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.

1. Introduction

Existence and stability of large foodwebs, where many species share a few of resources, is one of key problems in ecology (Hardin, 1960; Hutchinson, 1961; Volterra, 1990) as well as extinctions and mass extinctions in such systems under climate changes (Rothman, 2017). In this paper, we consider the model initiated in Kozlov et al. (2017a, 2016) 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 Huisman and Weissing (1999) 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 (Hsu, 2005; Smith and Waltman, 1995; Tilman, 1980) 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 (Hardin, 1960; Hutchinson, 1961)) has received a great attention in past decades (Roy and Chattopadhyay, 2007; Sommer and Worm, 2002). 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 (Roy and Chattopadhyay, 2007; Sommer and Worm, 2002). 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 (Huisman and Weissing, 1999) but extend that model in the two aspects. First, we take into account self-limitation effects (which are important for plankton populations (Roy and Chattopadhyay, 2007) and to explain stability of large foodwebs (Allesina, 2012; Allesina and Tang, 2012)). Roughly speaking when we introduce a weak self-limitation we replace equations of Maltus type on Verhulst type equations. Second, following (Kozlov et al., 2016) we take into account species extinction thresholds, however, in contrast to (Kozlov et al. 2016); Sudakov et al. (2017) 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

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earlier in Kozlov et al. (2017a,b) 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 holds 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 (Fisher et al., 1999; Tilman, 1982). 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 Rothman (2017). 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

$x(t) = (x_1(t), ..., x_M(t))$	the vector of species abundances
$v(t) = (v_1(t), ..., v_m(t))$	the vector of resource abundances
μ_i, γ_i	the mortality and the self-limitation constant of species i
D_j, S_j	the turnover rate and the supply of resource v_j
c_{ij}	the content of resource j in species i
ϕ_i	the specific growth rates of species i
K_{ij}	the half-saturation constant for resource j of species i, page 4
(x^{eq}, v^{eq})	the special equilibrium state, page 5
$X_{ext}^{(i)}$	the extinction threshold of species i, page 6

$N_e(t)$	the number of species which exist at the time t, page 7

2. Preliminaries

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

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

is the closed box with vertices at a and b.

We consider the following system of equations:

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

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

Here $x = (x_1, x_2, ..., x_M)$ is the vector of species abundances and $v = (v_1, ..., v_m)$ is a vector of resource amounts, where v_k is the resource of kth type consumed by all ecosystem species, μ_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 kth resource in the ith species. The coefficients $\gamma_i > 0$ describe self-limitation effects (Kozlov et al., 2017a; 2016; Roy and Chattopadhyay, 2007).

We consider general ϕ_j which are bounded, non-negative and Lipshitz continuous

$$|\phi_j(v) - \phi_j(\tilde{v})| \le L_j \|v - \tilde{v}\| \tag{3}$$

and

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

We use the norm notation $\|x\| = \max_{1 \le i \le m} |x_i|$.

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 as the amount of jth resource increases all the functions ϕ_l also increase.

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

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

where r_i and K_{ij} are positive coefficients, $i = 1, ..., M$. Here, r_i is the maximal level of the resource consumption rate by ith 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 ϕ_i satisfying all above conditions is

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

For $\gamma_i = 0$ system (1), (2) was considered in the studies of the plankton paradox, see, for example, Huisman and Weissing (1999). Following Roy and Chattopadhyay (2007) and Kozlov et al. (2017a) we assume $\gamma_i > 0$ since it is known that self-limitation is essential for large ecosystem (Allesina, 2012; Allesina and Tang, 2012) and plankton or plant ecosystems can induce effects leading to self-limitation. We complement system (1), (2) by non-negative initial conditions

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

where