_{n-1} - S_0^{-1}\sum_{j=1}^{n-1}\left(a_{j-1}x_{j-1}x_j - x_j^2\right)$. If this point of $(n-1)$-dimensional system is stable, then $(n-1)$ eigenvalues are negative.

Consider the eigenvalue λ. Note that the coordinates of the stationary point are determined by the system

$$a_{k-1}x_{k-1} - x_k - S_0^{-1}\sum_{j=1}^{n}\left(a_{j-1}x_{j-1}x_j - x_j^2\right) = 0, 1 \leq k \leq n-1,$$

here k are the numbers of nonzero coordinates. Therefore, we can write the expression

$$\lambda = a_{n-1}x_{n-1} - \left(a_{n-2}x_{n-2} - x_{n-1}\right).$$

Then, the eigenvalue λ is negative, if the following inequality is correct

$$\frac{x_{n-2}}{x_{n-1}} > \frac{a_{n-1}+1}{a_{n-2}}.$$

The theorem is proved. □

Obviously if coordinate x_{n-2} of the point from Theorem 3.4 is zero, then this point is unstable.

Example 3.1 It is obvious that there is a subset

$$\Big\{ (x_1, \dots, x_k, 0 \dots, 0) | \, x_j = N \prod_{i=1}^{j-1} a_i, j = \overline{1, n}, 1 < k < n \Big\}$$

of the set of stationary points of model (1). Using Theorems 3.3 and 3.4 it is easy to show that each point of this set is unstable.

4 The Two-dimensional Model of Open Eigen's Hypercycle

It was determined in [10] that the two-dimensional model of open Eigen's hypercycle has 6 stationary 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). The Lyapunov direct method is used for definition of their type and stability. The results are presented in Table 1.

Points	$S_0 \in$			
	$\left(0, \frac{1}{a_1+1}\right)$	$\left(\frac{1}{a_1+1}, 1\right)$	$(1, a_1+1)$	$(a_1+1, +\infty)$
$(0, S_0)$	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

Table 1: The stability of the stationary points.

The method described in [3] is used for definition of behavior of trajectories near complex (degenerate) stationary point. Thus, $(0,0)$ is a complex stationary point of "saddle-node" type for any positive values of the parameters; $(N,0)$ if $S_0 = N$; $(S_0, 0)$ if $S_0 = N(a_1+1)^{-1}$; (N, a_1N) if $S_0 = (a_1+1)N$.

Theorem 4.1 *There are no limit cycles in the phase portrait of two-dimentional model of open Eigen's hypercycle.*

Proof. It is easy to show that points $(0,0)$, $(0,S_0)$, $(N,0)$, $(S_0,0)$, $\left(\frac{S_0+N}{a_1+2}, \frac{S_0(a_1+1)-N}{a_1+2}\right)$ are on the integral lines $x_1=0$, $x_2=0$, $x_1+x_2=S_0$. So there is no a limit cycle around these points. As for the point (N,a_1N), it is saddle or node-saddle if $\frac{S_0}{N}\in(0,a_1+1]$ (there is no a limit cycle around this point). If $\frac{S_0}{N}\in(a_1+1,+\infty)$ then it is a stable node. Consider this case. If $\frac{S_0}{N}\in(a_1+1,+\infty)$ then (N,a_1N) is inside the triangle formed by the integral lines $x_1=0$, $x_2=0$, $x_1+x_2=S_0$.

Use Dulac theorem. Take $F(x_1,x_2)=x_1^{-2}x_2^{-2}$ as Dulac function, then

$$\frac{\partial(PF)}{\partial x_1}+\frac{\partial(QF)}{\partial x_2}=-\frac{NS_0-x_1(N-S_0a_1)}{S_0x_1^2x_2^2}.$$

Here P and Q are the left-hand sides of equations of the two-dimensional model of open Eigen's hypercycle. As we consider only the triangle, then $x_1\leqslant S_0$. Hence

$$-\frac{NS_0-x_1(N-S_0a_1)}{S_0x_1^2x_2^2}\leqslant-\frac{NS_0-S_0(N-S_0a_1)}{S_0x_1^2x_2^2}=-\frac{S_0a_1}{x_1^2x_2^2}.$$

This expression has a constant sign in the triangle, hence there is no a limit cycle in the triangle. Therefore there is no a limit cycle in the phase portrait. The theorem is proved. □

There is only one attractor, namely node, in the system for any positive values of the parameters. The stable point is always in the first quarter of the phase portrait. If $0<S_0<(a_1+1)^{-1}N$, only one association is able to exist in the ecosystem. When $S_0=(a_1+1)^{-1}N$, there is a bifurcation (if we consider only the first quarter). It is interpreted as the inclusion of the second association in the ecological system and it defines a new stage of succession process.

If $(a_1+1)^{-1}N<S_0<(a_1+1)N$, $\left(\frac{S_0+N}{a_1+2}, \frac{S_0(a_1+1)-N}{a_1+2}\right)$ is a stable point. Note that the first association is dominant, if $a_1<1$. If $a_1>1$, the first or the second one is dominant depending on the size of the ecological niche.

If $S_0>(a_1+1)N$, there is an excess of resources in the system. Both associations reach maximum capacity. Moreover the first association is dominant if $a_1<1$. Otherwise the second association is dominant.

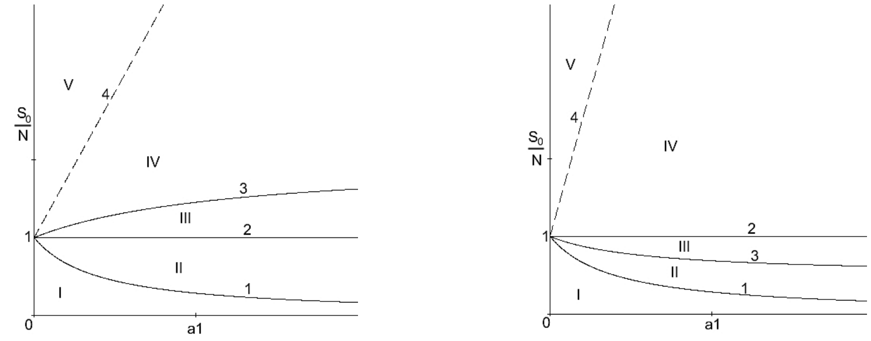
5 The Three-Dimensional Model of Open Eigen's Hypercycle

It was determined that there are 11 stationary points of phase space of three-dimensional model of open Eigen hypercycle: $P_1:(0,0,0)$, $P_2:(N,0,0)$, $P_3:(N,a_1N,0)$, $P_4:(N,a_1N,a_1a_2N)$, $P_5:(S_0,0,0)$, $P_6:(0,S_0,0)$, $P_7:(0,0,S_0)$, $P_8:\left(\frac{N+S_0}{a_1+2}, \frac{S_0(a_1+1)-N}{a_1+2}, 0\right)$, $P_9:\left(\frac{S_0+N}{2}, 0, \frac{S_0-N}{2}\right)$, $P_{10}:\left(0, \frac{S_0}{a_2+2}, \frac{S_0(a_2+1)}{a_2+2}\right)$, $P_{11}:\left(\frac{S_0+N(a_2+2)}{a_1a_2+a_1+a_2+3}, \frac{(a_1+1)S_0+N(a_1-1)}{a_1a_2+a_1+a_2+2}, \frac{(a_1a_2+a_2+1)S_0-N(a_1+a_2+1)}{a_1a_2+a_1+a_2+3}\right)$.

Using Theorems 3.1, 3.2 and 3.4 it can be shown that points P_1 and P_2 are complex (degenerate) stationary points; point P_3 is a saddle with two-dimension unstable subspace if $S_0/N\in(0,a_1+1)$, or two-dimension stable sub-space if $S_0/N\in(a_1+1,+\infty)$; point 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 $S_0/N \in (1, +\infty)$; point P_6 is unstable node; point P_8 is stable node if $S_0/N \in \left((1+a_1)^{-1}, \frac{1+a_1+a_2)}{1+a_2+a_1a_2}\right)$, a saddle with two-dimension stable subspace if $S_0/N \in (0, (a_1+1)^{-1}) \cup \left(\frac{1+a_1+a_2)}{1+a_2+a_1a_2}, 1+a_1\right)$, and a saddle with two-dimension unstable subspace if $S_0/N \in (1+a_1, +\infty)$.

The Lyapunov method is used for definition of the type and stability of the last five stationary points: point P_7 is an unstable point; point P_{10} is a saddle with two-dimension unstable subspace if $\left\{\begin{array}{l} S_0/N \in \left(\frac{1-a_1}{1+a_1}, 1\right) \cup (1, +\infty), \\ a_1 \in (0,1), \end{array}\right. \cup \left\{\begin{array}{l} S_0/N \in (0,1) \cup (1, +\infty), \\ a_1 \in [1, +\infty), \end{array}\right.$ and a saddle with two-dimension stable subspace if $\left\{\begin{array}{l} S_0/N \in \left(0, \frac{1-a_1}{1+a_1}\right) \cup (1, +\infty), \\ a_1 \in (0,1), \end{array}\right.$ point P_{11} is a stable stationary point if $S_0/N \in \left(\frac{1+a_1+a_2}{1+a_2+a_1a_2}, 1+a_1+a_1a_2\right)$, an unstable point with two-dimension unstable subspace if $\left\{\begin{array}{l} S_0/N \in \left(0, \frac{1-a_1}{1+a_1}\right) \cup (1, +\infty), \\ a_1 \in (0,1), \end{array}\right.$ an unstable point with two-dimension stable subspace if $\left\{\begin{array}{l} S_0/N \in \left(\frac{1-a_1}{1+a_1}, \frac{1+a_1+a_2}{1+a_2+a_1a_2}\right), \\ a_1 \in (0,1), \end{array}\right. \cup \left\{\begin{array}{l} S_0/N \in \left(0, \frac{1+a_1+a_2}{1+a_2+a_1a_2}\right), \\ a_1 \in [1, +\infty), \end{array}\right. \cup S_0/N \in (1+a_1+a_1a_2, +\infty)$; point P_4 is a stable stationary point if $S_0/N \in (1+a_1+a_1a_2, +\infty)$, and an unstable stationary point if $S_0/N \in (0, 1+a_1+a_1a_2)$.

The bifurcation diagram is shown in Figure 1 (a) , b)) on the basis of the analysis of stationary points. If $a_2 = 1$, the curve 3 and line 2 merge. Solid curves illustrate bifurcation values of parameters.



a) $a_2 \in (0,1)$ b) $a_2 \in (1, +\infty)$

Figure 1: Sections of the parametric surfaces $\big(1.S_0/N = (1+a_1)^{-1},\ 2.S_0/N = 1,\ 3.S_0/N = (1+a_1+a_2)/(1+a_2+a_1a_2),\ 4.S_0/N = 1+a_1+a_1a_2\big)$.

Point P_5 is a stable stationary point for the values of the parameters from region I $(0 < S_0/N < (1+a_1)^{-1})$. In this case the size of ecological niche is so small, that only one association is able to exist in the ecosystem. When $(1+a_1)^{-1} < S_0/N < \frac{1+a_1+a_2}{1+a_2+a_1a_2}$, point P_8 appears in the first octant (regions II and III in case a) or region II in case b)). In this case the second association can compete with the less demanding first one. If $S_0/N > \frac{1+a_1+a_2}{1+a_2+a_1a_2}$, the size of the ecological niche is so big, that three associations are able to coexist in the biogeocoenose (region IV in case a) or regions III and IV in case b)). Note, that they use all resourses if $\frac{1+a_1+a_2}{1+a_2+a_1a_2} < S_0/N < 1+a_1+a_1a_2$ (point P_{11} is stable); there is an excess of resourses if $S_0/N > 1+a_1+a_1a_2$ (point P_4 is stable, region V). So, the appearance of each new association in the system corresponds to the bifurcation of the first octant of phase space. During the bifurcations the stationary points that correspond to the neighboring states of ecological systems, merge and "exchange stability".

6 Conclusion

The main focus in this paper is to study the evolution of biogeocoenose during primary succession. It can be seen from the study of two- and three-dimentional models that there are self-organizing processes in the system. When ecological niche reaches certain size (it is smaller than the limit of occurrence of resources excess), new association is included in the system. Thus, under the influence of the flow of matter and energy the ecosystem evolves. A control parameter is the size of the ecological niche.

Note that similar process is described in the papers on theoretical ecology [18]: first, poor soil is ocuppied by lichens, further by mosses, grass and etc. Moreover, climatic conditions determine the maximum number of primary succession stages and flora forms soil, and thus it determines the time of transition to a new stage.

Note that the described dynamics is typical for natural ecological systems: volcano in Kamchatka [13], sulfur deposits in Lviv region, Ukraine [6], coal mining dumps of Donetsk and Chervonograd industrial areas, Ukraine [4], wetland [24], Glacier Bay, Alaska [9].

Also we can observe a discrete change of state of the ecological system, although the process is described by the continuous model. Discreteness of the process is explained by the presence of bifurcation phenomena in nonlinear models.

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