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Closure and stability of trophic chains

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Motivation and Aim: The emergence of oscillatory regimes in fully or partially closed trophic chains of various lengths is considered in detail in the monograph [1, pp. 242-268]. Three types of trophic functions were used for the analysis: linear (Volterra), hyperbolic and S-shaped. However, there are quite a few trophic functions of a different type, which well describe the experimental data [2]. The question arises whether it is possible to say something about the change in the stability of the trophic chain with a change in the degree of closure of the nutrient flow without specifying the type of trophic functions and for different modes of external biogen exchange.

Methods and Algorithms: Consider first a closed trophic chain that has one exchange channel with the environment (Fig. 1, B). The ecosystem of an isolated lake, where carbon acts as a biogen, can serve as a real analogue of such a chain.

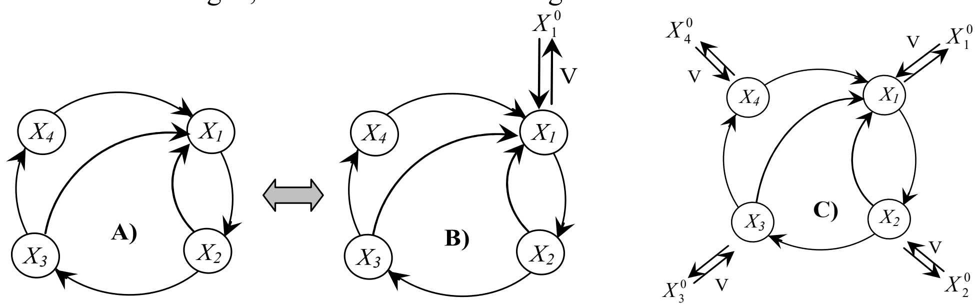

Fig. 1. Various options of matter exchange of a closed trophic chain with an environment

In general, this scheme can be described by the following system of equations:

$$\begin{cases} \dot{X}_1 = F_1(\vec{X}) + V(X_1^0 - X_1) \\ \dot{X}_i = F_i(\vec{X}) \end{cases} \quad (1)$$

where V is the rate constant of exchange with the environment; $\vec{X}$ – vector of concentrations of substances or numbers of organisms in the ecosystem; X_1^0 – the concentration of a substance or the number of organisms of a given species in the environment.

The stationary state of the system is reached at $X_1^* = X_1^0$. Note that for system (1) the stationary state is the same for any non-zero values of V. Let us formally consider the process of increasing closure in this system, which corresponds to a decrease in the exchange rate constant V. In the limit, at $V = 0$, the system takes the form:

$$\dot{X}_i = F_i(\vec{X}) \quad (2)$$

Note that system (2) is qualitatively different from the original system (1), since the order of the system decreases by one due to the conservation law. Let us consider the stability of the stationary points of these two systems. The eigenvalues of the systems can be found by solving the following equations respectively:

$$\Delta_{NC}^{n} \equiv \begin{vmatrix} \frac{\partial F_1}{\partial X_1} - V - \lambda & \frac{\partial F_1}{\partial X_2} & \cdots & \frac{\partial F_1}{\partial X_N} \\ \frac{\partial F_2}{\partial X_1} & \frac{\partial F_2}{\partial X_2} - \lambda & \cdots & \frac{\partial F_2}{\partial X_N} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial F_N}{\partial X_1} & \frac{\partial F_N}{\partial X_2} & \cdots & \frac{\partial F_N}{\partial X_N} - \lambda \end{vmatrix} = 0 \quad \Delta_{C}^{n-1} \equiv \begin{vmatrix} \frac{\partial F_2}{\partial X_2} - \frac{\partial F_2}{\partial X_1} - \lambda & \frac{\partial F_2}{\partial X_3} - \frac{\partial F_2}{\partial X_1} & \cdots & \frac{\partial F_2}{\partial X_N} - \frac{\partial F_2}{\partial X_1} \\ \frac{\partial F_3}{\partial X_2} - \frac{\partial F_3}{\partial X_1} & \frac{\partial F_3}{\partial X_3} - \frac{\partial F_3}{\partial X_1} - \lambda & \cdots & \frac{\partial F_3}{\partial X_N} - \frac{\partial F_3}{\partial X_1} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial F_N}{\partial X_2} - \frac{\partial F_N}{\partial X_1} & \frac{\partial F_N}{\partial X_3} - \frac{\partial F_N}{\partial X_1} & \cdots & \frac{\partial F_N}{\partial X_N} - \frac{\partial F_N}{\partial X_1} - \lambda \end{vmatrix} = 0$$

where *NC* means incompletely closed, *C* means closed trophic chains, *n* is the order of the determinant.

Let's formally describe a smooth transition from a partially closed to a completely closed system, which in this case undergoes a qualitative change – it loses one variable. To do this, we need to find a relationship between the above determinants. Shown, that

$$\Delta_{NC}^{n} = -V\Delta_{NC}^{n-1} - \lambda\,\Delta_{C}^{n-1} \text{ and } V\Delta_{NC}^{n-1} + \lambda\,\Delta_{C}^{n-1} = 0 \quad (3)$$

is the equation for finding the eigenvalues of the food web model.

Results. It can be seen from this equation that if the connection with the external environment (V) weakens for the system (1), then one of the eigenvalues also tends to zero, that is, one degree of freedom disappears. In this case, the equation for calculating the eigenvalues takes the form $\Delta_{C}^{n-1} = 0$. An equation with similar properties was also obtained for the case when each of the components of the ecosystem exchanges with the environment with the intensity specified by the parameter V (see Fig. 1, C).

Since we do not know the specific form of the right-hand sides of the equations, we cannot calculate the eigenvalues, and can only ask in which direction the eigenvalues will shift when V changes. The Gershgorin's circle method allows localizing eigenvalues by elements of the determinant and thereby estimating the stability of the system [3]. With an increase in V, the Gershgorin's circle corresponding to the first variable shifts to the left towards negative values. This does not guarantee decreasing probability of oscillatory and chaotic modes, since the eigenvalues are localized in the union of all Gershgorin's circles, however, the stability of the system does not exactly decrease. At the same time numerous computational experiments with have shown that the stability of the system with increasing V, increases as a rule. In the case of a trophic web with the exchange of all components (see Fig. 1, C) all diagonal elements tend to shift to the negative region with increasing V, however a change in V causes a change in stationary values and, potentially, a loss of stability can be observed in some part of the change in V. However computational experiments have not confirmed that this sometimes happens. Nevertheless it is clear that at very large V, the values of the food chain variables are determined by the values of the corresponding variables in the environment. That is, the variables themselves become unchanged, but at the same time it is hardly possible to speak of a trophic chain or an ecosystem itself – it has disappeared.

References

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