Minor climatic fluctuations lead to species extinction in a conceptual ecosystem model

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Abstract

The extinction of species is a core process that affects the diversity of life on Earth. One way of investigating the causes and consequences of extinctions is to build conceptual ecological models, and to use the dynamical outcomes of such models to provide quantitative formalization of changes to Earth’s biosphere. In this paper we propose and study a conceptual resource model that describes a simple and easily understandable mechanism for resource competition, generalizes the well-known Huisman and Weissing model, and takes into account species self-regulation, extinctions, and time dependence of resources. We use analytical investigations and numerical simulations to study the dynamics of our model under chaotic and periodic climate oscillations, and show that the stochastic dynamics of our model exhibit strong dependence on initial parameters. We also demonstrate that extinctions in our model are inevitable if an ecosystem has the maximal possible biodiversity and uses the maximal amount of resources. Our conceptual modeling provides theoretical support for suggestions that non-linear processes were important during major extinction events in Earth history.

Lead Paragraph

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. Well-known examples of extinction events in Earth history include the event that destroyed the dinosaurs, and the process of extinction is of particular current scientific interest because it is thought that we may be approaching a mass extinction driven by anthropogenic activities. In this paper, we
have developed a new conceptual ecosystem model that allows us to investigate how chaotic
and period oscillations in Earth’s climate affect biodiversity and extinction. This model is
an extension of the well-known Huisman and Weissing model 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, and using analytical investigations and numerical simulations we show
that non-linear processes are likely to be important aspects of extinction. In our model, ex-
tinctions are inevitable if an ecosystem has the maximal possible biodiversity and uses the
maximal amount of resources. Our conceptual modeling provides a quantitative frame-
work in which to investigate the dynamics of biospheric change.

1 Introduction

The current state of the biosphere is a product of the evolutionary process that began with the origin of
life around 3.5Ga. Since this time, life has expanded from a single common ancestor to the diversity of
biological forms that are present on the Earth today. 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 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. Of these, several stand out for their
sheer magnitude. 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 wide-spread higher taxon
during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing
diversity” (Sepkoski (1986), p. 278).

Paleobiological studies indicate that extinction events are frequently associated with major environ-
mental 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 event, or to the opening of the Atlantic ocean in the case of the late Triassic extinction. 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. 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 ecosystems beyond their resilience. Ecosystems represent functional en-
tities 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. Conceptual
ecological models do not represent every single complex biotic and abiotic interaction that leads to ecosys-
tem assembly and disruption, but nevertheless, the dynamical outcomes of such models can provide a
quantitative formalization for dynamical biospheric change, and can serve as a counterpoint to empirical
studies of biospheric evolution based on observational data.

In this paper, we consider a new conceptual ecosystem model that not only gives a quantitative formal-
ization but also 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 climatic
change, for example), self-limitation effects, as well as extinctions are accounted for. Our conceptual model
represents an extension of the Huisman and Weissing model, which accounts for extinctions but only in-
cludes a single resource and does not include any climatic variation. The parameters of our model depend on
the state of the environment via time dependent coefficients. This system is inspired by some phytoplankton
models, and under certain assumptions can be derived from them, and if the resource turnover rate is
large enough our model reduces to a Lotka-Volterra system.

Our paper is organized as follows: (1) we first state the standard model of species coexistence; (2) we
then extend the standard model of species coexistence by introducing extinctions and climate, and assuming that the parameters depend on some environmental forcing that can oscillate (for example temperature); (3) we then consider the problem of extinction in our extended model in more detail; (4) finally, we use analytical investigations and numerical simulations to study the dynamics of our extended model under chaotic and periodic climate oscillations. Our principal results are that the stochastic dynamics of our model exhibit strong dependence on initial parameters. We show that extinctions are inevitable if an ecosystem 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 extinctions. \[18\]

### 2 The standard model of species coexistence

We consider the following standard model of population of biodiversity: \[14\]

\[
\frac{dx_i}{dt} = x_i(-r_i + \phi_i(v) - \sum_{j=1}^{N} \gamma_{ij} x_j), \tag{1}
\]

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

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

\[
\phi_j(v) = \min\left\{ \frac{a_j v_1}{K_{1j} + v_1}, \ldots, \frac{a_j v_M}{K_{Mj} + v_M} \right\}. \tag{3}
\]

where \(a_j\) and \(K_{ij} > 0\). The terms \(\gamma_{ij} x_i\) 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 \(c_{jk}\) 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. \[19\] 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 \(\phi_j\) satisfying the conditions

\[
\phi_j(v) \in C^1, \quad 0 \leq \phi_j(v) \leq C_+, \tag{4}
\]

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

\[
\phi_k(v) = 0, \quad \forall k \quad v \in \partial R^N_+, \tag{5}
\]

where \(\partial R^N_+\) denotes the boundary of the positive cone \(R^N_+ = \{v : v_j \geq 0, \forall j\}\). Note that condition (5) holds if \(\phi_j\) 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 system (1), (2) on a time interval \([0, \tau]\), where initial data are given by

\[
x_i(0) = X_i > 0, \quad v_k = V_k \in (0, S_k), \tag{6}
\]

and \(\tau\) 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 log-normal law with parameters \(a, \sigma\). The corresponding distribution density is given by

\[
f(x) = \frac{1}{x\sigma \sqrt{2\pi}} \exp \left[ \frac{-(\ln x - a)^2}{2\sigma^2} \right]. \tag{7}
\]
Suppose we simplify the problem that concurrence is absent and
\[ \gamma_{ij} = \gamma \delta_{ij}, \quad \gamma > 0. \] (8)

One can show, by standard estimates, that the Cauchy problem (1), (2) and (6) is 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\(^{20}\) since \( \frac{\partial F_j(x)}{\partial x_i} > 0 \) for \( j \neq i \).

**Assertion.** Under condition (5) the dynamical system defined by (1), (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. (2017) and Sudakov et al. (2017).\(^{21,22}\) The resource \( R(\bar{x}) \) 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 system (1), (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 follows from Theorem 1 in Kozlov et al. (2017).\(^{21}\)

The problem can be simplified for large turnovers \( (D_k > 1) \). Then one can show \(^{22}\) that systems (1) and (2) reduce to Lotka-Volterra systems of a special form.

3 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 environmental influence on the dynamics of the modified systems (1) and (2). That effect will be considered in the next section.

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 parameter \( \delta > 0 \) and suppose that if the \( i \)-th species abundance \( x_i(t) \) becomes less than \( \delta \), i.e., \( x_i(t_0) = \delta \) and \( \frac{dx_i(t_0)}{dt} < 0 \) for some \( t \) 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 \( t > t_0 \). For the case of a single resource this extended model is proposed and investigated in more detail in Kozlov et al. (2017).\(^{21}\)

Note that after this modification the model stays mathematically well posed.\(^{21}\) 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 \( t_0 < t_1 < \ldots < t_m < \ldots \) 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 \( \lim_{t \to +\infty} N_e(t) = N_\infty = 0 \), then all the species vanish. If \( N_\infty > 0 \), then on some infinite semiaxis \( (t_m, +\infty) \) the modified system is equivalent to model (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.\(^{6,21}\) For some initial abundances all species coexist, whereas for other initial data only a few species can survive over long timescales. Usually, the environmental influence diminishes the number of surviving species. Nonetheless sometimes the environmental chaos can stabilize the ecosystem, increasing the number of coexisting species. Systems with large numbers of species are stabler than 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.

4 A more detailed look at extinctions in our model

We follow Kozlov et al. (2017)\(^{21}\) but will consider the problem of extinction in more detail. Let us consider the case of a single resource \( M = 1, v_1 = v \) for large \( D \). Let \( \phi_i = a_i \phi(v) \), where \( \phi(v) = \frac{1}{\pi+v} \). Then, according
corresponding decrease of the consumed resource amount. We also include stochastic effects. For example, we can suppose that a small number of species leads to a small variation in the abundance of each species. In this section, we consider extinctions in our model forced by chaotic and periodic environmental temperature changes. While we have studied this situation numerically and the results obtained are shown in Fig. 1.

5 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 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

$$S = S_0 + r \sin(\omega t) + \epsilon \eta(t)$$  \hspace{1cm} (12)
Figure 1: a) This graph shows the number of coexisting species $N_e(t)$ in the two cases. In case 1, the number of species $N_e(t)$ coexists in a system depending on $t$ when the nutrient supply $S$ is a constant, $S_0 = 200$ and $S_1 = 0$. In the case 2, the number of species $N_e(t)$ coexists in a system with time varying resource, $S_0 = 200, S_1 = 180$. b) This plot shows the dependence of the number of coexisting species (vertical axis) on $S$ (horizontal axis) for a random population composed as follows. The parameter $K = 4$ and $\gamma = \gamma = 1$. The parameters $a_i$ are chosen according to log-normal law with average 1 and $\sigma = 0.03$. The mortality parameter $r_i = R$ is chosen so that the species abundances are close to the limit value $\delta = 1$, $R = 14$. The parameters $c_i = c(1 + \tilde{c}_i)$ where $c = 0.1$ and $\tilde{c}_i$ are uniformly distributed on $[0, 1]$. The red curve line corresponds to the non-perturbed case and the blue curve describes biodiversity when the resource limit $S$ is diminished on 10 percents with respect to the non-perturbed value.

where $S_0, S_1 > 0$ are parameters, $\omega$ is a frequency, $\eta$ is standard white noise and $\varepsilon$ 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

$$S = S_0 + r\theta(q(t))$$

(13)

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

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

(14)

where $B(t)$ is the standard Brown motion and $Q$ is a smooth vector field. In the case $\varepsilon = 0$ we are dealing in (14) with a system of differential equations, and we will suppose that its dynamics are well posed and has a compact attractor $\mathcal{A}_0$. Then for small $\varepsilon$ we can use the Freidlin-Wentzell theory,[23] and the properties of the noisy dynamical system (14) depend heavily on the attractor structure.

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

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

(15)

where $\alpha, \beta, \rho$ are parameters, and $\tau > 0$ is a parameter that controls the speed of the trajectories. For $\varepsilon = 0$ that system shows a chaotic behaviour for $\alpha = 10, \beta = 8/3$ and $\rho = 28$. We construct $\theta$ as follows. The
third component $z$ in (15) describes the time evolution of temperature. We set $θ(t) = (z(t) - ̄z)/μ_z$, where $μ_z = \max(|z(t)|)$ on a large interval $[0, T]$ and $̄z$ is the average of $T^{-1} \int_0^T z(t) dt$ on this interval.

The time extended model reduces to the time independent model with constant $S$ in the two opposite cases: (A) $ω >> 1$ and (B) $ω << 1$. Assume $S = S(t)$ is defined by (12). In case (A), we can apply the averaging principle to (1), (2) and replace $S(t)$ by $S_0$ in (2). This averaging also works for $S(t)$ defined by (13). 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 $tilde{t} = ωt$ and use a quasistationary approximation. Then we obtain that the equilibria $tilde{z}(tilde{t}), tilde{v}(tilde{t})$ are functions of slow time. The number $N_e$ of coexisting species is also a function of $tilde{t}$. Note that $N_e$ is a measure of biodiversity in our model.

Before we present some numerical results, we will show (using methods of the Freidlin-Wentzell theory [23]) the existence of three sharply different extinctions scenarios in our model, which can be generated by random and non-random climate variation induced by (14).

Our primary goal here is to find the probabilities of extinctions in our model. For simplicity, we consider the case of a single resource and denote by $ΔS_c$ the critical value of supply change that leads to an extinction, and let $O(ΔS_c)$ be the set of values $q$ corresponding to that value:

$$O(ΔS_c) = \{q : θ(q) = ΔS_c\}.$$  

Following [23] we define distance between $d(q, q')$ between two points $q$ and $q'$ by

$$d_{FW} = \inf_{p(t), p(0) = q, p(T) = q'} \int_0^T (dq/dt - Q(q))^2 dt.$$  

The distance between the two sets $A$ and $B$ is defined as $dist(A, B) = \inf_{q \in A, q' \in B} d_{FW}(q, q')$. We note in particular that if $q, q'$ lies in the same connected component of the attractor then $d_{FW}(q, q') = 0$. We assume first that the attractor consists of a single connected component. Then the probability $P_{c, ε}$ to attain the critical value starting from a point on the attractor satisfies the estimate

$$\lim_{ε→0} ε^{-1} \log P_{c, ε} = \inf_{q \in A, q' \in O(ΔS_c)} d_{FW}(q, q').$$  

Figure 2: The plots show the dependence of the number of coexisting species (vertical axis) on time (horizontal axis). The blue line corresponds to the case when all parameters do not depend on time and periodic environmental forcing does not influence the system; the red line describes time evolution under periodic environmental forcing influence. a) The plot shows environmental forcing dependence diminishes biodiversity. b) The plot shows environmental forcing dependence increases biodiversity.
Using that relation and known results \[23\] we obtain that there are three possible extinction probability scenarios as a function of \( \varepsilon \).

**I** If the intersection \( I = \mathcal{O}_1 \cap \mathcal{O}(\Delta S_c) \) is not empty for all \( \Delta S_c \) then the probability \( P_{c,\varepsilon} \) is not exponentially small, i.e., \( \lim_{\varepsilon \to 0} \varepsilon^{-1} \log P_{c,\varepsilon} = 0 \). It is a catastrophic scenario when the extinction of all species is quite probable.

**II** The intersection \( I = \mathcal{O}_2 \cap \mathcal{O}(\Delta S_c) \) is empty for all \( \Delta S_c \). Then the probability \( P_{c,\varepsilon} \) are exponentially small both for large and small extinctions.

**III** The intersection \( I = \mathcal{O}_3 \cap \mathcal{O}(\Delta S_c) \) is not empty for some \( \Delta S_c \) but it is empty for larger \( \Delta S_c \). Then it is possible that the probability \( P_{c,\varepsilon} \) is not small for extinctions involving relatively few species but that probability is exponentially small for extinctions involving relatively many species. In this case, there is a sharp transition in the probabilities of small losses of biodiversity and great losses of biodiversity.

If the attractor consists of \( n_A > 1 \) connected components \( \mathcal{O}_i^{(i)} \) we observe that there are possible additional effects that may be caused by climate bifurcations (tipping points). Then the climate bifurcation can correspond to a transition from a connected component to another one that may lead for example to a transition from scenario I to scenario II (or III), and vice versa.

The numerical results for periodical and chaotic cases are as follows. For large values of \( S_0 \) and \( \omega \in (3,8) \), when the period of time oscillations is much less, system (1), (2) with \( M = 1 \) shows formidable stability even for \( r \) close to 0. The periodic and chaotic oscillations always decrease biodiversity, but the effect on coexisting species is small: the numbers \( N_i(T) \) remain close or they coincide. To obtain diminishing biodiversity, it is necessary to take \( r = 0.05S_0 \) which corresponds to the case of very strong oscillation. In rare situations, the counterintuitive effect of biodiversity increasing under oscillations is possible. It may happen when the averaged resource \( S_0 \) is not large. Note that this effect can be explained. In fact, the time oscillations and increasing supply can conserve some species that were close to extinction.

Typical situations showing the dynamics of the number of coexisting species and how the environmental forcing changes that number, are illustrated in Fig. 2. Here we assume that the \( i \)-th species survives while \( x_i(t) > X_{ext} \), where \( X_{ext} \) is a small parameter. The initial species abundances and all parameters are defined by log-normal distributions, \( \phi_i(t) \) are distributed by the standard normal law \( N(0,1) \). Initially the number of species is \( N = 100 \). We see that initially the number of coexistence species declines rapidly. This effect has a clear interpretation: the resources can only support some bounded number of species. Further, we observe a slow extinction process, which progresses differently according to whether there is or is not an environmental influence in the model evolution (see Fig. 3).

These plots and other numerical results can be interpreted as follows.

1) If the population is stable, i.e. all species survive, then periodic temporal dynamics of the environment increase the species abundances and the total biomass. If the environment evolves with chaotic or random components, this effect diminishes.

2) If the population experiences harsher conditions, environment oscillations can lead to extinction of all species. However, if the species survive, the environmental oscillations can increase biomass.

### 6 Concluding remarks

In this paper, a conceptual resource model for biodiversity is proposed and studied. Our conceptual model describes a simple and easily understandable mechanism for resource competition, and generalizes the well-known Huisman and Weissing model, [14] taking into account species self-regulation, extinctions, and time dependence of resources. Our numerical results show that when the averaged resource supply level is large enough, fast time oscillations in resource supply do not effect essential 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, although in some cases oscillations with a noise component can increase biodiversity.
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 (sensu Sepkoski (1986)[6]) as a quantitatively different regime (e.g. Jablonski (2005)[24]). This is likely to be because our conceptual model currently does not include trophic levels such as primary producers, herbivores and predators, or evolutionary processes such as speciation (cf. Sole et al. (2002)[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 conceptual 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 million 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 ecosystems 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 Benton and Emerson (2007)[2]) are not incompatible with the results of our conceptual modeling.

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