

Extinction Events and Species Lifetimes in a Simple Ecological Model

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A model for large-scale evolution recently introduced by Amaral and Meyer is studied analytically and numerically. Species are located at different trophic levels and become extinct if their prey becomes extinct. It is proved that this model is self-organized critical in the thermodynamic limit, with an exponent of 2 characterizing the size distribution of extinction events. The lifetime distribution of species, cutoffs due to finite-size effects, and other quantities are evaluated. The relevance of this model to biological evolution is critically assessed. [S0031-9007(98)07821-1]

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In complex systems, not everyone is equal. In a human society, different individuals fulfill different roles. Similarly, companies occupy different niches in an economic system, and species occupy different niches in an ecosystem. Among the rich variety of possible structures in these systems, power laws take a prominent place and characterize the size distribution of cities [1], incomes [2], and ecological extinction events [3]. Several models that lead to such a scaling behavior have been introduced in the literature (for some recent examples see [4–9]); however, the picture is far from complete.

While reality is certainly best described by a complicated web of interactions at all levels, the simplest type of models that incorporate qualitative differences between individuals (or companies or species) are hierarchical or layered models, where individuals in a given layer affect individuals in the neighboring layer. Such a structure can, e.g., be found in ecosystems, where species are at different levels in a food chain, or in economic systems, where different types of producers are located at different places in a production chain. Recently, Amaral and Meyer [10] introduced a model for large-scale evolution that contains several trophic levels. Using computer simulations, they found a power-law size distribution of extinction events. It is the intention of this paper to prove that this model is indeed critical in the thermodynamic limit, and to evaluate some of its properties analytically and numerically.

The model is defined as follows: Species can occupy niches in a model ecosystem with L levels in the food chain and N niches in each level. Species from the first level $l = 0$ do not depend on other species for their food, while species on the higher levels l feed each on k or less species in the level $l - 1$. Changes in the system occur due to two processes. (a) Creation of new species with a rate μ in each empty niche. If the new species arises in a level $l > 0$, k prey species are chosen at random from the layer below. A species never changes its prey after this initial choice. (b) Extinction: At rate p , species in the first level $l = 0$ become extinct. Any species in layer $l = 1$ and subsequently in higher levels, for which all preys have become extinct, also become extinct immediately. This

rule leads to avalanches of extinction that may extend through several layers and will be shown below to obey a power-law size distribution. These rules are slightly different from [10]; however, the results can be expected to be the same. Since the dynamics of the model are characterized by slow driving (speciation), and by rare and fast avalanches (or extinction events), the model is self-organized critical [11].

Let us first discuss the case $k = 1$, where each species in layers $l > 0$ feeds on one prey species only. In this case, each species is connected to exactly one species in layer $l = 0$ via a food chain. Since several species can feed on the same prey, the structure of the ecosystem looks like a set of trees, each consisting of all species that are connected to the same bottom species. If a bottom species has existed for a long time, the tree connected to it extends through many layers and consists of a large number of species. If a bottom species is young, only a few species of the lowest layers are connected to it, and the corresponding “tree” is small. When a bottom species becomes extinct, the whole tree of species connected to it also becomes extinct. Since each bottom species becomes extinct with the same rate p , the size distribution of extinction events is identical to the size distribution of trees.

After some time, the system can be expected to be in a stationary state where the speciation and extinction rates balance each other within each layer, leading to constant mean species densities. Of course, for a finite system size N , there may exist considerable fluctuations around the mean density. Let ρ_l denote the species density in layer l . The equation of motion for ρ_l is

$$d\rho_l/dt = \mu(1 - \rho_l) - p\rho_l, \quad (1)$$

leading to a stationary density $\rho_l = \mu/(p + \mu)$ in each layer. The lifetime distribution of species is an exponential,

$$p_T(T) = p \exp(-pT), \quad (2)$$

and is the same for each species. Let $s_l^{(i)}(t)$ denote the number of species in layer l that are connected to bottom

species i . Since each newly created species picks its prey species at random among the existing species in layer $l - 1$, the growth of $s_l^{(i)}(t)$ is given by

$$ds_l^{(i)}/dt = [\mu(1 - \rho_l)/\rho_{l-1}]s_{l-1}^{(i)} = ps_{l-1}^{(i)}, \quad (3)$$

as long as bottom species i does not become extinct. The second identity holds in the stationary state. The size of a tree, $S^{(i)} = \sum_l s_l^{(i)}$ obeys consequently $dS^{(i)}/dt = pS^{(i)}$, leading to

$$S^{(i)}(t) = S^{(i)}(0) \exp(pt), \quad (4)$$

where the initial tree size is $S^{(i)}(0) = 1$, since only the bottom species is present (the age of a tree is measured from the creation of the bottom species on).

The size distribution of trees, $P(S)$, is related to the age distribution of trees, $P(t)$, via

$$P(S) = P(t)dt/dS. \quad (5)$$

Now, $P(t)$ obeys the equation $dP(t)/dt = -pP(t)$, or $P(t) \propto \exp(-pt)$, which can be combined with Eqs. (5) and (4) to give

$$P(S) \propto S^{-2}. \quad (6)$$

Since the size distribution of trees is identical to the size distribution of extinction events, the exponent characterizing the extinction events is $\tau = 2$, in excellent agreement with the numerical findings by Amaral and Meyer [10].

There are two types of finite-size effects that modify this power law: First, there are effects due to the finite size of N , when the number of layers L is large. Since the height of a tree is proportional to its age, the number of trees extending up to layer l decreases as $\exp(-l)$, and the mean number of species within layer l that belong to the same tree is proportional to $\exp(l)$. Thus, all species in layers $l > \ln N$ belong to the same tree and are simultaneously destroyed. Consequently, trees cannot become much higher than $\ln N$ layers, and there is a cutoff to the power law $P(S) \propto S^{-2}$ at $S_{\max} \sim N \ln N$. If the number of layers L is of the order $\ln N$, the size of the largest extinction event is of the order NL , which is the total system size. Indeed, events of this size are reported in [10], where $N = 1000$ and $L = 6 \simeq \ln N$. (These authors probably have chosen $k > 1$.)

Since real ecological systems have only a few trophic levels, it is important to also study the case $L < \ln N$, where the properties of the system do not depend on N and finite-size effects are due to the finite number of layers, L . Since the height of trees grows linearly in time, while their size S grows exponentially, the typical size of the largest trees is now given by $S_{\max} \propto \exp L$. On the other hand, each extinction event destroys on an average the same number of species in each layer, since the same number of species are created in each layer. Since each extinction

event destroys one species in the bottom layer, the mean number of species destroyed per extinction event is $\bar{S} = L$. Together with the relation

$$\bar{S} = \int_0^{S_{\max}} SP(S) dS$$

and the assumption that $P(S)$ obeys a power law, this leads again to $P(S) \propto S^{-2}$ for $S < S_{\max}$.

Figure 1 shows the size distribution of extinction events for different values of L . The size S is scaled by $\exp(L)$, and curves for different L collapse nicely. The number of layers in this simulation is not large enough to show the power-law exponent τ over a large scaling regime, but it is chosen such that it is close to the number of layers in real ecosystems.

The results obtained so far hold for a broad range of values of the parameters μ and p . Of course, since μ and p are defined as rates, one must make sure in simulations with discrete time steps that they are small enough so that no artificial effects occur due to the parallel updating of many sites. Also, there is assumed to be a time scale separation between extinction events which are fast on evolutionary time scale, and the creation rate of new species, which is much slower. Only in this case one can neglect the interference between new speciations and the extinction avalanches.

Let us next discuss the properties of the model in the case $k > 1$. Each newly created species feeds on k species in the layer below, and becomes extinct only after all k prey species have become extinct. Older species feed on less and older prey species and are therefore more likely to become extinct during a given time interval than younger species. In contrast, for $k = 1$ each species becomes extinct with the same probability, irrespective of its age. This feature seems to be present in the fossil data [12]. Choosing $k > 1$ introduces correlations in age and extinction

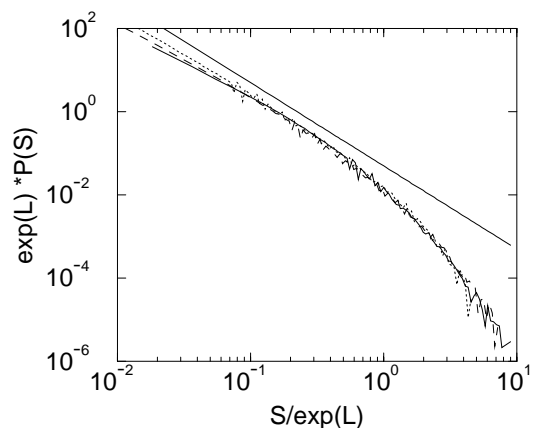


FIG. 1. The size distribution of extinction events for $k = 1$, $p = 0.05$, $\mu = 0.02$, and $L = 4$ (solid line), $L = 5$ (dashed line), and $L = 6$ (dotted line). The straight line is a power law with the exponent $\tau = 2$.

probability between species and their preys that make analytic treatment harder.

Figure 2 shows the size distribution of extinction events for $k = 3$, $L = 6$, and $N = 999$. As in a similar plot in [10], this size distribution appears to be a power law with extinction events up to the system size. In order to decide whether the system is indeed in a critical state, or whether the apparent power law is just due to a lucky choice of parameters, we have to discuss the system in the thermodynamic limit $N, L \rightarrow \infty$ with $L < \ln N$.

Let $P_T^{(l)}(T)$ denote the lifetime distribution of newly created species in layer l . The following calculation relates $P_T^{(l)}(T)$ to $P_T^{(l-1)}(T)$. The preys of a newly created species in layer l are chosen at random from all the species in layer $l - 1$. Since species are created with a constant rate in each layer, the distribution of the remaining lifetime τ of the prey species of a newly created species is given by $P_T^{(l-1)}(\tau)$, which is related to $P_T^{(l-1)}(T)$ via

$$\begin{aligned} P_T^{(l-1)}(\tau) &= \frac{\int_{\tau}^{\infty} dT P_T^{(l-1)}(T)}{\int_0^{\infty} d\tau \int_{\tau}^{\infty} dT P_T^{(l-1)}(T)} \\ &= \int_{\tau}^{\infty} dT P_T^{(l-1)}(T) / \bar{T}^{(l-1)}, \end{aligned} \quad (7)$$

where $\bar{T}^{(l-1)}$ is the mean lifetime of species in layer l . The probability that a species created at time $T = 0$ lives for a time T is identical to the probability that the last of its prey species becomes extinct at time T , leading to

$$\begin{aligned} P_T^{(l)}(T) &= \left[1 - \int_T^{\infty} P_T^{(l-1)}(\tau) d\tau \right]^{k-1} k P_T^{(l-1)}(T) \\ &= \frac{\partial}{\partial T} \left[\int_0^T d\tau P_T^{(l-1)}(\tau) \right]^k. \end{aligned} \quad (8)$$

The asymptotic lifetime distribution of newly created species for large l is obtained from Eqs. (7) and (8) by

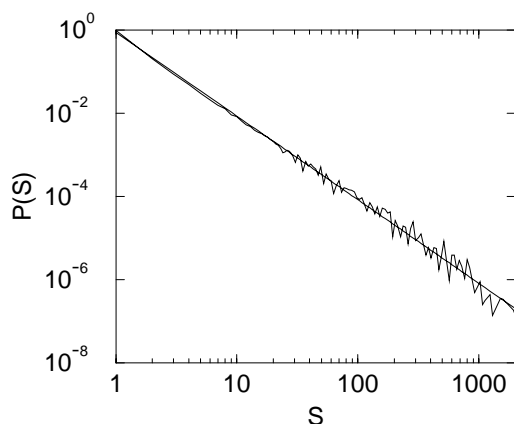


FIG. 2. The size distribution of extinction events for $k = 3$, $L = 6$, $N = 999$, $p = 0.05$, and $\mu = 0.01$. The straight line is a power-law fit with an exponent $\tau = 2.009$.

dropping the l dependence in P_T and P_τ . After a few steps, one obtains the following differential equation for P_τ :

$$\frac{dP_\tau(\tau)}{[1 - \bar{T}P_\tau(\tau)]^{1-1/k} P_\tau(\tau)} = -kd\tau/\bar{T}. \quad (9)$$

Integration of both sides, together with the condition $P_\tau(0) = 1/\bar{T}$, gives an implicit solution for P_τ . For very large τ , the first factor in the denominator on the left-hand side is close to 1 and can be neglected, leading to

$$P_\tau(\tau) \sim \exp(-k\tau/\bar{T})$$

for large τ . On the other hand, for very large τ the lifetime of a species is limited only by the lifetime of the bottom species to which it is connected. The bottom species is destroyed with a rate p , leading to $k/\bar{T} = p$, or

$$\bar{T} = k/p. \quad (10)$$

Thus, after a few transient layers, the mean lifetime of newly created species saturates at k/p , which is k times the lifetime of species in the bottom layer. Figure 3 shows the lifetime distribution of species in the higher layers for different values of k , as obtained by numerically iterating the recursion relations Eqs. (7) and (8). One can see that the distribution becomes more peaked with increasing k .

The fact that the lifetime distribution of species does not change any more after a few transient layers means that each extinction event destroys on an average the same number of species on each of the higher levels. Consequently, the rate of species production is also the same at each of these levels. Let us now define a tree with index m to be the set of all species that would go extinct if bottom species m went extinct. Only species with one prey belong to those trees, and there are species with one prey that do not belong to a tree. The growth rate of such

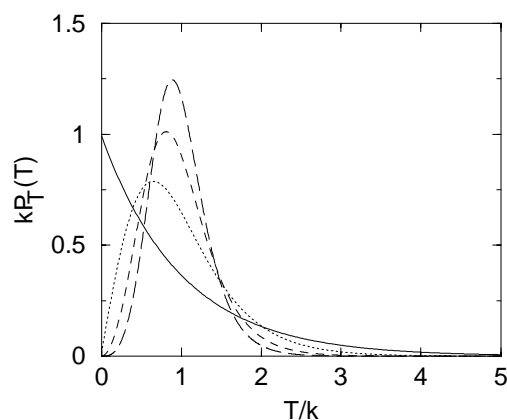


FIG. 3. The lifetime distribution of species in the higher layers for $k = 1$ (solid line), $k = 2$ (dotted line), $k = 3$ (dashed line), and $k = 4$ (long-dashed line). The time axis is scaled by $1/k$.

a tree must be proportional to its size, just as in the case $k = 1$, since in each layer (above the transitional layers) species with one prey are generated (from species with two preys) at the same rate. We can now repeat the derivation of $P(S)$ and S_{\max} from above (case $k = 1$), and we find again $\tau = 2$ and $S_{\max} \sim \exp(L)$. The species density in levels above the transient levels is $\rho = \mu/(\mu + p/k)$.

The properties of the model may change when the rules are changed to equally plausible ones. If, e.g., rule (b) is modified such that a species goes extinct as soon as one of its k prey species goes extinct, the number of species decreases exponentially with the level number: Each species is now connected to k^l bottom species, so that the death rate of species increases with layer number as k^l/p . If the speciation rate is constant in each layer, the species density decreases as k^{-l} , while the size distribution of extinction events is still a power law with $\tau = 2$ in the thermodynamic limit. However, this power law cannot be seen for the system sizes used in the simulations. If the speciation rate is chosen to be proportional to the density of species in a layer, the density in the stationary state decreases as $k^{-l(l-1)/2}$, and the size distribution of extinction events has a cutoff after a few layers, even in the thermodynamic limit.

To summarize, the model discussed in this paper is self-organized critical with a power-law size distribution of extinction events in the thermodynamic limit. Finite systems with only a few layers show this power law only if k is larger than 1 or 2, and a modified version of the model either does not show a power law in systems with few layers or is not critical at all. Thus, power-law extinction events are not a generic feature of food-chain models in general, but occur only in some versions of these models. Also, a more detailed food-chain model [13] that includes adaptation of species to their prey and that evaluates the transfer of resources from one layer to the next was shown to be not critical.

Dependencies between species in nature are not limited to predator-prey relationships, leading to interaction networks instead of nice hierarchies. The layered model studied in this paper must therefore be considered as a mean-field-like approximation to the more complicated reality.

Other ecological models, while not containing a layered structure, take into account the fitness of species [6–8].

The resulting power laws have in general an exponent different from 2. A model in which extinction is entirely caused by the action of environmental stresses on species also gives a power-law size distribution of extinction events [9].

While the study of simple models like the ones mentioned here is a necessary stage in the attempt to understand complex phenomena like large-scale evolution, all of them are unrealistic in many respects, and it can be doubted that they are capable of grasping all important features of evolutionary dynamics. Certainly, far more research is needed to gain a deeper understanding of the processes that lead to the observed patterns in the fossil record.

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