Modeling of biotic cycle formation in closed ecological systems

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Abstract. The biotic turnover formation in closed ecological system (CES) is analyzed by means of mathematical and computer modeling. The model CES hierarchical structure formation is ruled by the energy flow through the ecosystem which increases after the introduction of a predator in the steady state of “production - reduction” systems. The model analysis shows that the presence of the primary predator under certain conditions leads to the acceleration of the biotic turnover because of its higher mineralization ability (in comparison with the same of decomposer). The most acceptable predator which is able to bring the system towards the higher biotic turnover rate and energy consumption can be found for each system.

1. Introduction
For mathematical analysis of closed ecological system (CES) the equations describing the population dynamics and resource concentration are usually used (known Lotka-Volterra equations) [1-3]. Unfortunately, the applicability of this standard model approach is limited. It does not allow to formulate the general criteria, which would help to predict the result of competition of several populations on resources, limits of turnover sustainability, the direction of succession. This indicates the narrowness of this model approach. Sequential application of the functional approach is the solution to this situation. Firstly, the analysis of level dynamics of one or more key factors limiting the population development is required. Generally, it is necessary to study the function of the system acting as a single whole [4-7].

This work considers biotic turnover in closed ecological system (CES) with an external flow of energy. We use ordinary differential equation systems to represent the main types of natural or laboratory ecosystems (biotic cycles) with a few interacting species [1, 8, 9]. These ecosystems are nutrient-limited and display mass balance.

2. Results and Discussion
The simplest biotic cycle we use to deal with a "producer-consumer-decomposer" food chain (Fig. 1). A nutrient limited plant or algae (X) consume a nutrient resource (N), two predators (Y1, Y2) consume a producer. Then it dies and is reduced by decomposers (D), therefore matter recycles and meanwhile initially captured energy dissipates (ED).
**Figure 1.** Scheme of ecosystem with "production- consumption- reduction" food chain.

The dynamics of this system is characterized by the four differential equations:

\[
\begin{align*}
\frac{dX}{dt} &= \mu X - \varepsilon_X X - nY \\
\frac{dY}{dt} &= nY - \varepsilon_Y Y - mY \\
\frac{dD}{dt} &= \varepsilon_X X + \varepsilon_Y Y - dD \\
\frac{dN}{dt} &= dD + mY - \mu X \\
\end{align*}
\]

(1)

where \(X, Y, D, N\) - concentrations of producers, predator, detritus and limiting substance, respectively; \(\mu\) is specific growth rate of producers, \(n\) is specific rate of producer's consumption; \(\varepsilon_X, \varepsilon_Y\) - specific rates of mortality of producers and predators, respectively; \(d\) is a specific rate of dead biomass reduction; \(m\) - specific rate of predator's biomass expenditure for the processes of life support, and \(m \gg d\), because the growth rate of predators is supposed to be limited not with a substance, but the energy resources.

To gain more simplicity, instead of biomass values we use nutrient content in producers and detritus. Characteristic growth rate of the producers depends on the limiting nutrient concentration (the Monod function). To simplify the analytical study we use the following approximation:

\[
\mu = \frac{\mu_m N}{K_N + N} \approx \varepsilon_i N
\]

(2)

This equation is corresponds the case of deep limitation.

System (1) characterizes the matter flows and provides the closure of the ecosystem. As can be seen \(d(X + D + N) = 0\), or \(X + D + N = \text{const} = N_i\), where \(N_i\) is the total amount of limiting nutrient in ecosystem.

In this case only producers capture energy from outside the system. So, we can assume that the energy flow into ecosystem is proportional to the primary production of the ecosystem \(P\), which is product of specific growth rate and biomass of producers:

\[
\frac{dE_o}{dt} = eP = e\mu X
\]

(3)

where \(e\) is characteristic energetic content of producers biomass. Producers bound much more energy into biomass, than dissipate. Therefore energetic activity of producers equals
\[ a_p \approx -\frac{dE_O}{dt} = -eP \]  

(4)

Energetic activity of decomposer link is

\[ a_D = \frac{dE_D}{dt} \]  

(5)

Equations (4) and (5) describe the energy flows, meanwhile the system (1) shows matter flows. Been brought together, assuming that characteristic energetic content of producers, consumers and decomposers is the same, we'll get the steady-state energy balance for the system (6): 

\[ a_D = \frac{dE_D}{dt} \]  

(6)

It can be seen, that the system (1) contains both energy and matter conservation laws.

The growth of predators is supposed to be limited not with a substance, but the energy resources, bounded in producer’s biomass. Predators consume much more prey biomass, than it is needed to build its own. The extra biomass is spent for the energy requirements. While the energy used for the processes of life support is dissipated, the correlated substance is immediately released into the medium, and therefore recycled. The nonliving predator's biomass is reduced by the decomposers.

Predator consumes the prey with specific rate:

\[ \nu = \frac{\nu_m X}{K_X + X} \approx c_2 X \]  

(7)

where \( \nu \) is the maximal specific rate of prey's consumption, \( K \)-prey's concentration, when the rate of its consumption is half of maximal. To simplify the analytical study we'll assume, that the rate of prey's consumption is proportional to the predator and prey concentrations (Lotka-Volterra model). Producer dies with specific rate \( \varepsilon_X \) and predator with \( \varepsilon_Y \). Moreover, the part of predators biomass (properly its energetic content) is expended for the processes of life support and so on with the specific rate \( m \), which is proportional to the energetic activity of predator according to (4):

\[ mY = \frac{dN_Y}{dt} = k_Y \alpha_Y \]  

(8)

where \( k_Y \) is characteristic energy content of predator's biomass. Predator is releasing energy with the rate \( \alpha_Y \), meanwhile excreting extra substance with the rate \( \mu_Y \). We also can treat this system for the energy conservation law, and it will show that \( E_O = E_D + E_Y \).

Solving the system (1) for the steady state we’ll find the value of primary production:

\[ \bar{p} = \frac{\varepsilon_Y + m}{C_2} \cdot \frac{C_2 N_1 - \varepsilon_Y - m + \varepsilon_X - m \varepsilon_X / d}{1 + C_2 / C_1 + \varepsilon_Y / d}, \]  

(9)

where \( N \) is total amount of limiting substance in ecosystem. Systems (1) were simulated on the computer with the values of coefficients common for the aqua systems (program Stella II, High Performance System, USA). Succession was modeled so that predators were introduced into the steady state of the “production - reduction” system and a new steady state were achieved. Dynamics of links and changes are shown in Fig. 2.
Figure 2. Computer simulation of ecosystem (1). The moment of predator's appearance is arrowed.

After appearance of predators in the ecosystem the primary production increases. Also number of decomposers decreases due to the lowering of their role in mineralization (recycling). Fig. 3 shows the dependence of ecosystem's primary production (formula (9)) on the characteristic energetic activity of predator \( \frac{a_Y}{Y} = \frac{m}{k_Y} \), with the different values of \( N_t \) in the system. It can be seen, that productivity of the ecosystem increases and has a maximum (some optimal value). This graph can be called predator optimization curve.

Figure 3. The dependence of the steady state primary production of production-consumption-reduction system on the characteristic activity of predator, shown for the different \( N_t \) in the system.
Having higher energetic activity, the predators are more active mineralizes than decomposers. Therefore its appearance in the system leads to the increasing of the recycling rate, which is proportional to the primary production. We can assume that the process of predators’ competition leads to the appearance of more active organisms.

3. Conclusion
The main difference between our model ecosystem and previously advanced models of closed ecosystems is that in our model the growth of consumers is limited by the available energy in preys but not the amount of nitrogen stored in preys [1, 8, 9]. Most of these previous estimates support the viewpoint that the growth of predators is constrained by energy but not by nutrient availability. Limitation of consumers by available energy enhances their importance in biotic cycles functioning because they allow a very rapid return of free nutrient to the environment whereas such return through mineralization of non-living matter is much slower process (see, for example, [3, 10, 11]). Due to this reason we cannot get rid of detritus and reducer chains by assuming the rate of decomposition to be high enough.

There are simulated elementary biotic cycles in the main types presented in the nature CES. It is shown, that in model CES hierarchical structure formation is ruled by the energy consumption: the primary production in the ecosystem increases after introduction of predator in the steady state of “production-reduction” system and achievement of the new steady state. The model analyses shows, that the presence of the primary predator under certain conditions leads to the acceleration of the biotic turnover, because of its higher mineralization ability (by a comparison with decomposer). This is the most general conclusion, which is interesting for solving the problems of predator introduction into the certain ecosystems.

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