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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):

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

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

where

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

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 moralities, 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 ith 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 $v(t) \to S$ 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 γ_{ij} are formulated below, at the beginning of Section 3.

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

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

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

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

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

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

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

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

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

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

2.2. Extended standard model with climate influence

We extend the system (4) and (5) to describe potential effects connected with an influence of the climate. In fact, temperature has a significant effect on the maximum growth rate of phytoplankton (Richardson et al., 2000), and can be considered as a crucial factor in population dynamics.

For one and two species ($N = 1, 2$), a model of climate influence was proposed in Sekerci and Petrovskii (2015). We consider the case of arbitrary N. In certain aspects, however, our model is simpler than in Sekerci and Petrovskii (2015). In particular, we do not account for zooplankton and, therefore, do not take into account possible predator-prey interactions in an explicit form.

Let us assume that the resource supplies S_k can depend on the environmental parameters, for example, temperature T: $S_k = S_k(T)$. In turn, T may depend on species abundances, for example, via albedo (Chapin et al., 2002). We assume, for simplicity, that this effect is linear:

$$T = \overline{T} + \Delta T, \quad \Delta T = \sum_{k=1}^{N} \mu_{kj} x_j, \tag{9}$$

where μ_{ik} are coefficients and $\overline{T}$ is a reference temperature corresponding to the albedo of the ecosystem environment, such as the upper ocean, without the ecosystem influence. If the temperature variations ΔT induced by the species are small, we have

$$S_k = \overline{S}_k(\overline{T}) + \Delta S_k + O(\Delta T^2), \quad \Delta S_k = \sum_{k=1}^{N} b_{kj}(\overline{T}) x_j, \tag{10}$$

$$k = 1, \ldots, M,$$

where $b_{kj} = \frac{dS_k(\overline{T})}{d\overline{T}} \mu_{kj}$. If all $b_{kj} > 0$ we are dealing with purely positive feedback (then species abundance increases resources), and if all $b_{kj} < 0$ one has purely negative feedback.

There is, however, an interesting case where some of the coefficients b_{kj} are positive numbers and others are negative (mixed feedback). For mixed feedback a cumulative effect of the climate–ecosystem feedback on the resource supplies may be small since the different terms in ΔS_k may cancel each other. On other hand, when the signs of the b_{jk} alternate, but these coefficients are sufficiently large, there may be complicated large time behavior. We discuss this problem in more detail in Section 5.

There are also possible alternative physical mechanisms leading to relations like (10). An important resource for phytoplankton is oxygen (Sekerci and Petrovskii, 2015). The production of oxygen is proportional to the phytoplankton concentration and depends on temperature T.

Finally, the extended model takes the form

$$\frac{dx_i}{dt} = x_i \left(-r_i + \phi_i(v) - \sum_{j=1}^{N} \gamma_{ij} \, x_j \right), \quad 1 \leq i \leq N, \tag{11}$$

$$\frac{dv_j}{dt} = D_j(S_j(x) - v_j) - \sum_{k=1}^{N} c_{jk} \, x_k \, \phi_k(v), \quad 1 \leq j \leq M, \tag{12}$$

where

$$S_k(x) = \overline{S}_k + \sum_{k=1}^{N} b_{kj} x_j, \quad k = 1, \ldots, M. \tag{13}$$

This model is an approximation of the model with temperature dependent S only up to the terms of order ΔT^2.

In the next section we show that under some assumptions this model is well posed.

3. General properties of the model

Let us first describe some sufficient conditions which guarantee that systems (1), (2), (4), (5), (11) and (12) are dissipative and have an attractor, and recall some basic notions. Since there are variations in the definition of attractor, for correctness, we follow (Hofbauer and Schreiber, 2010).

Let us consider the Cauchy problem defined by Eqs. (11) and (12) and positive initial data in (16) below. The solution $z(t, z_0) = (x(t), v(t))^{tr}$ with initial data $z_0 = (x(0), v(0))^{tr}$ (where the ^{tr} superscript denotes transpose) is unique and is defined for all $t \geq 0$ (see Lemma 1). We then obtain the map $S^t : z_0 \to z(t, z_0)$ defining a global semiflow S^t, $t \geq 0$ in a cone $\mathbf{C} = \mathbf{R}_+^{N+M}$, which serves as a phase space.

Given an interval $I \subset R_+$ and a set $K \subset \mathbf{C}$, let $K(I) = \{u \in \mathbf{C} : u = z(t, z_0), t \in I, z_0 \in K\}$. We denote $K(t) = K([t, t])$. A set K is invariant if $K(t) = K$ for all t, and forward invariant if $K(t) \subset K$ for all $t > 0$. The omega limit set $\omega(K)$ is the intersection of all $K([t, +\infty))$ over all $t \geq 0$. Given a forward invariant set K a subset B of K is an attractor for the semiflow S^t restricted to K provided there exists an open neighborhood $U \subset K$ of B such that $\omega(U) = B$.

The stable set $W^s(K)$ of a compact invariant set K is defined by

$$W^s(K) = \{z \in \mathbf{C} : \omega(z) \neq \emptyset \quad and \quad \omega(z) \subset K\}.$$

In other words, the stable set of K consists of points where trajectories enter inside the set K, and stay in K for large times t.

The semiflow is dissipative if there exists an attractor B such that $W^s(B) = \mathbf{C}$. In other words, for dissipative semiflows the attractor is a minimal invariant set, which attracts all points. If the attractor consists of a single isolated point, then this point is stable in the standard Lyapunov sense.

Define the matrix Γ with the entries γ_{ij} to satisfy one of the following conditions:

Assumption 1A. The matrix Γ with the entries γ_{ij} has a positive dominant diagonal:

$$\gamma_{ii} - \sum_{j=1, \ldots, N, j \neq i} |\gamma_{ij}| = \kappa_i > 0 \quad 1 \leq i \leq N. \tag{14}$$

Assumption 1B. The matrix Γ has non-negative entries

$$\gamma_{ij} \geq 0, \quad \gamma_{ii} > 0, \quad 1 \leq i, \quad j \leq N. \tag{15}$$

Assumption 1A means that species self-regulation is stronger than species interaction, while assumption 1B implies that all species in our ecosystem compete. Let us show that the solutions to (11) and (12) exist, and that they are non-negative and bounded.

Lemma 1. *Assume the functions ϕ_j satisfy (6). Let us consider for Eqs. (11) and (12) the Cauchy problem with positive initial data for x and positive initial resources*

$$x_i(0) > 0, \quad v_j(0) > 0, \quad \forall i \in \{1, \ldots, N\}, \quad \forall j \in \{1, \ldots, M\}. \tag{16}$$

Then, if either assumption 1A or 1B holds, solutions of this Cauchy problem exist for all $t \geq 0$, are positive and bounded for large times t, that is,

$$0 < x_i(t) < X(t) = X_0 + |X_0 - \max_i x_i(0)| \exp(-\kappa t), \quad t > 0, \tag{17}$$

where X_0 is a positive constant, $\kappa = \gamma X_0$, and

$$0 < v_j(t) < v_j(0) \exp(-D_j t) + \max_{s \in [0, t]} V_j(s), \tag{18}$$

where

$$V_j(t) = \bar{S}_j + \bar{b}_j X(t), \quad \bar{b}_j = \sum_{i=1}^{N}(b_{ji})_+.$$

Proof. For a proof, see the Appendix.

Due to boundness of solutions for large t we then obtain the following corollary.

Theorem 1. *Under the conditions of the previous lemma, system (11) and (12) defines a global semiflow in the cone $\mathbf{R}_+^{N+M}$. This semiflow is dissipative and has a compact attractor.*

4. Asymptotic approach

Our next step is to find asymptotic solutions of the system in (11) and (12), where the S_k are defined by (10). We consider the case of large $D_j \gg 1$. Note that a reduction to a Lotka–Volterra system described below also holds for bounded D and large resource supplies $S_k \gg 1$. To simplify the statement, we assume that $D_j = D$ for all j. Let us make the change of variables

$$v_k = S_k(x) - \tilde{v}_k, \quad \tau = Dt. \tag{19}$$

System (11) and (12) then takes the form

$$\frac{dx_i}{d\tau} = \epsilon x_i \left(-r_i + \phi_i(S(x) - \tilde{v}) - \sum_{j=1}^{N} \gamma_{ij} \, x_j \right), \tag{20}$$

$$\frac{d\tilde{v}_j}{d\tau} = -\tilde{v}_j - \epsilon U_j(x, \tilde{v}), \tag{21}$$

where $\tilde{v} = (\tilde{v}_1, \ldots, \tilde{v}_M)$, $\epsilon = D^{-1} \ll 1$ and

$$U_j(x, v) = \sum_{k=1}^{N} c_{jk} \phi_k(S(x) - \tilde{v})$$

$$+ \sum_{k=1}^{N} b_{jk}(\phi_k(S(x) - \tilde{v}) - r_k - \sum_{kl} \gamma_{kl} x_l). \tag{22}$$

For small ϵ Eqs. (20) and (21) form a typical system with slow variables x_j and fast variables $\tilde{v}$. We can find an asymptotic solution of (21), which has the form

$$\tilde{v}_j = \epsilon U_j(x, 0) + O(\epsilon^2). \tag{23}$$

Finally, for the species abundances x_i we obtain

$$\frac{dx_i}{dt} = x_i \left(\phi_i(S(x)) - r_i - \sum_{j=1}^{N} \gamma_{ij} x_j \right) + O(\epsilon). \tag{24}$$

5. Qualitative analysis of large time behavior

If the coefficients b_{lj} are small, i.e., the feedback between the resource supply and the climate is weak, then the system (24) can be simplified by the Taylor expansion

$$\phi_i(S(x)) = \phi_i(\bar{S}) + \sum_{l=1,\ldots,M} \sum_{j=1,\ldots,N} \frac{\partial \phi_i}{\partial S_l}(\bar{S}) b_{lj} x_j + \cdots.$$

Removing terms quadratic in x_i, Eq. (24) reduces to the Lotka–Volterra system

$$\frac{dx_i}{dt} = x_i \left(R_i - \sum_{j=1}^{N} A_{ij} x_j \right). \tag{25}$$

where

$$R_i = \phi_i(\bar{S}) - r_i, \quad A_{ij} = \gamma_{ij} - \sum_{l=1}^{M} a_{il} b_{lj}, \tag{26}$$

and

$$a_{il} = \frac{\partial \phi_i}{\partial S_l}(\bar{S}). \tag{27}$$

The Lotka–Volterra systems are very well studied (see, for example, Hofbauer and Sigmund, 1988; Takeuchi, 1996) and we can use these results to help understand how climate warming can affect ecosystems. We assume that 1B holds and consider the two limiting cases, the "weak climate" (**WC**) regime and the "strong climate" (**SC**) regime. The **WC** case corresponds to weak climate influence, where the ecosystem–climate interaction via the coefficients b_{ik} is much weaker than the competition effects associated with the coefficients γ_{ij}. This means that all the $|b_{ik}| \ll \gamma$, where $\gamma = \|\Gamma\|$ is a characteristic magnitude of the entries γ_{ij}.

In the **SC** case (regime of strong climate influence; coefficients determining climate feedback are stronger than the coefficients that define species interaction), we assume that $|b_{ik}| \gg \gamma$.

In the **WC** case, system (25) is close to so-called competitive systems, which are well studied (Hirsch, 1985; Smith, 1981; Smith and Thieme, 1991; Zeeman, 1995; Van den Driessche and Zeeman, 1998). Under some conditions (Hirsch, 1985; Hofbauer and Sigmund, 1988; Van den Driessche and Zeeman, 1998) these systems exhibit no stable periodic or chaotic regimes: almost all trajectories converge to equilibria, which will be investigated in Section 6 for the case of a single resource.

Consider the **SC** case. We set $\gamma_{ij} = 0$ for all i, j. Then Eq. (25) represent a Lotka–Volterra system of a special structure. An analysis (Hofbauer and Sigmund, 1988) shows that, for general R_i, no more than M species can coexist – an expression of the competitive exclusion principle. Mathematically this means that if $N > M$ then for some i either the corresponding $x_i(t) \to 0$ or $x_i(t) \to +\infty$ as $t \to +\infty$, i.e., the system is not permanent (Hofbauer and Sigmund, 1988). However, if the condition

$$R_i = \sum_{k=1}^{M} a_{ik} \theta_k, \quad \forall i = 1, \ldots, N \tag{28}$$

for some θ_k is fulfilled, then it is possible that all N species can coexist. In this case system (25) can be studied by an idea proposed by Volterra (1931). We introduce new variables q_j, named the qualities of life in Volterra (1931), where $j = 1, \ldots, M$. Then Eq. (25) reduces to a system involving only the variables q_j (Kozlov and Vakulenko, 2013):

$$\frac{dq_j}{dt} = G_j(q), \tag{29}$$

$$G_j(q) = -\theta_j + \sum_{i=1}^{N} b_{ji} C_i \exp\left(-\sum_{j=1}^{M} a_{ij} q_j \right), \tag{30}$$

where the C_i are arbitrary positive constants. The species abundances x_i can be expressed via q_j by

$$x_i = C_i \exp\left(-\sum_{j=1}^{M} a_{ij} q_j \right), \quad i = 1, \ldots, N.$$

Note that $C_i = x_i(0)$ and therefore the vector field $G(q)$ depends on initial data and the species number N. So, system (29) completely determines dynamics of x_i.

The main results on system (29) can be outlined as follows (see Kozlov and Vakulenko, 2013 for more details). Let Ω be a compact

connected domain in $\mathbf{R}^M$ with a smooth boundary, $F(q)$ be a compact C^1 smooth field on Ω, and $\epsilon > 0$ be a real number. Then there exist a number N and coefficients $a_{ij} > 0$, $C_i > 0$ and b_{il} such that the corresponding field G approximates F in the domain Ω in C^1-norm with accuracy ϵ. This approximation result implies that system (29) with M variables q_j can generate all structurally stable dynamics in dimension M. In particular, due to the Theorem on Persistence of hyperbolic sets (Ruelle, 1989), system (29) can exhibit all (up to topological orbital equivalences) hyperbolic dynamics, including periodic and chaotic, including for example, the Smale horseshoe, Anosov flows, etc.

Under condition (28) we find that the time behavior of solutions of system (25) depends sharply on M. Assume that $a_{ik} > 0$. Note that this assumption looks natural since it means that ϕ_i increases as a resource supply S_i increases.

If $M = 1$ it is possible that all N species survive in an equilibrium state, and N may be large. Although periodic and chaotic trajectories are impossible, we can observe multistability (coexistence of many equilibria).

For $M = 2$ and b_{ik} of different signs, system (25) can have time periodic solutions and for $M > 2$ this system can produce time chaotic solutions (we can then obtain all possible hyperbolic invariant sets of dimension $\leq M$). If all $b_{ik} < 0$ or all $b_{ik} > 0$ we have no complex behavior for the trajectories and they are convergent. Therefore, the most interesting situation arises in the biodiversity case when b_{ik} have different signs. Finally, we conclude that in the **SC** regime there are possible chaotic phenomena and periodic oscillations if there exist at least three resources ν_j.

In the next subsection we will study the case $M = 2$ and we will see that in this case Andronov-Hopf bifurcations are possible.

5.1. Bifurcations, complexity and biodiversity

If there exists a positive climate–ecosystem feedback, and $b_{ik} > 0$, then time periodic (for $M > 1$) or even chaotic (for $M > 2$) behavior, as well as complicated bifurcations, can occur.

We consider two cases: $M = 1$ (a single resource) and $M = 2$, and investigate the existence of different bifurcations, in particular, the Andronov-Hopf bifurcations. If $M = 1$ there are possible saddle-node, pitchfork, and transcritical bifurcations, but the Andronov-Hopf does not occur. The main climate effect in the case $M = 1$ is a destruction of the ecosystem under climate forcing that can be described as follows. Let us consider a population consisting of N species with random parameters, and denote $q = q_1$, $G = G_1$. We can assume, for example, that the parameters a_i and K_i in (3) and b_{1i} in (10) are normally distributed random variables. The equilibria are defined by roots of equation $\theta = G(q)$.

Let us consider system (29) for $M = 2$. Let (Q_1, Q_2) be a steady state for this system, and we define a 2×2 matrix **M** with entries

$$M_{lj} = \frac{\partial G_l}{\partial q_j}(Q_1, Q_2).$$

We introduce vectors $b^{(l)} = col(b_{l1}, b_{l2}, \ldots, b_{lN})$ and

$$E_a(Q)^{(j)} = col(a_{1j}\exp(-a_{11}Q_1 - a_{12}Q_2), \ldots, a_{Nj}\exp(-a_{N1}Q_1 - a_{N2}Q_2)).$$

Then we obtain

$$M_{kl} = \langle b^{(k)}, E_a(Q)^{(l)} \rangle_C, \quad l, k \in \{1, 2\}.$$

An Andronov-Hopf bifurcation occurs if the trace Tr_M of the matrix **M** changes its sign as the bifurcation parameter b goes through a critical value b_c and if the determinant det_M of **M** is positive at this

critical value. Using the notation in (8) we obtain

$$Det_M = M_{11}M_{22} - M_{12}M_{21}, \tag{31}$$

$$Tr_M = \langle b^{(1)}, E_a(Q)^{(1)} \rangle_C + \langle b^{(2)}, E_a(Q)^{(2)} \rangle_C. \tag{32}$$

These relations allow us to see connections between bifurcations, feedback, and diversity. First let us observe that components of the vectors $E_a(Q)^j$ are always positive. Note that if the climate influence is absent, then all the components of b^l are negative, and it is clear that Tr_M does not change its sign. Thus in this case the Andronov-Hopf bifurcations are absent. The same fact holds if all the climate–ecosystem feedbacks are negative. For purely positive or mixed feedbacks these bifurcations are possible under additional conditions. In order to find a biological meaning of these conditions, we define $\phi_{lj}(C)$ as the angles between the vectors $b^{(l)}$ and $E_a(Q)^{(j)}$. We then have

$$\phi_{lj}(C) = \langle b^{(l)}, E_a(Q)^{(j)} \rangle_C ||b^{(l)}||_C^{-1} ||E_a(Q)^{(j)}||_C^{-1}.$$

Then the condition $Det_M > 0$ reduces to

$$\phi_{11}(C)\phi_{22}(C) > \phi_{12}(C)\phi_{21}(C). \tag{33}$$

The condition $Tr_M = 0$ implies that $\phi_{11}(C)$ and $\phi_{22}(C)$ have opposite signs. Then (33) means that $\phi_{12}(C)$ and $\phi_{21}(C)$ also have opposite signs. If all the species affect the climate in a similar manner (the coefficients b_{kj} have the same signs) then all the quantities ϕ_{lj} have the same sign. Therefore, Andronov-Hopf bifurcations are impossible in this case.

We conclude that not only feedback positivity but also biodiversity and a complex ecosystem structure support complicated time periodic behavior. Moreover, all bifurcation conditions depend on the initial data C. From a biological point of view, this means that bifurcation effects have a "memory", i.e., they depend on the choice of initial data.

6. Equilibria

The aim of this section is to show that the cases of negative (**NF**) and positive (**PF**) feedback between climate and ecosystem are markedly different. In the **NF** case, positive equilibria with many species can exist. In the **PF** case, such equilibria vanish for some critical feedback level; this can be interpreted as a *mass extinction*. We compute this critical level.

On the attractor structure, one can say more for the particular case of system (11) and (12), where we have a single resource, $M = 1$. We use Eqs. (1) and (2), where $K_i = K$ and thus $\phi_i = a_i \phi(\nu)$, where $\phi(\nu) = \nu/(K + \nu)$. Let us set $\rho_i = r_i/a_i$. These quantities are important characteristics of species. The species with smaller ρ_i have a greater chance to survive. Moreover, using an analogue of (13) for the case a single resource $M = 1$, we assume that S depends on x as follows:

$$S(x) = \overline{S} + \sum_{k=1}^N b_k x_k,$$

where b_k are the coefficients.

6.1. Equation for equilibrium resource value

Moreover, for simplicity, let us set

$$\gamma_{ij} = \gamma_i \delta_{ij}, \quad \gamma_i > 0. \tag{34}$$

In this case numerical simulations show that all trajectories tend to equilibria. As was pointed out by V. Kozlov, using the theory of decreasing operators and an assumption that $\phi_i(\nu)$ increases in the

resource v and $D \gg 1$, one can prove this fact by analytic methods (a detailed analysis of this question will appear in future work, since the proof is quite involved). The resting points $(\bar{x}, \bar{v})$ of systems (1) and (2) can be found as follows.

Setting $dx_i/dt = 0$ in (1), we obtain $\bar{x}_i = a_i \gamma_i^{-1} (\phi(\bar{v}) - \rho_i)_+$. This gives the following nonlinear equation for $\bar{v}$:

$$D(\bar{S} - \bar{v}) = G(\bar{v}), \tag{35}$$

where

$$G(v) = \sum_{j=1}^{N} a_j \gamma_j^{-1} (c_j a_j \phi(v) - b_j)(\phi(v) - \rho_j)_+. \tag{36}$$

We have obtained a complicated equation with non-smooth nonlinearities. An important characteristic of the solutions $\bar{v}$ is $N_B(\bar{v})$, the number of positive $\bar{x}_j(\bar{v})$ involved in the sum in the right hand side of (36). The number N_B can be interpreted as biodiversity.

Note that, for any N, in the **NF** case a solution $\bar{v}$ with $\bar{v} \in (0, \bar{S})$ always exists under the following condition:

$$\phi(\bar{S}) > \rho_0 = \min_j \rho_j. \tag{37}$$

Indeed, observe that $D(\bar{S} - v)$ is a decreasing function of v, while $G(v)$ is increasing. The solution $\bar{v}$ is given by an intersection of the curve $G(v)$ and the right line $D(\bar{S} - v)$, which exists if (37) holds.

Moreover, the same geometrical argument shows that the resource $\bar{v}$ is an increasing function of b_j. Therefore, in the case of negative feedback the biodiversity N_B is larger (if a solution $\bar{v} > 0$ exists). However, for negative b_j that are too large, the positive solution $\bar{v}$ does not exist.

Consider a large ecosystem with random parameters ρ_j. We suppose that $N \gg 1$ and ρ_j are selected randomly according to a distribution with probability density function $\xi(\rho)$, which is positive on some open interval $I_\rho = (R_0, R_1)$.

Assertion 1. Consider the case of negative feedback ($b_j \geq 0$). If

$$\phi(\bar{S}) > R_0, \tag{38}$$

then for any N there exists a positive solution $\bar{v}(N)$ of Eq. (35) with biodiversity $N_B(\bar{v})$ such that $N_B \to \infty$ as $N \to \infty$.

Proof. The existence of solutions is obvious from geometrical arguments (see remarks on the monotonicity of $D(\bar{S} - v)$ and $G(v)$ above). To show that N_B is large for $N \gg 1$, we observe that for any fixed R_0 and R_1 such that $R_0 < R_1$, the interval (R_0, R_1) contains N_c points ρ_j, with $N_c \to +\infty$ as $N \to +\infty$. For large N we seek a solution of (35) in the form $\bar{v} = S - w$, where $0 < w \ll 1$. Since (38) holds, such a solution exists. The number N_b approximately equals the number N_c for $R_1 \approx \phi(\bar{S})$, and the assertion is proved.

In the **PF** case this assertion, in general, does not hold. Using the arguments from the proof, we note that all species die if the following relation holds:

$$R_0 \sum_{j=1}^{N} a_j^2 \gamma_j^{-1} c_j < \sum_{j=1}^{N} b_j a_j \gamma_j^{-1}. \tag{39}$$

This relation shows that mass extinction inevitably arises if the $b_j > 0$ are sufficiently large.

Results on a numerical solution of Eq. (35) are discussed below. They confirm that mass extinctions are possible as the feedback magnitude increases.
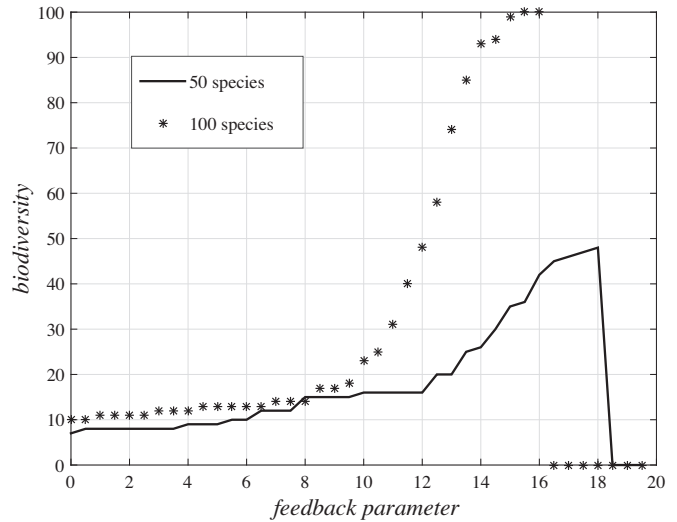

Fig. 1. The graph shows the dependence of the biodiversity N_B on the magnitude of positive feedback b_F, in the case of $N = 50$ and $N = 100$. We see that the biodiversity increases as b_F grows, but beyond a critical value of the climate–ecosystem feedback b_F, all the species become extinct.

6.2. Numerical results

In the general case Eq. (35) for equilibria can be resolved numerically for $N = 50$. We choose the coefficients in Eq. (35) as follows. The positive coefficients a_i are random numbers subject to log-normal distributions. This means that $\ln(a_i)$ are distributed normally, $\ln a_i \in \mathbf{N}(E_a, s_a)$, where E_a is the mean and s_a is the deviation. The same distribution is taken for c_i, with the parameters E_c and s_c.

We assume that the R_i and b_i are distributed normally, namely, $R_i \in \mathbf{N}(R_0, s_R)$ and $b_i = b_F \beta_i$, where $\beta_i \in \mathbf{N}(b_0, s_b)$, and b_F is the magnitude of the feedback level. The other parameters were taken as follows: $D = 1, K = 2, \bar{S} = 10, E_a = 1, s_a = 0.1, E_b = 1, s_b = 0.3, R_0 = 0.7, s_R = 0.05$ and $\gamma_i = 1$.

The results are shown by Fig. 1. Comparison of the two plots shows that when the number of species increases, so does the likelihood of a sharp drop in species number as the climate changes and feedback processes grow stronger. These findings are consistent with analytical results. Biodiversity grows with the feedback parameter b_F, until at some critical level we observe a mass extinction.

7. Conclusions

In this paper, a consumer-resource model for a system of many coexisting species is proposed. It is a generalization of the well known model in Huisman and Weissing (1999), takes into account species self-regulation and a dependence on the environment, and is the first model of an ecosystem with many species and feedback which couples climate and population dynamics. Such conceptual models describe a simple and easily understandable mechanism for resource competition. For the case of fixed parameters, a general assertion on attractor existence for this model is proved. One of the sufficient conditions for the existence of an attractor is that species self-regulation is stronger than species competition.

Climate–ecosystem feedbacks are an important problem in terms of uncertainty in predictions and modeling future climate change. The proposed model allows us not only to investigate climate–ecosystem feedbacks for large ecosystems, but also to show that coexistence of many species feeding on a few resources is possible. In the case of positive feedback in the ecosystem–climate interaction, the numerical results show a possibility of

catastrophic bifurcations, when all (or almost all) species become extinct under the impact of climate warming. The ecosystem biodiversity increases with the magnitude of positive feedback b_F, but at some critical level of feedback, a mass extinction occurs. For negative climate–ecosystem feedback we observe smaller biomass and biodiversity values, but we do not observe catastrophes. Note that in the contemporary world, human impact on the climate system can possibly lead to positive feedback in the above context.

To investigate more complicated situations, where complex dynamics may be possible, we have considered the case of just a few resources. We find asymptotic solutions for the case of a large resource turnover. This allows us to reduce this system to the Lotka–Volterra model, which is well studied. The existence of two sharply different regimes of ecosystem behavior is proven: the weak climate regime (**WC**), and the strong climate regime (**SC**). This behavior depends on a parameter that determines the intensity of ecosystem-climate interactions. Note that this analytical result is consistent with experimental data (Crampton et al., 2016), where it is shown that two distinct regimes of extinction dynamic are present in the major marine plankton group. Results in (Crampton et al., 2016) suggest that the dominant, primary controls on extinction were abiotic (environmental), which corresponds to the **SC** case.

If the ecosystem – climate interaction involves terms of different signs, then there are possible Andronov-Hopf bifurcations, time periodic behavior for the case of two resources, and chaotic behavior for more than three resources. We conclude that not only feedback positivity, but also biodiversity and a complex ecosystem structure (when different species affect climate differently creating positive and negative feedback ecosystem–climate loops) support complicated temporal dynamics of the ecosystem.

For the case of a single resource the ecosystem equilibria can be described implicitly. We find these equilibria by a nonlinear equation for the equilibrium resource level. We show that, due to self-limitation effects, the system can support equilibria with a number of species sharing the same single resource.

Appendix

We state here the proof of Lemma 1. The proof proceeds in the following steps.

Step 1. Positivity of the x_i follows from the fact that the ith right hand side of system (4) is proportional to x_i, thus, $x_i(t) = x_i(0) \exp(-\xi_i(t))$, where ξ_i is a function.

Step 2. Let us prove that $v_j(t) > 0$. Assume that this fact is violated. Then there exists an index j_0 and a time $t_0 > 0$ such that

$$v_{j_0}(t_0) = 0, \quad \frac{dv_{j_0}}{dt} \leq 0, \quad v_j(t_0) \geq 0, \quad \forall\ j. \quad (40)$$

Condition (7) entails the term $\sum_{k=1}^N c_{jk}\, x_k\, \phi_k(v)$ equaling zero. Then we substitute these inequalities into the j_0th Eq. (12) and obtain a contradiction.

Step 3. Let us prove estimate (17). First let us suppose that assumption 1B is satisfied. Let $E(t) = \max\{x_1(t), \ldots, x_N(t)\}$. Let us estimate dE/dt for large E. Let $i_0(t)$ be an index such that $E(t) = x_{i_0}(t)$. According to (6) the ϕ_i are uniformly bounded by C_+. Therefore within any open interval I_{i_0}, where i_0 is fixed, one has

$$\frac{dE}{dt} \leq ER_{i_0}, \quad R_{i_0} \leq C_+ - \gamma E(t), \quad (41)$$

where $\gamma = \min_i \gamma_{ii} > 0$ due to assumption (14) on Γ.

In the case 1A we note that

$$\sum_{j=1}^N \gamma_{i_0 j} x_j \geq \gamma_{ii} E - \sum_{j \neq i_0} |\gamma_{i_0 j}| x_j \geq \kappa E,$$

and we have an inequality analogous to (41):

$$\frac{dE}{dt} \leq ER_{i_0}, \quad R_{i_0} \leq C_+ - \kappa E(t). \quad (42)$$

Note that the sequence of intervals I_{i_0} is not bounded and these intervals cover all $\mathbf{R}_+$ since, according to the Lemma, the solutions exist for all $t > 0$.

Inequality (41) implies that $E(t) \leq X(t)$, where $X(t)$ is the solution to the Cauchy problem

$$\frac{dX}{dt} = X(C_+ - \gamma_0 X), \quad X(0) = \max_i x_i(0), \quad (43)$$

where γ_0 equals γ in the case 1B and κ in the case 1A. Let $X_0 = C_+/\gamma_0$. If $X(0) < X_0$, then Eq. (43) shows that $X(t) \leq X_0$ for all t and (17) follows. If $X(0) > X_0$, then Eq. (43) shows that $X(t) > X_0$ for all t. By the change of variables $\tilde{X} = X - X_0$ we obtain that $\tilde{X} > 0$ and thus

$$\frac{d\tilde{X}}{dt} = -\gamma_0(X_0 + \tilde{X})\tilde{X} \leq -\gamma_0 X_0 \tilde{X},$$

which implies $\tilde{X}(t) \leq \tilde{X}(0)\exp(-\gamma_0 X_0 t)$, and we obtain (17).

Step 4. Having (17), we can prove (18). Indeed, using the non-negativity of the c_{jk} and ϕ_k, one obtains

$$\frac{dv_j}{dt} \leq D_j(S_j(x(t)) - v_j).$$

Therefore,

$$v_j(t) = \exp(-D_j t)\left(v_j(0) + \int_0^t S_j(x(s))\exp(D_j s)ds\right)$$

which yields

$$v_j(t) \leq \exp(-D_j t)v_j(0) + \max_{s \in [0,t]} S_j(x(s)).$$

Here $S_j(x(t)) \leq \overline{S}_j + \overline{b}_j X(t)$. These two last inequalities imply $v_j(t) \leq V_j(t)$, which completes the proof.

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