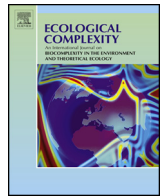




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Original Research Article

## Large ecosystems in transition: Bifurcations and mass extinction

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### ABSTRACT

We propose a model of multispecies populations surviving on distributed resources. System dynamics are investigated under changes in abiotic factors such as the climate, as parameterized through environmental temperature. In particular, we introduce a feedback between species abundances and resources via abiotic factors. This model is apparently the first of its kind to include a feedback mechanism coupling climate and population dynamics. Moreover, we take into account self-limitation effects. The model explains the coexistence of many species, yet also displays the possibility of catastrophic bifurcations, where all species become extinct under the influence of abiotic factors. We show that as these factors change there are different regimes of ecosystem behavior, including a possibly chaotic regime when abiotic influences are sufficiently strong.

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## 1. Introduction

Models of ecosystems form an important class of dynamical systems generating complex dynamics, bifurcations and strange attractors (Ulanowicz and Kemp, 1979). However, modeling these large systems is made difficult by rapid, large scale biological evolution and gaps in observations to use for comparison. Also, there is uncertainty in how to set up reliable experiments on such ecosystems.

Recent observations have shown that climate change may be a leading factor influencing ecosystem behavior (Walther, 2010). Large multispecies marine ecosystems are sensitive indicators of climate change (Doney et al., 2012; Kedra et al., 2015). As a key part of the global ecosystem, they influence climate feedback processes and possible tipping points (Selkoe et al., 2015). A well studied example is the ocean ecosystem, where phytoplankton are the main resource for many species. Phytoplankton populations play an important role in the dynamics of the climate system through the oceanic carbon cycle – by removing about half of all carbon dioxide from the atmosphere during photosynthesis (Field et al., 1998). Previous studies (Arhonditsis and Brett, 2004; Travers et al.,

2007) have shown that phytoplankton communities respond to climate warming through changes in diversity and productivity. However, it was recently determined (Toseland et al., 2013) that changing the climate temperature directly impacts the chemical cycles in plankton, affecting the system as much as nutrients and light.

We consider here a model of a large ecosystem where many species share few resources. It extends the model of phytoplankton species competition in Huisman and Weissing (1999), by taking into account that the resources depend on environmental factors, in particular, climate, as well as self-limitation and competition effects. Our aim is to explore the connections among complexity of the temporal behavior, biodiversity, and the structure of the climate–ecosystem interaction.

Note that competition may occur as a result of the following mechanism (Roy and Chattopadhyay, 2007). There are a number of species of phytoplankton which have the ability to produce some toxic or inhibitory compounds. These toxic materials compensate for the competitive disadvantages among phytoplankton species which leads to self-limitation effects. Moreover, resource levels may depend on the environment via temperature or greenhouse gas concentration.

Many mathematical models (Hofbauer and Sigmund, 1988; Takeuchi, 1996; Zeeman, 1995) show that only a single species can survive in an ecosystem for certain fixed parameters. Biologically,

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this is the competitive exclusion principle. In the framework of the phytoplankton model, it is known as the so-called *plankton paradox* studied in many interesting works (Hutchinson, 1961; Tilman, 1977; Huisman and Weissing, 1999; Irigoien et al., 2004; Ryabov et al., 2015). In particular, it is sometimes observed in nature that numerous species can coexist while depending on the same resource, even though competition tends to exclude species. In fact, in contrast to the exclusion principle, we observe here the coexistence of many plankton species sharing the same niche and resources. Numerical simulations (Hutchinson, 1961; Tilman, 1977; Huisman and Weissing, 1999) have shown that in such systems chaos and unpredictable behavior occur. In Hsu et al. (1977) and Smith (1981) it was shown that temporal variability of the nutrient supply can lead to coexistence of species.

The environment may alter the distribution and abundance of the species in a population. Such effects have been studied in terms of internal processes within the population, like competition for resources and conditions for chemical reactions. However, current models have not been linked to feedback with the environment. Feedback between a population and the environment can occur as a result of changes in abiotic factors such as temperature, nutrient concentrations, and light intensity.

The main results of this paper show that the population dynamics depends sharply on feedback with the environment. For simplicity, hereinafter we refer to this as *climate–ecosystem feedback*. If the abiotic factor is temperature  $T$ , for example, then it is natural to talk about the feedback between an ecosystem and the climate system, which can be parameterized as a function of a rate of change of the resource supply with respect to temperature. If that feedback is negative – where species abundance decreases resources – then an ecosystem can support a number of species and the dynamics is relatively simple (non-chaotic and non-periodic). If the feedback is positive – where species abundance increases resources – then for a sufficiently large feedback level there are possible mass extinctions which occur suddenly, and moreover, there are possible chaotic or periodic dynamics.

The paper is organized as follows. In the next section we formulate the standard model of species coexistence and the extended model, which takes into account climatic factors. Further, in Section 3 we prove a general assertion on the existence of an attractor for this model. In Section 4 it is shown that for large turnover rates  $D$  the system admits an asymptotic solution and, under additional assumptions, can be reduced to the Lotka–Volterra model (Vakulenko, 2013; Kozlov and Vakulenko, 2013). This model is well studied (Hofbauer and Sigmund, 1988; Takeuchi, 1996; Zeeman, 1995; Van den Driessche and Zeeman, 1998) and known results allow us to describe the influence of climate and climate warming in large ecosystems (see Section 5). In Section 6, for the case of a single resource, we show that the global attractor consists of equilibria and derive an equation for the species abundances. This investigation is aimed at describing the influence of climate on biodiversity.

## 2. Models of large ecosystems

### 2.1. Standard model

Consider the following model of an ecosystem with  $N$  species, which extends the model of resource competition in Huisman and Weissing (1999):

$$\frac{dx_i}{dt} = x_i \left( -r_i + \phi_i(v) - \sum_{j=1}^N \gamma_{ij} x_j \right), \quad 1 \leq i \leq N, \quad (1)$$

$$\frac{dv}{dt} = D(S-v) - \sum_{j=1}^N c_j x_j \phi_j(v), \quad (2)$$

where

$$\phi_j(v) = \frac{a_j v}{K_j + v}, \quad a_j, K_j > 0, \quad (3)$$

is the specific growth rate of species  $j$  as a function of the availability  $v$  of the resource (also known as Michaelis–Menten’s function),  $x_i$  are species abundances,  $r_i$  are the species mortalities,  $D$  is the resource turnover rate,  $S$  is the supply concentration of the resource, and  $DS$  can be interpreted as the supply rate. The dynamics of the species depend on the availability of the resource, which in turn depends on the rate of resource supply and the amount of resource used by the species.

The coefficient  $c_j$  is the content of the resource in the  $i$ th species. The constants  $c_j$  define how different species share resources. Note that if all  $c_j = 0$  then the equation for  $v$  becomes trivial and  $v(t) \rightarrow S$  for large times  $t$ , i.e., the resource equals the resource supply. We consider this system in the non-negative cone:  $x \in \mathbf{R}_+^N$ ,  $v > 0$ , where  $\mathbf{R}_+^N = \{x : x_j \geq 0, \forall j\}$ . The coefficients  $a_i$  are specific growth rates and the  $K_i$  are self-saturation constants.

We assume that the  $\gamma_{ii} > 0$ . The terms  $\gamma_{ii}x_i$  define self-regulation of species populations that restricts their abundances. In the case  $\gamma_{ij} > 0$  with  $i \neq j$  these terms describe competition between species. These effects can appear as a result of an ability to produce some toxic or inhibitory compounds (Roy and Chattopadhyay, 2007). However, we admit the possibility of mutualistic interactions, in which case  $\gamma_{ij} < 0$ . Assumptions on  $\gamma_{ij}$  are formulated below, at the beginning of Section 3.

For the case of  $M$  resources, we have the more complicated equations

$$\frac{dx_i}{dt} = x_i \left( -r_i + \phi_i(v) - \sum_{k=1}^N \gamma_{ik} x_k \right), \quad 1 \leq i \leq N, \quad (4)$$

$$\frac{dv_j}{dt} = D_j(S_j - v_j) - \sum_{k=1}^N c_{jk} x_k \phi_k(v), \quad 1 \leq j \leq M, \quad (5)$$

where  $v = (v_1, v_2, \dots, v_M)$ , and the  $\phi_j(v)$  are smooth functions. We consider general  $\phi_j$  satisfying the conditions

$$\phi_j(v) \in C^1, \quad 0 \leq \phi_j(v) \leq C_+, \quad (6)$$

where  $C_+ > 0$  is a positive constant, and

$$\phi_k(v) = 0, \quad \forall k, \quad v \in \partial \mathbf{R}_+^M, \quad (7)$$

where  $\partial \mathbf{R}_+^M$  denotes the boundary of the cone  $\mathbf{R}_+^M = \{v : v_j \geq 0, \forall j\}$ . Condition (6), in particular, means that  $C_+$  forms a uniform upper bound for the  $\phi_j(v)$ . We assume that  $c_{jk} > 0$ . This model is widely used for primary producers like phytoplankton, and can also be applied to describe competition for terrestrial plants (Tilman, 1977).

When  $\gamma_{ij} = 0$  for all  $i, j$  this system is equivalent to those in works where the plankton paradox is studied (Huisman and Weissing, 1999). The choice  $\gamma_{ii} = \gamma_i > 0$  and  $\gamma_{ij} = 0$  for  $i \neq j$  allows us to take into account self-limitation effects, which is important in these systems, as shown by Roy and Chattopadhyay (2007).

Below we use the notation  $f_+ = \max\{f, 0\}$ . We define the scalar product in  $\mathbf{R}^N$  together with the corresponding norm by

$$\langle f, g \rangle_C = \sum_{j=1}^N C_j f_j g_j, \quad \|f\|_C^2 = \langle f, f \rangle_C. \quad (8)$$

This scalar product is defined for  $N$ -component vectors and depends on non-negative coefficients  $C_j > 0, j = 1, \dots, N$ .

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