

COENOME MODEL: ELEMENTARY ECOLOGICAL CYCLE AS A DYNAMICAL UNIT

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ABSTRACT

A general approach to modelling of ecosystem dynamic is considered. The special term "coenome" is proposed for basic dynamic element of biogeocoenoses. The coenome is an association of populations which have complementary properties (up to symbioses) or united by trophical links. Each succession stage is characterised by a major dominant coenome. The succession process is considered as a process of step-by-step changing dominating coenome. Sketch models of the coenome are considered. The application of M. Eigen's hypercycle for modelling of ecosystem successions is proposed. The model describes a specific interaction between coenomes, which are similar, but not equivalent to the competition and "host-parasite" relations. As a result of the interaction, a redistribution of ecological resources may take place. During several steps of the succession process, the ecosystem "selects" its optimal dimension and complexity. Succession process is considered as reaching optimal complexity of ecosystems.

COENOME AS A UNIT OF ECOSYSTEM DYNAMIC STRUCTURE

The method of mathematical modelling become a traditional tool of ecology. The modern approach to theoretical ecology modelling is founded by the famous monographs of A. Lotka (1925) and V. Volterra (1931). The chief purpose of this kind of modelling is not an exact quantitative simulation of natural ecosystems, but determining and formal description of main properties of ecosystems' behaviour. In the nature there is no pair of populations absolutely corresponding to the Volterra's "predator-pray" style of relations, as well as there is no "material points" in real physical systems. At the same time such abstract objects are extremely useful as elements of complex mathematical models. Within voluminous literature on the dynamical analysis in ecology one can mention classical monographs of E.P. Maynard Smith (1974), Yu.M. Svirezhev and D.O. Logofet (1978), E.C. Pielou (1977).

Let's concentrate on some aspects of long-term ecosystem dynamics and consider the succession phenomenon as a result of ecosystem property of self-recovery (or

homeostasis). The traditional succession models (Horn 1976; Lepš 1988; Perry and Millington 2007) are based on using stochastic models and such parameter as "a probability of transition" between different ecosystem states. The parameter is considered as external one, and, as a result, the model structure does not reflect adaptive nature of the succession process (Begon et al. 1986). Modelling of ecosystem transforming on the base of adaptation approach looks more interesting from theoretical point of view. The idea is to describe changes of ecosystem structure as a result of changing ecological conditions determined by internal and external factors.

The phenomenon of homeostasis is not determined directly by complexity of real ecosystems. Mathematical modelling shows that, in general, growth of complexity leads to reduction of ecosystem stability, or does not influence it (May, 1973). Stability of real ecosystems is a result of very special character of interaction between their elements. It is not only trophic and topic relations between populations or individuals. Another kind of dynamical units should be found to describe this aspect of ecosystem dynamics (Chernyshenko 1996).

Let's consider "succession generations" (intermediate dominate ecosystems) as units, interaction between which is a driving force of successions. Each succession generation is identified by an unequal association of species with complementary ecological properties (up to symbioses) or united by trophical links. We propose a special term "coenome" for such associations. "Coenomes" are considered as main elements of forest ecosystem (or biogeocoenosis) useful for purposes of modelling long-term dynamic processes. Each succession stage is characterised by main dominant coenome. The succession process is considered as a process of step-by-step changing dominant coenome.

An association of species, forming coenome, includes populations of producers, consumers, and reducers. The central position of producers in coenome is determined by their role as an energy source for the whole ecosystem. The role of consumers is not such important, although there are situations, when activity of consumers determines a tendency of succession (Begon et al., 1986). An energetic role of reducers consists in restoring some biomass to biota by detrital trophic webs, but their major importance for biogeocoenose is explained by the necessity "to close" biogeochemical cycles. The simplest artificial stable ecosystems, functioned in closed flasks, included populations of producers (unicellular algae) and reducers (fungus) (Lappo, 1987).

Theoretically, it is possible to envision producers, independently realising the function of decomposition regarding own biomass. But this possibility is not realised in reality. If the hypotheses of E. Odum (1971) about origin of heterotrophs before phototrophs is correct, first producers had no problems with utilisation of died biomass and products of metabolism, and there were no evolutionary reasons for forming “self-sufficient” organisms. Stable biogeochemical cycles were formed gradually, during the process of co-adaptation of producers and reducers. The formation of a first stable “producers-reducers” cycle meant origin of a first ecosystem. The cyclic character of ecological stability creates an analogy between the beginnings of ecosystems and first organisms in accordance with the “hypercyclic” model of M. Eigen (1979).

We propose a special term “coenome” for the elementary biogeocoenotic cyclic element. The coenome includes one or several populations of producers (as a source of energy and a kernel of the association); reducers, which “close” biogeochemical cycles; and consumers, which stimulate energetic processes in the system (Chernyshenko 2008a). Naturally, the areas of the ecological optimum of coenome species must have common parts. Coenome species are characterised by some level of co-adaptation. The main features of cross-population relations in a coenome are the following: a) a low level of competition, as a result of effective separation of niches; b) a high level of mutualism, especially, in pairs “producer-reducer”; c) an optimal (energetically determined) level of trophic relationship.

The coenome closely corresponds to the sinusia of 3-rd order of H. Gams (1918). The “stable” group of populations forms a dominant coenome, the “regressive” populations represent previous coenomes (succession generations), the “progressive” populations reflect forming a next coenome. Interaction of producers from the different groups is very important for the course of succession. It can not be described by the traditional schemes like “++” or “--”, and need in more detailed analysis.

A principal scheme of matter and energy flows in coenome (without consumers) is represented in Fig.1. The symbols x , y , p , q denote contents of some chemical elements, correspondingly: in the biomass of producers; in the biomass of reducers; in the dead biomass; in the inorganic matter, accessible for producers. Characteristic intensity of the element cycling is symbolised by M . The coefficient α ($0 < \alpha < 1$) determines a part of the element, escaping the populations of producers as an organic matter, and λ ($0 < \lambda < 1$) determines the same for populations of reducers.

MATTER, ENERGY, AND INFORMATION FLOWS IN COENOMES

The simplest model of matter cycling in coenome (the unbroken lines in Fig.1) can be designing on the base of the Lotka-Volterra model (Lotka, 1925; Volterra, 1931).

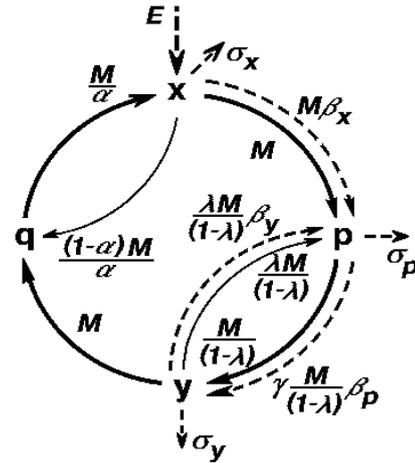


Figure 1: Matter and energy flows in a coenome

In the case without effects of saturation and self-limitation of populations, it can be written as

$$\begin{aligned} dx/dt &= a q x - b x \\ dp/dt &= \alpha b x + \lambda s y - r y p \\ dy/dt &= r p y - s y \\ dq/dt &= (1-\alpha) b x + (1-\lambda) s y - a x q \end{aligned} \quad (1)$$

The coefficients b and s are coefficients of mortality of producers and reducers; a and r estimate a rate of the use of, correspondingly, inorganic matter by producers and dead biomass by consumers. The model (1) can be considered as a modification of the model of V.V. Alekseev (1976). The value M for the model is equal to $\alpha b x$, that is to say, it is determined by the intensity of the element transferring from producer populations to the dead biomass.

Although the model (1) is only a sketchy model, it is characterised by some special features. The concentration of the element in inorganic matter, accessible for producers (“in soil”), is determined in the steady-state by the ratio of the coefficient of producer mortality to the rate of producer absorption of the element: $q_{st} = b/a$. Similarly, but on the base of ecological features of reducers, the stable level of the element concentration in the dead biomass (“in litter”) is found from the equation $p_{st} = s/r$. The model does not determine the stable values of x and y , but only their ratio: $x/y = (1-\lambda)s/\alpha b$. It is explicable both from mathematical point of view (the sum of the right-hand sides of the equations equals to zero, and the sum $(x+y+p+q)$ is not changed during the process), and from biological reasons (the model describe closed circulation of the element, its amount in the cycle have to be determined by some external factors). The system (1) is not asymptotically stable, but under natural assumptions that $A > b$, $R > s$, the own numbers of the linearised system have negative real parts (except one, which equals zero).

A more realistic model of the coenome is arrived by the use of equations with Michaelis-Menten functions in the right-hand sides (Thornley 1976):

$$\frac{dx}{dt} = A \left(\frac{X}{x+X} - \frac{b}{A} \right) x \quad (2)$$

where X means the concentration of semisaturation, which is proportional to the concentration of controlling factor. The equation (1) assumes the form:

$$\begin{cases} \frac{dx}{dt} = A \left(\frac{cq}{x+cq} - \frac{b}{A} \right) x \\ \frac{dp}{dt} = \alpha bx + \lambda sy - R \frac{hp}{y+hp} y \\ \frac{dy}{dt} = R \left(\frac{hp}{y+hp} - \frac{s}{R} \right) y \\ \frac{dq}{dt} = (1-\alpha)bx + (1-\lambda)sy - A \frac{cq}{x+cq} x \end{cases} \quad (3)$$

The system (3) dictates the same parameter $M = \alpha bx$ and the same ratio between biomass of populations as the model (1). However, the quantities p and q depend on populations' sizes in this case by the following way:

$$\begin{aligned} y &= \frac{\alpha b}{(1-\lambda)s} x, & q &= \frac{b}{c(A-b)} x \\ p &= \frac{s}{h(R-s)} y = \frac{\alpha b}{(1-\lambda)h(R-s)} x, \end{aligned} \quad (4)$$

In the vicinity of an arbitrary equilibrium point the characteristic equation for the own numbers have the form:

$$\Lambda^4 + (\Phi + \Psi) \Lambda^3 + (\Phi\Psi + \Gamma + \Xi) \Lambda^2 + (\Phi\Gamma + \Psi\Xi) \Lambda = 0,$$

where $\Phi = (A-b)(b+c(A-b))/A$, $\Psi = (R-s)(s+h(R-s))$, $\Gamma = \alpha bc(A-b)^2/A$, $\Xi = (1-\lambda)sh(R-s)^2/R$. One of the eigenvalues is equal to zero, but others have negative real parts. In the vicinity of any equilibrium points of the system (3) there are an infinite number of other equilibrium points, and any of them is not asymptotically stable. At the same time the set of the equilibrium points (as a whole) is a global attractor. The fact is confirmed by numerical experiments.

Let us consider energetic flows in coenome (the dotted lines in the Fig. 1). On the base of the model (3) it is possible to write the following system:

$$\begin{cases} \frac{de_x}{dt} = (E - \alpha b - \sigma_x) e_x \\ \frac{de_p}{dt} = \alpha b e_x + \lambda s e_y - R \frac{h e_p}{e_y + h e_p} e_y - \sigma_p e_p \\ \frac{de_y}{dt} = \left(\gamma R \frac{h e_p}{e_y + h e_p} - \lambda s - \sigma_y \right) e_y \end{cases} \quad (5)$$

where e_x , e_y , e_p - the variables, which estimate, correspondingly, the energy amount in biomass of producers, reducers, and dead biomass; $\sigma_x e_x$, $\sigma_y e_y$, $\sigma_p e_p$ - the losses of energy for each of this groups; $E e_x$ - the intensity of energy flow into populations of producers; $\gamma (0 < \gamma < 1)$ - the part of energy of the dead biomass, which passes to energy of the biomass of reducers.

As it is easy to see, the first equation of the system (5) does not depend on the other. The condition of existing a stationary nonzero value of e_x is $\sigma_x = E - \alpha b$. The stationary value of e_x is depend on initial conditions, as well as the variation x in the model (3). With the natural supposition of $s_p=0$ (the role of abiotic degrading the dead biomass is not essential) the stationary values for other co-ordinates are determined by the equations:

$$\begin{aligned} e_y &= \frac{\gamma \alpha b}{(1-\gamma)\lambda s + \sigma_y} e_x; & e_p &= \frac{(\lambda s + \sigma_y)}{h(\gamma R - \lambda s - \sigma_y)} e_y = \\ &= \frac{\gamma(\lambda s + \sigma_y) \alpha b}{h((1-\gamma)\lambda s + \sigma_y)(\gamma R - \lambda s - \sigma_y)} e_x. \end{aligned} \quad (6)$$

The conditions of positivity of the steady-state are the following: $\gamma > \lambda s / R$, $\sigma_y < \gamma R - \lambda s$. If they assert, the steady-state (6) is stable.

Let's consider the problem of the interplay of the matter and energy flows in the coenome. Let β_x , β_y , β_p be the measure of energy per the biomass unit of, correspondingly, producers, reducers, and dead biomass. Then $e_x = \beta_x x$, $e_y = \beta_y y$, $\beta_p = \beta_p p$. Let us substitute to (6) the values x , y , p from the model (3) and arrive:

$$\begin{aligned} \beta_y &= \frac{\gamma(1-\lambda)s}{(1-\gamma)\lambda s + \sigma_y} \beta_x; & \beta_p &= \frac{(R-s)(\lambda s + \sigma_y)}{s(\gamma R - \lambda s - \sigma_y)} \beta_y = \\ &= \frac{\gamma(1-\lambda)(R-s)(\lambda s + \sigma_y)}{((1-\gamma)\lambda s + \sigma_y)(\gamma R - \lambda s - \sigma_y)} \beta_x. \end{aligned} \quad (7)$$

The formulas (7) supposedly describe more realistic relationship between energy concentration in biomass of different groups, than the equations, derived on the base of the quadratic model (Ulanowicz 1972).

From equations (3), (5) one can obtain the system, describing the dynamics of variables $\beta_x, \beta_y, \beta_p$:

$$\begin{cases} \frac{d\beta_x}{dt} = A \left(E + (1-\alpha)b - A \frac{c}{x_q + c} - \sigma_x \right) \beta_x \\ \frac{d\beta_p}{dt} = \alpha b x_p \beta_x + \left(\lambda s - R \frac{h \beta_p}{y_p \beta_y + h \beta_p} \right) y_p \beta_y + \\ \quad + \left(R \frac{h}{y_p + h} - \alpha b x_p - \lambda s y_p - \sigma_p \right) \beta_p \\ \frac{d\beta_y}{dt} = \left(\gamma R \left(\frac{h \beta_p}{\beta_y y_p + h \beta_p} - \frac{h}{y_p + h} \right) + (1-\lambda)s - \sigma_y \right) \beta_y \\ \frac{dx_p}{dt} = \left(A \frac{c}{x_q + c} - b - \alpha b x_p - \lambda s y_p + R \frac{h}{y_p + h} y_p \right) x_p \\ \frac{dy_p}{dt} = \left(R \frac{h}{y_p + h} - s - \alpha b x_p - \lambda s y_p + R \frac{h}{y_p + h} y_p \right) y_p \\ \frac{dx_q}{dt} = \left(A \frac{c}{x_q + c} - b - (1-\alpha) b x_q + (1-\lambda) s y_q - A \frac{c}{x_q + c} x_q \right) x_q \\ \frac{dy_q}{dt} = \left(R \frac{h}{y_p + h} - s - (1-\alpha) b x_q + (1-\lambda) s y_q - A \frac{c}{x_q + c} x_q \right) y_q \end{cases} \quad (8)$$

Here the co-ordinates are defined as $x_p = x/p$, $y_p = y/p$, $x_q = x/q$, $y_q = y/q$. Their dynamics is not depend on β_x, β_p ,

β_y , and they may be described in the vicinity of the equilibrium point by the first three equations from (8), where the values of biomass from (4) are used:

$$\begin{cases} \frac{d\beta_x}{dt} = (E - \alpha b - \sigma_x)\beta_x \\ \frac{d\beta_p}{dt} = h(R-s)(1-\lambda)\beta_x + h(R-s)\left(\lambda - R\frac{\beta_p}{(R-S)\beta_y + s\beta_p}\right)\beta_y \\ \frac{d\beta_y}{dt} = \left(\gamma R\frac{s\beta_p}{(R-s)\beta_y + s\beta_p} - \lambda s - \sigma_y\right)\beta_y \end{cases} \quad (9)$$

The steady-state is specified by equation (7) and it is stable. The variables β_x , β_p , β_y can be used as a measure of the level of organisation (or thermodynamic instability) of population biomass. It is possible to interpret the system (9) as the model of information transformation in the coenome, if to use the term "information" as a synonym of negentropy.

The flows of matter, energy, and information, describing by the models (3),(5),(9), are ultimately determined by producer activity. The variables x , e_x , and β_x are external parameters of the models in some sense. Particularly, it is evident from formulas (4), (6), (7), where other coordinates of the steady-state are expressed by these variables. It is reasonable to use models (3), (5), (9) without first equations, and to consider variables x , e_x , β_x as external parameters, describing by some additional equations.

The value of e_x is determined by the energetic potential of producers. The stable value e^* can be derived from a model of productivity (Thornley 1976; Berezovskaya et al. 1991). Particularly, it is possible to use models of such type as (2):

$$\frac{de_x}{dt} = \left(A \frac{E(u_s, u_c, u_h, u_t)}{e_x + E(u_s, u_c, u_h, u_t)} - b(u_t) \right) e_x \quad (10)$$

The variables E (the intensity of the flow of physiologically accessible energy) and b (the intensity of energy spending in the course of vital activity) depends on such parameters as u_s (the intensity of the flow of solar energy), u_c (the concentration of accessible carbonic acid gas), u_h (the concentration of accessible water), u_t (the temperature), and other factors, which can be included in the model too. For the model (10) one can obtain:

$$e^* = E(u_s, u_c, u_h, u_t) \left(\frac{A}{b(u_t)} - 1 \right)$$

The energy flow to the coenome can be limited by scantiness in the environment of some chemical elements or substances in accessible forms. Besides carbonic acid gas and water it can be such elements as N, P, K, microelements, etc. Each i -th critical element or substance can be characterise by two indices. The first one, $x_i^{(\min)}$ is a physiologically necessary concentration of the element in the producer biomass. If $x_i < x_i^{(\min)}$, the productivity of the producer decreases proportionally to x_i . The second index, $x_i^{(\text{nom})}$ ($x_i^{(\text{nom})} > x_i^{(\min)}$) is a physio-

logically optimal concentration of the element. Let $X_i^{(c)}$ be a general amount of the element in the coenome. Than, in accordance with (6), its amount in the producers biomass will be

$$x_i^{(c)} = \left(\frac{cA - (c-1)b}{c(A-b)} + \frac{hR - (h-1)s}{h(R-s)} \frac{\alpha b}{(1-\lambda)s} \right)^{-1} X_i^{(c)}$$

The value of x_i^* and the corresponding value of e_{xi} can be defined by the following formulas:

$$\begin{cases} x_i^* = x_i^{(\text{nom})}, e_{xi} = e^*, & \text{when } x_i^{(c)} > x_i^{(\text{nom})} \\ x_i^* = x_i^{(c)}, e_{xi} = e^*, & \text{when } x_i^{(\min)} < x_i^{(c)} < x_i^{(\text{nom})} \\ x_i^* = x_i^{(c)}, e_{xi} = e^* x_i^{(c)} / x_i^{(\min)}, & \text{when } x_i^{(c)} < x_i^{(\min)} \end{cases} \quad (11)$$

In accordance with the principle of minimum of J. Liebig (1847) the productivity of a plant is determined by the amount of a substance, which is physiologically minimal. Consequently, the final value of the intensity of stable energy flow in a coenome can be defined as

$$e_x^* = \min_i e_{xi}$$

In the case, when the energy flow is limited by climatic factors only, $e_x^* = e^*$. In the opposite case, $e_x^* < e^*$.

The variable β_x appears to be determined physiologically, and only slightly ecologically. It is confirmed by the wide variation of energy concentration in biomass of different producers. For example, it has a minimal value for trees, which are characterised by high development of support organs, and it is essentially higher for phytoplankton. In accordance with the definition, $\beta_x^* = e_x^* / x^*$. Based on (11), one can suppose that the energy concentration in biomass have to be higher in a condition of deficiency of necessary substances. However, this is not correct always, particularly, as a result of variation of the substance concentration during year and effects of accumulation.

THE MODEL OF DIRECT INTER-COENOME RELATIONS

Let us consider the direct inter-coenome relations, without taking into account their mutual influence by the way of changing environmental conditions. It is possible to recognise two components in this relation: competition and facilitation.

By the Lotka-Volterra equation, the competition between two populations can be describing as

$$\frac{dx_i}{dt} = x_i \left(a_i - b_i \sum_{j=1}^n d_{ij} x_j \right), \quad i = \overline{1, n}$$

After some generalisation it can be written as

$$\frac{dx_i}{dt} = \Gamma_i(x) - b_i x_i \sum_{j=1}^n \Gamma_j(x), \quad i = \overline{1, n} \quad (12)$$

The system (12) has some special features, when b_i do not depend on i . This is a case, when the competition oppresses equally all interacting coenomes (an analogue of third Newton's law is true). The system assumes the following form:

$$\frac{dx_i}{dt} = \Gamma_i(x) - \frac{x_i}{C_0} \sum_{j=1}^n \Gamma_j(x), \quad i = \overline{1, n}. \quad (13)$$

Models of the form (13) have been used by M. Eigen (Eigen and Schuster 1979) for describing the evolutionary process of self-organisation of organic macromolecules. The functions $\Gamma_i(x)$ have been decided as:

$$\begin{aligned} \Gamma_1(x) &= k_1 x_1, \\ \Gamma_i(x) &= x_i (k'_{i-1} x_{i-1} + k'_i x_i), \quad i = \overline{2, n} \end{aligned} \quad (14)$$

The functions (14) describe limitless increase of sizes of isolated populations and their mutual stimulation (with simultaneous competition for ecological resources in accordance with structure of the equation (13)). In the case of self-restriction of the populations the “functions of growth” $\Gamma_i(x)$ (Allen 1976) can be written in the following form:

$$\begin{aligned} \Gamma_1(x) &= x_1 (N - x_1), \\ \Gamma_i(x) &= x_i (a_{i-1} x_{i-1} - x_i), \quad i = \overline{2, n} \end{aligned} \quad (15)$$

The parameters C_0 , a_i , and N are presumed positive. Initial conditions are supposed positive and essentially less than the parameters N and C_0 . The modification (13), (15) of the M. Eigen’s model was proposed in the article (Chernyshenko, 1995). Equilibrium points of the system (13) can be classified for two groups. The first one is defined by the following formulas:

$$\sum x_i = C_0, \quad \frac{x_i}{\Gamma_i(x)} = \text{const} \quad \text{for all } i, \quad (16)$$

and for the second group it is true

$$\Gamma(x_1, \dots, x_n) = 0, \quad i = \overline{1, n}. \quad (17)$$

The level of the competition between the coenomes varies in inverse proportion to the value of C_0 . Considering that by (16) a limiting value of the total biomass of all coenomes is equal to C_0 (for the case (17) it does not exceed this value too) it is possible to interpret the parameter C_0 as a “environmental capacity”, which limits a maximal total biomass of the ecosystem.

The system (13), (15) has

$$n + 2 + \sum_{i=1}^{n/2+1} C_n^i$$

equilibrium points, with $(n+1)$ points X_k can be stable:

$$\begin{cases} X_k = \{x_k^{(1)}, x_k^{(2)}, \dots, x_k^{(k)}, 0, \dots\}, & k = \overline{1, n}, \\ X_{n+1} = \{N, a_1 N, \dots, a_1 \dots a_{n-1} N\}, \end{cases} \quad (18)$$

The variables $x_k^{(i)}$ are defined by the following equations:

$$\begin{aligned} x_k^{(i)} &= (R_i^{(k)} N + B_i^{(0)} C_0) / \sum_{j=1}^k B_j^{(0)}, \quad i = \overline{1, k}, \\ R_i^{(k)} &= \prod_{j=1}^{i-1} a_j \sum_{j=1}^{k-i} B_j^{(i)} - \sum_{j=1}^{i-1} \left(B_{i-j}^{(j)} \prod_{l=0}^{j-1} a_l \right), \quad a_0 = 1, \end{aligned}$$

The variables $B_j^{(i)}$ can be obtained from the recurrent formula of the Fibonacci type:

$$B_0^{(i)} = 0, \quad B_1^{(i)} = 1, \quad B_j^{(i)} = (a_{i+j-1} + 1) B_{j-1}^{(i)} - a_{i+j-2} B_{j-2}^{(i)}.$$

It is true that for any k :

$$\sum_{i=1}^k R_i^{(k)} = 0, \quad \sum_{i=1}^k x_k^{(i)} = C_0.$$

A concrete value of k for the steady-state (its dimension) is determined by values of the parameters C_0 , a_i , and N . The value of k increases simultaneously with growth of the parameter C_0 . The dimension of the system in a steady-state (or the number of succession steps before a climax stage) increases simultaneously with increasing “environmental capacity”.

Let us consider the two-dimensional system:

$$\begin{cases} \frac{dx_1}{dt} = \Gamma_1(x_1, x_2) - \frac{x_1}{C_0} \sum_{i=1}^2 \Gamma_i(x_1, x_2), \\ \frac{dx_2}{dt} = \Gamma_2(x_1, x_2) - \frac{x_2}{C_0} \sum_{i=1}^2 \Gamma_i(x_1, x_2) \end{cases} \quad (19)$$

There are three (excluding the infinity) potentially steady equilibrium points:

$$\begin{cases} X_1^{(1)} = C_0 \\ X_1^{(2)} = 0 \end{cases}, \quad \begin{cases} X_2^{(1)} = \frac{C_0 + N}{a_1 + 2} \\ X_2^{(2)} = \frac{(a_1 + 2)C_0 - N}{a_1 + 2} \end{cases}, \quad \begin{cases} X_3^{(1)} = N \\ X_3^{(2)} = a_1 N \end{cases}$$

For fixed values of the parameters of the system there is only one steady-state. The state X_1 is steady when

$$C_0 < \frac{N}{a_1 + 1}, \quad (20)$$

the state X_2 is steady under the condition

$$\frac{N}{a_1 + 1} < C_0 < (a_1 + 1)N, \quad (21)$$

and the state X_3 is steady if

$$C_0 > (a_1 + 1)N. \quad (22)$$

All steady equilibrium points are nodes, unsteady points are nodes or saddles. The system has no focal equilibrium points under any values of the parameters. Oscillatory regimes are not possible in the model. In the bifurcation points $N/(a_1 + 1)$ and $(a_1 + 1)N$ a change of steady-states takes place. Under the critical values of C_0 two equilibrium points are merged into a point of the “saddle-node” type.

The cases (20)-(22) determine different scenarios of the system development. Under small value of C_0 (“environmental capacity”) the second coenome can not develop and its biomass x_2 in the steady-state is equal zero. Under middle values of C_0 (the case (21)) the second coenome has possibility of growth after attainment by the first coenome of some level of development. In this case both coenomes share the resources ($x_2^* > 0$, $x_1^* + x_2^* = C_0$). Finally, for large values of C_0 the coe-

nomes progress to the maximal possible values and do not exhaust the capacity of the environment.

The qualitative graphic representation of the system's dynamics in the case (21) is shown in the Fig.2. The initial conditions are perceived to be small. On the first interval $[t_0, t_1]$ the progressive increasing x_1 take place. When the critical value x_1^* is reached, the development of the second coenome starts, with x_1 begins to decrease. Then the dynamics of the system is gradually stabilised. In (Chernyshenko, 1995) it is shown for the model (19) that under the condition

$$\frac{N}{a_1 + 1} < C_0 < \frac{N}{a_1}$$

an "internal catastrophe" take place. If this take place, the value of x_1^* equals $N - a_1 C_0$.

In the Fig. 3-6 phase-portraits of the system (19) are represented. One can see that in the different cases an area of attraction of an finite steady-state includes the neighbourhood of the origin of co-ordinates. The dynamics of the system in this area is in agreement with ecological reasons. In the same time the each phase-portrait includes an area of attraction of the infinite equilibrium point. This fact illustrates that for large values of the co-ordinates the model is not correctly describe a succession process.

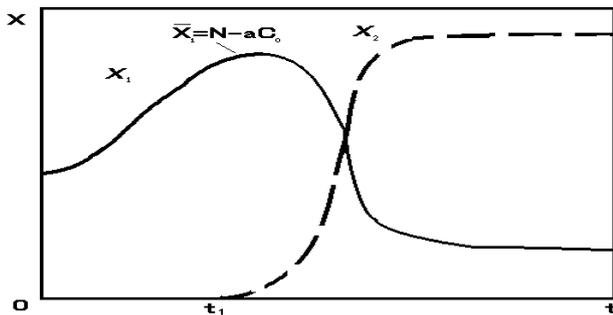


Fig.2: Biomass dynamics in the succession model (19).

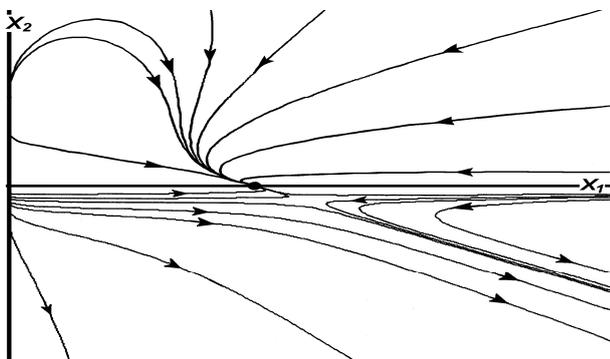


Fig. 3: The phase portrait of the model (19). The case (20) ($a=3, N=1, C_0=0.2$). A neighbourhood of the origin of co-ordinates.

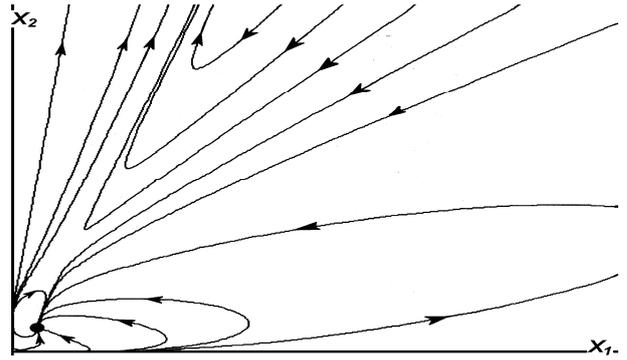


Fig. 4. The phase portrait of the model (19). The case (21) ($a=3, N=1, C_0=1$).

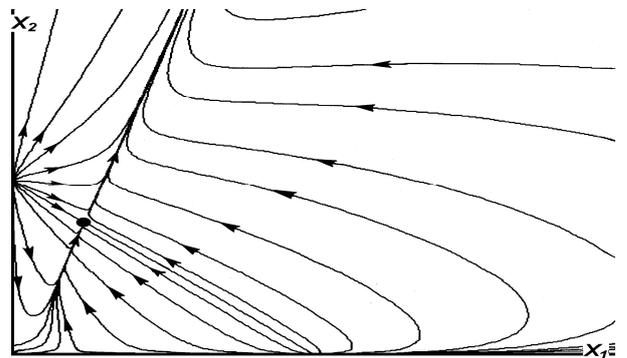


Fig. 5. The phase portrait of the model (19). The degenerate case (21),(22) when $C_0=(a_1+1)N$ ($a=3, N=1, C_0=4$). The equilibrium point of the "saddle-node" type.

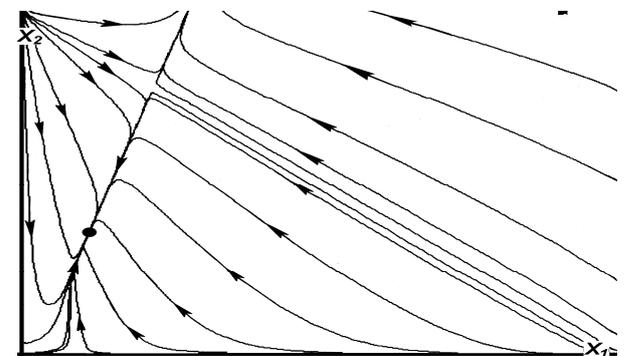


Fig. 6. The phase portrait of the model (19). The case (22) ($a=3, N=1, C_0=10$).

CONCLUSION

The model (13),(15) describes the succession process as a result of ecosystem ability of self-recovery and homeostasis. Coenome is considered as a major dynamic element of ecosystems in long-term dynamic processes. It is an association of species which have complementary properties (up to symbioses) or united by trophical links. Each succession stage is characterised by a main dominant coenome. The succession process is considered as a process of step-by-step changing the dominant coenome.

The model is an “open” modification of M. Eigen’s hypercycle. The model describes a specific inter-coenomes interaction, which are similar, but are not equivalent to the competition and “host-parasite” relations. As a result of the interaction and redistribution of ecological resources, several “succession steps” may take place (Fig.2). The number of the steps depends on the major system bifurcation parameter C_0 , which is determined by accessible energetic resources. During the succession process the ecosystem “selects” own optimal dimension and complexity. Additional coordinates appear as a result of “technological innovations” in the ecosystem, which increase the flow of accessible energy. Succession process is the process of recreation of optimal complexity level.

In the framework of the model (13), (15) succession process is explained by a low level of the solar energy utilisation by first “undemanding” succession stages. They leave “energetic space” for the development of next, more effective coenomes. The evolution of biogeocoenose proceeds in the direction of a maximal utilisation of the solar energy. The succession process is a process of producing information, if the information is understood as the evaluation of system complexity or complexity of system response to variations of environmental conditions (Eigen and Schuster 1979). A information measure peaks in a climax state. Correspondingly, the entropy decreases during successions. This statement is in agreement with modern ecological conceptions (Brooks and Wiley 1988; Chernyshenko 2008b). The model (13), (15) describes the process of entropy decrease and its characteristic properties: discrete nature of the process and the limitation of the information growth by amount of the energy, accessible for the system.

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