

The influence of environmental forcing on biodiversity and extinction in a resource competition model

Sergey A. Vakulenko, Ivan Sudakov, and Luke Mander

Citation: *Chaos* **28**, 031101 (2018); doi: 10.1063/1.5017233

View online: <https://doi.org/10.1063/1.5017233>

View Table of Contents: <http://aip.scitation.org/toc/cha/28/3>

Published by the [American Institute of Physics](#)

Articles you may be interested in

[Prediction of flow dynamics using point processes](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **28**, 011101 (2018); 10.1063/1.5016219

[Stochastic mixed-mode oscillations in a three-species predator-prey model](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **28**, 033606 (2018); 10.1063/1.4994830

[Solitary states for coupled oscillators with inertia](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **28**, 011103 (2018); 10.1063/1.5019792

[Introduction to Focus Issue: Time-delay dynamics](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **27**, 114201 (2017); 10.1063/1.5011354

[Wavefront cellular learning automata](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **28**, 021101 (2018); 10.1063/1.5017852

[Dynamic modes in a network of five oscillators with inhibitory all-to-all pulse coupling](#)

Chaos: An Interdisciplinary Journal of Nonlinear Science **28**, 033105 (2018); 10.1063/1.5004015

Welcome to a

Smarter Search



PHYSICS
TODAY

with the redesigned
Physics Today Buyer's Guide

Find the tools you're looking for today!

The influence of environmental forcing on biodiversity and extinction in a resource competition model

Sergey A. Vakulenko,^{1,2,3} Ivan Sudakov,^{4,a)} and Luke Mander⁵

¹*Institute for Problems in Mechanical Engineering, Russian Academy of Sciences, Bolshoy pr. V.O., 61, St. Petersburg 199178, Russia*

²*Laboratory of Power Electronics and Automated Electric Drive, ITMO University, Kronverkskiy pr., 49, St. Petersburg 197101, Russia*

³*Department of Mathematics and Informatics, Saint-Petersburg State University of Industrial Technologies and Design, 18, Bolshaya Morskaya Str., St. Petersburg 191186, Russia*

⁴*Department of Physics, University of Dayton, 300 College Park, Dayton, Ohio 45469, USA*

⁵*School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes MK-7 6AA, United Kingdom*

(Received 26 November 2017; accepted 12 February 2018; published online 1 March 2018)

In this paper, we study a model of many species that compete, directly or indirectly, for a pool of common resources under the influence of periodic, stochastic, and/or chaotic environmental forcing. Using numerical simulations, we find the number and sequence of species going extinct when the community is initially packed with a large number of species of random initial densities. Thereby, any species with a density below a given threshold is regarded to be extinct. *Published by AIP Publishing.* <https://doi.org/10.1063/1.5017233>

The history of life on Earth is one of continually fluctuating diversity. In general terms, the diversity of life, as measured by the number of species or higher taxa such as genera or families, represents the balance between the process of speciation (which adds species to the biosphere) and extinction (which removes species from the biosphere). Palaeobiological work has shown that the history of life is characterized by many extinction events that have at various times decimated the Earth's biota. The process of extinction is of particular current scientific interest because it is thought that we may be approaching a mass extinction driven by some kind of environmental forcing (for example, climate change, anthropogenic activities, extreme weather, etc.). In this paper, we consider a resource competition model, which allows us to investigate how chaotic and period oscillations of resource supply affect the number of coexisting species (biodiversity) and how these oscillations can lead to species extinction. Using analytical investigations and numerical simulations, we find model parameters that characterize extinction under environmental forcing. In our model, extinctions are inevitable if population has the maximal possible biodiversity level (a certain number of survived species) and exploits the maximal amount of resources.

where the number of taxa has declined rapidly. Such intervals represent extinction events, and reviews of the history of life indicate that there have been 61 such events in Earth history.^{3,4} Of these, several stand out for their sheer magnitude.⁵ These are mass extinctions, which are defined as “any substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically widespread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity”(see Ref. 6 p. 278).

Palaeobiological studies indicate that extinction events are frequently associated with major environmental change. For example, several of Earth's largest extinction events occur during intervals of elevated volcanic activity, either due to the intrusion of large igneous bodies of rock as in the case of the Toarcian extinction event⁷ or to the opening of the Atlantic ocean in the case of the late Triassic extinction.⁸ There are also examples of extinction events on much more recent timescales, such as the disappearance of the spruce tree species *Picea critchfieldii* during the last deglaciation in North America.^{9,10} Such studies can provide empirical data on the sensitivity of the Earth's biota to environmental change and can identify factors that can lead to the proliferation of species as well as the broad abiotic conditions under which species are lost from the Earth's biota.

A general trait that emerges from empirical palaeobiological studies of the biosphere is that extinctions reflect perturbations that stress populations beyond their resilience.¹¹ Species populations represent functional entities that are produced by assembly processes, and if they are subject to perturbations that are greater in magnitude or duration than they can accommodate, then they are disrupted in some way.^{11,12} Many ecological models do not represent every single complex biotic and abiotic interaction that leads to population assembly and disruption, but nevertheless, the dynamical outcomes of such models^{11,13} can provide a quantitative

I. INTRODUCTION

The current state of the biosphere is a product of the evolutionary process that began with the origin of life around 3.5 Ga.¹ Since this time, life has expanded from a single common ancestor to the diversity of biological forms that are present on the Earth today.² However, the diversification of life over this time interval has not been smooth or steady, and the fossil record indicates that there have been periods

^{a)}Electronic mail: isudakov1@udayton.edu

formalization for dynamical biospheric change¹¹ and can serve as a counterpoint to empirical studies of biospheric evolution based on observational data.

In this paper, we consider a resource competition model that allows us to investigate how biodiversity affects the mechanism of extinction. In this model, a number of species share resources, and oscillations in these resources (as might be induced by some kind of environmental forcing: from periodic environmental temperature changes to chaotic dynamics defined by the Lorenz model), self-limitation effects, as well as extinctions are accounted for. Our model represents an extension of the Huisman and Weissing model,¹⁴ which does not include any environmental variations. The parameters of the model depend on the state of the environment via time dependent coefficients (i.e., we consider an external forced competition model). This system is inspired by some phytoplankton models,^{15,16} and under certain assumptions can be derived from them. If the resource turnover rate is large enough our model reduces to a Lotka-Volterra system.¹⁷

Externally forced competition models have been studied in various papers,^{18–24} and here we briefly recapitulate their main findings. Bagchi and Mohanty¹⁸ presented a microscopic model of biological evolution that takes into account both external stresses as well as biotic interactions between species as contributory factors for species extinction. However, this model does not consider competition for resources. Caraballoa *et al.*¹⁹ develop a general theory of pullback attractor, while in the paper by Kremer and Klausmeier,²⁰ a competition model with fluctuations is considered and these authors showed that, by numerical simulations, identical fluctuations are capable of supporting the coexistence of multiple species. Amritkar and Rangarajan²¹ studied a general resource competition model with time dependent parameters. It was shown that under a common external forcing the species with a quadratic saturation term first undergoes spatial synchronization and then extinction. Ovaskainen and Meerson²² proposed a simple model of species extinction using the Verhulst equation with fluctuating parameters. In the paper by Sun *et al.*,²³ a spatial version of the predator prey model with Holling III functional response and two species, which includes external periodic forces, noise, and diffusion processes, was studied. Finally, in the work by Smith and Meerson,²⁴ extinction of oscillating populations in a stochastic version of the Rosenzweig-MacArthur predator-prey model was found.

In Sec. II, we first state the model of species coexistence; In Sec. III, we then extend the standard model of species coexistence by introducing extinctions and external forcing (assuming that the dynamics depends on some environmental parameters that can oscillate (for example, environmental temperature)). In Sec. IV, we then consider the problem of extinction in our extended model in more detail; In Sec. V, we use analytical investigations and numerical simulations to study the dynamics of our extended model under chaotic and periodic forcing.

Our principal results are that the stochastic dynamics of our model exhibit strong dependence on initial parameters. Also, we show that extinctions are inevitable if species

community has the maximal possible biodiversity and uses the maximal amount of resources, a conclusion which underscores the importance of studying the role of stability thresholds in mass extinction (the species with a density below a certain threshold).²⁵

II. THE STANDARD MODEL OF SPECIES COEXISTENCE

We consider the following standard model of species biodiversity:¹⁴

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

$$\frac{dv_j}{dt} = D_j(S_j - v_j) - \sum_{k=1}^N c_{jk} x_k \phi_k(v), \quad (2)$$

where $v = (v_1, v_2, \dots, v_M)$, and

$$\phi_j(v) = \min \left\{ \frac{a_j v_1}{K_{1j} + v_1}, \dots, \frac{a_j v_M}{K_{Mj} + v_M} \right\}. \quad (3)$$

where a_j and $K_{ij} > 0$. In these equations, $x = (x_1, x_2, \dots, x_M)$ are unknown species abundances, $v = (v_1, \dots, v_M)$ is a vector of unknown resource amounts, where v_k is the resource of k -th type consumed by all species, r_i are the species mortalities, $D_k > 0$ are resource turnover rates, S_k is the supply of the resource v_k , and the coefficients c_{jk} determine how the species share the resources (nutrients). If all $x_i = 0$, then the initial nutrient supply of k -th type is S_k . Note that S_k and D_k are characteristics of the environment, in particular, the coefficient D_k describes the resumption rate of k -th resource.

The terms $\gamma_{ii} x_i$ define self-regulation of species populations that restrict the species abundances, and $\gamma_{ij} x_j$ with $i \neq j$ define a possible competition between species for resources. The coefficients a_j are specific growth rates and the K_{ij} are self-saturation constants. The coefficients c_{jk} determine how the species share the resource (nutrient supply).

This model is widely used for primary producers like phytoplankton and it can also be used to describe competition among terrestrial plants.²⁶ When $\gamma_{ij} = 0$, this system is equivalent to models used to study the plankton paradox, which describes the phenomenon where a limited range of resources supports an unexpectedly large number of different species.¹⁴

Relation (3) corresponds to the von Liebig minimum law, but we can consider even more general ϕ_j satisfying the conditions

$$\phi_j(v) \in C^1, \quad 0 \leq \phi_j(v) \leq C_+, \quad (4)$$

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

$$\phi_k(v) = 0, \quad \forall k \quad v \in \partial \mathbf{R}_>^N, \quad (5)$$

where $\partial \mathbf{R}_>^N$ denotes the boundary of the positive cone $\mathbf{R}_>^N = \{v : v_j \geq 0, \forall j\}$. Note that condition (5) holds if ϕ_j are defined by (3), so our conditions can be considered a generalization of the von Liebig law, when the species abundance

growth stops if at least one resources vanishes. Thus, each resource is necessary for species survival.

We consider the Cauchy problem for the systems (1) and (2) on a time interval $[0, \tau]$, where initial data are given by

$$x_i(0) = X_i > 0, \quad v_k = V_k \in (0, S_k), \quad (6)$$

and τ is a positive number. We assume that $N \gg 1$ (the case of a large species community) and $X_i > 0$ is distributed randomly according to a log-normal law with parameters a^*, σ . The corresponding distribution density is given by

$$f(x) = \frac{1}{x\sigma\sqrt{2\pi}} \exp \left[\frac{-(\ln x - a^*)^2}{2\sigma^2} \right]. \quad (7)$$

Suppose we simplify the problem that a direct competition between species is absent and

$$\gamma_{ij} = \gamma_i \delta_{ij}, \quad \gamma_i > 0. \quad (8)$$

One can show that, by standard estimates, the Cauchy problems (1), (2), and (6) are well posed and that the corresponding $x_i(t)$ are defined for all $t > 0$, bounded and take positive values. Therefore, we are dealing with a dynamical system. Moreover, we observe that this system is cooperative,²⁷ since $\frac{\partial F_i(\bar{x})}{\partial x_j} > 0$ for $j \neq i$, where F_i is the right side of the equation (1).

Assertion. *Under condition (8), the dynamical system defined by (1) and (2) has a compact global attractor. In the case of a single resource ($M = 1$) and sufficiently large turnover $D = D_1$, all trajectories of that system are convergent, and there are no locally attracting stable limit cycles.*

Outline of the proof. We follow Kozlov *et al.*²⁸ and Sudakov *et al.*²⁹ The resource is a uniformly bounded function. This fact, in a standard way, implies uniform boundedness of $x_i(t)$ for large times t and shows that the systems (1) and (2) defines a global semiflow, which has an absorbing set. Thus, this semiflow is dissipative and has a compact global attractor. The claim on trajectories convergence formally follows from Theorem I in Ref. 28. Non-formally, it can be explained as follows. For large turnovers, the resources are fast variables, whereas the species populations are slow. Under condition (8), the system is dissipative, and typically in such systems the large time dynamics of the fast modes is captured by the dynamics of slow modes. In our case, the slow dynamics are defined by a single differential equation for v , thus the stable limit cycles are impossible.

For $M > 1$, the problem can be also simplified for large turnovers ($D_k \gg 1$). Then, one can show²⁹ that systems (1) and (2) reduce to Lotka-Volterra systems of a special form.

III. THE MODEL WITH EXTINCTIONS

We extend systems (1) and (2) to describe two important effects. The first effect is species extinctions, and in this section we focus on it. The second effect is a result of external forcing in the dynamics of the modified systems (1) and (2). That effect will be considered in Sec. V.

In reality, abundances x_i are discrete numbers; therefore, if the abundance becomes too small, the corresponding species must become extinct. To describe this effect

mathematically, we introduce a threshold parameter $\delta > 0$ and suppose that if the i -th species abundance $x_i(t)$ becomes less than δ , i.e., $x_i(t_0) = \delta$ and $\frac{dx_i(t_0)}{dt} < 0$ for some i and $t_0 > 0$, then the corresponding species should be excluded from systems (1) and (2). We then set formally that $x_i(t) \equiv 0$ for all $t > t_0$. Note that this modification follows to the persistence concept studied in detail in the book by Hofbauer and Sigmund.³⁰ For the case of a single resource, this extended model is used and investigated in Ref. 28.

Note that after this modification the model stays mathematically well posed.²⁸ Next, we introduce a function $N_e(t)$, which is the number of surviving species at time t , i.e., the number of the indices i such that $x_i(t) > \delta$. It is clear that $N_e(t)$ is a piecewise constant non-increasing function. Let $t_0 < t_1 < \dots < t_m < \dots$ be the points of discontinuity of this function. Within the intervals $[t_k, t_{k+1}]$, the Cauchy problem for systems (1) and (2) is well posed, and therefore the Cauchy problem is well posed for the modified systems (1) and (2) with extinctions. There are two possible situations. If $\lim_{t \rightarrow +\infty} N_e(t) = N_\infty = 0$, then all the species vanish. If $N_\infty > 0$, then on some infinite semiaxis $(t_m, +\infty)$, the modified system is equivalent to models (1) and (2), which, according to our Assertion, has a compact global attractor. Therefore, in this case, the modified model with extinctions also has a compact global attractor.

The model with extinctions exhibits a highly stochastic behavior. The final population state depends dramatically on initial data (6).²⁸ For some initial abundances, all species coexist, whereas for other initial data only a few species can survive over long timescales. Usually, the external forcing diminishes the number of surviving species. Nonetheless, sometimes the environmental chaos can stabilize the population, increasing the number of coexisting species. Systems with large numbers of species are more stable than the ones with few species. This multistability, which is present in a system with fixed parameters, means that in a system with slowly evolving parameters we can observe jumps between equilibria.

IV. A MORE DETAILED LOOK AT EXTINCTIONS

We follow Kozlov *et al.*²⁸ but will consider the problem of extinction in more detail. Let us consider the case of a single resource $M = 1$ for large $D = D_1$. For brevity and simplicity, we use notation $v_1 = v, c_i = c_{i1} > 0, S = S_1$ and that $\gamma_{ij} = \delta_{ij}\gamma_i$ with $\gamma_i > 0$. Let $\phi_i = a_i\phi(v)$, where $\phi(v) = \frac{v}{K+v}$. Then, according to our Assertion, all trajectories are convergent to equilibria. Let N be the number of coexisting species for such equilibria and v_{eq} is the equilibrium amount of the resource. Then, the equilibrium abundances \bar{x}_i are²⁸

$$\bar{x}_i = (\gamma_i^{-1}(a_i\phi(v_{eq}) - r_i))_{+, \delta}, \quad (9)$$

where $a_{+, \delta}$ is truncated at level $\delta > 0$, the number a : $a_{+, \delta} = a$ for $a > \delta$ and $a = 0$ otherwise. It is useful to introduce normalized variables $u = v/S, \bar{K} = K/S, p_i = r_i/a_i$, and $\bar{\delta}_i = \delta\gamma_i$.

For the normalized equilibrium consumed resource amount $u_{eq} = v_{eq}/S$, we then obtain

$$1 - u_{eq} = \bar{\phi}(u_{eq}) \sum_{i=1}^N \frac{a_i^2 c_i}{DS\gamma_i} (\bar{\phi}(u_{eq}) - p_i)_{+, \delta_i}, \quad (10)$$

where $\bar{\phi}(u) = u/(\bar{K} + u)$ and we assume that $c_i > c_0 > 0$. Note that u_{eq} depends on S and N . That dependence on S is monotonic: as S decreases, v_{eq} also decreases. Moreover, it is useful to note that the properties of the system when all $\gamma_{ij} = 0$ [the case **(a)**] and when $\gamma_{ij} = \delta_{ij}\gamma_i$ with $\gamma_i > 0$ [case **(b)**] are strongly different. The case **(a)** is studied in detail by many works (see Refs. 31 and 32). Then, in a generic situation, a single species survives and, in order to obtain coexistence of many species, we should impose special restrictions on parameters ($p_i = \bar{p}$ for all i). Then, actually the equilibrium resource value does not involve the resource supply S . In the case **(b)**, even if $\gamma_i > 0$ are small, the large time behaviour properties of the systems (1) and (2) completely change since that systems become dissipative that, under some conditions, makes possible coexistence of many species.

The equilibrium abundances \bar{x}_i decrease in $v_{eq} = Su_{eq}$ and for some i the value \bar{x}_i defined by (9) equals zero. Then, the corresponding species suffers extinction and the species number N takes a smaller value, for example, $N - 1$. That is a typical picture for general S and not too large N .

To understand how extinctions occur in our model, we consider the case of the maximal biodiversity. To simplify our analysis, we suppose first that all species have identical properties, i.e., all $p_i = \bar{p}$ and $a_i = a$, $c_i = c$, $\gamma_i = \gamma$. Then, from (10), one has

$$N = \frac{DS\gamma}{a^2 c} \frac{1 - u_{eq}}{\bar{\phi}(u_{eq})(\bar{\phi}(u_{eq}) - \bar{p})_{+, \delta\gamma}}. \quad (11)$$

An analysis of this equation allows us to note that in (11) the numerator decreases in u_{eq} and the denominator is an increasing function of u_{eq} . Thus, the number of survived species (for brevity, we call it biodiversity) N is a decreasing function of the v_{eq} . On the other hand, N is an increasing function of resource supply S . Therefore, one can say that the maximal N can be obtained when the resource supply, which still exist in an environment and not consumed by species, is maximal.

Moreover, let us note that the large number of coexisting species N can be obtained for a more realistic situation when the species parameters are not identical. It is possible if δ is small and all fundamental parameters p_i (which are consuming rates divided mortality rates) are close to a value \bar{p} . Equation (11) also shows that the biodiversity N depends on the parameter

$$P_{stress} = (DS\gamma)^{-1} \langle a^2 c \rangle, \quad (12)$$

where $\langle a^2 c \rangle$ denotes the value of the quantities $a_i^2 c_i$ averaged over all the population

$$\langle a^2 c \rangle = N^{-1} \sum_{i=1}^N a_i^2 c_i.$$

The quantity P_{stress} is a dimensionless parameter and can be interpreted as a level of environmental pressure on the population.

Consider now how extinctions can occur. While $\phi(u_{eq}) - \bar{p} \gg \delta\gamma$, a small variation ΔS in the resource S leads to either a small variation in N or N conserves. In fact, a decrease in S can be compensated by the corresponding decrease in the normalized consumed resource amount u_{eq} . In this case, we observe the extinction of a small number of species.

However, in the case of the maximal possible biodiversity N that can be attained, if all the equilibrium abundances \bar{x}_i are close to δ , the situation dramatically changes when the normalized consumed resource amount u_{eq} is close to the maximal value of 1. In this situation, a decrease in u_{eq} leads to extinction of many or even all species in the model because for smaller u_{eq} we have $a\phi(u_{eq}) < \bar{p} + \delta\gamma$.

This effect is weaker if the species parameters are different (i.e., the parameters a_i , c_i , γ_i , and p_i are different).

From this study of our model, we can formulate the following assertion:

Extinction principles (a) *If a community consisting of species that share the same resource attains its maximum possible biodiversity, then relatively small changes in the environment can lead to species extinction. (b)* *If the biodiversity of a species community is at its maximal possible value and simultaneously the species in that community consume resources close to a maximal value, then the community is fragile: it can be destroyed completely or almost completely as a result of species extinction under very small environmental changes. This effect is weaker for community consisting of a random mix of species that have different mortality and resource consumption parameters.*

V. THE POPULATION MODEL UNDER PERIODIC AND CHAOTIC ENVIRONMENTAL FORCING

In this section, we consider extinctions in our model forced by chaotic and periodic environmental temperature T changes. We assume that the resource supply depends on T and that T is a periodic function of time. We also include stochastic effects. For example, we can suppose that

$$S = S_0 + R \sin(\omega t) + \varepsilon \eta(t), \quad (13)$$

where $S_0, R > 0$ are parameters, ω is a frequency, η is standard white noise, and ε is the noise amplitude. This means that the temperature changes periodically in time. The parameter S_0 represents nutrient supply (the resource available to species), and the parameter r describes the intensity of periodic forcing.

To simulate chaotic time forcing, we set

$$S = S_0 + R\theta(q(t)), \quad (14)$$

where $\theta(q)$ is a smooth function of the vector argument q , $q = (q_1, \dots, q_n)$ which describes a state of the population environment, and the dynamics of q is governed by trajectories of the noisy dynamical system, written in the Ito form:

$$dq = Q(q)dt + \sqrt{\varepsilon} dB(t), \quad (15)$$

where $B(t)$ is standard Brownian motion and Q is a smooth vector field. In the case $\varepsilon = 0$, we are dealing in (15) with a

system of differential equations, and we will suppose that its dynamics are well posed and has a compact attractor \mathcal{A}_Q . Then, for small ε , we can use the Freidlin-Wentzell theory,³³ and the properties of the noisy dynamical system (15) depend on the attractor structure of (15). For simplicity, we will consider here the case $\varepsilon = 0$.

For example, we can set $q = (x, y, z)$ and consider the Lorenz system, a simplified model of atmospheric dynamics given by

$$\begin{aligned} dx/dt &= \tau^{-1}(\alpha(y - x)), \\ dy/dt &= \tau^{-1}(x(\rho - z) - y), \\ dz/dt &= \tau^{-1}(xy - \beta z), \end{aligned} \tag{16}$$

where α, β, ρ are parameters, and $\tau > 0$ is a parameter that controls the speed of the trajectories. For $\varepsilon = 0$, this system shows a chaotic behaviour for $\alpha = 10, \beta = 8/3$ and $\rho = 28$. We construct θ as follows. The third component z in (16) describes the time evolution of temperature. We set $\theta(t) = (x(t) - \bar{x})/\mu_x$, where $\mu_x = \max(|x(t)|)$ on a large interval $[0, T]$ and \bar{x} is the average of $T^{-1} \int_0^T x(t) dt$ on this interval.

The time extended model reduces to the time independent model with constant S in the two opposite cases: (A) $\omega \gg 1$ and (B) $\omega \ll 1$. Assume $S = S(t)$ is defined by (13). In case (A), we can apply the averaging principle to (1) and (2) and replace $S(t)$ by S_0 in (2). This averaging also works for $S(t)$ defined by (14). The number $N_e(t)$ of coexisting species tends to a constant for large t . This asymptotic averaging is confirmed by numerical results, see below.

In case (B), we introduce a slow time $\bar{t} = \omega t$ and use a quasistationary approximation. Then, we obtain that the equilibria $\bar{x}(\bar{t}), \bar{v}(\bar{t})$ are functions of slow time. The number N_e of coexisting species is also a function of \bar{t} . Note that N_e is a measure of biodiversity in our model.

The numerical results for periodical and chaotic cases are as follows. For chaotic and fast periodic forcing and for large values of the resource supply S_0 systems (1) and (2) with $M = 1$ shows formidable stability when relative variations of S are not small, for example, have the order 40% (see Fig. 1) and even 80% (see Fig. 2). The fast periodic and chaotic oscillations usually decrease biodiversity, but the effect on the number of coexisting species is small: the numbers $N_e(T)$ of finally survived species (biodiversity) remain close for $R = 0$ (forcing is absent) and $R > 0$ (under forcing).

Typical situations, showing the dynamics of the number of coexisting species and how the environmental forcing sharply changes that number, are illustrated by Fig. 1 for the case of slow periodic forcing (see the black curve on that plot). This numerical result can be explained by the results of Sec. IV. In fact, for slow forcing, we can apply a quasistationary approximation, when at each time moment the population state is determined by the resource supply at that moment. Note that for $R = 0.8$ the slow periodic forcing leads to a catastrophe, when all the species go to extinct.

So, we observe that for the fast environmental oscillations our resource competition model is sufficiently stable even for large forcing amplitudes, whereas slow forcing can lead to mass extinctions.

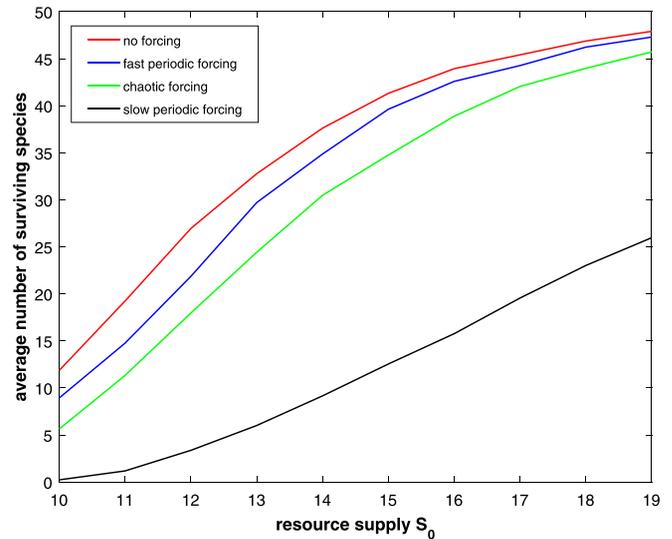


FIG. 1. This graph shows the number of coexisting species N_e for the model defined by (1) and (2) with $M = 1$ (a single resource v) on time interval $[0, 50]$ and with $N = 50$ species. The three cases are considered: (a) $S = S_0$ (no forcing), (b) $S = S_0 + R \sin(\omega t + \pi/2)$ (periodic external forcing), with $\omega = \pi$ (fast oscillations) and $\omega = 0.1$ (slow periodic forcing), and (c) $S_0 + R(x(t) - x_0)$, where $x(t)$ is a chaotic solution of the Lorenz system (16) and $R = 0.4S_0$. The threshold parameter δ for species abundances equals 0.5. To make comparison correct, we set x_0 equals to the time average of $x(t)$, and define α by $\alpha = R \max|x(t) - x_0|^{-1}$, then the maximal amplitudes of periodic forcing and chaotic one are close. For each of 10 values S_0 within the interval $[10, 20]$, we have made 100 tests, where for each test at initial time moment parameters of a random system (1) and (2) were taken as follows. The parameters were chosen as follows: $K_i = K = 3, \gamma_i = \gamma = 1, c_i = c = 0.1, D = 1, a_i$ are sampled according to the normal law $\mathbf{N}(2, 0.2)$. The mortality parameter r_i equal $R = 1$. The initial species abundances $x_i(0)$ were chosen as $X_0 z_i$, where $X_0 = 3$ and z_i are random positive numbers sampled according to the log-normal law, $\log z_i \in \mathbf{N}(-1, 0.2)$.

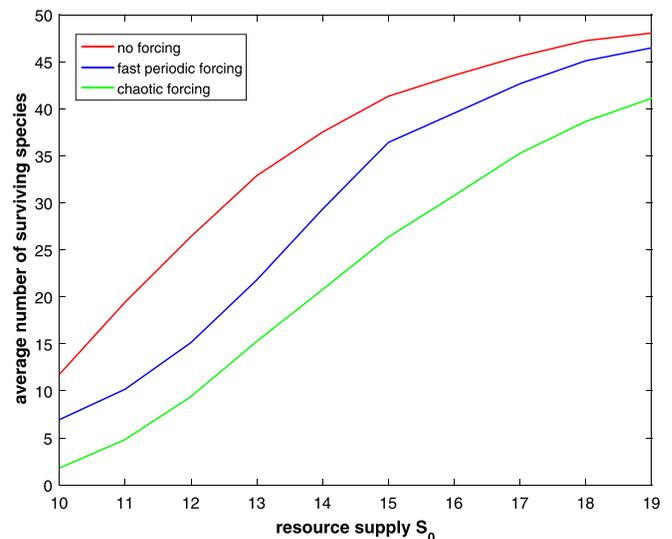


FIG. 2. This graph shows the number of coexisting species N_e for the model defined by (1) and (2) with $M = 1$ (a single resource v) on time interval $[0, 50]$ and with $N = 50$ species which extinct at $x_i(t) = \delta = 0.5$. The three cases are considered: (a) $S = S_0$ (no forcing), (b) $S = S_0 + R \sin(\omega t + \pi/2)$ (periodic external forcing), with $\omega = \pi$ (fast oscillations), and (c) $S_0 + R(x(t) - x_0)$, where $x(t)$ is a chaotic solution of the Lorenz system (16) and for large resource supply variations $R = 0.8S_0$. All other parameters are same as in Fig. 1.

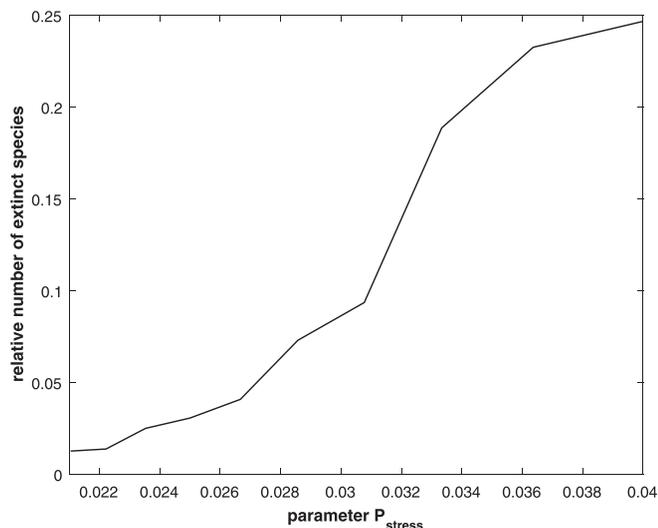


FIG. 3. For populations with parameters as mentioned in Fig. 1, this plot shows the dependence of extinctions size on the stress parameter P_{stress} for the models (1) and (2) under the fast periodic forcing. Here, $Z = (N - N_f)/N$, where N is the number of finally ($t = 50$) survived species when the forcing is turned off and N_f is where N is the number of finally ($t = 50$) survived species when the forcing is turned on, with $R = 0.4S_0$.

To conclude this section, let us note that according to Sec. IV, the robustness of resource competition system with respect to forcing should depend on the parameter P_{stress} . The numerical computations confirm this fact (see Fig. 3).

VI. CONCLUDING REMARKS

In this paper, a resource competition model for biodiversity is studied. The model describes a simple and easily understandable mechanism for resource competition and extends the well-known Huisman and Weissing model,¹⁴ taking into account species self-regulation, extinctions, and time dependence of resources. Our results show that when the averaged resource supply level is large enough, fast time oscillations in resource supply do not materially affect biodiversity (the number of coexisting species). This result is valid both for chaotic and periodic oscillations. The effect of oscillations becomes observable when the averaged resource value is sufficiently small. Then, typically, the oscillations (both chaotic and periodic) diminish biodiversity substantially, and this effect is stronger for slow environmental oscillations.

In our model, the largest extinctions occur when resource consumption reaches a maximal possible value, but there is a smooth continuum from extinctions of relatively small magnitude (the loss of a few species) to extinctions of relatively large magnitude (the loss of a great many species). Thus, we are not able to identify mass extinctions (in the sense of mass extinctions definition from Ref. 6 p. 278) as a quantitatively different regime (e.g., as it was obtained in Ref. 34). This is may be because our model does not include trophic levels such as primary producers, herbivores, and predators, or evolutionary processes such as speciation (cf. Ref. 11) Similarly, our analyses have focused on the conditions that lead to extinction. Representation of ecological structure and evolutionary processes such as these in future extensions of our

model will allow us to investigate the dynamics of recoveries from extinction, and this will permit investigations of how ecosystems rebuild and new ecologies emerge from the aftermath of extinction events.

Nevertheless, our model provides support, on theoretical grounds, for the importance of non-linear processes during the various extinction events that have punctuated Earth history. For example, the rapid loss of plant biodiversity during an extinction event in the Late Triassic period (200×10^6 years ago) has been attributed partly to a threshold response of plants to relatively minor increases in the concentration of carbon dioxide in Earth's atmosphere at this time.⁷ Additionally, when species reach maximal biodiversity in our model, the risk of large extinction events strongly increases, even under small environment changes, and random, chaotic, or periodic environment oscillations can also dramatically affect biodiversity. Thus, suggestions that the global diversity of life on Earth is capped somehow (see discussion in Ref. 2) are not incompatible with the results of our paper.

ACKNOWLEDGMENTS

We would like to thank Professor V. Kozlov, Professor U. Wennergren, and Professor V. Tkachev (Linköping University) for their useful discussion. The authors are grateful for the financial support from the Government of the Russian Federation through the Mega-Grant No. 074-U01. We also acknowledge the support from the Russian Foundation for Basic Research (RFBR) under the Grant Nos. 16-34-00733mol_a and 16-31-60070mol_a_dk. In addition, we gratefully acknowledge the support from the Division of Physics at the U.S. National Science Foundation (NSF) through Grant No. PHY-1066293. Finally, we thank the Statistical and Applied Mathematical Sciences Institute (SAMSI) and the Mathematical Biosciences Institute (MBI) for their support of this work.

- ¹M. R. Walter, R. Buick, and J. S. R. Dunlop, *Nature* **284**, 443–445 (1980).
- ²M. J. Benton and B. C. Emerson, *Palaeontology* **50**, 23–40 (2007).
- ³O. Walliser, *Global Events and Event Stratigraphy in the Phanerozoic* (Springer-Verlag, Berlin, 1996), p. 333.
- ⁴R. K. Bambach, *Annu. Rev. Earth Planet. Sci.* **34**, 127–155 (2006).
- ⁵M. J. Benton, *Science* **268**, 52–58 (1995).
- ⁶J. J. Sepkoski, “Phanerozoic overview of mass extinction,” in *Patterns and Processes in the History of Life*, edited by D. M. Raup and D. Jablonski (Springer-Verlag, Berlin, 1986), pp. 277–279.
- ⁷J. C. McElwain, J. Wade-Murphy, and S. P. Hesselbo, *Nature* **435**, 479–482 (2005).
- ⁸B. Schoene, J. Guex, A. Bartolini, U. Schaltegger, and T. J. Blackburn, *Geology* **38**(5), 387–390 (2010).
- ⁹S. T. Jackson and C. Weng, *Proc. Natl. Acad. Sci. U. S. A.* **96**, 13847–13852 (1999).
- ¹⁰L. Mander, J. Rodriguez, P. G. Mueller, S. T. Jackson, and S. W. Punyasena, *J. Quat. Sci.* **29**(7), 711–721 (2014).
- ¹¹R. V. Sole, J. M. Montoya, and D. H. Erwin, *Philos. Trans. R. Soc. London, Ser. B.* **357**, 697–707 (2002).
- ¹²R. Margalef, *Perspectives in Ecological Theory* (University of Chicago Press, Chicago, 1968).
- ¹³R. E. Plotnick and M. McKinney, *Palaios* **8**, 202–212 (1993).
- ¹⁴J. Huisman and F. J. Weissing, *Nature* **402**, 407 (1999).
- ¹⁵G. E. Hutchinson, *Am. Nat.* **95**, 137 (1961).
- ¹⁶X. Irigoien, J. Huisman, and R. Harris, *Nature* **429**, 863 (2004).
- ¹⁷S. Vakulenko, *Complexity and Evolution of Dissipative Systems: An Analytical Approach* (Walter de Gruyter, Berlin/Boston, 2013).

- ¹⁸D. Bagchi and P. K. Mohanty, *Phys. Rev. E* **84**, 061921 (2011).
- ¹⁹T. Caraballo, R. Colucci, and X. Han, *Nonlinear Anal. Real.* **31**, 661–680 (2016).
- ²⁰C. T. Kremer and C. A. Klausmeier, *Ecol. Lett.* **20**, 1158–1168 (2017).
- ²¹R. E. Amritkar and G. Rangarajan, *Phys. Rev. Lett.* **96**, 258102 (2006).
- ²²O. Ovaskainen and B. Meerson, *Trends Ecol. Evol.* **25**, 643–652 (2010).
- ²³G. Q. Sun, Z. Jin, Q. X. Liu, and B. L. Li, *BioSystems* **100**, 14–22 (2010).
- ²⁴N. R. Smith and B. Meerson, *Phys. Rev. E* **93**, 032109 (2016).
- ²⁵D. H. Rothman, *Sci. Adv.* **3**, e1700906 (2017).
- ²⁶D. Tilman, *Ecology* **58**, 338 (1977).
- ²⁷M. Hirsch, *SIAM J. Math. Anal.* **16**, 423 (1985).
- ²⁸V. Kozlov, S. Vakulenko, and U. Wennergren, *Phys. Rev. E* **95**, 032413 (2017).
- ²⁹I. Sudakov, S. A. Vakulenko, D. Kirievskaya, and K. M. Golden, *Ecol. Complexity* **32**, 209–216 (2017).
- ³⁰J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1988).
- ³¹S. B. Hsu, *Taiwanese J. Math.* **9**, 151–173 (2005).
- ³²H. L. Smith, “Dynamics of competition,” in *Mathematics Inspired by Biology*, Springer Lecture Notes in Mathematics, Vol. 1714 (Springer, 1999), pp. 191–240.
- ³³M. I. Freidlin and A. D. Wentzell, “Random perturbations of dynamical systems,” *Grundlehren der Mathematischen Wissenschaften [Fundamental Principles of Mathematical Sciences]* (Springer-Verlag, New York, 1998), Vol. 260, p. 430.
- ³⁴D. Jablonski, *Paleobiology* **31**, 192–210 (2005).