

Simple model of evolution with variable system size

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A simple model of biological extinction with variable system size that exhibits a power-law distribution of extinction event sizes is presented. The model is a generalization of a model recently introduced by Newman [Proc. R. Soc. London Ser. B **263**, 1605 (1996)]. Both analytical and numerical analysis show that the exponent of the power-law distribution depends only marginally on the growth rate g at which new species enter the system and is equal to that of the original model in the limit $g \rightarrow \infty$. A critical growth rate g_c , below which the system dies out, can be found. Under these model assumptions stable ecosystems can only exist if the regrowth of species is sufficiently fast. [S1063-651X(97)09912-1]

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The fact that extinction events seem to be episodic on all scales, as noted by Raup [1], has aroused much interest in the last few years. Throughout the history of life on Earth there have been many small extinction events, but very big ones have happened only rarely. A histogram of the frequency of extinction events of different sizes indicates a power-law distribution $p(s) = s^{-\tau}$, where s denotes the number of species that go extinct in one event and $p(s)$ denotes the frequency of events of size s .

There are two mechanisms to explain mass extinctions. On the one hand, it is argued that coevolution can drive large proportions of an ecosystem into extinction and produce extinction events on all scales. Ecosystems might drive themselves into a critical state in which a small change (e.g., the mutation of a single species) can trigger an ‘‘avalanche’’ that may span the whole system. For this kind of dynamic Bak *et al.* [2] have coined the name self-organized criticality (SOC). Several simple models of evolution exhibiting SOC have been proposed, among them models by Kauffman and Johnsen [3], Bak and Sneppen [4], and Manrubia and Paczuski [5].

On the other hand, it is argued that mass extinctions find their origin in external influences. That situation is modeled by some recent work of Newman [6]. He used a model belonging to the new class of so-called ‘‘coherent noise’’ models recently introduced by Newman and Sneppen [7]. These models are clearly not SOC but they nevertheless show a power-law distribution of avalanche sizes. Newman compared his model with the analysis of the fossil record performed by Raup. The exponent τ close to 2 that arises in this model is in good agreement with the fossil record. Thus Newman came to the conclusion that there is no evidence for SOC as the major driving force for extinction.

It can be generally observed that the majority of the models for biological evolution and extinction up to now considered work with a fixed number of species. This is a major drawback since it is in clear contrast with the biological reality. After a major extinction event, the number of species in the ecosystem is significantly reduced, and the process of regrowth of new species can take a long time. The fossil record [8] shows that the process of growth of species is commonly interrupted by extinction events.

To our knowledge, models with variable system size have only been studied by Vandewalle and Ausloot [9] and by Head and Rodgers [10]. But in both cases the models do not explain the distribution of extinction events seen in the fossil record. The model of Vandewalle and Ausloot is a tree model that grows infinitely, while the model of Head and Rodgers reaches a steady state in which no major extinctions occur. As far as we know, none of the models with variable system size up to now considered can explain the distribution of extinction events seen in the fossil record.

But every mechanism proposed for the explanation of mass extinctions must (i) explain the distribution seen in the fossil record, and (ii) face the fact that the number of species is not constant, but is reduced significantly after a major extinction event. *A priori* it is not at all clear if a mechanism producing a certain distribution of extinction events will show the same distribution when the constraint of a fixed system size is released. Therefore it is very important to study models with variable system size.

We propose here a generalization to the coherent noise model used by Newman, where the refilling of the system is done in finite time. Newman’s model is defined as follows. The system consists of N species, each possessing a threshold x_i of tolerance against stress, chosen from a probability distribution $p_{\text{thresh}}(x)$. At each time step, a stress η is generated at random with a distribution $p_{\text{stress}}(\eta)$, and all species with $x_i < \eta$ are removed from the system and immediately replaced with new ones. Furthermore, a small fraction f of the species is chosen at random and given new thresholds. That corresponds to a probability of f for every species to undergo spontaneous mutation.

In our model the fraction of species with $x_i < \eta$ is removed permanently from the system, but in every time step there is some growth of new species.

Note that the generalized model, like the original one, does not include explicitly interaction between species. There are two reasons to justify this model assumption. Firstly, previous work [11] has shown that the coherent noise dynamic is very strong and can dominate interaction dynamic. Secondly, the investigation of a model without interaction, which can reproduce important features of the fossil record, helps to clarify the influence of species’ interaction on mass extinctions.

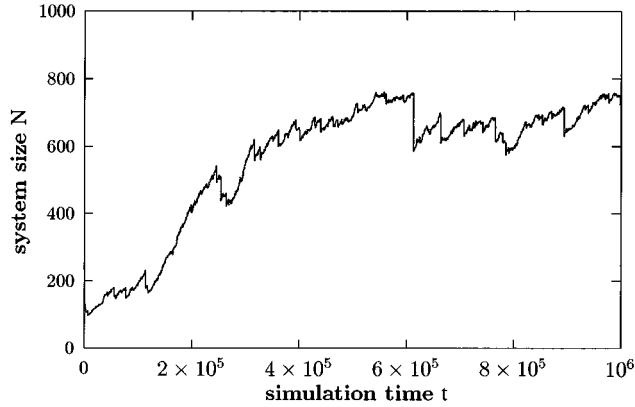


FIG. 1. The evolution of the system size N in time. The parameters are $g=4 \times 10^{-5}$, $\sigma=0.05$, $f=10^{-5}$, and $N_{\max}=1000$ with exponentially distributed stress.

The amount of newly introduced species per time step should be proportional to the number of already existing species, with some constant of proportionality g (the growth rate). This gives an unbounded exponential growth, which is in good agreement with the data of Benton [8]. However, since recourses on Earth are finite, the growth of the species must be limited as well. Therefore, we believe it is justified to introduce a logistic factor $(1 - N/N_{\max})$, where N_{\max} is the maximal number of species that can be sustained with the available resources. With this factor it is possible to work with a finite model. A few comments on the fact that in nature this N_{\max} is probably not constant in time will be given later.

For the above reasons we want our system to grow according to the differential equation

$$\frac{dN}{dt} = gN \left(1 - \frac{N}{N_{\max}} \right). \quad (1)$$

Since our model is discrete, in time as well as in the number of species, instead of Eq. (1) we use the corresponding difference equation

$$\Delta N(t + \Delta t) = \frac{N(t)N_{\max}e^{g\Delta t}}{N_{\max} + N(t)(e^{g\Delta t} - 1)} - N(t), \quad (2)$$

where Δt is one simulation time step (usually set equal to 1). As ΔN has to be an integer, we use the fractional part of ΔN as the probability to round up or down. In the limit $g \rightarrow 0$ (which corresponds to $\Delta t \rightarrow 0$) Eq. (2) reduces to Eq. (1). In the limit $g \rightarrow \infty$ Eq. (2) becomes $\Delta N = N_{\max} - N$, which means that our model reduces to the original one in the limit of an infinite growth rate.

Now we can formulate our model: we set $\Delta t = 1$. At every time step, a stress value η is chosen and all species with $x_i < \eta$ are removed. Then, an amount ΔN of new species is introduced into the system. Finally, a fraction f of the species is assigned new thresholds.

A typical evolution of the system size N in time is presented in Fig. 1. The process of growth of new species is constantly disrupted by small extinction events. From time to time, bigger events, which disturb the system significantly,

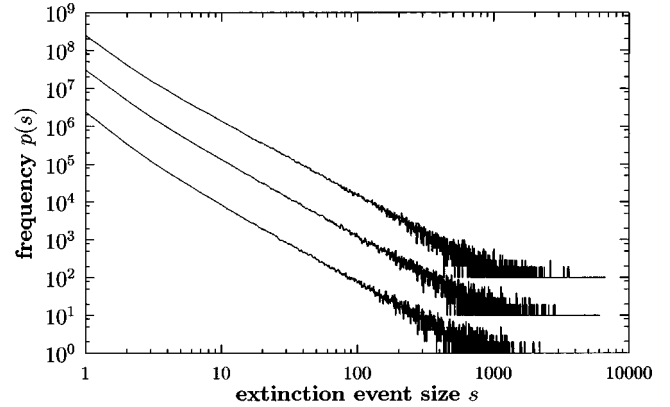


FIG. 2. The distribution of extinction events for a system with exponentially distributed stress, $\sigma=0.05$ and $N_{\max}=10\,000$. The growth rate is, from bottom to top, $g=4 \times 10^{-5}$, $g=0.002$, $g=10$. It can be seen that the power-law behavior does depend only marginally on the growth rate. The curves have been rescaled so as not to overlap.

occur. A plot of the distribution of extinction events (Fig. 2) shows a power-law decrease. Variation of the growth rate over several orders of magnitude does change the exponent only slightly.

We can explain the exponent of the power law by extending the analysis of Sneppen and Newman to our model. The probability that species leave a small interval dx of the time-averaged distribution $\bar{\rho}(x)$ is proportional to $[f + p_{\text{move}}(x)]\bar{\rho}(x)$, where $p_{\text{move}}(x)$ is the probability that a species with threshold x is hit by stress. Let α be a variable that measures the ‘‘emptiness’’ of the system, i.e., $\alpha \propto (1 - N/N_{\max})$. The rate at which the interval dx is repopulated is then proportional to $[f(1 - \alpha) + g\alpha(1 - \alpha)]p_{\text{thresh}}(x)$ in the limit $\Delta t \rightarrow 0$. In equilibrium the rates of species’ loss and repopulation balance, and we find the master equation

$$[f + p_{\text{move}}(x)]\bar{\rho}(x) = [f(1 - \bar{\alpha}) + g\bar{\alpha}(1 - \bar{\alpha})]p_{\text{thresh}}(x). \quad (3)$$

Note that we had to replace α by its time-averaged value $\bar{\alpha}$ and that we can always take the limit $\Delta t \rightarrow 0$ in the steady state. After rearranging Eq. (3), we find

$$\bar{\rho}(x) = [f(1 - \bar{\alpha}) + g\bar{\alpha}(1 - \bar{\alpha})] \frac{p_{\text{thresh}}(x)}{f + p_{\text{move}}(x)}. \quad (4)$$

Equation (4) can be solved if we choose how to normalize $\bar{\rho}(x)$ and $\bar{\alpha}$. Since we can think of the system as containing N_{\max} species at any time step, from which there are N active and $N_{\max} - N$ dead, it makes sense to normalize the sum of $\bar{\alpha}$ and $\bar{\rho}(x)$ to unity, viz.,

$$1 = \bar{\alpha} + \int \bar{\rho}(x) dx. \quad (5)$$

That implies, nevertheless, that we do not normalize $\bar{\rho}(x)$ to unity. Rather, $\int \bar{\rho}(x) dx$ gives the ratio \bar{N}/N_{\max} .

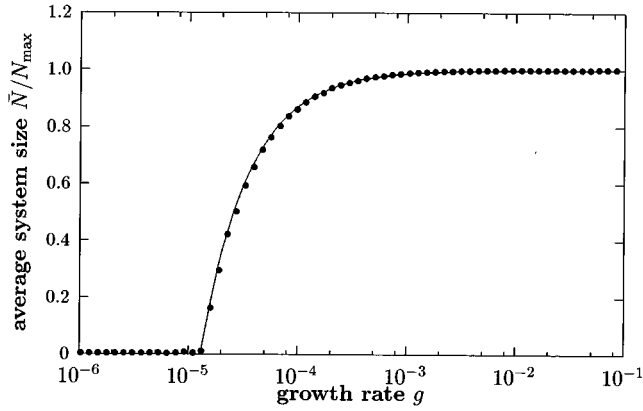


FIG. 3. The average system size \bar{N} vs the growth rate g . We used exponentially distributed stress with $\sigma=0.05$ and $f=10^{-5}$. The solid line is the analytic expression, the points are the simulation results.

For $\bar{\alpha}$ we find, apart from the trivial solution $\bar{\alpha}=1$, the solution $\bar{\alpha}=(A-f)/g$, with

$$A^{-1} = \int \frac{p_{\text{thresh}}(x)}{f + p_{\text{move}}(x)} dx. \quad (6)$$

For $\bar{\rho}(x)$, we find

$$\bar{\rho}(x) = A \left(1 - \frac{A-f}{g} \right) \frac{p_{\text{thresh}}(x)}{f + p_{\text{move}}(x)}. \quad (7)$$

We thus have the interesting result that apart from the overall factor $1 - \bar{\alpha}$, which determines the average system size, the shape of $\bar{\rho}(x)$ is identical to that found by Sneppen and Newman. Since only the shape $\bar{\rho}(x)$, but not the overall factor, is responsible for the power-law distribution of extinction events (for details see [7]) we find that, within the time-averaged approximation, the exponent τ of the power-law decrease is exactly the same as in the original model, even for very small g .

If we take the limit $g \rightarrow \infty$ in Eq. (7) we can restore the expression found by Sneppen and Newman, which was to be expected since our model reduces to the original one in that limit. In the region of very small g , we can read off from Eq. (7) that the system breaks down at a critical growth rate $g_c = A - f$. This is the case when the growth rate is so small that the regrowth of species cannot compensate the successive extinction events. Every system with $g < g_c$ will eventually end up with $N=0$, regardless of the number of species at the beginning of the simulation.

For the simulation results presented here we have used exponentially distributed stress only, i.e., $p_{\text{stress}}(\eta) = \exp(-\eta/\sigma)/\sigma$. We did simulations with N_{\max} between 1000 and 10 000. Figure 3 shows the dependence of the average system size \bar{N} of g . We can clearly see the breakdown of the system at g_c . A measurement of the time-averaged distribution of thresholds $\bar{\rho}(x)$ is presented in Fig. 4. The exponent τ of the power-law distribution of extinction events is found to be $\tau = 1.9 \pm 0.1$ for $g = 10$, $\tau = 2.0 \pm 0.1$ for

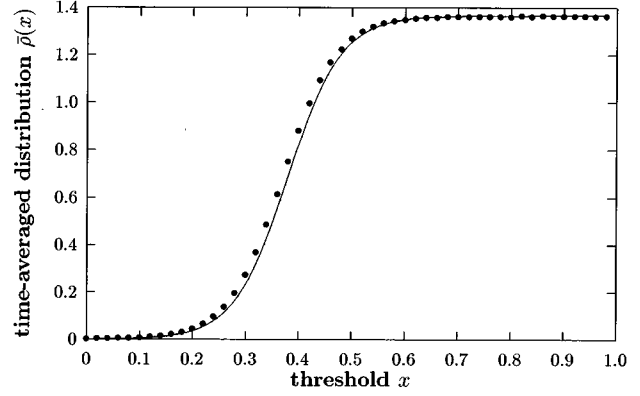


FIG. 4. The time-averaged distribution $\bar{\rho}(x)$. The parameters used are $g=0.002$, $\sigma=0.05$, and $f=5 \times 10^{-4}$ with exponentially distributed stress. The solid line is the analytic expression, the points are the simulation results.

$g=0.002$, $\tau=2.05 \pm 0.1$ for $g=4 \times 10^{-5}$ (for exponentially distributed stress, $\sigma=0.05$, $f=10^{-5}$, Fig. 2). The exponent decreases slightly with increasing g . For $g=10$, we have already good agreement with the exponent found by Newman and Sneppen [7] for $g=\infty$, viz., $\tau=1.85 \pm 0.03$.

An interesting feature of the original model by Newman and Sneppen is the existence of aftershocks, a series of smaller events following a large one. These aftershocks have their origin in the fact that after a large event the introduction of new species reduces significantly the mean threshold value, thus increasing the probability to get further events. Since the existence of aftershocks is a result of the immediate refilling of the system after an event, we cannot necessarily expect to see aftershocks when the refilling is done in finite time, especially at a small growth rate. Numerical simulations show that there are aftershocks for larger values of g , but when g approaches g_c , aftershocks cannot clearly be identified anymore. The region where this happens is that in which the average system size decreases rapidly with g . For these values of g , the typical time the system needs to regrow the amount of species lost in a major event exceeds the typical time needed to create a major stress value. In Fig. 3, the region in which we do not find aftershocks is between $g=g_c=1.3 \times 10^{-5}$ and about $g=5 \times 10^{-4}$. A typical example for a series of events in a system with g close to g_c is presented in Fig. 5.

Sneppen and Newman argued that the existence of aftershocks might provide a measure to distinguish between coherent-noise driven systems and SOC systems. This is certainly true in the sense that systems exhibiting aftershocks are better candidates for coherent-noise driven systems rather than for SOC systems. But our simulations show that there are systems without clear aftershocks that still should be classified as coherent-noise driven.

We have focused on logistic growth since we believe it is suitable for the study of mass extinctions. In principle it is possible to use different types of growth. We have done some simulations with linear growth, where in every time step a fixed amount of new species is introduced into the system, as long as $N < N_{\max}$. These simulations indicate that the respective type of growth used does not affect the appearance of a power-law distribution with exponent almost inde-

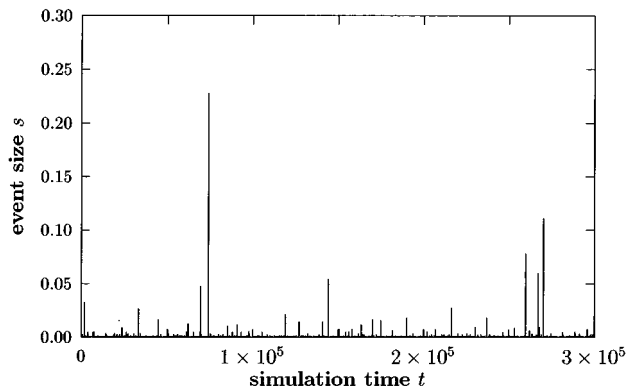


FIG. 5. A series of extinction events. The parameters used are $g = 4 \times 10^{-5}$, $\sigma = 0.05$, and $f = 5 \times 10^{-4}$ with exponentially distributed stress. Aftershocks cannot clearly be identified.

pendent from the growth rate. But whether aftershocks appear or not, is indeed dependent on the type of growth we choose. In a system with linear growth aftershocks can be seen clearly even for small growth rates.

If we want to use a coherent noise model with variable system size as a model of biological evolution, some remarks about the meaning of N_{\max} are necessary. The fact of allowing the regrowth of species in finite time, instead of refilling the system immediately, represents a first step closer to reality. But for ecosystems it is certainly not a good assumption to keep the maximal system size N_{\max} fixed, since the number of species an ecosystem can contain depends on the interaction of species themselves. Therefore, a next step could

be to change N_{\max} after every extinction, e.g., up or down by chance and by an amount proportional to the size of the event. This is motivated by the fact that bigger events are expected to be correlated with a more profound restructuring of the ecosystem, and as simulations show we still find power-law distributions with exponents $\tau \approx 2$. The behavior of such a system has a very rich structure with long times of relatively little change (stasis) and sudden bursts of evolutionary activity (punctuated equilibrium), where a major extinction event is followed by a regrowth of species to a system size much bigger than the one before the event. The so found curves of the system size N agree qualitatively well with the fossil record [8].

We have generalized a coherent noise model to a model with variable system size. The most important feature of coherent noise models, the power-law distribution of event sizes with an exponent close to 2, does not change under the generalization. This means that the validity of Newman's approach to explain biological extinction with a coherent noise model is not affected by the regrowth of species in finite time. An interesting new feature that emerges from a variable system size is the existence of a critical growth rate g_c . Systems with $g < g_c$ will always end up with $N = 0$ after some time. Therefore in a world in which the regrowth of species is too slow to compensate external influences no stable ecosystems can exist. In the framework of our model we conclude that the process of mutation and diversification of species at sufficiently high rate is necessary for the stability of life on earth.

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