Species extinction at the various environmental forcing in a stochastic ecosystem model

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Abstract. This paper considers a stochastic multi-species single resource population model. The stochastic model is obtained from perturbing the supply of resource by a time dependent force. We use analytical investigations and numerical simulations to study the dynamics of our model under chaotic and periodic environmental oscillations, and show that the stochastic dynamics of our model exhibits a strong dependence on initial parameters.

1. Introduction

Currently, some ecosystems that previously exhibited stable dynamics are gaining or losing biomass under environmental temperature rise. It may lead to instability in both an ecosystem and its environment. For example, an unusual plankton biodiversity shift has been found in the Chukchi Sea [1, 2] and it may correlate with planetary warming. The plankton population expansion/decline could affect surface ocean temperature and delay sea ice re-freezing. How such ecosystems interact with the environment and if these interactions can modify the earth into a new state and, in turn, decline actively gaining biomass into mass extinction, are all poorly constrained.

In this paper, we have developed a new stochastic ecosystem model that allows us to investigate how the various environmental forcing affect biodiversity (the number of coexisting species), biomass (the number of species in an ecosystem) and extinction. This model is an extension of the well-known Huisman and Weissing model [3] that has been used to study phytoplankton. Our model accounts for species self-regulation, extinctions, and time dependence of resources. The stochastic dynamics of our model are strongly dependent on initial parameters. Using analytical investigations and numerical simulations we show that stochastic and nonlinear processes are likely to be important aspects of extinction. Our modeling provides a quantitative framework in which to investigate the dynamics of biospheric change.

First of all, we formulate the standard model of species coexistence. Next, we state the extended model which takes into account species extinctions and time oscillations of the resource. The chaotic forcing of the environment is described the Lorenz system. Follow the ideas of the
Freidlin-Wentzell theory [4], the theory of large deviations, we describe influences of a weak noise in the model. Finally we provide the results of some numerical simulations for this model.

2. The standard model of biodiversity

We consider the following standard model of biodiversity [3]:

\[ \frac{dx_i}{dt} = x_i(-r_i + \rho_i(v) - \sum_{j=1}^{N} \gamma_{ij} x_j), \]  
\[ \frac{dv}{dt} = D(S - v) - \sum_{j=1}^{N} c_j x_j \rho_j(v), \]

where

\[ \rho_j(v) = \frac{a_j v}{K_j + v}, \quad a_j, K_j > 0, \]

are Michaelis-Menten’s functions, \( x_i \) are species abundances, \( r_i \) are the species mortalities, \( D \) is the resource turnover rate, \( S \) is the supply of resource \( v \), and \( c_i \) is the content of the resource in the \( i \)-th species. These constants define how different species share resources. Note that if \( c_i = 0 \) then the equation for \( v \) becomes trivial and \( v(t) \rightarrow S \) for large times \( t \), i.e., the resource equals the resource supply.

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 \( a_i \) are specific growth rates and the \( K_i \) are self-saturation constants. The coefficients \( c_i \) determine how the species share the resource (nutrient supply).

When \( \gamma_{ij} = 0 \) this system is equivalent to those in works where the plankton paradox [3] is studied. For the case of \( M \) resources we have more complicated equations

\[ \frac{dx_i}{dt} = x_i(-r_i + \phi_i(v) - \sum_{j=1}^{N} \gamma_{ij} x_j), \]  
\[ \frac{dv}{dt} = D_j(S_j - v_j) - \sum_{k=1}^{N} c_{jk} x_k \phi_k(v), \]

where \( v = (v_1, v_2, ..., v_M) \), and

\[ \phi_j(v) = \min\left\{ \frac{a_j v_1}{K_{1j} + v_1}, ..., \frac{a_j v_M}{K_{Mj} + v_M} \right\}. \]

where \( a_j \) and \( K_{ij} > 0 \). This model is widely used for primary producers like phytoplankton and it can also be applied to describe competition for terrestrial plants [5]. Relation (6) corresponds to the von Liebig minimum law, but we can consider even more general \( \phi_j \) satisfying the conditions

\[ \phi_j(v) \in C^1, \quad 0 \leq \phi_j(v) \leq C_+, \]

where \( C_+ > 0 \) is a positive constant, and

\[ \phi_k(v) = 0, \quad \forall k \quad v \in \partial \mathbb{R}^N_+ \]

where \( \partial \mathbb{R}^N_+ \) denotes the boundary of the positive cone \( \mathbb{R}^N_+ = \{ v : v_j \geq 0, \forall j \} \). Note that condition (8) holds if \( \phi_j \) are defined by (6). Similarly as above, we assume that \( \sum_{k=1}^{N} c_{ik} = 1, \quad c_{ik} > 0 \).
3. The ecosystem model under noisy periodic and chaotic environmental forcing
In the remaining part of the paper we consider the case of a single resource $v$ (see eqs. 1, 2).

In this section, we consider our model forced by chaotic or periodic environmental forcing via the resource supply time variations as a periodic function of time [6]. We also include stochastic effects.

To simulate forcing we set
\[ S = S_0 + r \theta(q(t)) \]  
(9)
where the parameter $S_0$ represents nutrient supply (the resource available to species), and the parameter $r$ describes the intensity of periodic forcing. In equation 9 the function $\theta(q)$ is a smooth function of the vector argument $q$, $q = (q_1,...,q_n)$ which describes a state of the ecosystem environment (for example, a state of the atmosphere), and the dynamics of the $q$ is governed by trajectories of the noisy dynamical system, written in the Ito form:
\[ dq = Q(q)dt + \sqrt{\epsilon} dB(t), \]  
(10)
where $B(t)$ is the standard Brown motion and $Q$ is a smooth vector field, $\epsilon > 0$. In the case $\epsilon = 0$ we are dealing in (10) with a system of differential equations
\[ \frac{dq}{dt} = Q(q), \]  
(11)
and we will suppose that its dynamics are well posed and has a compact attractor $A_Q$.

Choosing different $Q$, we can obtain different kinds of forcing. For example, to obtain a periodical forcing we can take $q = (q_1,q_2)$, $\theta = q_1$ and $Q_1 = q_2, Q_2 = -\omega^2 q_1$ that gives
\[ S = S_0 + r \sin(\omega t) + \sqrt{\epsilon} B(t) \]  
(12)
where $\omega$ is a frequency of the periodic noisy forcing, and $\epsilon > 0$ defines a noise amplitude.

To describe chaotic forcing, we can set $q = (x,y,z)$ [6] and consider the Lorenz system [7], a rough model of atmospheric dynamics given by
\[ \frac{dx}{dt} = \tau^{-1}(\alpha(y-x)), \frac{dy}{dt} = \tau^{-1}(x(\rho-z)-y), \frac{dz}{dt} = \tau^{-1}(xy-\beta z), \]  
(13)
where $\alpha, \beta, \rho$ are parameters, and $\tau > 0$ is a parameter that controls the speed of the trajectories. For $\epsilon = 0$ that system shows a chaotic behaviour for $\alpha = 10, \beta = 8/3$ and $\rho = 28$. We assign the function $\theta$ as follows. The third component $z$ in (13) describes the time evolution of temperature $T = z$. Then, assuming that $S = S_0 + rz$ we obtain a chaotic forcing.

In the noisy case for small $\epsilon > 0$ we can use the Freidlin-Wentzell theory [4]. The time extended model reduces to the time independent model with constant $S = S_0$ in the two opposite cases: (A) $\omega \gg 1$ and (B) $\omega \ll 1$. Assume $S = S(t)$ is defined by (12). In case (A), we can apply the averaging principle to (4), (5) and replace $S(t)$ by $S_0$ in (5). This averaging also works for $S(t)$ defined by (9). The number $N_e(t)$ of coexisting species tends to a constant for large $t$. This asymptotic approach is confirmed by numerical results in a large diapason of parameter values.

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.

4. Biodiversity and resource supply in the ecosystem model
Let us consider the Cauchy problem for the system given by (1) and (2) on a time interval $[0,T]$,
where the initial data are given by
\[ x_i(0) = X_i > 0 \]  
(14)
This graph shows that in some rare cases the time oscillating supply $S(t)$ can increase biodiversity. Here, $S_1 = 0.8S_0$ for time depending model and $S_1 = 0$ for time independent one. In case 1, the probability that the $N_e(T_t)$ for the time dependent model is larger than $N_e(T_t)$ for the time independent model with $S_1 = 0$. In case 2, the probability that the $N_e(T)$ for the time dependent model is larger than $N_e(T_t)$ for the model with $S_1 = 0$.

and $T_t$ is a positive number. We assume that $N >> 1$ (the case of a large ecosystem) and $X_i > 0$ is distributed randomly according to a lognormal law with parameters $a, \sigma$. The corresponding distribution density is given by

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

We assume that the coefficients $a_i$ are random numbers obtained from the normal distribution $\mathbf{N}(\bar{a}, \sigma_a)$. Similarly $K_i$ are distributed by $\mathbf{N}(\bar{K}, \sigma_K)$, $r_i$ are distributed by $\mathbf{N}(\bar{r}, \sigma_r)$ etc. The share coefficients $c_i$ are taken as random numbers uniformly distributed on $[0, 1/N]$.

In some cases the strongly time oscillating supply $S(t)$ defined by (12) can increase biodiversity, $N_e(T_t)$ at $S_1 = 0.8S_0$ is grater than $N_e(T_t)$ at $S_1 = 0$, see Figure 1. In case 1, we calculate the probability that the periodic oscillations of the nutrient resource will increase biodiversity. Also, we define the probability (case 2) that the periodic oscillations of the nutrient resource will decrease biodiversity. We note this plot (Figure 1) is obtained by the Euler method with the time step 0.001 for the following parameter values: $N = 20, \bar{a} = 10, \sigma_a = 2, \bar{r} = 1, \sigma_r = 1, D = 3, T_t = 10, \delta = 0.1, X_0 = 1, V_0 = 10, \bar{K} = 5, \sigma_K = 1$. When the value of $\epsilon$ is large ($\epsilon = 10$) the noise is large. To compute the probabilities, $M = 50$ solutions to the Cauchy problems were obtained with random data. The procedure was the same for both the time dependent and time independent models.
Figure 2. This graph shows the dependence of the number $N_e$ of coexisting species on the parameter $\tau$ in the case of chaotic supply dynamics defined by the Lorenz system. The time interval $T_t = 80$, $S_0 = 5$ and $S_1 = 4$.

For large values $S_0$ and $\omega \in (3, 8)$, when the period of time oscillations is much less that the system from (1) and (2) shows formidable stability even for $S_1$ close to $S_0$. The periodic and chaotic oscillations always decrease biodiversity, but diminishing the numbers of coexisting species is small: the numbers $N_e(T_t)$ are close or they coincide. To obtain an essential biodiversity diminishing, it is necessary to take $S_1 = 0.95S_0$ that corresponds to the case of very strong oscillation. The counterintuitive effect of biodiversity increasing under oscillations is possible when the averaged resource $S_0$ is not large (see Figure 1). Note that this effect can be explained. In fact, the time oscillations, increasing supply, can conserve some species which were close to extinction.

Figure 2 shows the dependence of the number $N_e$ on the speed parameter $\tau$ when the resource $S(t)$ evolves chaotically according to (13). We observe that the biodiversity is a decreasing function of the speed parameter. This decrease depends on the averaged supply level $S_0$, for larger $S_0$ the effect is weaker.

5. Conclusion and discussion

In this paper, a resource model for species ecosystem is developed, which generalizes the well known model [3] and takes into account species self-regulation, extinctions, and time dependence of resources. Such conceptual models describe a simple and easily understandable mechanism for resource competition.

In the case of time dependent resource oscillations two regimes are found which can be investigated analytically. The first regime describes fast oscillations. Then one can proceed by averaging the resource over time. The second regime arises when the resources change slowly, here we use the quasistationary approximation.

The numerical results show that when the averaged supply level is large enough, sufficiently fast resource time oscillations do not affect essential biodiversity, i.e., 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, however, in some cases oscillations with a noise component can increase biodiversity.

The proposed model can be extended to the case when the environment has feedback with the ecosystem [8] or to the case when the resource is consuming randomly [9]. We also apply the ideas of the Freidlin-Wentzell theory to ecological niche modeling [10]. These results can be interesting for the future investigation of the biodiversity problems.

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