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COMPLEX SYSTEMS BIOPHYSICS

Abundances of Species and Limitation Strata in a Variational Model of an Ecological Community

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Abstract—A variational problem is posed to find the relative abundances of species in a community in the stationary growth phase, and a stratification theorem is formulated. Algorithms are derived to determine the relative abundances of species in communities consisting of two or three species consuming two or three resources. The boundaries are described for limitation strata where there are one, two, or three limiting resources. For a community consisting of two species consuming two resources, an explicit expression is obtained for the relative abundance of species as a function of the ratio between the contents of the resources, and the form of this expression for actual demands of organisms for environmental resources is demonstrated.

Key words: community ecology, variational modeling, abundance, limiting resources

INTRODUCTION

The main problem of quantitative community ecology is to calculate the abundance of each of the populations of organisms in a community as a function of the contents of available environmental resources. The purpose of this work is to derive an algorithm for finding the abundances of species constituting an ecological community, using methods of optimal control theory. The point is that methods of modeling using sets of differential equations, which are conventionally used in ecology, are extremely cumbersome, difficult to observe, and have low efficiency when applied to studying communities consisting of many (w) species consuming many (m) resources. For example, a phytoplankton community in an ordinary pond comprises more than a hundred of species, which consume dozens of noninterchangeable resources (a realistic simulation model [1] of such a community involves $m + w + mw$ equations and $2w + 4mw$ parameters). Another problem of ecology is to rigorously select, from the entire set of resources, the ones that actually control or limit the abundances of species to be found. It is proposed to solve the two problems through solving a variational problem of determining a constrained extremum under inequality constraints. The constraints describe the balance of consumption of environmental resources by organisms, and before solving the problem, it is unknown which of the resources are consumed completely or, in other words, which of the inequalities can be written as strict equalities. The model proposed has already been applied to phytoplankton communities [2, 3], in which the number of species is usually much greater than the number of resources being consumed. This work considers cases where the number of species is small and is comparable to or smaller than the number of resources (this is characteristic of communities of microorganisms [4, 5]).

VARIATIONAL MODEL

A community of unicellular organisms is modeled. The organisms consume resources, which are not interchangeable, because the functions of these resources with respect to the cell growth are different. It is assumed that cell division and cell death are possible, whereas cell fusion is not. As applied to laboratory conditions, the proposed model describes accumulative cultivation, when resources and microorganisms are neither added nor removed. The development of the polyculture is studied until it ceases because of depletion of one of the resources, but not due to any other causes.

It is postulated that dynamic systems from a given state pass into a state where the structure is extremal (within the limits governed by the resources available). The corresponding variational problem of determining a constrained extremum has the form [6–8]

$$\begin{cases} H(n_1,\dots,n_w) = \left(\sum_{i=1}^{w} n_i\right)\ln\left(\sum_{i=1}^{w} n_i\right) - \sum_{i=1}^{w} n_i \ln n_i \to \text{extr}, \\ \sum_{i=1}^{w} q_i^k n_i \le L^k,\ k = \overline{1,m}, \\ n_i \ge 0,\ i = \overline{1,m} \end{cases} \quad (1)$$

where n_i is the final total abundance to be found and the abundances of each of the species to be found, q_i^k is the amount of the kth resource that is necessary for the ith species to grow per cell (i.e., the demand), m is the total number of noninterchangeable resources consumed by the community, w is the number of species in the community, and L^k is the initial content of the kth resource in the environment ($L^k \ge 0$).

Note that the functional $H(\vec{n})$, $\vec{n} = (n_1, \dots, n_w)$, which is called the generalized entropy, is not postulated but derived using a category–functor method for comparing mathematical structures (the community itself is described by a mathematical structure of sets of n elements, each divided into w disjoint classes of n_i elements) [6].

The main result on which the further investigation of the problem formulated is based is the stratification theorem [2, 7]. According to this theorem, the entire space $\prod_{k=1}^{m} L^k$ of resource factors is stratified into $2^m - 1$ disjoint strata, each corresponding to one of the subsets of the set of resources consumed by the community. For the stratum S^J, where $J \ne \varnothing$ is a subset of the set of resources $\{1, 2, \dots, m\}$, (1) the solution $n_i(\vec{L})$ of problem (1), where $\vec{L} \equiv L^1, L^2, \dots, L^m$, depends on only those L^k for which $k \in J$; and (2) for this solution, the nonstrict inequalities $\sum_{i=1}^{w} q_i^k n_i \le L^k$ become strict equalities for all $k \in J$ and strict inequalities for all $k \notin J$. The stratification theorem reduces problem (1) to the problems

$$\begin{cases} H(\vec{n}) \to \text{extr}, \\ \sum_{i=1}^{w} q_i^j n_i \le L^j,\ j \notin J, \\ n_i \ge 0,\ i = \overline{1,w}, \end{cases} \quad (2)$$

formulated for any $J \subset \{1, 2, \dots, m\}$.

The theorem provides an algorithm for calculating the strata for a given set of demands q_i^k in a community and also allows one to rigorously predict which resources limit the community growth (i.e., which resources are completely consumed from the environment).

The solution of problems (2) is called the species structure formula

$$n_i(\vec{L}^J) = n\exp\left\{-\sum_{k\in J} \lambda^k q_i^k\right\},$$

where $n = \sum_{i=1}^{w} n_i$; and the vector $\vec{L}^J$ has the components j from the set J, which identifies the stratum to which the vector $\vec{L}^J$ belongs. The Lagrange multipliers λ^k and the total abundance n as functions of the contents $\vec{L}^J$ of the resources consumed completely in the stratum S^J are found from the algebraic equations

$$\begin{cases} \sum_{i=1}^{w} \exp\left\{-\sum_{k\in J} \lambda^k q_i^k\right\} = 1, \\ n\sum_{i=1}^{w} q_i^j \exp\left\{-\sum_{k\in J} \lambda^k q_i^k\right\} = L^j,\ j \in J. \end{cases}$$

SOLUTIONS FOR SOME PARTICULAR CASES OF THE VARIATIONAL PROBLEM

The stratification theorem and also the existence and uniqueness theorem [7] give an algorithm for solving the variational problem (1). Initially, it is necessary to find the boundaries of the strata into which the resource space is stratified according to the stratification theorem (the method for finding the strata follows directly from the proof). Then, in each of the strata, problem (2) where the nonstrict inequalities are replaced by equalities is solved. When the number of limiting factors coincides with the number of species, it is sufficient to solve the set of the inequality

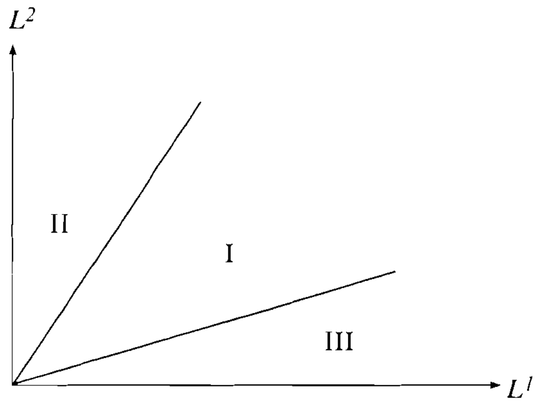

Fig. 1. Stratification of the space of resource factors being consumed at $m = 2$. In stratum I, the limiting factors are L^1 and L^2; in stratum II, the limiting factor is L^1; and in stratum III, the limiting factor is L^2.

constraints. Below, the solutions of the problem in some particular cases are presented.

Solution for the Case where $w = 2$ and $m = 2$

Let a community consist of two species consuming two resources, L^1 and L^2. Let the demands of the species for the resources are known: $\{q_i^k\}$, $k = 1, 2$; $i = 1, 2$ (the superscript k denotes resources, and the subscript i stands for species). According to the variational model of community, the abundances of species in the stationary growth phase are found as follows. Initially, it is necessary to find the strata into which the resource space is stratified according to the stratification theorem. Let x_0 be the root of the equation $x^{q_1^1} + x^{q_2^1} = 1$ and y_0 be the root of the equation $y^{q_1^2} + y^{q_2^2} = 1$. Then, the slopes of the rays that are the boundaries of the limitation strata (Fig. 1) are determined as

$$\nu = \nu(q_i^k) = \frac{q_1^1 x_0^{q_1^1} + q_2^1 x_0^{q_2^1}}{q_1^2 x_0^{q_1^1} + q_2^2 x_0^{q_2^1}};$$

$$\eta = \eta(q_i^k) = \frac{q_1^1 y_0^{q_1^2} + q_2^1 y_0^{q_2^2}}{q_1^2 y_0^{q_1^2} + q_2^2 y_0^{q_2^2}}.$$

The resource space is stratified into three strata: in stratum I, the limiting resources are L^1 and L^2; in stratum II, the limiting resource is L^1; and in stratum III, the limiting resource is L^2.

Let us find the relative abundances of species in the stationary growth phase in each of the strata separately.

In stratum I, where $\nu \le \frac{L^1}{L^2} \le \eta$, both inequalities of the initial variational problem appear as the equalities

$$\begin{cases} q_1^1 n_1 + q_2^1 n_2 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 = L^2. \end{cases}$$

Let us denote $\frac{n_1}{n} = s$, $\frac{n_2}{n} = t$, $\frac{L^1}{L^2} = \chi$. Then, the set has the solution

$$\begin{cases} s = \dfrac{q_2^2 \chi - q_2^1}{q_2^2 \chi - q_2^1 + q_1^1 - q_1^2 \chi}, \\ t = \dfrac{q_1^1 - q_1^2 \chi}{q_2^2 \chi - q_2^1 + q_1^1 - q_1^2 \chi}. \end{cases}$$

In stratum II, where $\frac{L^1}{L^2} < \nu$, the variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^1 n_1 + q_2^1 n_2 = L^1. \end{cases}$$

The solution of this problem is given by the species structure formula $n_i = n\exp(-\lambda^1 q_i^1)$, $i = 1, 2$, where n and λ^1 are the solution of the set

$$\begin{cases} \sum_{i=1}^{2} \exp(-\lambda^1 q_i^1) = 1, \\ \lambda^1 (n \sum_{i=1}^{2} q_i^1 \exp(-\lambda^1 q_i^1) - L^1) = 0, \\ \lambda^1 \ge 0. \end{cases}$$

Let us make the change of variables $\exp(-\lambda^1) = x$; then, the relative abundances $s = x_0^{q_1^1}$ and $t = x_0^{q_2^1}$ are found from the equation $x_0^{q_1^1} + x_0^{q_2^1} = 1$.

In stratum III, where $\frac{L^1}{L^2} > \eta$, the initial variational problem appears as the problem involving a single equality:

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^2 n_1 + q_2^2 n_2 = L^2. \end{cases}$$

Reasoning similar to that in stratum II yields $s = \frac{n_1}{n} = y_0^{q_1^2}$ and $t = \frac{n_1}{n} = y_0^{q_2^2}$; moreover, $y_0^{q_1^2} + y_0^{q_2^2} = 1$.

Solution for the Case where $w = 3$ and $m = 2$

Let a community consist of three species consuming two resources, L^1 and L^2. Let the demands of the species for the resources are known: $\{q_i^k\}$, $k = 1, 2$; $i = 1, 2, 3$ (the superscript k denotes resources, and the subscript i stands for species). According to the variational model of community, the abundances of species in the stationary growth phase are determined as follows. Three strata, into which the resource space is stratified, are given similarly to the previous case. Let x_0 be the root of the equation $x^{q_1^1} + x^{q_2^1} + x^{q_3^1} = 1$ and y_0 be the root of the equation $y^{q_1^2} + y^{q_2^2} + y^{q_3^2} = 1$. Then, the slopes of the rays that are the boundaries of the limitation strata (Fig. 1) are determined as

$$\nu = \nu(q_i^k) = \frac{q_1^1 x_0^{q_1^1} + q_2^1 x_0^{q_2^1} + q_3^1 x_0^{q_3^1}}{q_1^2 x_0^{q_1^1} + q_2^2 x_0^{q_2^1} + q_3^2 x_0^{q_3^1}};$$

$$\eta = \eta(q_i^k) = \frac{q_1^1 y_0^{q_1^2} + q_2^1 y_0^{q_2^2} + q_3^1 y_0^{q_3^2}}{q_1^2 y_0^{q_1^2} + q_2^2 y_0^{q_2^2} + q_3^2 y_0^{q_3^2}}.$$

In the stratum where $\nu \le \frac{L^1}{L^2} = \chi \le \eta$, the limiting resources are L^1 and L^2; in the stratum where $\frac{L^1}{L^2} < \nu$, the limiting resource is L^1; and in the stratum where $\frac{L^1}{L^2} > \eta$, the limiting resource is L^2. Let us find the relative abundances of species in each of the strata.

In the stratum where $\nu \le \frac{L^1}{L^2} \le \eta$, the variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^1 n_1 + q_2^1 n_2 + q_3^1 n_3 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 + q_3^2 n_3 = L^2. \end{cases}$$

By taking into account that the solution of this problem is given by the species structure formula, and introducing new variables $\exp(-\lambda^1) = x$ and $\exp(-\lambda^2) = y$, the set of equations for the relative abundances $\frac{n_i}{n}$ is obtained in the form

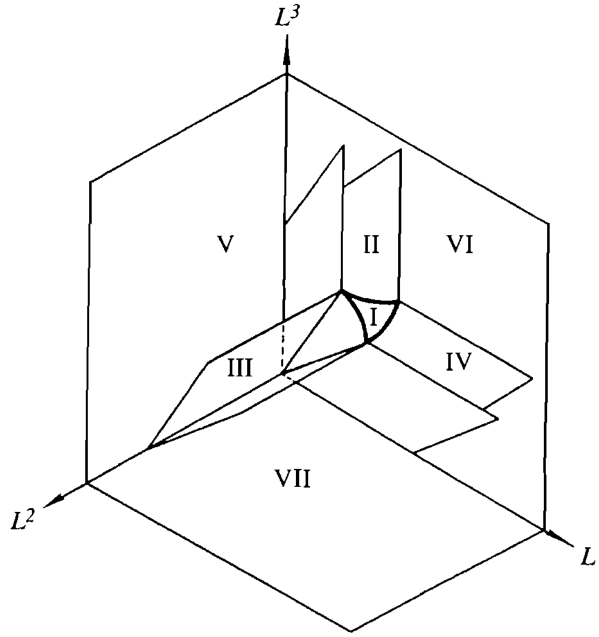

Fig. 2. Stratification of the space of resource factors being consumed at $m = 3$. In stratum I, the limiting factors are L^1, L^2, and L^3; in stratum II, L^1 and L^2; in stratum III, L^1 and L^3; in stratum IV, L^2 and L^3; in stratum V, L^1; in stratum VI, L^2; and in stratum VII, L^3.

$$\begin{cases} \frac{n_i}{n} = x^{q_i^1} y^{q_i^2}, i = 1,2,3, \\ x^{q_1^1} y^{q_1^2} + x^{q_2^1} y^{q_2^2} + x^{q_3^1} y^{q_3^2} = 1, \\ \frac{q_1^1 x^{q_1^1} y^{q_1^2} + q_2^1 x^{q_2^1} y^{q_2^2} + q_3^1 x^{q_3^1} y^{q_3^2}}{q_1^2 x^{q_1^1} y^{q_1^2} + q_2^2 x^{q_2^1} y^{q_2^2} + q_3^2 x^{q_3^1} y^{q_3^2}} = \chi. \end{cases}$$

In the strata where there is only one limiting factor, the relative abundances of species in the stationary growth phase are found as follows.

In the stratum where $\frac{L^1}{L^2} < \nu$, i.e., where the limiting factor is L^1, the variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^1 n_1 + q_2^1 n_2 + q_3^1 n_3 = L^1. \end{cases}$$

By taking into account the species structure formula and introducing the variable $\exp(-\lambda^1) = x$, the set of equations for the relative abundances $\frac{n_i}{n}$ is obtained in the form

$$\begin{cases} n_i = n x^{q_i^1}, \\ x^{q_1^1} + x^{q_2^1} + x^{q_3^1} = 1, \\ n(q_1^1 x^{q_1^1} + q_2^1 x^{q_2^1} + q_3^1 x^{q_3^1}) = L^1. \end{cases}$$

Thus, the relative abundances are $\frac{n_i}{n} = x_0^{q_i^1}$, where x_0 is the root of the equation $x^{q_1^1} + x^{q_2^1} + x^{q_3^1} = 1$. Similarly, in the stratum where the limiting factor is L^2, i.e., where $\frac{L^1}{L^2} > \eta$, the solution is $\frac{n_i}{n} = y_0^{q_i^2}$, where y_0 is the root of the equation $y^{q_1^2} + y^{q_2^2} + y^{q_3^2} = 1$.

Solution for the Case where $w = 3$ and $m = 3$

Let a community consist of three species consuming three resources, L^1, L^2, and L^3. Let the demands of the species for the resources are known: $\{q_i^k\}$, $k = 1, 2, 3$; $i = 1, 2, 3$ (the superscript k denotes resources, and the subscript i stands for species). According to the variational model of community, the resource space is stratified into seven strata. In one of these strata, there are three limiting factors; in three strata, two limiting factors; and in three strata, one limiting factor (Fig. 2).

The strata are described as follows. Let z_k^0, $k = 1, 2, 3$, is the root of the equation $z_k^{q_1^k} + z_k^{q_2^k} + z_k^{q_3^k} = 1$, $k = 1, 2, 3$. Let us now consider the equation $z_1^{q_1^1} z_2^{q_1^2} + z_1^{q_2^1} z_2^{q_2^2} + z_1^{q_3^1} z_2^{q_3^2} = 1$. This equation defines a certain function $z_2 = z_2(z_1)$; then, the equations

$$\chi_1(z_1) = \frac{q_1^1 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^1 z_1^{q_2^1} z_2(z_1)^{q_2^2} + q_3^1 z_1^{q_3^1} z_2(z_1)^{q_3^2}}{q_1^2 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^2 z_1^{q_2^1} z_2(z_1)^{q_2^2} + q_3^2 z_1^{q_3^1} z_2(z_1)^{q_3^2}},$$

$$\chi_2(z_1) = \frac{q_1^1 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^1 z_1^{q_2^1} z_2(z_1)^{q_2^2} + q_3^1 z_1^{q_3^1} z_2(z_1)^{q_3^2}}{q_1^3 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^3 z_1^{q_2^1} z_2(z_1)^{q_2^2} + q_3^3 z_1^{q_3^1} z_2(z_1)^{q_3^2}}$$

at $z_1^0 \le z_1 \le 1$ define a certain line in the plane (χ_1, χ_2), and if $\chi_1 = \frac{L^1}{L^2}$ and $\chi_2 = \frac{L^1}{L^3}$, then this line is in a section $L^3 = \text{const}$.

Similarly, the equations $z_1^{q_1^1} z_3^{q_1^3} + z_1^{q_2^1} z_3^{q_2^3} + z_1^{q_3^1} z_3^{q_3^3} = 1$ and $z_2^{q_1^2} z_3^{q_1^3} + z_2^{q_2^2} z_3^{q_2^3} + z_2^{q_3^2} z_3^{q_3^3} = 1$ are considered, and the functions $z_1 = z_1(z_3)$ and $z_3 = z_3(z_2)$ are derived. Two more lines in the section $L^3 = \text{const}$ are obtained.

At $z_3^0 \le z_3 \le 1$,

$$\chi_1(z_3) = \frac{q_1^1 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^1 z_1(z_3)^{q_2^1} z_3^{q_2^3} + q_3^1 z_1(z_3)^{q_3^1} z_3^{q_3^3}}{q_1^2 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^2 z_1(z_3)^{q_2^1} z_3^{q_2^3} + q_3^2 z_1(z_3)^{q_3^1} z_3^{q_3^3}},$$

$$\chi_2(z_3) = \frac{q_1^1 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^1 z_1(z_3)^{q_2^1} z_3^{q_2^3} + q_3^1 z_1(z_3)^{q_3^1} z_3^{q_3^3}}{q_1^3 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^3 z_1(z_3)^{q_2^1} z_3^{q_2^3} + q_3^3 z_1(z_3)^{q_3^1} z_3^{q_3^3}}.$$

At $z_2^0 \le z_2 \le 1$,

$$\chi_1(z_2) = \frac{q_1^1 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^1 z_2^{q_2^2} z_3(z_2)^{q_2^3} + q_3^1 z_2^{q_3^2} z_3(z_2)^{q_3^3}}{q_1^2 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^2 z_2^{q_2^2} z_3(z_2)^{q_2^3} + q_3^2 z_2^{q_3^2} z_3(z_2)^{q_3^3}},$$

$$\chi_2(z_2) = \frac{q_1^1 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^1 z_2^{q_2^2} z_3(z_2)^{q_2^3} + q_3^1 z_2^{q_3^2} z_3(z_2)^{q_3^3}}{q_1^3 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^3 z_2^{q_2^2} z_3(z_2)^{q_2^3} + q_3^3 z_2^{q_3^2} z_3(z_2)^{q_3^3}}.$$

Thus, in the section $L^3 = \text{const}$, a curvilinear triangle is obtained, which is the boundary of the stratum where there are three limiting resources. By plotting rays, the boundaries of the other strata are determined.

Let us find the relative abundances of species in the stationary growth phase. In the stratum where there are three limiting factors, the problem has the form of the set of three inequalities

$$\begin{cases} q_1^1 n_1 + q_2^1 n_2 + q_3^1 n_3 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 + q_3^2 n_3 = L^2, \\ q_1^3 n_1 + q_2^3 n_2 + q_3^3 n_3 = L^3. \end{cases}$$

The solution of this set in terms of variables $\frac{n_1}{n} = s$, $\frac{n_2}{n} = t$, $\frac{n_3}{n} = u$, $\frac{L^1}{L^2} = \chi_1$, and $\frac{L^1}{L^3} = \chi_2$ has the form

$$u = \frac{(\chi_1 q_1^2 - q_1^1)(q_1^2 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_2^3) - (\chi_2 q_1^3 - q_1^1)(q_2^1 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_2^2)}{(q_1^3 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_3^2)(q_2^1 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_2^3) - (q_3^1 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_3^3)(q_2^1 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_2^2)},$$

$$t = \frac{(\chi_1 q_1^2 - q_1^1)(q_3^1 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_3^3) - (\chi_2 q_1^3 - q_1^1)(q_3^1 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_3^2)}{(q_2^1 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_2^2)(q_3^1 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_3^3) - (q_2^1 - q_1^1 + \chi_2 q_1^3 - \chi_2 q_2^3)(q_3^1 - q_1^1 + \chi_1 q_1^2 - \chi_1 q_3^2)},$$

$$s = 1 - t - u.$$

In the stratum where the limiting factors are L^1 and L^2, the variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^1 n_1 + q_2^1 n_2 + q_3^1 n_3 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 + q_3^2 n_3 = L^2. \end{cases}$$

The relative abundances are found as

$$\begin{cases} \dfrac{n_i}{n} = x^{q_i^1} y^{q_i^2}, \ i = 1, 2, 3, \\ x^{q_1^1} y^{q_1^2} + x^{q_2^1} y^{q_2^2} + x^{q_3^1} y^{q_3^2} = 1, \\ \dfrac{q_1^1 x^{q_1^1} y^{q_1^2} + q_2^1 x^{q_2^1} y^{q_2^2} + q_3^1 x^{q_3^1} y^{q_3^2}}{q_1^2 x^{q_1^1} y^{q_1^2} + q_2^2 x^{q_2^1} y^{q_2^2} + q_3^2 x^{q_3^1} y^{q_3^2}} = \dfrac{L^1}{L^2}. \end{cases}$$

In the strata where the limiting factors are L^1 and L^3, or L^2 and L^3, the solutions are obtained similarly.

In the strata where there is only one limiting factor, L^k, $k = 1, 2, 3$, the relative abundances in the stationary growth phase are found by solving the variational problem

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^k n_1 + q_2^k n_2 + q_3^k n_3 = L^k \end{cases}$$

and are given by the expressions $s = x_0^{q_1^k}$, $t = x_0^{q_2^k}$, and $u = x_0^{q_3^k}$, where x_0 is the root of the equation $x^{q_1^k} + x^{q_2^k} + x^{q_3^k} = 1$.

Solution for the Case where $w = 2$ and $m = 3$

Let a community consist of two species consuming three resources, L^1, L^2, and L^3. Let the demands of the species for the resources are known: $\{q_i^k\}$, $k = 1, 2, 3$; $i = 1, 2$ (the superscript k denotes resources, and the subscript i stands for species). According to the variational model of community, the resource space is stratified into seven strata. In one of these strata, there are three limiting factors; in three strata, two limiting factors; and in three strata, one limiting factor (Fig. 2). The strata are described as follows. Let z_k^0, $k = 1, 2, 3$, is the root of the equation $z_k^{q_1^k} + z_k^{q_2^k} = 1$, $k = 1, 2, 3$. Let us now consider the equation $z_1^{q_1^1} z_2^{q_1^2} + z_1^{q_2^1} z_2^{q_2^2} = 1$. This equation defines a certain function $z_2 = z_2(z_1)$; then, the equations

$$\chi_1(z_1) = \frac{q_1^1 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^1 z_1^{q_2^1} z_2(z_1)^{q_2^2}}{q_1^2 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^2 z_1^{q_2^1} z_2(z_1)^{q_2^2}},$$

$$\chi_2(z_1) = \frac{q_1^1 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^1 z_1^{q_2^1} z_2(z_1)^{q_2^2}}{q_1^3 z_1^{q_1^1} z_2(z_1)^{q_1^2} + q_2^3 z_1^{q_2^1} z_2(z_1)^{q_2^2}}$$

at $z_1^0 \le z_1 \le 1$ define a certain line in the plane (χ_1, χ_2), and if $\chi_1 = \dfrac{L^1}{L^2}$ and $\chi_2 = \dfrac{L^1}{L^3}$, then this line is in a section $L^3 = \text{const}$.

Similarly, the equations $z_1^{q_1^1} z_3^{q_1^3} + z_1^{q_2^1} z_3^{q_2^3} = 1$ and $z_2^{q_1^2} z_3^{q_1^3} + z_2^{q_2^2} z_3^{q_2^3} = 1$ are considered, and the functions $z_1 = z_1(z_3)$ and $z_3 = z_3(z_2)$ are derived. Two more lines in the section $L^3 =$ are obtained.

At $z_3^0 \le z_3 \le 1$,

$$\chi_1(z_3) = \frac{q_1^1 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^1 z_1(z_3)^{q_2^1} z_3^{q_2^3}}{q_1^2 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^2 z_1(z_3)^{q_2^1} z_3^{q_2^3}},$$

$$\chi_2(z_3) = \frac{q_1^1 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^1 z_1(z_3)^{q_2^1} z_3^{q_2^3}}{q_1^3 z_1(z_3)^{q_1^1} z_3^{q_1^3} + q_2^3 z_1(z_3)^{q_2^1} z_3^{q_2^3}}.$$

At $z_2^0 \le z_2 \le 1$,

$$\chi_1(z_2) = \frac{q_1^1 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^1 z_2^{q_2^2} z_3(z_2)^{q_2^3}}{q_1^2 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^2 z_2^{q_2^2} z_3(z_2)^{q_2^3}},$$

$$\chi_2(z_2) = \frac{q_1^1 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^1 z_2^{q_2^2} z_3(z_2)^{q_2^3}}{q_1^3 z_2^{q_1^2} z_3(z_2)^{q_1^3} + q_2^3 z_2^{q_2^2} z_3(z_2)^{q_2^3}}.$$

Thus, in the section $L^3 = \text{const}$, a curvilinear triangle is obtained, which is the boundary of the stratum where there are three limiting resources. By plotting rays, the boundaries of the other strata are determined.

Let us find the relative abundances of species in the stationary growth phase. In the stratum where there are three limiting factors, the initial variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^1 n_1 + q_2^1 n_2 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 = L^2, \\ q_1^3 n_1 + q_2^3 n_2 = L^3. \end{cases}$$

By taking into account that the solution of this problem is given by the species structure formula, and introducing variables $\exp(-\lambda^1) = x$, $\exp(-\lambda^2) = y$, and $\exp(-\lambda^3) = z$, the set of equations for the relative abundances $\dfrac{n_i}{n}$ is obtained in the form

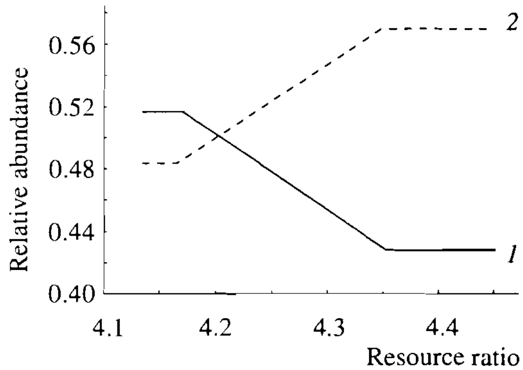

Fig. 3. Relative abundances (*1*) *t* and (*2*) *s* of two species as functions of the ratio between the contents of two limiting resources.

$$\begin{cases} \dfrac{n_i}{n} = x^{q_i^1} y^{q_i^2} z^{q_i^3}, \; i = 1, 2, \\ x^{q_1^1} y^{q_1^2} z^{q_1^3} + x^{q_2^1} y^{q_2^2} z^{q_2^3} = 1, \\ \dfrac{q_1^1 x^{q_1^1} y^{q_1^2} z^{q_1^3} + q_2^1 x^{q_2^1} y^{q_2^2} z^{q_2^3}}{q_1^2 x^{q_1^1} y^{q_1^2} z^{q_1^3} + q_2^2 x^{q_2^1} y^{q_2^2} z^{q_2^3}} = \chi_1, \\ \dfrac{q_1^1 x^{q_1^1} y^{q_1^2} z^{q_1^3} + q_2^1 x^{q_2^1} y^{q_2^2} z^{q_2^3}}{q_1^3 x^{q_1^1} y^{q_1^2} z^{q_1^3} + q_2^3 x^{q_2^1} y^{q_2^2} z^{q_2^3}} = \chi_2. \end{cases}$$

In the stratum where the limiting factors are L^1 and L^2, the variational problem has the form

$$\begin{cases} q_1^1 n_1 + q_2^1 n_2 = L^1, \\ q_1^2 n_1 + q_2^2 n_2 = L^2. \end{cases}$$

Similarly to the case where $w = 2$ and $m = 2$, the relative abundances are found as

$$\begin{cases} s = \dfrac{q_2^2 \chi - q_2^1}{q_2^2 \chi - q_2^1 + q_1^1 - q_1^2 \chi}, \\ t = \dfrac{q_1^1 - q_1^2 \chi}{q_2^2 \chi - q_2^1 + q_1^1 - q_1^2 \chi}, \\ \text{where } \chi = \dfrac{L^1}{L^2}. \end{cases}$$

In the strata where the limiting factors are L^1 and L^3, or L^2 and L^3, the solutions are obtained similarly.

In the strata where there is only one limiting factor, L^k, $k = 1, 2, 3$, the variational problem has the form

$$\begin{cases} H(\vec{n}) \to \max, \\ q_1^k n_1 + q_2^k n_2 = L^k, \; k = 1, 2, 3. \end{cases}$$

Solving this problem similarly to the case where $w = 2$ and $m = 2$ yields $s = x_0^{q_1^k}$, and $t = x_0^{q_2^k}$; moreover, $x_0^{q_1^k} + x_0^{q_2^k} = 1$.

Calculations for the Case where $w = 2$ and $m = 3$

To perform illustrative calculations using the algorithms described, the demands of species for resources were taken from the results of microbiological studies [4, 5]: $q_1^1 = 55$, $q_1^2 = 10$, $q_2^1 = 50$, and $q_2^2 = 15$. The boundaries of strata are determined by solving the equations $x^{50} + x^{55} = 1$ and $y^{10} + y^{15} = 1$. Their solutions are $x_0 = 0.986874$ and $y_0 = 0.945312$. The slopes η and ν of the rays that are the boundaries of the limitation strata are

$$\nu = \frac{55 x_0^{55} + 50 x_0^{50}}{10 x_0^{55} + 15 x_0^{50}} = 4.165884;$$

$$\eta = \frac{55 y_0^{10} + 50 y_0^{15}}{10 y_0^{10} + 15 y_0^{15}} = 4.3494.$$

Then, the relative abundances of species in each of the strata are calculated.

In the stratum where $\nu \le \chi \le \eta$, $s = 3 - \dfrac{13}{\chi + 1}$; $t = -2 + \dfrac{13}{\chi + 1}$.

In the stratum where $\chi < \nu$, $s = x_0^{55} = 0.483497$, $t = x_0^{50} = 0.5116518$.

In the stratum where $\chi > \eta$, $s = y_0^{10} = 0.569841$, $t = y_0^{15} = 0.43016$.

The relative abundances t and s of species as functions of the ratio χ between the contents of resources are presented in Fig. 3.

CONCLUSION

The results obtained, in particular, the explicit expressions for the relative abundances of species as functions of the ratio between the contents of resources, demonstrated the possibility of controlling the community structure, i.e., the possibility of selecting such contents of resources in the environment early in the experiment that, by the time the community attains the stationary growth phase, the relative abundances of species vary regularly (Fig. 3). The complete proof of the existence of this possibility is given by the optimization theorem [9], according to which (1) the relative abundances of species depend on the ratios between the contents of environmental resources consumed completely by the community; (2) to a given set L of environmental resources, the only state $\vec{n} = (n_1, \ldots, n_w)$ of the community corresponds; and (3) the relative abundance of a given species takes the maximal value (the value that is maximal among all the possible values throughout the range of factors being modified) when the ratio between the contents of resource factors is equal to the ratio between the demands for them for the given species.

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