HIERARCHICAL HETEROGENITY OF POPULATIONS: MODELING BY THE OPEN EIGEN HYPERCYCLE

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ABSTRACT

The case of a biological population, which consists of several sub-populations (different kinds of the population ”social” groups: families, bevies, etc.), has been considered. For description of non-trivial interactions between these groups, a model of ”open the Eigen hypercycle” has been proposed. Its bifurcation analysis for 3-dimension case has been carried out. Ecological interpretation of the results has been discussed.

INTRODUCTION

A huge number of mathematical models of ecological population structure (for example, (Allen 1974; Austin 1990; Billik and Case 1994; Chernyshenko 1995; Maurer 1999; Williamson 1990)) are designed for the description of population dynamics while taking into account different kinds of physiological differences between specimens (of age, sex, size, etc.) At the same time it is known (Breder 1959; Urich 1938) another form of population heterogeneity, based on the ”social” population structure.Contrary to sex difference, specimens can change their group membership (though this changes are not as mechanistic as change of age). The main feature of social groups is an hierarchical character of the ”social structure” and dependence of the existance of higher groups on the proper functionality of the lower ones. Big populations of relatively ”intellectual” animals form new levels of population organization. The most bright example is the row ”specimen – family – bevy” and, correspondingly, different kind of specimens (ordinary specimen, head of family, bevy leader) (Manteyfel 1992).

In the famous hypercycle model, proposed by Eigen and Shuster (Eigen and Schuster 1979; May 1991), similar relationship between system elements is described. At the same time, relations between ”social groups” are not cyclic, and worsening of life conditions of the populations leads to elimination of higher levels while keeping lower ones. That gives an idea to use an open modification of the hypercycle model, which was proposed initially for the description of ecological successions and some social processes (Sole and Bascompte 2006; Ellner and Rees 2006).

The open hypercycle model is based on a matrix representation, which is non-linear (it is natural for a model of ”social self-organization” of the population). In the article we focus on a continuous case, although the results may be used for discrete versions also. The model shows dependence of a complexity of population ”social structure” from the size of its niche. Population ”chooses” its complexity (or dimension) itself. We show it exactly for 3-dimension case (as well as for 2-dimension earlier (Chernyshenko 2005); generalization for N-dimension case is matter of further research.

1. OPEN HYPERCYCLE MODEL.

Let's consider the dynamic behavior of the heterogeneous biological population $\mathbf{x}(t) = (x_1(t), ..., x_n(t))^T$, which describing by Eigen's model hypercycle (here and further symbol T signifies transposition)

$$\left\{ \begin{array}{l} \dot{x}_1(t) = x_1(t)\left(F_1(t) - \dfrac{1}{S_0}\sum\limits_{j=1}^{n} x_j(t)F_j(t)\right), \\ \cdots\cdots\cdots\cdots\cdots\cdots, \\ \dot{x}_n(t) = x_n(t)\left(F_n(t) - \dfrac{1}{S_0}\sum\limits_{j=1}^{n} x_j(t)F_j(t)\right), \end{array} \right. \quad (1)$$

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(here $S_0 > 0$). The population consists of n subpopulations $x_i(t), i = 1, ..., n,$, which represent different levels of "social" hierarchy. The vector of initial values is $\mathbf{x}^T(0) = (x_{10}, ..., x_{n0})$.

We will consider that $F_1(t) = N - x_1(t), F_i(t) = a_{i-1}x_{i-1}(t) - x_i(t); i = 2, ..., n$, where $N, a_1, ..., a_{n-1}$ are positive numbers. (The functions $F_1(t), ..., F_n(t)$ are called as Allen's functions (Allen 1974).)

These functions determine very special interaction between the sub-populations, whene each of them depends on all the previous ones. Contrary to Eigen's hypercycle, the dependence has no cyclic character, so we can call this model as 'open' hypercycle.

2. THE EQUILIBRIUM POINTS OF THE SYSTEM (1).

Let's investigate analytically main features of the model dynamics.

Let's define as $i_1, ..., i_k$ $(k \le n)$ permutations of any k symbols $1, 2, ..., n$, for which the condition

$$1 \le i_1 < ... < i_k \le n$$

is fulfilled.

Assume that $x_{i_1} \ne 0, ..., x_{i_k} \ne 0$ and $x_{i_{k+1}} = 0, ..., x_{i_n} = 0$. Then the system of equations that define equilibriums has the form

$$\begin{pmatrix} 1-\frac{x_{i_1}}{S_0} & -\frac{x_{i_2}}{S_0} & \cdots & -\frac{x_{i_k}}{S_0} \\ -\frac{x_{i_1}}{S_0} & 1-\frac{x_{i_2}}{S_0} & \cdots & -\frac{x_{i_k}}{S_0} \\ \vdots & \vdots & \ddots & \vdots \\ -\frac{x_{i_1}}{S_0} & -\frac{x_{i_2}}{S_0} & \cdots & 1-\frac{x_{i_k}}{S_0} \end{pmatrix} \cdot \begin{pmatrix} F_{i_1} \\ F_{i_2} \\ \vdots \\ F_{i_k} \end{pmatrix} = 0,$$

$$x_{i_{k+1}} = ... = x_{i_n} = 0. \quad (2)$$

A determinant of the first k equations of system (2) may be presented as:

$$\det \begin{pmatrix} 1-\frac{x_{i_1}}{S_0} & -\frac{x_{i_2}}{S_0} & \cdots & -\frac{x_{i_k}}{S_0} \\ -\frac{x_{i_1}}{S_0} & 1-\frac{x_{i_2}}{S_0} & \cdots & -\frac{x_{i_k}}{S_0} \\ \vdots & \vdots & \ddots & \vdots \\ -\frac{x_{i_1}}{S_0} & -\frac{x_{i_2}}{S_0} & \cdots & 1-\frac{x_{i_k}}{S_0} \end{pmatrix} =$$

$$= 1 - \frac{x_{i_1} + ... + x_{i_k}}{S_0}.$$

Here we may face two cases: 1)$1 - \frac{x_{i_1} + ... + x_{i_k}}{S_0} \ne 0$ and 2)$1 - \frac{x_{i_1} + ... + x_{i_k}}{S_0} = 0$.

2.1. Determinant of the first k equations of the system (1) is not equal to zero.

In this case, according to (2) we get that $F_{i_1} = ... = F_{i_k} = x_{i_{k+1}} = ... = x_{i_n} = 0$. Condition $F_{i_1} = 0$ leads to $x_1 \ne 0$, then $x_1 = N, x_2 = a_1N, x_3 = a_1a_2N, ..., x_n = a_1 \cdot ... \cdot a_{n-1}N$; in this case the condition

$$S_0 \ne N(1 + a_1 + a_1a_2 + ... + a_1 \cdot ... \cdot a_{n-1})$$

has to be fulfilled.

Let $x_1 \ne 0, x_2 = 0$. Then $x_3 = ... = x_n = 0$. Assume $x_1 \ne 0$, $F_2 = 0$. Then $x_1 = N, x_2 = a_1N, x_3 = ... = x_n = 0$.

It is easy to find out that in this case we have $n+1$ equilibriums:

$$E_1 = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, ..., E_{k+1} = \begin{pmatrix} 1 \\ a_1 \\ \vdots \\ a_1 \cdot ... \cdot a_{k-1} \\ 0 \\ \vdots \\ 0 \end{pmatrix} N, ...,$$

$$E_{n+1} = \begin{pmatrix} 1 \\ a_1 \\ \vdots \\ a_1 \cdot ... \cdot a_{n-1} \end{pmatrix} N \in \mathbb{R}^n.$$

2.2. Determinant of the first k equations of the system (1) is equal to zero.

Here, we have $x_{i_k} = S_0 - x_{i_1} - ... - x_{i_{k-1}}$. Substituting the last formula in the system (2) we derive $F_{i_1} = F_{i_2} = ... = F_{i_k} = F$, where F is a nonzero function. Taking into account the last equations, system (2) may be presented as

$$\begin{cases} x_{i_1}(a_{i_1-1}x_{i_1-1} - x_{i_1} - F) = 0, \\ \cdots\cdots, \\ x_{i_k}(a_{i_k-1}x_{i_k-1} - x_{i_k} - F) = 0, \\ x_1 + ... + x_n = S_0, \\ x_{i_{k+1}} = 0, \\ \cdots\cdots, \\ x_{i_n} = 0, \end{cases} \quad (3)$$

where $F \ne F_{i_{k+1}}, ..., F \ne F_{i_n}$.

From this system we derive that $x_{i_1} \ne 0, ..., x_{i_k} \ne 0$. As $k = 1, 2, ..., n-1$, we get $C_n^1 + C_n^2 + ... + C_n^{n-1} + C_n^n$ solutions. Here C_n^i is a number of combinations of k sets from n elements ($k < n$).

Taking into account the case when determinant of the rst k equations of the system (1) is not equal to zero, we get for this system (1) $n + 1 + C_n^1 + ... + C_n^{n-1} + 1 = 2^n + n$ equilibriums.

2.3. Jacobian matrix building.

The Jacobi matrix for arbitrary n can be evaluated as $J = A + B + C$, where:

$$A = \begin{pmatrix} F_1 - \frac{1}{S_0}\sum_{j=1}^{n} x_j F_j & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & F_n - \frac{1}{S_0}\sum_{j=1}^{n} x_j F_j \end{pmatrix};$$

$$B = \begin{pmatrix} -x_1 & 0 & 0 & \cdots & 0 \\ x_2 a_1 & -x_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & x_n a_{n-1} & -x_n \end{pmatrix};$$

$$C = -\frac{1}{S_0} \begin{pmatrix} x_1(N - 2x_1 + a_1 x_2) & \cdots & x_1(a_{n-1}x_{n-1} - 2x_n) \\ \vdots & \cdots & \vdots \\ x_n(N - 2x_1 + a_1 x_2) & \cdots & x_n(a_{n-1}x_{n-1} - 2x_n) \end{pmatrix}.$$

3. EIGENVALUES OF JACOBI MATRIX IN EQUILIBRIUM POINTS FOR n = 3.

Let $n = 3$ and $F_1(t) = N - x_1(t)$, $F_2(t) = a_1 x_1(t) - x_2(t)$,$F_3(t) = a_2 x_2(t) - x_3(t)$, where $N > 0, a_1 > 0, a_2 > 0$.

Here we come to two cases: 1)$x_1 + x_2 + x_3 \neq S_0$ and 2)$x_1 + x_2 + x_3 = S_0$.

In the first case ($x_1 + x_2 + x_3 \neq S_0$) we have four equilibriums:

$$(0,0,0)^T, (N,0,0)^T, (N, a_1 N, 0)^T, (N, a_1 N, a_1 a_2 N)^T.$$

In the second case ($x_1 + x_2 + x_3 = S_0$) we have seven systems of equations, watch (3), to determine additional seven equilibriums:

$$\begin{cases} a_1 x_1 - x_2 - F = 0 \\ a_2 x_2 - x_3 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_1 = 0 \end{cases}, \begin{cases} N - x_1 - F = 0 \\ a_2 x_2 - x_3 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_2 = 0 \end{cases},$$

$$\begin{cases} N - x_1 - F = 0 \\ a_1 x_1 - x_2 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_3 = 0 \end{cases}, \begin{cases} a_2 x_2 - x_3 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_1 = 0 \\ x_2 = 0 \end{cases},$$

$$\begin{cases} N - x_1 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_2 = 0 \\ x_3 = 0 \end{cases}, \begin{cases} a_1 x_1 - x_2 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \\ x_1 = 0 \\ x_3 = 0 \end{cases},$$

$$\begin{cases} N - x_1 - F = 0 \\ a_1 x_1 - x_2 - F = 0 \\ a_2 x_2 - x_3 - F = 0 \\ x_1 + x_2 + x_3 = S_0 \end{cases}.$$

(Indefinite form of function F doesn't affect the present analysis.)

So, for the system (1) where $n = 3$ we got following 11 equilibriums:

E_1 :

$$x_1 = 0, x_2 = 0, x_3 = 0.$$

E_2 :

$$x_1 = 0, x_2 = \frac{S_0}{a_2 + 2}, x_3 = \frac{(a_2 + 1)S_0}{a_2 + 2}.$$

E_3 :

$$x_1 = \frac{S_0 + N}{2}, x_2 = 0, x_3 = \frac{S_0 - N}{2}.$$

E_4 :

$$x_1 = \frac{S_0 + N}{a_1 + 2}, x_2 = \frac{(a_1 + 1)S_0 - N}{a_1 + 2}, x_3 = 0.$$

E_5 :

$$x_1 = N, x_2 = a_1 N, x_3 = 0.$$

E_6 :

$$x_1 = 0, x_2 = 0, x_3 = S_0.$$

E_7 :

$$x_1 = 0, x_2 = S_0, x_3 = 0.$$

E_8 :

$$x_1 = S_0, x_2 = 0, x_3 = 0.$$

E_9 :

$$x_1 = N, x_2 = 0, x_3 = 0.$$

E_{10} :

$$F_1 = F_2 = F_3 = 0;$$

in this case

$$x_1 = N, x_2 = a_1 N, x_3 = a_1 a_2 N.$$

E_{11} :

$$F_1 = F_2 = F_3 \neq 0, x_1 + x_2 + x_3 = S_0;$$

then

$$x_1 = \frac{S_0 + (a_2 + 2)N}{3 + a_1 + a_2 + a_1 a_2}, x_2 = \frac{(a_1 + 1)S_0 + (a_1 - 1)N}{3 + a_1 + a_2 + a_1 a_2},$$

$$x_3 = \frac{(1 + a_2 + a_1 a_2)S_0 - (a_1 + a_2 + 1)N}{3 + a_1 + a_2 + a_1 a_2}.$$

(It is easy to find that all equilibriums do exist in the first orthan, necessary and sufficient criteria are: $S_0 \geq N$ and $a_2 \geq 1$ will be fulfilled.)

Now we are going to find a positive invariant set of the system (1) in case $n = 3$. Sum of all equations of system (1) is equal to:

$$\frac{d(x_1 + x_2 + x_3 - S_0)}{dt} = (x_1 + x_2 + x_3 - S_0)*$$

$$*\frac{1}{S_0}(-Nx_1 - a_1x_1x_2 - a_2x_2x_3 + x_1^2 + x_2^2 + x_3^2). \quad (4)$$

The behavior of solutions of (7) is described by the matrix

$$\begin{pmatrix} 1 & -a_1/2 & 0 \\ -a_1/2 & 1 & -a_2/2 \\ 0 & -a_2/2 & 1 \end{pmatrix}.$$

As $x_1 \geq 0, x_2 \geq 0, x_2 \geq 0$, then it follows from the equation (7) that if $x_{10} + x_{20} + x_{30} \leq S_0$, in case $t \geq 0$, $x_1 + x_2 + x_3 \leq S_0$. Let's define by V a domain in the first orthant bounded by coordinate planes $x_1 = 0$, $x_2 = 0$, $x_2 = 0$ and $x_1 + x_2 + x_3 = S_0$.

Recasting the equation (7) by successively completing the squares, we obtain:

$$\frac{d(x_1 + x_2 + x_3 - S_0)}{dt} =$$

$$= (x_1 + x_2 + x_3 - S_0)\frac{1}{S_0}(-Nx_1 + (x_1 - 0.5a_1x_2)^2$$

$$+(x_3 - 0.5a_2x_2)^2 + (1 - 0.25a_1^2 - 0.25a_2^2)x_2^2) =$$

$$= (x_1 + x_2 + x_3 - S_0)\frac{1}{S_0}\Big[\Big(x_1 - \frac{a_1}{2}x_2 - \frac{N}{2}\Big)^2 +$$

$$+\frac{4 - a_1^2 - a_2^2}{4}\Big(x_2 - \frac{2a_1N}{4 - a_1^2 - a_2^2}\Big)^2 + \Big(x_3 - \frac{a_2}{2}x_2\Big)^2 -$$

$$-\frac{N^2}{4} - \frac{a_1^2N^2}{4 - a_1^2 - a_2^2}\Big].$$

Let $a_1^2 + a_2^2 < 4$. Define by W an ellipsoid with center in point

$$K\left(\frac{N}{2} + \frac{a_1^2N}{4 - a_1^2 - a_2^2}, \frac{2a_1N}{4 - a_1^2 - a_2^2}, \frac{a_1a_2N}{4 - a_1^2 - a_2^2}\right)$$

and product of semiaxes

$$\frac{N^3(4 + 3a_1^2 - a_2^2)^{3/2}}{4(4 - a_1^2 - a_2^2)^2}.$$

If $a_1^2 + a_2^2 < 4$, $x_{10} + x_{20} + x_{30} \geq S_0$ and $(x_{10}, x_{20}, x_{30})^T \in W$, then a vector $(x_1(t), x_2(t), x_3(t))^T \in W$, and the formula in big rectangular brackets is negative. Therefore $\lim_{t\to\infty}(x_1(t), x_2(t), x_3(t))^T = E_{11}$. (Let $u = x_1(t) + x_2(t) + x_3(t) - S_0$. Then the equation (7) may be written in the form $\dot{u} = \xi(u)u$, where $\xi(u) < 0$; we derive the analog of a linear equation, the solution of which tends to zero.) Further we will consider the case $(x_{10}, x_{20}, x_{30})^T \in V$ only.

4. ANALYSIS OF THE EQUILIBRIUMS.

In all computations elements of Jacobian matrix divided on S_0 (so eigenvalue λ is replaced by the construction λ/S_0).

Let $\mu = N/S_0$. This value characterizes the ecological niche's size (it is inversely proportional the size). Let's analyse a behavior of the system (1) in the vicinity of all equilibriums.

Let's estimate all eigenvalues:

E_1. In this point eigenvalues $\lambda_1 = \mu, \lambda_2 = \lambda_3 = 0$. Equilibrium is a degenerative unstable node.

E_2. In this point eigenvalues

$$\lambda_1 = \mu + \frac{1}{a_2 + 2}, \lambda_2 = -\frac{a_2 + 1}{a_2 + 2}, \lambda_3 = \frac{1}{a_2 + 2}.$$

As $\mu > 0$, $a_2 \geq 0$ and $\lambda_2 \leq 0$, equilibrium is a saddle-node.

E_3. Here

$$\lambda_1 = \frac{\mu(a_1 - 1)}{2} + \frac{a_1 + 1}{2}, \lambda_2 = -\frac{1 - \mu^2}{2}, \lambda_3 = \frac{1 - \mu}{2}.$$

If $\mu \neq 1$, then from condition $\lambda_2\lambda_3 < 0$ it follows that this point is saddle-node. If $\mu = 1$, then

$$\lambda_1 = a_1, \lambda_2 = \lambda_3 = 0,$$

and we get a degenerative unstable node.

E_4. Here

$$\lambda_1 = -\frac{\mu(1 + a_1 + a_2)}{a_1 + 2} + \frac{1 + a_2 + a_1a_2}{a_1 + 2},$$

$$\lambda_2 = -\frac{\mu(1 + a_1)}{a_1 + 2} + \frac{1}{a_1 + 2}, \lambda_3 = \frac{(\mu + 1)(\mu - 1 - a_1)}{a_1 + 2}.$$

A simple analysis shows that if

$$\frac{1 + a_2 + a_1a_2}{1 + a_1 + a_2} < \mu < 1 + a_1, \quad (5)$$

then this point is a stable node. If $\mu > 1 + a_1$, then it is a saddle-node.

E_5. Here

$$\lambda_1 = a_2a_1\mu, \lambda_{2,3} = -\frac{\mu(a_1 + 1 - \mu)}{2} \pm$$

$$\pm\frac{\mu}{2}\sqrt{(a_1 + 1 - \mu)^2 + 4a_1(a_1\mu + \mu - 1)}.$$

As $\lambda_1 > 0$, then equilibrium is either a saddle or an unstable node.

E_6. Here $\lambda_1 = 1 + \mu, \lambda_{2,3} = 1$. Equilibrium is an unstable node.

E_7. Here $\lambda_1 = 1 + \mu, \lambda_2 = 1, \lambda_3 = a_2 + 1$. Equilibrium is an unstable node.

E_8. Here $\lambda_{1,2} = 1 - \mu, \lambda_3 = a_1 + 1 - \mu$. This point is either an unstable node or a stable node or a saddle-node.

E_9. Here $\lambda_1 = \mu(\mu-1), \lambda_2 = a_1\mu, \lambda_3 = 0$. This point is an unstable node or saddle.

E_{10}. It is clear that $N(1+a_1+a_1a_2) \le S_0$ or

$$\mu = \frac{S_0}{N} \le \frac{1}{1+a_1+a_1a_2} \qquad (6)$$

then $E_{10} \subset V$.

The Jacobi matrix in point E_{10} may be presented as:

$$J_{10}/S_0 = \mu \begin{pmatrix} -1 & 0 & 0 \\ a_1^2 & -a_1 & 0 \\ 0 & a_1a_2^2 & -a_1a_2 \end{pmatrix} +$$

$$+\mu^2 \left[\begin{pmatrix} 1 \\ a_1 \\ a_1a_2 \end{pmatrix} \cdot \begin{pmatrix} (1-a_1^2), a_1(1-a_2^2), a_1a_2 \end{pmatrix} \right].$$

A characteristic polynomial of the Jacobi matrix in point E_{10} is:

$$\det(\lambda I - J_{10}/S_0) = \lambda^3 + p_1\lambda^2 + p_2\lambda + p_3 =$$

$$= \lambda^3 + [\mu(1+a_1+a_1a_2) - \mu^2]\lambda^2 + [a_1(1+a_2+a_1a_2)\mu^2 -$$

$$-a_1(1+a_1+a_2)\mu^3]\lambda + a_1^2a_2[\mu^3 - (1+a_1+a_1a_2)\mu^4].$$

Let's assume that the condition (6) is satisfied. Then $E_{10} \subset V$. If $\mu \to 0$, then this point is asymptotic stable. In case when μ is increasing, but inequality (6) is satisfied, it easy to check that $p_1 > 0, p_2 > 0, p_3 > 0, p_1p_2 > p_3$. If $\mu = (1+a_1+a_1a_2)^{-1}$ (bifurcation point), then $\lambda_1 = 0$ and the point turns out to be unstable.

E_{11}. One of eigenvalues of the Jacobi matrix is

$$\lambda_1 = \frac{1-\mu(1+a_1+a_1a_2)}{3+a_1+a_2+a_1a_2}.$$

Therefore the inequality (6) is hold. So $\lambda_1 > 0$ and equilibrium E_{11} may be node or saddle.

If

$$\mu \approx \frac{1}{1+a_1+a_1a_2}$$

and

$$\mu > \frac{1}{1+a_1+a_1a_2},$$

then equilibrium is a stable node. Thus, if

$$\mu = \frac{1}{1+a_1+a_1a_2}$$

then points E_{10} and E_{11} are exchange.

Consider the case

$$\mu > \frac{1}{1+a_1+a_1a_2}.$$

It is clear that

$$\frac{1}{1+a_1+a_1a_2} \le \frac{1+a_2+a_1a_2}{1+a_1+a_2}.$$

Note, if

$$\mu = \frac{1}{1+a_1+a_1a_2}$$

then one of eigenvalues of the Jacobi matrix in the point E_{11} equal to zero; if

$$\mu = \frac{1+a_2+a_1a_2}{1+a_1+a_2},$$

then another eigenvalue of the Jacobi matrix equal to zero (other two eigenvalues have negative real parts).

If

$$\frac{1}{1+a_1+a_1a_2} < \mu < \frac{1+a_2+a_1a_2}{1+a_1+a_2},$$

then the point E_{11} is stable; if

$$\mu > \frac{1+a_2+a_1a_2}{1+a_1+a_2},$$

then the point E_{11} is unstable.

At last, if the condition (5) is fulfilled, then we have the stable equilibrium in E_4.

5. BIFURCATION POINTS.

Let's find a positive invariant set of the system (1) for $n = 3$. Add all equations of system (1):

$$\frac{d(x_1+x_2+x_3-S_0)}{dt} = (x_1+x_2+x_3-S_0)\frac{1}{S_0}(-Nx_1-$$

-a$_1x_1x_2 - a_2x_2x_3 + x_1^2 + x_2^2 + x_3^2$).(7)

Let's introduce a new variable $u(t) = x_1(t) + x_2(t) + x_3(t) - S_0$. Then equation (**??**) may be written as

$$\frac{du}{dt} = u\frac{1}{S_0}(-Nx_1 - a_1x_1x_2 - a_2x_2x_3 + x_1^2 + x_2^2 + x_3^2). \quad (8)$$

Theorem 1. *Any solution $u(t)$ (for any initial value $u_0 = u(0)$ and $\forall t \ge 0$) of equation (8) has the property: $u_0u(t) \ge 0$.*

Let $u_0 \le 0$. As $x_1 \ge 0, x_2 \ge 0, x_2 \ge 0$, then according to the Theorem 1 while $t \ge 0$, the function $u(t) = x_1(t) + x_2(t) + x_3(t) - S_0 \le 0$. We will define as V a domain in the first orthant, bounded by coordinate planes $x_1 = 0$, $x_2 = 0$, $x_2 = 0$ and $x_1 + x_2 + x_3 = S_0$. Then, we derive that V is an invariant set ($\forall t \ge 0$ from $x_{10} + x_{20} + x_{30} \le S_0$ it follows that $x_1(t) + x_2(t) + x_3(t) \le S_0$).

We will consider that $(x_{10}, x_{20}, x_{30})^T \in V$ is a vector of initial values. In this case we will have $\forall t > 0$ $(x_1(t), x_2(t), x_3(t))^T \in V$. Thus, V is a positive invariant set.

We suppose that $x_{10} > 0, x_{20} > 0, x_{30} > 0$. (If one initial value is zero, then we will come to a 2-D analysis.)

There are 4 different bifurcations points:

$$\mu_0 = 0, \mu_1 = \frac{1}{1 + a_1 + a_1 a_2}, \mu_2 = \frac{1 + a_2 + a_1 a_2}{1 + a_1 + a_2},$$

$$\mu_3 = 1 + a_1.$$

1.

$$0 < \mu < \frac{1}{1 + a_1 + a_1 a_2}.$$

The trajectory tends to the single equilibrium $E_{10} \in V$. Thus, for small μ (when the size of the ecological niche larger then the critical value: $S_0 > (1 + a_1 + a_1 a_2) \cdot N$), all sub-populations do exist and try to reach maximal possible size; on the other hand, their aggregate size is smaller then the size S_0 of the population niche.

2.

$$\frac{1}{1 + a_1 + a_1 a_2} < \mu < \frac{1 + a_2 + a_1 a_2}{1 + a_1 + a_2}.$$

The trajectory tends to the single equilibriums $E_{11} \in V$. With such a size of the ecological niche, all three sub-populations may be presented; they occupy whole ecological niche S_0 and are limited in size by the size of the niche.

3.

$$\frac{1 + a_2 + a_1 a_2}{1 + a_1 + a_2} < \mu < 1 + a_1.$$

The trajectory tends to the single equilibriums $E_4 \in V$. The niche size S_0 is so small that the third level of the sub-population "social" organization (the third sub-population) can not come into existence. Two other populations occupy the entire ecological niche.

4. $1 + a_1 < \mu < \infty$.

In this case the trajectory tends to the point $E_8 \in V$. In the environment of such a small ecological niche only the first subpopulation is able to exist. So population is limited only by the size of niche. It has no internal structure; second and third sub-populations are absent.

6. CONCLUSION.

The analysis of results which were resulted above, leads to the several observations. In case of small values of p, only the first subpopulation survives. Second and third subpopulations survive just with growth of p. In addition, all surviving populations occupy whole ecological niche. Finally, if $p > p_3$ then an "era of abundance" comes, when all populations survive, and ecological niche is filled partially (all resources of the niche are used not completely).

One should also mention the following: parameters S_0, N, a_1, a_2 have different influence on a character of flowing processes. The most important of these parameters are S_0, N. Parameter S_0 determines the maximal volume of resources, that can be used while populations development. Parameter N shows that at any nonzero S_0 the first population always survives. This conclusion allows to assert that in case of the Eygen model, the biological association remains (what is possible thanks to the reduced structure). Parameters $a_1 and a_2$ specify only a quantitative influence of one population on others. In addition, these parameters do not change the type of bifurcation points and their ammount.

Analysis of the 3-D open Eigen's model allows to propose the following suggestion sfor n-dimension case.

There do exist $n + 1$ bifurcation points :

$$0 = \mu_0 < \mu_1 < \mu_2 < ... < \mu_n < \infty,$$

where

$$\mu_1 = \frac{1}{1 + a_1 + a_1 a_2 + ... + a_1 \cdot ... \cdot a_{n-1}}.$$

If

$$0 < \mu < \mu_1,$$

then all populations survive and occupy only part of ecological niche; a volume of this niche is $N(1 + a_1 + a_1 a_2 + ... + a_1 \cdot ... \cdot a_{n-1}) < S_0$.

If:

$$\mu_1 \leq \mu < \infty,$$

then populations (but not all) occupy whole ecological niche S_0; if

$$\mu_i < \mu < \mu_{i+1}, 1 \leq i \leq n - 1,$$

then populations $1, 2, ..., n - i + 1$ remain and populations $n - 1, n - 2, ..., i - 1$ die out ; when

$$\mu_n < \mu < \infty,$$

then only unique population survive and fill whole ecological niche S_0.

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