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Multicomponent Gause's principle in models of biological communities

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Abstract — A generalization of the Gause competitive exclusion principle which guarantees the vanishing of at least one species in the community exceeding in number of species the number of available resources is presented. Theorems which guarantee the vanishing of a greater number of components under condition of the Malthusian vector function localizations in a set of smaller dimension are formulated. The theory developed here is applied to the case of Volterra type systems for which such vector functions are linear resource dependent and the number of resources is small.

Keywords: Gause competitive exclusion principle, component-wise subdivided system, dimensional localization of the Malthusian vector functions, resource dependent system, Lotka–Volterra system.

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The Gause competitive exclusion principle [2] states that populations of two different species cannot coexist in a common ecological niche. In this case, the niche means a set of conditions of existence of each species including the range of dietary preferences. The principle is based on a model representation of the dynamics of the community as a system of ordinary differential equations with vanishing right-hand sides for zero values of variables standing in the left-hand side and characterizing the population size of each species. The ratios of these right-hand sides to the indicated variables are usually called the Malthusian functions of appropriate species, and the vector composed of them is called the Malthusian community vector. The essence of the Gause principle in terms of such models is that if two species have the Malthusian functions differing only by a nonzero constant (in the biological interpretation this could mean, for example, that the species occupy the same territory and act synchronously against the same rations, but have different mortality rates), one of the species will disappear in the course of time in the sense that the lower limit of its population size must tend to zero. Note that in the case of complete coincidence of the Malthusian functions the species become indistinguishable in terms of their environmental behaviour, so from an ecological point of view they can be combined into a single species (see the ecological definition of a species comparing to, for example, the *perfect* definitions for bisexual species suggesting

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the absence of evolutionary forces shifting the frequencies of genotypes; see variants in [8, Chapter 4]). The indicated property of the Malthusian functions is just the localization of values of the Malthusian vector of the considered community of two species on a line with unit inclination and not including the origin. The latter property of the two ones mentioned here for the line is principal for disappearance of one of the species as well as the fact that its dimension is less than the total number of species in the considered community.

For a community of an arbitrary finite number of species in the case when its Malthusian vector is localized in a set of dimensions less than this number and not including the origin we also have the situation when at least one of the species disappears [1, Chapter 5]. This latter property is called the multidimensional Gause principle. We consider it as a special case in Section 7 of the present paper.

Note that we deliberately ignore here the possibility of any mathematical interpretation of the concept of ecological niche being meaningful from the biological point of view and restrict ourselves with formulations of Gause's principle in terms of the Malthusian vector localization. This approach creates a possibility to use the simplest mathematical construction leaving, however, a sense of incompleteness caused mainly by the presence of logical lacuna in the construction of a mathematical model as a system of ordinary differential equations for a biological community of species characterized, in particular, by those niches. A quite reasonable scheme to fill this gap can be found in [3, Ch. 5], see also [6, Ch. VI] or [4, Ch. 8].

We would like to draw the attention of the reader to the correspondence of the terminology used here with the terminology adopted in English-language publications. The phrase 'the disappearance of at least one species' in a community, where the 'disappearance' is understood in the sense described above without specific reference to the disappearing species corresponds to the phrase 'the absence of strong persistence' in that community. Concerning this issue, see [7, Ch. 3]. We do not use such terminology because of its focus on the dynamics of the community as a whole, which eliminates the ability to talk about disappearance of certain species.

In the present paper we demonstrate the result being a deep refinement of the multidimensional Gause principle and formulated briefly in the following way. In the rough case in the biological community of n species whose Malthusian vector is localized in a set of dimension m, exactly $n-m$ species will disappear.

A more detailed description includes the conditions of roughness; a counterexample for their violation; the lower estimate for the number of disappearing species for the known number of violated conditions of roughness; conditions providing the ability to use the estimates for systems of lesser dimensions; and also applications of the constructed theory to a system of Volterra type with a Malthusian vector function linearly dependent on the amounts of finite number of resources.

1. Definitions and preliminary results

We consider a component-wise subdivided system representing a sufficiently wide generalization of the classic Lotka–Volterra system used in description of the dynamics of biological communities

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = F_i(x,t), \quad i = 1,\dots,n, \quad t \geqslant 0 \tag{1.1}$$

and modelling the dynamics of a biological community with the vector $x = (x_1,\dots,x_n)^{\mathrm{T}} \in \mathbf{R}^n$ of sizes of particular species $x_i = x_i(t) \geqslant 0$, where $F_i(x,t) = g_i(x_i)f_i(x,t)$, $i = 1,\dots,n$, and $f = (f_1,\dots,f_n)^{\mathrm{T}}$ is the vector of (generalized) Malthusian functions with the components $f_i(x,t)$. A certain (not necessarily unique) nonnegative solution $x(t)$ to the Cauchy problem for system (1.1) with some initial condition $x(t_0) = x_0 \geqslant 0$ is taken as the solution to that system. We assume by default that the domain of its definition is unbounded in the case of bounded range of its values. Just this solution may participate in the conditions presented below.

We use standard notations for operations with sets $V \subset \mathbf{R}^{\mathrm{n}}$ and vectors $x \in \mathbf{R}^{\mathrm{n}}$. Thus, for example, the scalar product in $\mathbf{R}^{\mathrm{n}}$ is denoted by $(x,y)_n$; $\mathbf{R}_+^{\mathrm{n}+1} = \left\{(x,t) : x \in \mathbf{R}_+^{\mathrm{n}}, t \geqslant t_0\right\}$, where t_0 is the initial moment for the considered solution; the expression 'holds for $t+$' is equivalent to the expression 'holds for all $t > T$ with some T'. We also use the following notations for basis vectors: $e_j = (0,\dots,0,1,0,\dots,0)^{\mathrm{T}} \in \mathbf{R}^{\mathrm{n}}$ (the unit stands at the jth position). The other notations and terms (as, for example, binomial coefficients C_n^m, support vector, kernel (preimage of the origin, denoted by Ker) of an operator or matrix, etc.) are standard.

We assume the following conditions on the functions entering (1.1).

(G) The functions $g_i(s)$ are determined and continuous for all $s \geqslant 0$; in addition, $g_i(s) > 0$ for $s > 0$.

(F) The functions $f_i(x,t)$ are continuous in $\mathbf{R}_+^{\mathrm{n}+1}$ and we have $f_i(x,t) \geqslant 0$ for all (x,t) with $x_i = 0$ such that $g_i(0) > 0$.

(C) There exist a vector $c \in \mathbf{R}^{\mathrm{n}}$ and a constant $\delta > 0$ such that the inequality $(f((x(t),t),c)_n > \delta$ holds for $t+$ for the vector of Malthusian functions $f = (f_1,\dots,f_n)^{\mathrm{T}}$ with the components $f_i = f_i(x(t),t)$.

The following condition is considered as sufficient for (C):

(V) There exists a closed convex set $V \subset \mathbf{R}^n$ such that the origin $\mathbf{0} \in \mathbf{R}^{\mathrm{n}}$ satisfies the exclusion condition $\mathbf{0} \notin V$ and the inclusion $f(x(t),t) \in V$ holds for $t+$.

We have the following result.

Theorem 1.1. *Under conditions* (*G*), (*F*), *and* (*C*) *and for any pair* $(x^0,t_0) \in \mathbf{R}_+^{\mathrm{n}+1}$ *and any nonnegative bounded solution* $x(t) = (x_1(t),\dots,x_n(t))^{\mathrm{T}}$ *to the Cauchy problem for* (1.1) *with* $x(t_0) = x^0$ *there exist a number* $j(c)$ *and a sequence* $t_k \to +\infty$ *such that* $x_{j(c)}(t_k) \to 0$.

Proof. In the alternative case of logarithmic boundedness of the solution $x(t)$, conditions (G) and (F) imply that this solution can be extended forward in time infinitely far. For all $t > t_1$ and some $t_1 > 0$ from condition (C) we get

$$\sum_{i=1}^{n} \frac{c_i}{g_i(x_i)} \frac{\mathrm{d}x_i}{\mathrm{d}t} = \sum_{i=1}^{n} c_i f_i(x,t) > \delta$$

so that after integration for any $\tau \geqslant t_1$ and $T > 0$ we have

$$\sum_{i=1}^{n} c_i \int\limits_{x_i(\tau)}^{x_i(\tau+T)} \frac{\mathrm{d}s}{g_i(s)} > \delta T. \tag{1.2}$$

Inequality (1.2) cannot hold for sufficiently large T in the considered case. This implies the assertion of the theorem.

Remark 1.1. An alternative to the assertion of the theorem for bounded solutions is their logarithmic boundedness, the so-called *ecological stability* is its synonym in the biological terminology. If it is absent in any solution, then the system is called ecologically unstable. Theorem 1.1 presents sufficient conditions for such instability.

Remark 1.2. Some generalizations and refinements of this theorem taking into account the possibility of localization of the range of values of the tail of the Malthusian vector function in a convex domain not separated from the origin and even the possibility of such localization for its limit distributions can be found in [5].

2. Main result

Below we consider the particular case of fulfillment of conditions of Theorem 1.1 such that the dimension of the given set V including the values of the Malthusian vector $f(x(t),t)$ is less than the dimension of the entire phase space. For any vector $b \in V$ the linear hull of the given set translated by this vector

$$L_V = \mathrm{Lin}\,\{V - b\} = \left\{ y = \sum_{j=1}^{N} \alpha_j y_j, N \in \mathbf{N},\ \alpha_j \in \mathbf{R}, y_j \in V - b \right\}$$

forms a linear space parallel to V. In this case the dimension of V is defined as the dimension of L_V and is denoted by $\dim V = m \leqslant n$.

Below we use the following condition instead of (V).

(VL) Condition (V) holds with $V = b + L_V$, $\dim V = m < n$, and the support vector b to V at the point b.

In particular, (VL) implies $b \notin L_V$ and the vector $b \neq \mathbf{0}$ is orthogonal to V, i.e., the equality $(v - b, b)_n = 0$ is valid for any $v \in V$. By P_V we denote the projector onto $L_V \subset \mathbf{R}^n$ along b in the Euclidean space $\mathbf{R}^n$ (so that $b \in L_V^{\perp}$, where $L_V^{\perp} = \mathrm{Ker}\, P_V \subset \mathbf{R}^n$ is its kernel being the orthogonal supplement to L_V in $\mathbf{R}^n$). Since $\dim L_V^{\perp} = n - m$, then the intersection of $L_V^{\perp} \cap L$ in $\mathbf{R}^n$ with any linear space $L \subset \mathbf{R}^n$ having the dimension greater than m is not empty (i.e., its dimension is positive). We take linear hulls of minimal number of basis vectors as appropriate ones.

The conjecture presented further is the key technical condition for Theorem 2.1 formulated below. Let us assume $\mathrm{M}_{m+1} = \{M \in 2^{\{1,\dots,n\}} : \ |M| = m+1\}$ (as usual, $|A|$ is the cardinality of the set A, 2^A is the set of all its subsets).

(Z) For any set of indices $M \in \mathrm{M}_{m+1}$ there exists a vector $c_M \in L_V^{\perp} \cap \mathrm{Lin}\,\{e_j\}_{j \in M}$ satisfying the condition $(c_M, b)_n \neq 0$.

Note that the fulfillment of conditions (Z) is the case of general position due to relation of dimensions. The following assertion is valid.

Theorem 2.1. *Under conditions* (G), (F), (VL), *and* (Z) *and for any bounded nonnegative solution* $x(t) = (x_1(t), \dots, x_n(t))^{\mathrm{T}}$ *to the Cauchy problem for* (1.1) *with* $x(t_0) = x^0$ *there exist* $n-m$ *indices* $i \in \{1, \dots, n\}$ *such that for each of them there exists a sequence* $t_k \to +\infty$ *such that* $x_i(t_k) \to 0$.

Proof. The proof is reduced to selection of a certain set of vectors $\{c\}$ satisfying the conditions of Theorem 1.1 so that the set of indices $\{j(c)\}$ composed by application of that theorem constitutes the required set.

Due to condition (VL), any vector $c \in L_V^{\perp}$ satisfying the inequality $(c,b)_n \neq 0$ satisfies condition (C) up to its sign. In fact, for the decomposition $c = \alpha b + c'$ with $\alpha \neq 0$ and c' such that $(c',b)_n = 0$, for any $v \in V$ we obtain $(c,v)_n = (\alpha b + c', v)_n = \alpha (b,v)_n$, therefore, since the vector b satisfies this condition, it also holds for the vectors c or $-c$. Leaving the first sign and checking the conditions of Theorem 1.1, for the vector c we get that there exists the number $j(c)$ satisfying the assertion of the theorem.

We construct the set of vectors $\{c\}$ from $L_V^{\perp}$ in the following way: Fix some set of indices $M \in \mathrm{M}_{m+1}$ and take a certain nonzero vector $c_M \in L_V^{\perp} \cap \mathrm{Lin}\,\{e_j\}_{j \in M}$ satisfying the condition $(c_M, b) \neq 0$. The existence of such vector is provided by condition (Z). It occurs that the set $\{j(c_M)\}_{|M|=m+1}$ assuredly has not less than $(n-m)$ elements, i.e., regardless of the relation $c \to j(c)$.

The verification of the latter property has a purely combinatorial character. The problem is posed in the following way. Given a set of n elements (in our case those are the components), choose all possible subsets of size $(m+1)$ (in our case this is M) and mark one element in each of those subsets (in our case this is $j(c_M)$). The appearing question on the minimal possible total number of marked elements has the unique answer, it equals $(n-m)$.

In fact, mark some element $J(M) \in M$ in each set $M \in \mathrm{M}_{m+1}$. This set (we call it *marked*) is represented by the pair $[M, J(M)]$. By $M_J = \{[M, J(M)] : M \in \mathrm{M}_{m+1}, J(M) \in M\}$ we denote the *graph* of the particular mapping $J : \mathrm{M}_{m+1} \to \{1, \dots, n\}$ being the set of all marked sets, and by $R(M_J) \subset \{1, \dots, n\}$ we denote the range of values of this mapping. In other words, the inclusion $j \in R(M_J)$ holds for $j \in \{1, \dots, n\}$ if and only if the inclusion $[M, J(M)] \in M_J$ with $j = J(M)$ holds for some $M \in \mathrm{M}_{m+1}$.

Associate each graph M_J with its *compacted image* M_J^C constructed in the following way. Fix some order of elements $j \in \{1, \dots, n\}$, where the elements from $R(M_J)$ occupy the first positions (with an arbitrary order among them). Further, according to a prescribed rule, we replace each marked number $J(M)$ by less possible $J_{\min}(M)$. Therefore, if $M = \{j_1, \dots, j_{m+1}\}$ is an ordered set (i.e., $j_1 < \dots < j_{m+1}$), then $J_{\min}(M) = j_1$. In this case for any such M we have the inequality $J_{\min}(M) \leqslant J(M)$, which implies the lower estimate for the total number of marked elements of the original graph $|R(M_J)| \geqslant |R(M_J^C)|$. It remains to obtain the lower estimate for $|R(M_J^C)|$.

The compacted image M_J^C has the following structure. The element with the number one is marked in all sets M where it appears. The element with the number j is marked in each set M to which it belongs, but elements with lesser numbers do not belong. The estimate of the total number S_j of sets of the compacted image where the jth element is marked is determined by the number of possible remaining sets of m elements (supplements in sets of $(m+1)$ elements with a fixed first element) under their choice from the remaining ones with the highest numbers (for the number j there are $(n-j)$ such ones). We finally get $S_j \leqslant C_{n-j}^m$. In particular, $S_{n-m} \leqslant 1$ and $S_j = 0$ for $j > n-m$. Since $C_n^{m+1} = \sum_{j=1}^n S_j$, where the left-hand side contains the total possible number of sets and the right-hand side contains the same value, but with partition over marked elements and $C_n^{m+1} = \sum_{j=1}^{n-m} C_{n-j}^m$, then, due to the obtained inequalities, in the compacted image we have $S_j = C_{n-j}^m$ for $j \leqslant n-m$ and $|R(M_J^C)| = (n-m)$.

3. Some sufficient conditions

The following constructively verified conditions are sufficient for fulfillment of conditions (Z).

Let $\dim V = m < n$, $V = b + L_V$, and linearly independent vectors $a_j^{\mathrm{T}} \in \mathbf{R}^n$, $j \in \{1, \dots, m\}$ be known so that $L_V = \mathrm{Lin}\ \{a_j^{\mathrm{T}}\}_{j\in\{1,\dots,m\}}$, and a nonzero vector $b \in \mathbf{R}^n$ support to V be such that $(b, a_j^{\mathrm{T}})_n = 0$ for $j \in \{1, \dots, m\}$. Let $a^{\mathrm{T}} = (a_{ij})$ be a matrix of size $n \times m$ and rank m composed of the columns a_j^{T}. Its co-kernel $\mathrm{Coker}\, a^{\mathrm{T}} = L_V^{\perp}$ coincides with the kernel of the adjoint $m \times n$ matrix $a = (a_{ij})^{\mathrm{T}} = (a_{ji})$. We associate each ordered set $M = \{i_1, \dots, i_{m+1}\}$, $i_l \in \{1, \dots, n\}$, with the minor a_M of size $m \times (m+1)$ composed of the columns of the matrix a presented in the set M. Let $\mathrm{rank}\, a_M = k \leqslant m$ and $a_{M'}$ be some nondegenerate minor of size $k \times k$ of the matrix a_M constructed on columns of the ordered set $M' = \{i'_1, \dots, i'_k\} \subset M$.

Suppose the vectors in the set $\{a_j^{\mathrm{T}}\}_{j\in\{1,\dots,m\}}$ are ordered so that the minor $a_{M'}$ is positioned in the first k rows of the matrix a_M. Note that, first, this assumption holds always in the case $k = m$ and, second, it does not restrict the generality within consideration of a fixed set M. If we apply reenumeration to M so that the elements from M' stand at the first positions, then the matrix a_M takes the form $a_M = \begin{pmatrix} a_{M'} & a_{M\setminus M'} \\ & a_{m-k} \end{pmatrix}$, where $a_{M\setminus M'}$ is the matrix of size $k \times (m+1-k)$ composed of $(m+1-k)$ shortened (i.e., truncated to the first k rows) columns $a_i = \left(a_{M\setminus M'}\right)_i \in \mathbf{R}^k$

of the matrix a_M not contained in $a_{M'}$ (i.e., $i \in M \backslash M'$), and a_{m-k} is the matrix of size $(m-k)\times(m+1)$ composed of the last $(m-k)$ rows of the matrix a_M. Order the elements of the vector $b \in \mathbf{R}^n$ according to the choice of the set M so that the first $(m+1)$ positions were occupied by the elements with numbers from M according to the order specified before for the set M, therefore, the vector b truncated to these first $(m+1)$ positions has the form $b_M = (b_{M'}, b_{M\backslash M'}) \in \mathbf{R}^{m+1}$ with $b_{M'} \in \mathbf{R}^k$ and $b_{M\backslash M'} \in \mathbf{R}^{m+1-k}$. As usual, by b_i we denote the element of the vector b standing at the position $i \in M\backslash M'$ according to the indicated order. The condition corresponding to the set M takes the form:

(ZM) for a given set $M \in \mathrm{M}_{m+1}$, corresponding to it rank $a_M = k \leqslant m$, and the order in $M = \{M', M\backslash M'\}$ there exists a number $i \in M\backslash M'$ such that

$$\left(a_{M'}^{-1}\left(a_{M\backslash M'}\right)_i, b_{M'}\right)_k \neq b_i. \tag{3.1}$$

It occurs that the fulfillment of condition (ZM) does not depend on particular choice of the subset $M' \subset M$ providing the nondegeneracy of the matrix $a_{M'}$ and, moreover, the simultaneous fulfillment of all conditions (ZM) for M running over M_{m+1} is sufficient for fulfillment of condition (Z). More precisely, we have the following result.

Proposition 3.1. *Let condition* (*ZM*) *hold for some M and an appropriate set $M' \subset M$. In this case it holds for the indicated M and any $M' \subset M$ such that the matrix $a_{M'}$ is nondegenerate.*

Proof. The expression $\left(a_{M'}^{-1}(a_{M\backslash M'})_i, b_{M'}\right)_k - b_j$ determines the scalar product $(b_M, s_i)_{m+1}$ of the vector b_M and the vector $s_i = \big(a_{M'}^{-1}(a_{M\backslash M'})_i, 0, \ldots, 0, -1, 0, \ldots, 0\big) \in \mathbf{R}^{m+1}$ such that its first k positions are occupied by elements of the vector $a_{M'}^{-1}\left(a_{M\backslash M'}\right)_j$, and the other positions contain only one nonzero element standing at the position with the number $i \in M\backslash M'$. Obviously, the vectors s_j are linearly independent and form a $(m+1-k)$-dimensional linear space $\mathrm{Lin}\,\{s_i\}_{i\in M\backslash M'}$ being the kernel of the matrix $\begin{pmatrix} a_{M'} & a_{M\backslash M'}\end{pmatrix}$ of size $k \times (m+1)$. In fact, for any $i \in M\backslash M'$ we get

$$\begin{pmatrix} a_{M'} & a_{M\backslash M'}\end{pmatrix} s_i = \left(a_{M'}\left(a_{M'}^{-1}\left(a_{M\backslash M'}\right)_i\right) - \left(a_{M\backslash M'}\right)_i\right) = 0.$$

The violation of inequality (3.1) for all $i \in M\backslash M'$ is equivalent to the orthogonality of the vector b to the entire $(m+1-k)$-dimensional kernel of the matrix $\begin{pmatrix} a_{M'} & a_{M\backslash M'}\end{pmatrix}$ and, hence, the same is valid for the matrix a_M (because the lower $(m-k)$ rows in the representation $a_M = \begin{pmatrix} a_{M'} & a_{M\backslash M'} \\ \multicolumn{2}{c}{a_{m-k}} \end{pmatrix}$ are linear combinations of the upper ones). But this orthogonality does not depend on the choice of the nondegenerate minor $a_{M'}$ of size $k \times k$.

Proposition 3.2. *The fulfillment of conditions (ZM) for all $M \in \mathrm{M}_{m+1}$ is sufficient for fulfillment of condition (Z).*

Proof. For $c_M \in L_V^\perp \cap \mathrm{Lin}\,\{e_i\}_{i \in M}$ with given $M \in \mathrm{M}_{m+1}$ we can take the vector $(s_i, 0) \in \mathbf{R}^n$ with the vector $s_i \in \mathbf{R}^{m+1}$ for i chosen according to condition (3.1) whose components are positioned corresponding to chosen M and are zero at other $(n-m-1)$ positions (in the representation $c_M = (s_i, 0)$ we assume that the first positions correspond to M and $0 \in \mathbf{R}^{n-m-1}$). In this case the inclusion $c_M \in L_V^\perp$ follows from the inclusion $s_i \in \mathrm{Ker}\, a_M$ (see the proof of Proposition 3.1) and the supplement of s_i by zeros up to the vector c_M of dimension n.

Since the nature of conditions (ZM) is the absence of equalities and their number is finite, then the 'probability' when they do not hold equals zero, i.e., in the case of general position these conditions and hence condition (Z) must hold. In accordance with Theorem 2.1, this means that in the case of general position the localization of the vector of Malthusian functions on a linear manifold of codimension $d = n-m$ not containing the origin leads to the disappearing (in the sense formulated in Theorems 1.1 and 2.1) of not less than d components. Possible breaks in (ZM), i.e., fulfillment of equalities instead of inequalities may lead, as is seen from the example presented below, to decrease of the number of disappearing components. In this connection, it is interesting to reveal the relations between the amount of such decrease and the number of breaks. The theorem presented below is a formal generalization of Theorem 2.1 where condition (Z) is replaced by the conditions of Proposition 3.2.

Theorem 3.1. *Let all the conditions of Theorem* 2.1 *hold except for condition (Z) replaced by conditions (ZM) for $M \in Q \subset \mathrm{M}_{m+1}$ with the total number $|Q| \leqslant |\mathrm{M}_{m+1}| = C_n^{m+1}$. In this case the assertion of Theorem* 2.1 *is valid for not less than $\varkappa \leqslant n-m$ components, where $\varkappa = \max\{l \in \mathbf{N} : C_{n-l+1}^{m+1} > C_n^{m+1} - |Q|\}$.*

Proof. For the graph of the mapping $J : \mathrm{M}_{m+1} \to \{1, \ldots, n\}$ we compose its compacted image in the same way as in the proof of Theorem 2.1. The main difference consists in the total number of sets $M \in \mathrm{M}_{m+1}$ where marked elements are chosen, in this case it is equal to $|Q| \leqslant C_n^{m+1}$ so not all compacted image elements may be marked comparing to those marked in conditions of Theorem 2.1. If their total number equals $\varkappa \geqslant 1$, then by construction of the compacted image for the number of sets with marked jth element we get $S_j = C_{n-j}^m$ for $j < \varkappa$ and $1 \leqslant S_\varkappa \leqslant C_{n-\varkappa}^m$, and the equality $|Q| = \sum_{j=1}^{\varkappa} S_j$ is valid. The number of breaks is

$$q = C_n^{m+1} - \sum_{j=1}^{\varkappa} S_j = \sum_{j=1}^{n-m} C_{n-j}^m - \left(S_\varkappa + \sum_{j=1}^{\varkappa-1} C_{n-j}^m \right)$$

therefore,

$$q = \sum_{j=\varkappa}^{n-m} C_{n-j}^{m} - S_{\varkappa} = C_{n-\varkappa+1}^{m+1} - S_{\varkappa}.$$

Taking into account the above inequalities for $S_{\varkappa}$, we obtain the chain of relations

$$C_{n-\varkappa}^{m+1} = \sum_{j=\varkappa}^{n-m} C_{n-j}^{m} - C_{n-\varkappa}^{m} \leqslant q = \sum_{j=\varkappa}^{n-m} C_{n-j}^{m} - S_{\varkappa} \leqslant C_{n-\varkappa+1}^{m+1} - 1$$

from which, given the value $q = C_n^{m+1} - |Q|$, we calculate the value of $\varkappa$ by the formula indicated in the formulation of the theorem.

All other arguments including the use of the result obtained for the compacted image as an estimate for the case of original graph repeat the corresponding arguments in the proof of Theorem 2.1.

Remark 3.1. If the other (except for (Z)) conditions of Theorem 2.1 hold, then the equality $|Q| \geqslant 1$ evidently holds (because otherwise the vector b were orthogonal to all e_i). This implies that the maximum is always attainable and localized within $\varkappa \in \{1,\dots,n-m\}$. The sets $M \in \mathrm{M}_{m+1} \backslash Q$ are said to be *breaks* and so $q = |\mathrm{M}_{m+1} \backslash Q| = C_n^{m+1} - |Q| \geqslant 0$ is the number of breaks. For marginal values we get $|Q| = 1$ for $\varkappa = 1$ (the case of Theorem 1.1) and $q = 0$ for $\varkappa = n-m$ (the case of Theorem 2.1), respectively. According to the formula, for some other values we get that $q \in \{1,\dots,m+1\}$ implies $\varkappa = n-m-1$, $q \in \{m+2,\dots,(m+2)(m+3)/2-1\}$ implies $\varkappa = n-m-2$, etc.

4. Necessity of the conditions. Counterexample

If the conditions of Theorem 2.1 are violated, some situations may occur so that a lesser number of components disappears than that is indicated in Theorem 2.1.

Example 4.1. Let us consider the system

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i f_i(x)$$

with $x = (x_1, x_2, x_3, x_4)$, $f_1(x) = 1 - x_2$, $f_2(x) = x_1 - 1$, $f_3(x) = -1$, $f_4(x) = 0$, and the initial conditions $x_i(0) > 0$ for $i = (1,\dots,4)$. Independently of its argument, the vector function $f(x) = (f_1, f_2, f_3, f_4)$ takes values in a two-dimensional plane given parametrically as $V = \{x = (x_1, x_2, -1, 0)\}$. The constructed system satisfies conditions of Theorem 1.1. Concerning the conditions of Theorem 2.1, all of them also hold except for condition (Z), and the latter one does not hold, taking into account Proposition 3.2, due to absence of only one condition (ZM) for $M = \{1,2,4\}$. Such a break in conditions is quite sufficient for the disappearing of only one variable (according to Theorem 1.1) instead of expected two variables (according to

Theorem 2.1), namely, this is the variable $x_3(t) = x_3(0)\mathrm{e}^{-t} \to 0$, whereas all other variables remain bounded and separated from zero (because $x_4(t) \equiv x_4(0) > 0$ and the variables $x_{1,2}(t)$ determine the solution to the Volterra 'predator-prey' system, i.e., oscillate around a closed trajectory in the bounded domain of strictly positive values $0 < C_1 < x_{1,2}(t) < C_2 < \infty$).

5. The case of truncated system

The following result may be interesting in connection with the possibility to use, instead of original system (1.1), a *truncated* one, i.e., that constructed on the base of the original system and its known solution satisfying the conditions of Theorem 2.1 relative to only a part of variables and whose equations coincide with equations of the original system for this part with the only difference that the other variables are considered there as the known functions of time obtained from the solution. The application of such procedure may change the conditions of Theorems 2.1 and 3.1. As we will see below, these changes decrease their efficiency. Such decrease does not occur if the projection of the set of the Malthusian function values onto the phase space of the truncated system satisfies the conditions of Theorem 2.1 (see condition (VP) below). In this case both variants give the same results.

As above, let $m = \dim V < n$. We fix some subset $M^h \subset \{1, \ldots, n\}$ so that $|M^h| = h \geqslant m+1$ and assume $\mathrm{M}^h_{m+1} = \{M \in \mathrm{M}_{m+1} : M \subset M^h\}$. Let $P_h = P_{M^h}$, where P_M is the projector onto the space spanned on the basis vectors $\{e_i\}_{i\in M}$ along the others, i.e., $P_M\left(\sum_{i=1}^n x_i e_i\right) = \sum_{i\in M} x_i e_i$. Denote $\mathbf{R}^h = P_h(\mathbf{R}^n)$ and consider instead of (VL) the following stronger condition meaning the fulfillment of condition (VL) for a part of variables only:

(VP) Condition (VL) holds with $m = \dim V < n$, where the exclusion $\mathbf{0} \notin V$ is replaced by the exclusion $\mathbf{0} \notin P_h V$.

The fact that $\mathbf{0} \notin P_h V$ implies $\mathbf{0} \notin V$ is a corollary of the equality $P_h \mathbf{0} = \mathbf{0}$, therefore, if condition (VP) holds, then along with the vector $b \neq \mathbf{0}$ there exists a unique vector $b^h \neq \mathbf{0}$ determining the projection $\mathbf{0} \in \mathbf{R}^h$ onto $P_h V$ (i.e., being support to the set $P_h V$ at the given point $b^h \in P_h V$).

Proposition 5.1. *Under conditions (VP) and for given $M \in \mathrm{M}^h_{m+1}$ condition (ZM) is equivalent to itself with the replacement of the vector b by b^h.*

Proof. The proof is reduced to verification of inequality (3.1) with the corresponding replacements. As we have seen (see the proof of Proposition 3.1), inequality (3.1) is equivalent to the inequality $(s,b)_n \neq 0$ for some appropriate $s \in P_M(\mathbf{R}^n) \cap L_V^{\perp}$. In order to verify the declared equivalence, it is sufficient to prove the equivalence of this inequality to the inequality $(s,b^h)_n \neq 0$ for any $s \in P_M(\mathbf{R}^n) \cap L_V^{\perp}$.

Let $L_{P_h V} \subset P_h(\mathbf{R}^n)$ be a linear space spanned on $P_h V - b^h$, which gives $P_h V =$

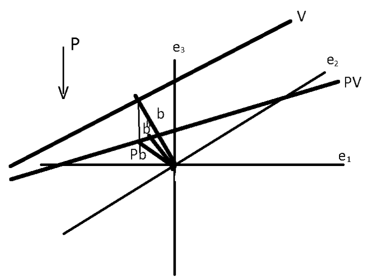

Figure 1. The case $n = 3$, $m = 1$, $P = P_h$ with $M_h = \{1,2\}$.

$b^h + L_{P_hV}$. Since $b \in V$, then $P_h b \in P_h V$, which implies $P_h b = b^h + \lambda$, where $\lambda \in L_{P_hV}$. Further, $(s,b)_n = (s,P_h b)_n + (s,(E-P_h)b)_n$, where E is the identity operator in $\mathbf{R}^n$. Since $M \in \mathrm{M}^h_{m+1}$, then $P_M(\mathbf{R}^n) \subset P_h(\mathbf{R}^n)$ and the second summand vanishes in the case $s \in P_M(\mathbf{R}^n)$. Substituting the expression for $P_h b$ into the first summand, we obtain $(s,b)_n = (s,P_h b)_n = (s,b^h)_n + (s,\lambda)_n$. Since $L_{P_hV} \subset L_V \oplus (E-P_h)(\mathbf{R}^n)$ (because for $v = P_h(b_1) - P_h(b_2) \in L_{P_hV}$ with $b_{1,2} \in V$ we get $\xi = b_1 - b_2 \in L_V$ such that $v = P_h \xi$), due to the previous arguments and the inclusion $s \in L_V^{\perp}$ we get the equality $(s,\lambda)_n = 0$, and, hence, we finally obtain $(s,b)_n = (s,b^h)_n$.

Taking the part of variables satisfying condition (VP) equivalent to condition (VL) for the truncated system and applying Proposition 5.1, we get the following theorem.

Theorem 5.1. *The assertion of Theorems* 2.1 *and* 3.1 *remain valid in the case of validity of their conditions for solutions considered as solutions to the truncated system relative to a certain part of variables.*

Figure 1 illustrates the case $n = 3$, $m = 1$, $P = P_h$ with $M_h = \{1,2\}$.

6. A model with lesser amount of resources

Let the dynamics of a biological community be described by nonnegative solutions to the following system of equations:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = g_i(x_i)\left(\beta_i + \sum_{j=1}^{m} \alpha_{ij} R_j(t)\right), \quad i \in \{1,\ldots,n\} \tag{6.1}$$

where the functions $g_i(s)$ determined for all $s \geqslant 0$ are continuous and positive for $s > 0$, and $g_i(0) = 0$. The functions $R_j(t)$, $j \in \{1,\ldots,m\}$, $m < n$, are arbitrary continuous functions of time describing the dynamics of resources. All other coefficients in (6.1) are real constants. Without loss of generality, we assume that the $n \times m$ matrix $\mathrm{A} = (\alpha_{ij})$ has the rank m and its minor $\mathrm{M} = (\alpha_{ij})$ for $i, j \in \{1,\ldots,m\}$ is nondegenerate. In the rough case for $m < n$ the vector of Malthusian functions with components from the expressions in parentheses in the right-hand side of (6.1) does not vanish and, hence, does not leave a certain linear manifold of dimension m separated from zero; therefore, according to Theorem 1.1, the boundedness of the solution implies the disappearing of at least one its component. Just this case was studied in [1]).

It occurs that Theorem 2.1 allows one to assert more in connection with system (6.1), in the rough case not one, but $(n-m)$ species will disappear. More subtle cases are described by Theorem 3.1 so that Theorem 5.1 presented below is valid in the general case. For its formulation we introduce the following notations.

For the coefficients from (6.1) we assume $\beta = (\beta_1, \ldots, \beta_n)^{\mathrm{T}}$, $a_{ij} = \alpha_{ji}$, and $\mathrm{A}^{\mathrm{T}} = (a_{ij})$. Assume also that $\beta \notin \operatorname{Ker} \mathrm{A}^{\mathrm{T}}$. The matrix A^{T} can be represented in the form $\mathrm{A}^{\mathrm{T}} = \begin{pmatrix} \mathrm{M}^{\mathrm{T}} & \mathrm{N} \end{pmatrix}$, where N is some $m \times (n-m)$ matrix supplementing M^{T} to A^{T}. Consider the extension of the matrix A to the $n \times n$ matrix A_n and the auxiliary matrix B of the form

$$\mathrm{A}_n = \begin{pmatrix} \mathrm{M} & -\left(\mathrm{M}^{\mathrm{T}}\right)^{-1} \mathrm{N}^{\mathrm{T}} \\ \mathrm{N} & \mathrm{E} \end{pmatrix}, \qquad \mathrm{B} = \begin{pmatrix} \mathrm{M}^{\mathrm{T}} & 0^{\mathrm{T}} \\ 0 & \mathrm{E} \end{pmatrix}$$

where E is the $(n-m) \times (n-m)$ identity matrix and 0 is the $m \times (n-m)$ zero matrix. The matrix $\mathrm{BA}_n + (\mathrm{BA}_n)^{\mathrm{T}}$ is positive definite and the matrix B is nondegenerate, hence, the matrix A_n is nondegenerate as well. This implies the uniqueness of the solution to the equation $\mathrm{A}_n u = \beta$ relative to the vector $u = \begin{pmatrix} u^1 & u^2 \end{pmatrix} \in \mathbf{R}^n$ with $u^1 \in \mathbf{R}^m$ and $u^2 \in \mathbf{R}^{n-m}$. It is not difficult to check (here we actually expand the vector β over the range of values of the operator A and its co-kernel) that the vector

$$b = \left(-\left(\mathrm{M}^{\mathrm{T}}\right)^{-1} \mathrm{N}^{\mathrm{T}} u^2 \quad u^2 \right) \in \mathbf{R}^n \tag{6.2}$$

is orthogonal to the linear manifold $\beta + \operatorname{Ran} \mathrm{A}$ containing all possible values of the Malthusian vector and ends at it, i.e., is a support vector appearing in the formulation of Theorem 2.1.

Formulate condition (ZM) relative to system (6.1). As before, for a set $M = \{i_1, \ldots, i_{m+1}\}$ the subscript corresponding to this set and standing at a matrix or a vector denotes their restriction in rows and columns onto this set.

(ZM) Given a set $M = \{i_1, \ldots, i_{m+1}\}$ and the corresponding to it matrix $\mathrm{A}_M^{\mathrm{T}}$ of rank $k \leqslant m$ and the set $M' = \{i'_1, \ldots, i'_k\} \subset M$ with a nondegenerate $k \times k$-minor $\mathrm{A}_{M'}^{\mathrm{T}}$, there exists a number $i \in M \backslash M'$ such that the inequality $\left((\mathrm{A}_{M'}^{\mathrm{T}})^{-1} (\mathrm{A}_{M \backslash M'}^{\mathrm{T}})_i, b_{M'}\right)_k \neq b_i$ holds for b from (6.2).

Theorem 6.1. *Let $r \leqslant C_n^{m+1}$ conditions from (ZM) hold for the vector b from* (6.2) *and the matrix* A^{T}. *Then any bounded nonnegative solution to system* (6.1) *has not less than $\varkappa = \max\{l \in \mathbf{N} : C_{n-l+1}^{m+1} > C_n^{m+1} - r\}$ disappearing components $x_i(t)$, i.e., there exists a sequence $t_k \to +\infty$ such that $x_i(t_k) \to 0$ (vanishing).*

Remark 6.1. The proof of the theorem directly follows from Theorems 2.1 and 3.1 for the case $r = |Q|$.

Remark 6.2. Equations in system (6.1) are formally independent. Their interrelation has sense only in connection with conditions (ZM). Taking into account Theorem 5.1, instead of this system we can consider its truncated variant where $i \in M^h = \{i_1, \ldots, i_h\} \subset \{1, \ldots, n\}$ with $m < h < n$ and the unique condition that for the vector β and matrix A truncated onto M^h and given as $\mathrm{A}_h = (\alpha_{ij})_{i \in M^h,\, j \in \{1,\ldots,m\}}$ and $\beta^h = (\beta_{i_1}, \ldots, \beta_{i_h})^{\mathrm{T}}$ the condition $\beta^h \notin \mathrm{Ker}\ \mathrm{A}_h^{\mathrm{T}}$ holds. In this case under the conditions of the theorem (only those $r^h \leqslant \min\{C_h^{m+1}, r\}$ conditions of (ZM) are sufficient that relate to subsets of the set M^h) bounded solutions to system (6.1) have the disappearing components from elements of M^h and their number is determined by calculations presented in the formulation of the theorem with the change of n by h and r by r^h.

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