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Biodiversity and robustness of large ecosystems

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Abstract

We study the biodiversity problem for resource competition systems with extinctions and self-limitation effects. Our main result establishes estimates of biodiversity in terms of the fundamental parameters of the model. We also prove the global stability of solutions for systems with extinctions and large turnover rate. We show that when the extinction threshold is distinct from zero, the large time dynamics of system is fundamentally non-predictable. In the last part of the paper we obtain explicit analytical estimates of ecosystem robustness with respect to variations of resource supply which support the $R^*$ rule for a system with random parameters.

Keywords: Foodweb, Biodiversity, Global stability, Extinction threshold, Ecological networks, the $R^*$ rule

1. Introduction

Existence and stability of large foodwebs, where many species share a few of resources, is one of key problems in ecology [4, 21, 9] as well as extinctions and mass extinctions in such systems under climate changes [14]. In this paper, we consider the model initiated in [11], [10] describing an ecological system, where several (many) species compete or fight for few limited resources.

The most typical examples are plant or plankton ecosystems. Sunlight, water, nitrogen, phosphorus and iron are all abiotic essential resources for phytoplankton and plant species. Resource competition models link the population dynamics of competing species with the dynamics of the resources. As it was mentioned in [7] an attractive feature of resource competition models is that they use the biological traits of species to predict the time evolution of competition. In fact, many rigorous results [5, 19, 16] show that, in general situation, a single species survives and to obtain coexistence of many species one needs very special assumptions to species parameters (mortalities and resource consumption rates). This paradox (the so-called paradox of plankton [9, 4]) has received a great attention in past decades [17, 15]. Several ways to explain the extreme diversity of phytoplankton communities have been proposed. In particular, the proposed mechanisms include spatial and temporal heterogeneity in physical and biological environments, horizontal turbulence of ocean, oscillation and chaos generated by several internal and external causes, stable coexistence and compensatory dynamics under fluctuating temperature in resource competition, and toxin-producing phytoplankton [17, 15]. Although the mathematical problem has been studied for more than two decades it is still far from to be well-understood. The most of available results do not give explicit estimates of biodiversity in terms of the fundamental observable ecosystem parameters (such as species mortality rates, rates of resource consumptions, resource supply and resource turnover rate).

The main goal of this paper is to present such estimates. To this end we consider dynamical equations are close to the model equations, which considered in the seminal paper [7] but extend that model in the two
aspects. First, we take into account self-limitation effects (which are important for plankton populations [15] and to explain stability of large foodwebs [1, 2]). Roughly speaking when we introduce a weak self-limitation we replace equations of Maltus type on Verhulst type equations. Second, following [11] we take into account species extinction thresholds, however, in contrast to [11, 18] we consider here the case of a few resources. Mathematically, our approach with extinction thresholds and self-limitation terms can be considered as a regularization of resource competition models.

Our main results can now be formulated as follows. A summary of the mathematical framework and the global stability results established earlier in [12], [10] for the model with zero extinction threshold is collected in Sections 2 and 3. In that case, a complete description of the system large time behaviour is obtained for systems with sufficiently large turnover rates and without extinctions. More precisely, the model exhibits the global stability: all positive trajectories converge to the same equilibrium state. This result holds due to two principal properties of our system. First, the system has a typical fast/slow structure for large turnover rates. Second, the system obeys a monotonicity property: if resources increase then species abundances also increase. We recall the principal ideas of the proof at the end of section 3.2.

Next, if one allows even small positive extinction threshold, the ecosystem behaviour exhibits new interesting effects. We study this in sections 4 and 5 below. We establish a weaker stability result: the limit equilibrium state still exists but it depends on the initial ecosystem state. This in particular implies that there can a priori exist several distinct equilibrium states.

In section 5, we establish explicit upper and below estimates of biodiversity expressed in terms of the fundamental ecosystem parameters (such as species mortalities, resource consuming rate etc.). Remarkably, the obtained estimates are universal for small extinction thresholds and self-limitation parameters. We point out that these results use no assumptions on the system dynamics and do not use our theorem on global stability.

In the part of the paper, we study large ecosystems with random fundamental parameters. Here the main assumption is that the system dynamics has no oscillating or chaotic regimes. Note that it follows from Theorem 3.2, that the assumption is automatically hold if, for example, turnovers rates are large enough. Recall that the $R^*$ rule (also called the resource-ratio hypothesis) is a hypothesis in community ecology that attempts to predict which species will become dominant as the result of competition for resources. It predicts that if multiple species are competing for a single limiting resource, then species, which survive at the lowest equilibrium resource level, outcompete all other species [20], [3]. In section 6 we obtain a complete description of parameters for survived species and establish the validity of the $R^*$ rule for systems with random parameters. We show that if the resources are limited and initially the number of species is sufficiently large then only species with the fitness which is close to maximal one can survive. In our model, the fitness is determined as the resource amounts available for an organism.

Finally, in section 7, we study sensitivity of those states with respect to a change of environmental parameters. This allows us to essentially extend recent results of [14]. Namely, not only the magnitude of environmental changes and their rates determine how much species will extinct but also the achieved biodiversity level, and some species parameters. For example, ecosystems where the species parameters are localized at some values are less stable than ecosystems with a large species parameter variation.

The basic notation

\[
x(t) = (x_1(t), \ldots, x_M(t)) \quad \text{the vector of species abundances}
\]
\[
v(t) = (v_1(t), \ldots, v_m(t)) \quad \text{the vector of resource abundances}
\]
\[
\mu_i, \gamma_i \quad \text{the mortality and the self-limitation constant of species } i
\]
\[
D_j, S_j \quad \text{the turnover rate and the supply of resource } v_j
\]
\[
e_{ij} \quad \text{the content of resource } j \text{ in species } i
\]
\[
\phi_i \quad \text{the specific growth rates of species } i
\]
\[
K_{ij} \quad \text{the half-saturation constant for resource } j \text{ of species } i, \text{ page 3}
\]
\[
(x_{eq}, v_{eq}) \quad \text{the special equilibrium state, page 4}
\]
2. Preliminaries

Given $x, y \in \mathbb{R}^n$ we use the standard vector order relation: $x \leq y$ if $x_i \leq y_i$ for all $1 \leq i \leq n$, $x < y$ if $x \leq y$ and $x \neq y$, and $x \ll y$ if $x_i < y_i$ for all $i$; $\mathbb{R}^n_+$ denotes the nonnegative cone $\{x \in \mathbb{R}^n : x \geq 0\}$ and for $a \leq b$, $a, b \in \mathbb{R}^n$ 

$$[a, b] = \{x \in \mathbb{R}^n : a \leq x \leq b\}$$

is the closed box with vertices at $a$ and $b$.

We consider the following system of equations:

$$\frac{dx_i}{dt} = x_i(\phi_i(v) - \mu_i - \gamma_i x_i), \quad i = 1, \ldots, M, \quad (1)$$

$$\frac{dv_k}{dt} = D_k(S_k - v_k) - \sum_{i=1}^M c_{ki} x_i \phi_i(v), \quad k = 1, \ldots, m. \quad (2)$$

Here $x = (x_1, x_2, \ldots, x_M)$ is the vector of species abundances and $v = (v_1, \ldots, v_m)$ is a vector of resource amounts, where $v_k$ is the resource of $k$-th type consumed by all ecosystem species, $\mu_i$ are the species mortalities, $D_k > 0$ are resource turnover rates, $S_k$ is the supply of the resource $v_k$, and $c_{ik} > 0$ is the content of $k$-th resource in the $i$-th species. The coefficients $\gamma_i > 0$ describe self-limitation effects [15], [11], [10].

We consider general $\phi_j$ which are bounded, non-negative and Lipshitz continuous

$$|\phi_j(v) - \phi_j(\tilde{v})| \leq L_j \|v - \tilde{v}\| \quad (3)$$

and

$$\phi_k(v) = 0, \quad \text{for all } k \text{ and } v \in \partial \mathbb{R}^m_+. \quad (4)$$

Furthermore, we shall assume that each $\phi_k(v)$ is a non-decreasing function of each variable $v_j$ in $\mathbb{R}^M_+$. This assumption means that the amount of $j$-th resource increases all the functions $\phi_l$ also increase.

Conditions (4) and (3) can be interpreted as a generalization of the well known von Liebig law, where

$$\phi_i(v) = r_i \min \left\{ \frac{v_1}{K_{i1} + v_1}, \ldots, \frac{v_m}{K_{im} + v_m} \right\} \quad (5)$$

where $r_i$ and $K_{ij}$ are positive coefficients, $i = 1, \ldots, M$. Here, $r_i$ is the maximal level of the resource consumption rate by $i$-th species and $K_{ij}$ is the half-saturation constant for resource $j$ of species $i$.

The Liebig law can be considered as a generalization of Holling functional response (Michaelis-Menten kinetics) for the case of many resources. It assumes that the species growth is determined by the scarcest resource (limiting factor). In particular, the Liebig law can be applied to ecosystem models for resources such as sunlight or mineral nutrients, for example, for plant ecosystems. For the case of a single resource $m = 1$ and $v = v_1 \in \mathbb{R}$ it reduces to the Holling response. In this case, a typical example of $\phi_i$ satisfying all above conditions is

$$\phi_i(v) = \frac{r_i v}{K_i + v}, \quad i = 1, \ldots, M. \quad (6)$$

For $\gamma_i = 0$ system (1), (2) was considered in the studies of the plankton paradox, see, for example, [7]. Following [15] and [10] we assume $\gamma_i > 0$ since it is known that self-limitation is essential for large ecosystem [2, 1] and plankton or plant ecosystems can induce effects leading to self-limitation. We complement system (1), (2) by non-negative initial conditions

$$x(0) = \bar{x}, \quad v(0) = \bar{v}, \quad (7)$$

where

$$\bar{x}_i > 0, \quad i = 1, \ldots, M, \quad \text{and} \quad 0 \leq \bar{v}_k \leq S_k, \quad k = 1, \ldots, m. \quad (8)$$
3. Estimates and equilibria

In this section, we study the stability and large time behavior of solutions to the Cauchy problem (1), (2) and (7). Using the standard partial order relations in \( \mathbb{R}^m \), we write \( v \leq w \) if \( v_i \leq w_i \) for each \( i \), and \( v \ll w \) if \( v_i < w_i \) for each \( i \). We also denote \( z_+ = \max\{z,0\} \).

3.1. Boundedness of solutions

Proposition 3.1. Solution \((x,v)\) of (1), (2) with initial data (8) is well defined for all positive \( t \), and it satisfies the estimates

\[
0 \leq x_i(t) \leq \frac{\bar{x}_i \exp(\bar{a}_i t)}{1 + \bar{x}_i \gamma_i \bar{a}_i^{-1} (\exp(\bar{a}_i t) - 1)} , \quad i = 1, \ldots, M ,
\]

where \( \bar{a}_i = \phi_i(S) - \mu_i \), and

\[
0 \leq v_i(t) \leq S_k (1 - \exp(-D_k t)) + \bar{v}_k \exp(-D_k t) , \quad k = 1, \ldots, m .
\]

Furthermore, if \( \phi_k(S) \leq \mu_k \) for some \( k \) then \( \lim_{t \to \infty} x_k(t) = 0 \).

In what follows, we make the following natural assumption:

\[
\phi_i(S) - \mu_i > 0 , \quad \text{for all } i = 1, \ldots, M .
\]

Indeed, if \( \phi_i(S) - \mu_i \leq 0 \) for a certain index \( i \) then according to Proposition 3.1 \( x_i(t) \to 0 \) as \( t \to \infty \), thus, species \( i \) will surely go extinct and therefore can be excluded from the analysis.

3.2. Equilibrium resource values and convergence to equilibria

Let \( E \) denote the set of nonnegative equilibrium points (stationary solutions) \((x,v)\) of (1)-(2). It is straightforward to see that \((0,S) \in E \). This point expresses the equilibrium resource availabilities in the absence of any species. Furthermore, it was shown in [10] that under assumption (11), for an arbitrary \((x,v) \in E \) such that \((x,v) \neq (0,S) \) there holds

\[
x > 0 \quad \text{and} \quad 0 \ll v \ll S .
\]

Among all equilibrium points in \( E \), we shall distinguish the special ones defined as follows: an equilibrium point \((x^{eq},v^{eq})\) is called special if \( v^{eq} \) is a solution of the fixed point problem

\[
D_k(S_k - v_k^{eq}) = F_k(v^{eq}) , \quad 1 \leq k \leq m ,
\]

where

\[
F_k(v) = \sum_{i=1}^{M} c_{ki} \phi_i(v) \phi_i(v) - \mu_i \),
\]

and \( x^{eq} \) is uniquely determined by

\[
x_i^{eq} = \frac{1}{\gamma_i} (\phi_i(v^{eq}) - \mu_i)_+ .
\]

Note that \( F_k \) can be interpreted as total consuming rates \( \frac{1}{\gamma_i} c_{ki} \phi_i(v) (\phi_i(v) - \mu_i)_+ \) over all the species \( \leq i \leq M \).

As a corollary of the monotonicity of \( \phi_i \), it can be shown that the set of special equilibrium points \((x^{eq},v^{eq})\) is nonempty for any choice of the fundamental parameters of the model, see [10] for the proof. If \( m = 1 \) then one can easily prove that there always exists a unique special point, see [11]. But, if \( m \geq 2 \) and \( D_i \) or \( \gamma_i \) are small enough, there can exist several special points. On the other hand, under some natural conditions, there exists a unique special equilibrium point. More precisely, we have the following result.
Theorem 3.2 (Corollary 7.2 in [10]). Assume that

\[ \rho := \max_{1 \leq i \leq m} \sum_{j=1}^{M} c_{ij} L_j (2\phi_j (S) - \mu_j) / D_i \gamma_j \leq 1 \]  

(15)

Then all the solutions \((x(t), v(t))\) of (1), (2) with positive initial data \(v(0) > 0, x(0) > 0\) converge, as \(t \to \infty\), to the unique special equilibrium point defined by (13) and (14).

In Section 3.2 we will see that the unique point \((x^e, v^e)\) is the right equilibrium point for the system (1)-(2), which attracts all trajectories. The proof of Theorem 3.2 is given in our recent paper [10]. Our approach is based on an iteration technique and two side estimates for period-two-points of nonincreasing maps and relies on the monotone properties of our system. More precisely, eliminating in an appropriate way the \(x\)-variables, we reduce the analysis to certain integral equations for \(v = (v_1, \ldots, v_m)\). It turns out that these integral equations give rise to a nonincreasing operator in an appropriate Banach space of functions \(0 \leq v \leq \bar{S}\). By the monotonicity, the solution \(v\) is estimated by the iterated sequences \(v^{(2n)}\) and \(v^{(2n+1)}\), which are shown to converge, say to limits \(v_{even}\) and \(v_{odd}\), respectively. The second part of the proof establishes the estimates on the difference \(v_{even} - v_{odd}\) in terms of \(\rho\) in (15) above. This implies that if the turnover rates \(D_i\) are large enough then the limits \(v_{even}\) and \(v_{odd}\) coincide, which yields the required stability result.

Alternatively, the main idea of the proof can be explained as follows. If the turnover rate \(D = \min_i \{D_i\}\) are large enough then our system has the standard structure typical for systems with slow/fast variables. More precisely, in that case the resources \(v_i\) evolve fast in time whereas the species abundances are slow variables. Using this property we make substitution \(v_i = S_i - \tilde{v}_i\), where \(\tilde{v}_i\) are new unknowns. This yields an a priori estimate \(|\tilde{v}_i| = O(D^{-1})\). Therefore, given \(x_i(t)\) we can solve the differential equations for \(v_i\) by iterations. The a priori estimates also imply that the first approximation for \(x_i\) can be determined by certain simplified equations which do not involve \(v\). Proceeding further, we get an approximation for \(v_i\) of order \(O(D^{-2})\), etc. This yields the convergence of the procedure by standard methods of theory of invariant manifolds for slow/fast systems.

4. Model with extinction threshold

4.1. Formulation of the model

System (1)-(2) does not take into account species extinctions due to extinction thresholds. To describe this effect, we follow [11] with certain simplifications. In order to describe species extinction we introduce small positive parameters \(X_{ext}^{(i)}\) being an extinction threshold and we will consider only solutions such that \(x_i(0) > X_{ext}^{(i)}\). Estimates of \(X_{ext}^{(i)}\) can be obtained by stochastic models, for example, [13], however, these models are rather complicated. The approach suggested below simplifies the problem and still allows us to obtain nontrivial effects.

Let \(S_e(t)\) denote the set of indices of those species which exist at the time \(t\) and let \(N_e(t)\) denote the cardinality of \(S_e(t)\). Then \(S_e(0) = \{1, 2, \ldots, M\}\) and \(N_e(0) = M\).

We say that \(x_k\) disappears at the moment \(t_*\) if

\[ x_k(t_*) = X_{ext}^{(k)} \quad \text{and} \quad x_k(t) > X_{ext}^{(k)} \quad \text{for} \quad t < t_* .\]

In this case we remove the index \(k\) from the set \(S_e(t)\), \(t \geq t_*\). The parameters \(X_{ext}^{(k)}\) can be interpreted as a thresholds for species abundances.

With modifications described above, equations (1) and (2) define the dynamics as follows. Within each time interval \((t_*, T_*\rangle\) between the subsequent species extinctions, the dynamical evolution of \(x_i(t)\) is determined by the system (1), (2). We obviously have

\[ S_e(t_2) \subset S_e(t_1), \quad 0 \leq t_1 \leq t_2, \]
therefore $N_e(t)$ is a piecewise constant decreasing function, hence there exist limits

$$S_e(t) \to S_e, \quad N(t) \to N_e, \quad \text{as } t \to +\infty,$$

where $N_e$ is the cardinality of the set $S_e$. Note that the set $S_e$ and its cardinality $N_e$ depend on the initial data as it is shown in [11]. By (16) there exists a time moment $T_e$ such that all extinctions have occurred and thus we can use Theorem 3.2 for the remained species. For $t > T_e$ system (1), (2) can be rewritten as follows:

\[
\frac{dx_i}{dt} = x_i(\phi_i(v) - \mu_i - \gamma_i x_i), \quad i \in S_e, \tag{17}
\]

\[
\frac{dv_k}{dt} = D_k(S_k - v_k) - \sum_{i \in S_e} c_{ki} x_i \phi_i(v), \quad k = 1, \ldots, m, \tag{18}
\]

where

\[
x_i(t) > X^{(i)}_{\text{ext}}, \quad \forall t > T_e. \tag{19}
\]

This system describes large time dynamics of ecosystem when all extinctions are finished. Note that the set of remaining species $S_e$ may be different for different initial data of original system (1), (2).

First let us consider the particular case of (17)-(18) is when all species disappear, i.e. $S_e = \emptyset$. Then (17)-(18) amounts to

\[
\frac{dv_k}{dt} = D_k(S_k - v_k) \quad k = 1, \ldots, m,
\]

hence the solution converges to the supply equilibrium state $(x, v) = (0, S)$. The dynamic in this case is trivial, therefore, we assume in what follows that $S_e \neq \emptyset$.

An analysis of the dependence of $S_e$ and $N_e$ on the initial data seems to be rather complicated, therefore, we consider instead the maximal possible number $N_{\text{max}}$ of species which may survive. More precisely, we define

\[
N_{\text{max}} = \max N_e \tag{20}
\]

where the maximum is taken over all possible sets $S_e \subset \{1, \ldots, M\}$ for which the problem (17)-(19) has a solution. We present some estimates of $N_{\text{max}}$ in section 5 below.

4.2. Dynamics of the model with extinction thresholds

To obtain equilibria for system (17), (18), we should take into account that $x_i(t) > X^{(i)}_{\text{ext}}$ for all $t > T_f$. Therefore, equations for equilibria take the form

\[
X_i(v^{eq}) = \frac{1}{\gamma_i} \left( \phi_i(v^{eq}) - \mu_i \right)_{+}, \quad \epsilon_i = \gamma_i X^{(i)}_{\text{ext}}, \tag{21}
\]

and

\[
D(S - v^{eq}) = F_{\text{ext}}(v^{eq}, b, K, p), \tag{22}
\]

where

\[
F_{\text{ext}}(v, b, K, p) = \sum_{i \in S_e} R_i(v, b, K, p). \tag{23}
\]

Here and in what follows, we denote by $z_{+, \delta}$ the cut-off function

\[
z_{+, \delta} = \begin{cases} 
0 & \text{if } z < \delta; \\
z & \text{if } z \geq \delta; 
\end{cases}
\]

Since the dynamics after the moment $T_f$ is completely determined by differential equations (17), (18), we obtain by Theorem 3.2:

**Corollary 4.1.** Suppose that $S_e$ is not empty and condition (15) holds. Let $(x, v)$ be solution of (17), (18) and (19). Then this solution converges, as $t \to \infty$, to an equilibrium point satisfied (21), (22), and (23).
5. Estimates of biodiversity

In the first three subsections of this section we derive general estimates of biodiversity which make no assumptions on large time behaviour of the system. In section 5.4, we obtain the biodiversity estimates which are asymptotically sharp. In the remaining part, we also establish estimates under assumption that there are not oscillating or chaotic regimes, and each trajectory converge to an equilibrium.

5.1. The general case

In the model with extinctions we are able to estimate the maximal biodiversity, i.e. the maximal possible value $N_c$ expressed by means of the ecosystem parameters. For this purpose we apply the averaging procedure similar to that considered in [11] for $m = 1$.

Let $f(t)$ be a continuous function which is uniformly bounded on $[0, +\infty)$. Then its $t$-average value $\langle f \rangle_t$ is defined by

$$\langle f \rangle_t = \frac{1}{t} \int_0^t f(s) ds.$$ 

Let $x = (x_1, \ldots, x_N), v = (v_1, \ldots, m)$ be a solution of (17)-(19). Applying the $t$-average to (17) and (18) and using the boundedness of $x$ and $v$, we obtain

$$\langle x_i \phi_i(v) \rangle_t - \mu_i \langle x_i \rangle_t - \gamma_i \langle x_i^2 \rangle_t = \xi_i(t)$$

and

$$D_k(S_k - \langle v_k \rangle_t) = \sum_{i \in S_k} c_{ki}(x_i \phi_i(v))_t + \tilde{\xi}_k(t),$$

where $\xi_i(t) = \frac{1}{t} \langle x_i(t) - x_i(0) \rangle, \tilde{\xi}_k(t) = \frac{1}{t} \langle v_k(t) - v_k(0) \rangle$. Since $x_i$ and $v_k$ are nonnegative and bounded from above, we obtain $\lim_{t \to +\infty} \xi_i(t) = \lim_{t \to +\infty} \tilde{\xi}_k(t) = 0$.

Next, since $x_i(t)$ is bounded from above and $x_i(t) > X_{ext}^{(i)} > 0$, we have

$$\eta_i(t) := \langle x'_i \rangle_t = \frac{1}{t} \int_0^t \frac{dx_i(s)}{x_i(s)} = \frac{1}{t} \ln \frac{x_i(t)}{x_i(0)} \to 0 \text{ as } t \to +\infty,$$

therefore dividing the left-hand and right-hand sides of (17) by $x_i(t)$ followed by the $t$-average we get

$$\langle \phi_i(v) \rangle_t = \mu_i + \gamma_i \langle x_i \rangle_t + \eta_i(t),$$

where $\eta_i(t) \to 0$ as $t \to +\infty$. Furthermore, by the Cauchy inequality we have $\langle x_i \rangle_t^2 \leq \langle x_i^2 \rangle_t$, hence we derive from (24) that

$$\langle x_i \phi_i \rangle_t \geq (\mu_i + \gamma_i X_{ext}^{(i)}(x_i) \langle x_i \rangle_t + \xi_i(t).$$

Relations (26) and (27) allow us to obtain a general estimate of consumed resources $v_k$ expressed only in the fundamental parameters of the main system (not involving $\gamma_i$ and $X_{ext}^{(i)}$).

Lemma 5.1. If the von Liebig law (5) holds, we have for sufficiently large $t$ and all $1 \leq k \leq m$

$$\langle v_k \rangle_t > V_k(S_k) := \max_{i \in S_k} \frac{\mu_i K_{ik}}{\gamma_i - \mu_i}.$$

Proof. Let $T > 0$ be chosen such that $|\eta_i(t)| < \gamma_i X_{ext}^{(i)}$ for all $t > T$. Next, note that the function $\phi_i(v)$ defined by (5) is concave as the minimum of concave functions. Therefore, combining Jensen’s inequality with (26) we obtain

$$\phi_i((v)'t) \geq \langle \phi_i(v) \rangle_t > \mu_i, \quad \forall t > T$$

which implies the desired estimate (28).
Remark 5.2. Note that in the case \( m = 1 \) one has
\[
\langle v \rangle_t > \bar{V} = \min_{i \in \{1, \ldots, M\}} \lambda_i,
\]
where
\[
\lambda_i = \frac{\mu_i K_i}{r_i - \mu_i}.
\]
The parameters \( \lambda_i \) represent break-even concentrations and appear in analysis of resource competition ecosystems as important species characteristics (see [5] and the references therein).

Now, combining (28) with (27) it follows from (25) that for large \( t \)
\[
D_k(S_k - V_k) \geq \sum_{i \in S_e} c_{ki} (\mu_i + \gamma_i X^{(i)}_{\text{ext}}) \langle x_i \rangle_t + \xi_k(t),
\]
where \( \xi_k(t) \to 0 \) as \( t \to +\infty \). Let us introduce the following averages:
\[
\theta_k(S_e) := \frac{1}{N_e} \limsup_{t \to \infty} \sum_{i \in S_e} c_{ki} (\mu_i + \gamma_i X^{(i)}_{\text{ext}}) \langle x_i \rangle_t,
\]
and also define
\[
\hat{\theta}_k = \min_{S_e \neq \emptyset} \theta_k(S_e), \quad \bar{V}_k = \min_{S_e \neq \emptyset} V_k(S_e),
\]
where we take the minima over all possible sets \( S_e \neq \emptyset \). Then (31) implies

**Proposition 5.3.** The number of survived species satisfies
\[
N_e \leq \min_k \frac{D_k(S_k - \bar{V}_k)}{\hat{\theta}_k}.
\]

Note that the latter estimate involves only the main observable fundamental ecosystem parameters. Furthermore, the obtained estimate is universal in the sense that it is valid without any assumptions on \( D_k \), the number of resources and the ecosystem dynamics.

5.2. Modifications of the main estimate

Estimate (25) can be simplified for small \( \gamma_i X^{(i)}_{\text{ext}} \ll \mu_i \). In that case, one has
\[
N_e \leq \min_k \frac{D_k(S_k - \bar{V}_k)}{\hat{\theta}_k},
\]
where
\[
\hat{\theta}_k = \min_{S_e \neq \emptyset} \frac{1}{N_e} \limsup_{t \to \infty} \sum_{i \in S_e} c_{ki} \mu_i \langle x_i \rangle_t.
\]
Taking into account that \( x_i(t) > X^{(i)}_{\text{ext}} \), we also have a rough estimate
\[
N_e \leq \min_k \frac{D_k(S_k - \bar{V}_k)}{Z_k},
\]
where
\[
Z_k = \min_{S_e \neq \emptyset} N_e^{-1} \sum_{i \in S_e} c_{ki} \mu_i X^{(i)}_{\text{ext}}.
\]
Now we want to estimate the biodiversity from below. We consider the case of a single resource \( m = 1 \). To this end, let us introduce the set
\[
\mathcal{B}_M = \left\{ i \in \{1, \ldots, M\} : \frac{r_i \bar{V}}{K_i + S} > \mu_i \text{ for all } i \right\},
\]
where \( \bar{V} \) is defined by (29). The cardinality of a set \( A \) will be denoted by \( |A| \).

**Proposition 5.4.**

a) Consider the dynamic without extinctions defined by (1) and (2), where \( \phi_i \) are defined by von Liebig's law (5). Then the number of species such that \( \liminf_{t \to +\infty} x_i(t) > 0 \) is not less than \( |\mathcal{B}_M| \).

b) In the model with extinctions, there holds \( N_e = 0 \) for some initial data (even if \( |\mathcal{B}_M| > 0 \)).

So, this claim shows in particular that models with and without extinctions have completely different behaviour. Remarkably, the obtained biodiversity estimate does not involve \( \gamma_i \), while the proof makes use the fact that \( \gamma_i > 0 \).

**Proof.** Consider a). We use (26) that gives
\[
\gamma_i(x_i)_t = \langle \phi_i(v) \rangle_t - \mu_i + \xi_i(t)
\]
where \( \xi_i(t) \to 0 \) as \( t \to \infty \). Since \( \frac{r_i}{K_i + S} > \frac{r_i}{K_i + S} v \), we find from (33) that
\[
\gamma_i(x_i)_t \geq \frac{r_i}{K_i + S} (v)_t - \mu_i + \xi_i(t).
\]
Now we use (29) and then a) is obtained from the last inequality as \( t \to \infty \).

Let us consider b). Let \( v(0) \) be small enough such that
\[
\phi_i(v(0)) - \mu_i = -2\kappa_i < 0
\]
holds for all \( i = 1, \ldots, M \). Note that \( v_l(t) < D_l S_l t + v_l(0) \). Then there exists \( \tau > 0 \) such that
\[
\phi_i(v(t)) - \mu_i < -\kappa_i < 0 \quad t \in (0, \tau).
\]
Therefore,
\[
x_i(t) < x_i(0) \exp(-\kappa_i t), \quad t \in (0, \tau)
\]
Therefore, if all \( x_i(0) \) are sufficiently close to \( X_{\text{ext}}^{(i)} \) all the species extinct.

To illustrate the dependence of the biodiversity the fundamental parameters, let us consider an example (see also Example 2 below). Let \( K_i = K \) for all \( i = 1, \ldots, M \) and \( a_i = \mu_i / r_i \). Then \( \lambda_i = K(1 - a_i)^{-1} \). Therefore, according to Proposition 5.4 all species \( x_j \) with
\[
a_j \left( 1 + \frac{S}{K} \right) < \min_{i=1, \ldots, M} (1 - a_i)^{-1}
\]
survive. The set of such species can have the maximal cardinality \( M \). Indeed, let \( a_i = \frac{1}{2} + \tilde{a}_i \), where \( 0 < \tilde{a}_i < \frac{1}{2} \) and let us assume that \( S/K < 1 \). Then the right hand side of (34) will be less than 2. Therefore, the species with the property
\[
\tilde{a}_i < 2 \left( 1 + \frac{S}{K} \right)^{-1} - \frac{1}{2}
\]
do certainly survive. Thus, if all \( \tilde{a}_i \) are small enough, all the species survive.
5.4. Three examples

We illustrate the obtained results by simple examples relating them to the (unified) neutral theory. Recall that neutrality means that at a given trophic level in a food web, species are equivalent in birth rates, death rates, dispersal rates and speciation rates, when measured on a per-capita basis. Mathematically this means that all basic parameters are almost equal, see [6]. In the all example we suppose that \( D_k \) are large.

**Example 1.** For large \( d = \min_k D_k \) system (13) becomes a fixed point problem with a contraction operator, therefore its solution \( v^\text{eq} \) is uniquely determined and

\[
v_k^\text{eq} = S_k - D_k^{-1} \sum_{i=1}^M c_{ki} \phi_i(S) \gamma_i^{-1} (\phi_i(S) - \mu_i)_+ + O(d^{-2}). \tag{35}
\]

By Theorem 3.2 all solutions \((x, v)\) of the system (1), (2) with the Cauchy data (8) have a limit

\[
v_k(t) \to S_k + O(d^{-1}), \quad k = 1, \ldots, m,
\]

\[
x_i(t) \to \frac{\phi_i(S) - \mu_i}{\gamma_i} + O(d^{-1}).
\]

So, if \( d \) is sufficiently large the system is persistent. Moreover, the number \( N_{\text{max}} \) is equal approximately to the cardinality

\[
\left| \left\{ i : \frac{\phi_i(S) - \mu_i}{\gamma_i} > X^{(i)}_{\text{ext}} \right\} \right|.
\]

**Example 2** (The case of a single resource). In the case \( m = 1 \) we set \( \phi_i = \frac{r_i u}{K + v} \) and suppose that

\[
\mu_i = \mu, \quad K_i = K, \quad r_i = r, \quad \gamma_i = \gamma, \quad \bar{C} = N^{-1} \sum_{i=1}^N c_i
\]

and \( X^{(i)}_{\text{ext}} = X_{\text{ext}} \). Let us introduce parameters

\[
p = \frac{\mu}{r}, \quad \tilde{S} = \frac{S}{K}, \quad \epsilon = \frac{\gamma X_{\text{ext}}}{r}, \quad R = \frac{KD\gamma}{r^2 C^2}.
\tag{36}
\]

We consider \( v^\text{eq} = Ku \), where \( u \) is to be determined. Then (13) becomes

\[
R(\tilde{S} - u) = N_x F(u), \tag{37}
\]

where

\[
F(u) = \frac{u}{1 + u} \left( \frac{u}{1 + u} - p \right)_{+, \epsilon}.
\]

Let

\[
u_{\epsilon} = \frac{p + \epsilon}{1 - p - \epsilon}. \tag{38}
\]

We seek a nontrivial solution of (37) such that \( u > u_{\epsilon} \). Equation (37) implies

\[
N_x(v^\text{eq}) \leq N_x(u) \leq N_x(v^\text{eq}) + 1, \tag{39}
\]

where

\[
N_x(v) = \left\lfloor \frac{R(S - v)(K + v) - \bar{C} v}{K v (\frac{K + v}{K + v} - p)_{+, \epsilon}} \right\rfloor \tag{40}
\]

and \( \lfloor x \rfloor \) is the floor of \( x \). Note that the function \( N_x(v^\text{eq}) \) is decreasing in \( v^\text{eq} \). Then since \( u > u_{\epsilon} \), relations (38) and (39) allows us to conclude that the maximal possible biodiversity \( N_{\text{max}} \) satisfies

\[
N_x(K u_{\epsilon}) < N_{\text{max}} < N_x(K u_{\epsilon}) + 1. \tag{41}
\]

In the Section 6 we shall see that this maximum of biodiversity is realizable for some initial data.
Example 3 (The multi-resource case). We assume that \( m \geq 2 \) and that the ecosystem is in an equilibrium state defined by (21), (13) and (23). We also assume that we are in the neutral position, i.e.

\[
K_{ki} = K, \quad r_i = r, \quad \mu_i = \mu, \quad \gamma_i = \gamma, \quad X_{\text{ext}} = X_{\text{ext}}^{(i)}.
\]

Then setting \( \phi(z) := \frac{r z K + z}{K + z} \) we obtain

\[
\phi_i(v) = \min_k \phi(v_k) = \phi(w),
\]

where \( w := \min_k v_k = v_{k^*} \). Then the equilibrium abundances and resources are determined respectively by

\[
x_i(w) = \gamma^{-1}(\phi(w) - \mu) + \gamma X_{\text{ext}}, \quad 1 \leq i \leq N_e,
\]

\[
v_{k^*}^{\text{eq}}(w) = \gamma^{-1}D_k \sum_{i=1}^{N_e} c_{k,i} \phi(w)(\phi(w) - \mu) + \gamma X_{\text{ext}}, \quad 1 \leq k \leq m.
\]

Since \( w = v_{k^*}^{\text{eq}}(w) = v_{k^*} \), we obtain

\[
w = \gamma^{-1}D_k \sum_{i=1}^{N_e} c_{k^*,i} \phi(w)(\phi(w) - \mu) + \gamma X_{\text{ext}}.
\]

The system (44), (45) and (46) determines an equilibrium state depending on the index \( k^* \in \{1, 2, \ldots, m\} \).

For any fixed \( k^* = 1, 2, \ldots, m \), we solve (44), (45) and (46). If \( v_{k^*}^{\text{eq}} < w \) is valid for all \( k \neq k^* \) then \( k^* \) is found.

Using change of the variables \( w = K u \), where \( u \) is a new variable, we obtain from (46) a similar relation (37) as in Example 2, where all parameters but \( R \) are defined by (36), and \( R = KD_k \gamma r^{-2} \bar{C}^{-1}_{m^*} \), where

\[
\bar{C}_{m^*} = M^{-1} \sum_{i=1}^{M} c_{k^*,i}.
\]

Then

\[
N^*(w) \leq N_e \leq N^*_e(w) + 1,
\]

where \( N(v) \) is defined by (40).

6. Asymptotically sharp estimate of biodiversity for systems with random parameters

In the remaining part of the paper we consider ecosystems with random parameters for large values of \( M \). Moreover, we suppose that the system is in an equilibria state, i.e. oscillating large time regimes are absent.

First let us suppose that at the initial moment there are \( M \gg 1 \) species with different (possibly random) parameters and that the resource supplies \( S_k \) are limited. We are going to address the following problem:

How many species \( N_e \) will survive?

It is clear that \( N_e \) is a priori bounded by \( M \). Below we obtain an asymptotically sharp estimate of \( N_e \).

We shall assume that \( m = 1 \) and the ecosystem has a globally convergent equilibrium state, \( v = v^{\text{eq}} \). We also assume that \( \phi_i \) are defined by the von Liebig law (5). Then, if the \( i \)-th species is survived for all times \( t > 0 \), we have

\[
\frac{r_i v^{\text{eq}}}{K_i + v^{\text{eq}}} - \mu_i > \gamma_i X^{(i)}_{\text{ext}}.
\]

Consequently,

\[
v^{\text{eq}} > \beta_i, \quad \beta_i = \frac{(\mu_i + \gamma_i X^{(i)}_{\text{ext}})K_i}{r_i - \mu_i - \gamma_i X^{(i)}_{\text{ext}}},
\]
and
\[ r_i > \mu_i + \gamma_i X_{\text{ext}}^{(i)}. \] (50)

Note also that for \( \gamma_i = 0 \) or \( X_{\text{ext}}^{(i)} = 0 \) the numbers \( \beta_i \) coincide with the parameters \( \lambda_i \) defined by (30). They determine survival of species in classical resource competition models without extinction thresholds and without self-limitation [5].

We introduce parameters
\[ \eta_i = D^{-1} c_i (\gamma_i X_{\text{ext}}^{(i)} + \mu_i) X_{\text{ext}}^{(i)}, \quad i = 1, \ldots, M \] (51)
and describe the choice of random values of the model parameters. Under assumptions (5), the main parameters of our model are the coefficients \( \mu_i, \gamma_i \) and the vectors \( K^{(i)} = (K_{i1}, \ldots, K_{im}) \), where \( i = 1, \ldots, M \), and \( r = (r_1, \ldots, r_M) \). As before, we consider \( U_M = (\mu, K, r, c, \Gamma) \in \mathbb{R}^{2M(m+2)} \). Note that \( c_i \) are species specific parameters which not necessary to be included in analysis, so we suppose that \( c_i \) are fixed.

Our basic assumption to \( \xi \) then can be formulated as follows:

**Assumption 6.1.** The probability density function \( \xi \) is a continuous function with a compact support in \( \mathbb{R}_+^n \). Moreover, as \( N \to \infty \) the parameters \( \beta_i \) are distributed on \((0, +\infty)\) with the smooth probability density \( \rho_0(\beta) \) such that
\[ \text{supp } \rho_0(\beta) \subset (\beta_{\text{min}}, \beta_{\text{max}}). \] (52)

The parameters \( \eta_i \) are distributed on \((0, +\infty)\) with a continuous probability density \( \rho_1(\eta) \). The densities \( \rho_0 \) and \( \rho_1 \) are mutually independent.

From Assumption 6.1 it follows that the function \( \xi \) is positive on \( S_{\xi} \), where \( S_{\xi} \) is an open bounded set. Assumption 6.1 also yields that the mortality rates do not approach zero and resource consumption is restricted. It is supposed that initial data \( \bar{x}_i = x_i(0) \) are random mutually independent with the density distribution
\[ \bar{x}_i \in \mathcal{X}(\bar{X}, \sigma_X) \]
with the mean \( \bar{X} \) and the deviation \( \sigma_X \). The random assembly of the species defines an initial state of the ecosystem for \( t = 0 \).

Let us order \( \beta_i \) so that
\[ \beta_{\text{min}} \leq \beta_1 \leq \beta_2 \leq \ldots \leq \beta_M \leq \beta_{\text{max}}. \]

Then
\[ \beta_{N_e} < \beta_{N_e+1}. \]

Therefore, we obtain
\[ \beta_{N_e+1} > S - D^{-1} \sum_{i=1}^{N_e} c_i \frac{r_i v_{\text{eq}}}{K_i + v_{\text{eq}}} (\frac{r_i v_{\text{eq}}}{K_i + v_{\text{eq}}} - \mu_i) \gamma_i^{-1}, \] (53)
\[ \beta_{N_e} < S - D^{-1} \sum_{i=1}^{N_e} c_i \frac{r_i v_{\text{eq}}}{K_i + v_{\text{eq}}} (\frac{r_i v_{\text{eq}}}{K_i + v_{\text{eq}}} - \mu_i) \gamma_i^{-1}, \] (54)
where by Assumption 6.1 one has that \( \delta_{\beta} = \beta_{N_e+1} - \beta_{N_e} = O(M^{-1}) \) as \( M \to +\infty \). Therefore, the last two inequalities are asymptotically exact.

**Lemma 6.2.** Let us define the probability \( \Pr_{\beta} \) by
\[ \Pr_{\beta} = \text{Prob} \{ \beta_n - \beta_{\text{min}} < M^{-1/3} \} \]
Then for sufficiently large \( M \)
\[ \Pr_{\beta} > 1 - C_n \exp(-c_n M^{-1/6}), \]
where \( C_n, c_n \) are positive constants.
Proof. Let us consider the probability $\Pr_{k, \delta}$ that a random sample consisting of $M$ numbers $\beta_i$ containing exactly $k$ numbers within the interval $J = [\beta_{\min}, \beta_{\min} + \delta]$, where $\delta$ is a small positive number. The probability that a random $\beta_i$ distributed according to the density $\rho_0$ lies within $J$ is

$$p_\delta = \int_{\beta_{\min}}^{\beta_{\min} + \delta} \rho_0(s)ds.$$ 

Since $\rho_0$ is smooth, the probability can be estimated as $p_\delta < c\delta^2$. Let us define

$$\Pr_{k, \delta} = \binom{M}{k} p_\delta^k (1 - p_\delta)^{M-k}.$$ 

Then

$$\Pr_{k, \delta} < C_k(Mp_\delta)^k \exp(-0.5Mp_\delta),$$

where the constants $C_k > 0$ do not depend on $M$. We set $\delta = M^{-1/3}$. Then

$$\Pr_{k, \delta} < C_k M^{-k/6} \exp(-c(k)M^{-1/6}). \quad (55)$$

We observe that

$$\Pr_{\beta} = 1 - \sum_{k=1}^{n} \Pr_{k, \delta} > 1 - n \max_{k \in \{1, \ldots, n\}} \Pr_{k, \delta}. \quad (56)$$

For fixed $n$ and $M$ large enough one has

$$\max_{k \in \{1, \ldots, n\}} \Pr_{k, \delta} = \Pr_{n, \delta}.$$ 

Combining this with (55) and (56) yields that for sufficiently large $M$

$$\Pr_{\beta} > 1 - n\Pr_{n, \delta} > 1 - C_n(M)^{-n/6} \exp(-c_nM^{-1/6}).$$

The latter estimate proves (6.2). \qed

Proposition 5.3 shows that $N_e \ll M$ and $\rho_0$ is a smooth density. Therefore, by Lemma 6.2 we conclude that

$$\beta N_e - \beta_{\min} < M^{-1/3}$$

and

$$\left( \frac{r_i v_{eq}}{K_i + v_{eq}} - \mu_i \right) = X_{\text{ext}}^{(i)} + O(M^{-1/3}),$$

with a probability exponentially close to 1 for large $M$. This yields the following relation which is asymptotically sharp:

$$\beta_{\min} + \sum_{i=1}^{N_e} \theta_i = S + O(M^{-1/3}).$$

Since the densities $\rho_0$ and $\rho_1$ are mutually independent, the sum in the left hand side of the last equation can be replaced by $N_e(\theta)$, where $\langle \theta \rangle = E\theta$ is the averaged value of $\theta$. Finally one has

$$N_e = (S - \beta_{\min})(\theta)^{-1} + O(M^{-1/3}). \quad (57)$$

The latter estimate considerably refines our previous result [11]. Moreover, we conclude that the final state of ecosystem originally consisting of many species with random parameters can be described by the so-called $R^*$ rule. The essential parameters $\beta_i$ are well localized in a narrow domain that follows from (53) and (54) (see Fig. 1) that confirms the $R^*$ rule. Recall that the $R^*$ rule (also called the resource-ratio hypothesis) is a hypothesis in community ecology that attempts to predict which species will become dominant as the result of competition for resources. It predicts that if multiple species are competing for a single limiting
resource, then species, which survive at the lowest equilibrium resource level, outcompete all other species [20]. Note that a generalized resource ratio value $\beta_i$ for small $\gamma_i X_{\text{ext}}^{(i)}$ is

$$\beta_i \approx \lambda_i,$$

where $\lambda_i$ are defined by (30), and it involves the mortality, sharpness of consuming rates, and consuming rates. Note, however, that the proof of (57) cannot be extended for $m > 1$.

To conclude this section, let us remark that (57) improves (32). Indeed, $N_e$ from (57) satisfies (32). Moreover, a difference between those estimate is that in (57) the nominator $S$ is replaced by $S - \beta_{\text{min}}$, therefore, for large resource supply these estimates coincide.

7. Extinctions and mass extinctions

7.1. Mass extinctions

Let us revisit our Examples 1 and 2 above, which describe the localized case (Assumption 6.1), where parameters of all species are localized in a narrow domain that consistent with the $R^*$-rule. Note that the nontrivial solution $u \neq 0$ of eq. (37) exists under condition $u_e < \tilde{S}$ thus

$$\frac{\mu + \gamma X_{\text{ext}}}{r - \mu - \gamma X_{\text{ext}}} < S/K.$$

The violation of this condition leads to a mass extinction, when all the species disappear. In [11], the following localization effect is described: in a long time evolving species population, which was randomly assembled at the initial moment (see Assumption 6.1 above), all species parameters converge to a limit value. Then one can show that this localized population state has an interesting property:

**All species die together:** As a result of a long evolution, initially randomly assembled population approaches to a neutral fitness invariant state, where, if an extinction occurs then the extinction is a mass extinction, i.e. all species die simultaneously.

So, we conclude that
1. extinctions are stronger if the variations of species parameters are smaller, i.e. localization of parameters is higher;
2. for well localized parameters ($\sigma_\mu$ and $\sigma_r$ are small) there is a critical domain of parameter values when a small variation in the resource supply $S_k$ can lead to a mass extinction.

These properties can be illustrated by Fig. 1.

We assume $m = 1$ and that coefficients $c_i, r_i, \gamma_i$ and $\mu_i$ satisfy

$$C_- r < r_i < C_+ r, \quad C_- c < c_i < C_+ c, \quad 1 \leq i \leq M, \quad (58)$$

$$C_- \gamma < \gamma_i < C_+ \gamma, \quad C_- \mu < \mu_i < C_+ \mu, \quad 1 \leq i \leq M \quad (59)$$

where $a, c, \gamma, r$ are characteristic values of the corresponding coefficients, $C_\pm$ are positive constants independent of $M, r, c, \gamma, \mu$.

Let us introduce the stress parameter by

$$P_{\text{stress}} = \frac{cr^2}{\gamma DS}$$

Let us find a relation between that parameter and the biodiversity robustness, which we define as a coefficient $R_b$ in the relation

$$\frac{\Delta N_e}{N_e} = R_b \frac{\Delta S}{S}, \quad (60)$$

where $\Delta S < 0$ is a small variation of the resource supply $S$ caused for instance by a climate change, and $\Delta N_e \leq 0$ is the corresponding variation of the number of coexisting species $N_e$. We suppose that relation (57) is fulfilled. Then comparing (57) and (60) we see that

$$\langle \theta \rangle = M^{-1} \sum_{i=1}^{M} \theta_i,$$

where $\theta_i$ are defined by (51). By (51) we note that in the case of large biodiversity $N_e \gg 1$ the coefficient $\langle \theta \rangle$ of same order that $S P_{\text{stress}}$. In fact, if all $r_1, \gamma_i$ and $\mu_i$ of the same order (as it was supposed above, in (58) and (59)), then $X_{\text{ext}}$ has order $r/\gamma$. Substituting this relation in (51), we obtain that $R_b$ has the same order $S P_{\text{stress}}$. Note that $P_{\text{stress}}$ is a dimensionless parameter.

8. Conclusions

The human activity affects ecosystems restricting their resources and producing climatic changes. The key question is about consequences of that activity, it will be an abrupt change of biodiversity comparable with famous mass extinctions such as the end-Permian extinction (252 million years ago (Ma)), and even more severe the Phanerozoic (the past 542 Ma), or we will observe a relatively smooth decline of biodiversity.

The history of the Earth system show that some changes were gradual, but others were sharp and produced catastrophic mass extinctions. To understand that wait us in Future we should investigate ecosystem biodiversity, find key factors affecting this biodiversity and estimate the sensitivity of ecosystems with respect to environmental parameters.

A number of works are devoted to biodiversity problem beginning with [21] (see, for example, [4, 1, 9, 20, 7, 8] this list does not pretend to be complete). However, mathematical methods developed up to now, does not allow us to obtain explicit estimate of ecosystem biodiversity via the fundamental and experimentally measurable ecosystem parameters. The main difficulty is competitive exclusion principle. According to [5] for the case of one fixed resource supply we obtained two situations. The species survival depends on "break-even" parameters $\lambda_i$ (see also (30) below). If $\lambda_1$ is less than all the rest $\lambda_i$ only the species number 1 survives. To obtain coexistence of $m$ species observed in many natural resource competition ecosystems ([9]) we must set $\lambda_1 = \lambda_2 = \ldots = \lambda_m$, where we, however, can take $m$ in an arbitrary way (only to be less than general species number). To get around this difficulty a number of different approach were suggested, for example, dynamical chaos in systems with more than 2 resources [7, 8], to take into account temporal
variations of parameters etc. (see for example [17] for an overview) but these ideas does not permit us to obtain an explicit analytic estimates for the number of coexisting species.

In this paper, we develop further two relatively new ideas: namely we take into account weak self-limitation effects [15] and extinction thresholds [11]. Although the modified models seem to be more sophisticated, these effects allow us to regularize the problem mathematically even in the case of a single resource and also to obtain explicit biodiversity estimates for diverse scenarios.

We also extend results [14] and show that for plant or plankton systems, the magnitude of the future catastrophe depends not only on the level of climate variations. The structure of ecosystems also influences the number of species that go to extinction. We establish estimates of biodiversity via the system parameters such as the mortality rate, the consuming rate, teh sharpness of consuming rate, self-limitation and the critical species abundance. Furthermore, we show that the ecosystems where these parameters are well-located are less stable that the ecosystems with large variations in these parameters. We also investigate how biodiversity depends on structure climate-ecosystem interactions.

In summary, or main results are:

1. The dynamics of model without extinctions is determined for large resource turnovers: we show that all trajectories converge to a unique equilibrium, system has no memory and forgets initial data completely.

2. For large resource turnovers, the dynamics of the model with extinctions is stable in a weaker sense: any trajectory goes to an equilibria which now may depend on the initial data. Thus, the ecosystem has memory and the final equilibria depend on initial data.

3. For models with extinctions, the ecosystem biodiversity can be explicitly estimated by a relation involving only measurable parameters (turnover and mortality rates, resource supplies and the species content coefficients). This estimate is asymptotically sharp under certain natural assumptions and in the case when the neutral theory correctly describes the ecosystem state. We show also that such a situation naturally occurs when the ecosystem is under stress, i.e. originally there exists species with randomly distributed parameters and the most of them disappear as a result of resource limitations.

4. In the stress situation, we also show that the final state of the system (after extinctions) can be determined according to the \( R^* \) rule.

5. The ecosystem robustness is investigated and conditions for mass extinctions are obtained. The robustness depends, in particular, on the dimensionless stress parameter introduced in [11]. Systems with a large stress parameter is less sensitive with respect to resource decrease, however, if an extinction is happened. Such an event is catastrophic and destroys an essential part of that ecosystem.

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