

Large-scale evolution and extinction in a hierarchically structured environment

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Abstract

A class of models for large-scale evolution and mass extinctions is presented. These models incorporate environmental changes on all scales, from influences on a single species to global effects. This is a step towards a unified picture of mass extinctions, which enables one to study coevolutionary effects and external abiotic influences with the same means. The generic features of such models are studied in a simple version, in which all environmental changes are generated at random and without feedback from other parts of the system.

Introduction

In the history of the Earth, there have been several catastrophic events which in a short period of time have wiped out large parts of the existing species. The amount of species annihilated in such events has been up to 96% of the biodiversity at that time (Raup 1986). It has often been argued that these mass extinctions must have been caused by some disastrous abiotic incidences like extraterrestrial impacts. Evidence in favor of that has been put forward (Alvarez 1987), but on the other hand, only 5% of the total loss of biodiversity in the fossil record can be connected to mass extinctions. The rest are the so-called background extinctions, which happen on much smaller scales. Interestingly, the two types of extinction cannot clearly be distinguished from another in the frequency distribution of extinction event sizes. The event sizes' distribution forms a smooth curve, very close to a power-law (Solé & Bascompte 1996).

In order to explain a single smooth distribution, the idea of coevolutionary avalanches has been developed (Kauffman 1992). The extinction of a single species might cause another species to die out, which might drive a third species into extinction and so on, producing an avalanche that in principle could span the whole system. Because of the diverging mean avalanche size, the distribution of extinction events

would then be a power-law, similar to the situation of thermodynamical systems at the point of a phase-transition. Nevertheless, this mechanism, called self-organized criticality, completely neglects external influences that certainly are present.

On the contrary, as it has recently been shown, a power-law distribution of extinction events can appear even in a system in which species are wiped out solely because of external influences (Newman 1996). However, this effect depends crucially on influences that are imposed on all species coherently.

From the point of view of a single species it does not really matter whether it has to struggle with bad conditions imposed externally, e.g., a global shift in temperature, or with bad conditions due to heavy competition with other species. All that counts for a single species is whether it can keep up with its environment or not.

A species goes extinct when its population decreases to zero. This can happen for several reasons. One is a loss of habitat. Climatic or tectonic changes affect the location and the size of a species' habitat. If the size decreases rapidly, the species may not be able to adapt fast enough to find a new niche. Then the population will drop below a level at which it can sustain itself and the species will die out. Another reason for species' extinction is the invasion of new competitors or new predators. Competitors that invade a territory may be better adapted to a niche than the species originally occupying this niche. In this case, the population of the native species can be decimated so effectively that it is wiped out. The same thing can happen because of an invading predator superior to the defense mechanisms of the species. Similarly, new parasites can significantly reduce the population of a species and drive it to extinction.

From the species point of view, all the above cases can be subsumed under the notion of stress. A species suffers stress of various kinds, stress because of climatic changes, stress because of competition and predation

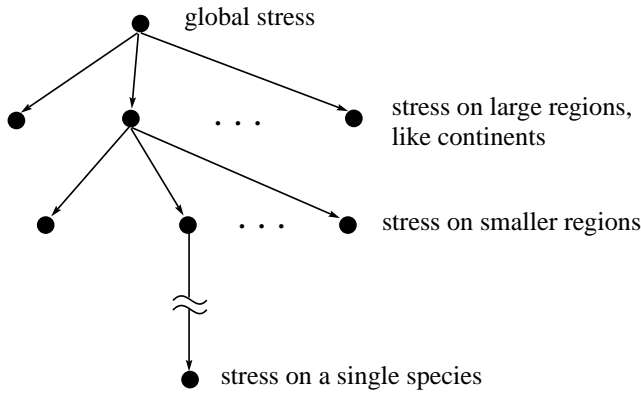


Figure 1: Stress is generated in a tree structure.

etc. If the stress exceeds the level a species can sustain, it will go extinct.

We are going to develop a model in which all causes for the extinction of a species will be regarded as stress. Every species i has a threshold x_i , or in general a vector \mathbf{x}_i , against stress. If a species suffers a stress $\eta_i > x_i$, or in the general case a vector of stresses $\boldsymbol{\eta}_i$, where at least one component exceeds the corresponding component of the threshold vector \mathbf{x}_i , it dies out. So far, this is a very general approach for a model in which species are the smallest units considered, i.e. a model that does not work with individuals or populations. Clearly, in such a model there will be stress on several scales. We have global stress like a global shift in temperature due to a slight change in the orbit of the Earth around the sun, or the impact of a very large meteor. Then we have stress that spans large parts of the Earth, e.g. a continent or a hemisphere, like the El Niño phenomenon that roughly spans the region about the tropical Pacific Ocean. And finally, we have stress that affects smaller regions, or only a single species. This leads us to a hierarchically ordered system of environmental stresses. The simplest way to model it is to generate stress in a tree structure, as it is shown in Fig. 1.

On all scales, the stress can be abiotic or biotic. This may sound a bit counter-intuitive, since abiotic changes are usually taken as large-scale phenomena, and biotic factors are usually taken as local phenomena. Abiotic changes happen often on a global scale, like the above mentioned examples of the orbit shift of the Earth or the meteor impact. But clearly there are more localized events. A small meteor or a small volcano may affect only a limited number of species. If a species happens to live only in a very small territory, and this territory gets destroyed by a meteor impact, the species may be the only one that goes extinct because of the impact.

On the other hand, biotic phenomena are not necessarily localized. Although direct species competition will usually be a local phenomenon, there can be also global biotic phenomena. The composition of the atmosphere, for example, depends strongly on biotic factors, and it can change significantly due to biotic effects.

So far, we have a model which represents the biosphere as a tree, with species situated at the leaves, and environmental stress generated at the nodes. Now we have to choose the rules that determine how stress is generated and what thresholds against stress the species are given. This is the crucial part where we decide what mechanisms we want to investigate. If we were interested mainly in coevolutionary effects, we would choose rules that link the properties and actions of the species directly to the generation of the stress. In such a model, for example, the global stress at time t could be some sort of a sum over all the adaptive moves of the species at time $t - 1$. In this work, however, we are mainly interested in the generic features we can expect from the hierarchical structure of the biosphere. Therefore, we will focus on a version of the model where the stresses and the species' thresholds are simply random variables. Species' interactions and abiotic effects can be so complicated and so unpredictable that in a first approximation we want to assume them to be completely random.

The model we study here is probably the simplest possible. Yet it has some intriguing features which are very similar to characteristics seen in the fossil record. To keep our model simple, we choose a homogenous tree, with l layers and n subtrees per node. In general, of course, one has to deal with inhomogenous trees. To each node of the final layer we connect exactly one leaf, where we put m species. An example of such a tree with $l = 4$ and $n = 2$ is displayed in Fig. 2. The total number of stresses that have to be generated in one time step is

$$N_{\text{stress}} = \sum_{i=0}^{l-1} n^i, \quad (1)$$

and the total number of species in the model is

$$N_{\text{species}} = mn^{l-1}. \quad (2)$$

Every species i has a single threshold x_i , chosen at random from the uniform distribution on the interval $[0; 1)$. At every node j , the stress η_j generated in one time step is a positive, real random variable drawn from a distribution with probability density function (pdf) $p_j(x)$. It is a reasonable assumption to expect smaller stresses to happen much more often than larger

stresses. Therefore, we use pdf's that fall off relatively fast with $x \rightarrow \infty$. An Exponential or Gaussian decrease should be a good choice, but the exact form of the pdf is not really important. We choose the pdf's $p_j(x)$ at the beginning of the simulation at random from some family of distribution functions and keep this choice fixed throughout the course of the simulation.

Finally, we have to fix the way a species is affected by stress generated on different levels of the tree. We simply take the maximum of all the stress values generated at nodes that lie above the species in the tree: if at any of these nodes a stress η_j is generated which exceeds the species threshold x_i , this species goes extinct. It is then immediately replaced by a new species with new random threshold.

In addition to the extinction dynamic, we introduce some sort of adaption. In agreement with our idea of a first, simple model, the adaption is a random walk: in every time step, a fraction f of the species is selected at random and given new thresholds.

There are certainly some oversimplifications in this model, such as the fixed number of species or the fact that all species have only one trait. We will return to this later and explain why we can still expect to cover the basic features of the extinction dynamic.

Analysis

The behaviour of the above introduced model can be understood to a large extent from analytical calculations. But before we begin with our analysis, we note that the mechanism for species extinction and adaption presented here is similar to the one of the so-called 'coherent-noise' models introduced by Newman and Sneppen (Newman & Sneppen 1996). These models display a distribution of extinction events that follows a power-law with exponent ≈ -2 , which is in good agreement with the fossil record. For this reason, they have already been used to study macroevolutionary phenomena (Newman 1996; Wilke & Martinetz 1997). The difference to our actual approach lies in the fact that we use a multitude of stresses in a hierarchically ordered system, whereas in the coherent-noise models there is only a single stress, acting on the whole system at once. Therefore, in the previous works the idea of stress imposed on the species has been linked to external influences like meteor impacts and was opposed to coevolutionary effects.

Note that we have effectively a coherent-noise model at every leaf of the tree if the number m of species located at one leaf is large.

The effective stress-distribution at a leaf of the tree

Every leaf of the tree feels a stress-distribution which depends on the distributions of the nodes above it. Let there be N nodes above a leaf. Then the N stress values having influence on this leaf are N random variables X_1, \dots, X_N with pdf's $p_1(x), \dots, p_N(x)$. We have to calculate the pdf $p_{\max}(x)$ of the random variable $X_{\max} = \max\{X_1, \dots, X_N\}$, i.e.,

$$p_{\max}(x) dx = P(x \leq \max\{X_1, \dots, X_N\} < x + dx). \quad (3)$$

With the partition theorem we can write the probability on the right-hand side as a weighted sum of conditional probabilities:

$$\begin{aligned} P(x \leq \max\{X_1, \dots, X_N\} < x + dx) \\ = \sum_{i=1}^N P(x \leq \max\{X_1, \dots, X_N\} < x + dx \\ \quad \left| \begin{array}{l} x \leq X_i < x + dx \\ \times P(x \leq X_i < x + dx). \end{array} \right. \end{aligned} \quad (4)$$

The conditional probabilities read

$$\begin{aligned} P(x \leq \max\{X_1, \dots, X_N\} < x + dx \\ \quad \left| \begin{array}{l} x \leq X_i < x + dx \\ = \frac{1}{P(x \leq X_i < x + dx)} \\ \quad \times P(x \leq \max\{X_1, \dots, X_N\} < x + dx \\ \quad \quad \wedge x \leq X_i < x + dx) \\ = \frac{P(x \leq X_i < x + dx) \prod_{j=1, j \neq i}^N P(x > X_j)}{P(x \leq X_i < x + dx)} \\ = \prod_{j=1, j \neq i}^N P(x > X_j). \end{array} \right. \end{aligned} \quad (5)$$

After inserting Eq. (5) into Eq. (4) we find

$$\begin{aligned} P(x \leq \max\{X_1, \dots, X_N\} < x + dx) \\ = \sum_{i=1}^N P(x \leq X_i < x + dx) \prod_{j=1, j \neq i}^N P(x > X_j). \end{aligned} \quad (6)$$

Consequently, for the pdf $p_{\max}(x)$ we have

$$\begin{aligned} p_{\max}(x) &= \sum_{i=1}^N p_i(x) \prod_{j=1, j \neq i}^N P(x > X_j) \\ &= \sum_{i=1}^N p_i(x) \prod_{j=1, j \neq i}^N \int_0^x p_j(x') dx'. \end{aligned} \quad (7)$$

We are interested in the tail of $p_{\max}(x)$. For coherent-noise models we know that a power-law distribution of event-sizes will appear if the stress-distribution $p_{\text{stress}}(x)$ satisfies

$$\int_{\eta}^{\infty} p_{\text{stress}}(x) dx \approx C p_{\text{stress}}^{\alpha}(\eta) \quad \text{for } \eta \rightarrow \infty, \quad (8)$$

where C and α are positive constants which depend on $p_{\text{stress}}(x)$ (Sneppen & Newman 1997). Therefore, we assume this condition to hold also for the distributions $p_j(x)$ in Eq. (7), with constants C_j and α_j , respectively. Then we can approximate the tail of $p_{\max}(x)$ by

$$p_{\max}(x) \approx \sum_{i=1}^N p_i(x) \prod_{j=1, j \neq i}^N \left(1 - C_j p_j^{\alpha_j}(x)\right) \quad \text{for } x \rightarrow \infty. \quad (9)$$

We proceed further by taking only linear terms in $p_i(x)$ and obtain

$$p_{\max}(x) \approx \sum_{i=1}^N p_i(x) \quad \text{for } x \rightarrow \infty. \quad (10)$$

For large x , this sum will be dominated by the $p_i(x)$ that is falling off slowest. We say that distribution $p_i(x)$ falls off slower than distribution $p_j(x)$ if there exists a x_0 such that

$$p_i(x) > p_j(x) \quad \text{for all } x > x_0. \quad (11)$$

For a set of reasonable stress-distributions it is always possible to identify one that is falling off slowest according to this definition.

The fact that the sum in Eq. (11) will asymptotically be dominated by a single term leads to the situation depicted in Fig. 2. The tree breaks down into several independent subsystems. The meaning of the numbers in the figure will be explained in detail later. In a nutshell, they indicate how slow a stress distribution is falling off. What interests us here is the breakup of the tree into several independent parts in the regime of large stresses. If these parts are not too small, they will behave like independent coherent-noise systems.

An ensemble of a finite number of independent coherent-noise systems

If the stress-distributions close to the root dominate the behaviour of the system, the tree will break down into independent coherent-noise systems, as we have mentioned above. Consequently, we proceed with the calculation of the distribution of extinction events in a system consisting of independent coherent-noise subsystems. In the calculation, however, we will deviate

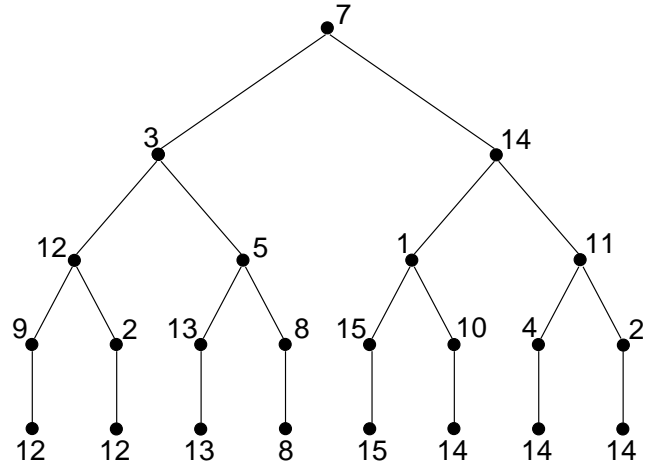


Figure 2: The tree breaks down into virtually independent parts in the limit of large stresses.

slightly from the actual situation in the tree model by assuming the subsystems to have each an infinite size. This allows for an easy calculation, and the main results should also hold for large but finite sizes.

In the case of an infinite system size, the event distribution of a coherent-noise model possesses a power-law tail that extends to arbitrary large events. Therefore, the task of calculating the event distribution of the compound system equals to the task of calculating the sum of a finite number of nonidentically distributed random variables with power-law tail. The latter can be treated mathematically exact under relatively weak assumptions (Wilke unpublished). But since the exact calculations are too extensive to be included in this work, we will here give only an intuitive argument about the tail behaviour of the sum.

We begin with the sum of two positive, real random variables X_1 and X_2 , where the pdf's $p_1(x)$ and $p_2(x)$ have a power-law tail $x^{-\tau_1}$ and $x^{-\tau_2}$, respectively. We assume the pdf's to be continuous, non-singular, and reasonably smooth. Under these conditions, we can write $p_1(x)$ and $p_2(x)$ in the form

$$p_1(x) = \frac{f_1(x)}{(x+1)^{\tau_1}}, \quad (12)$$

$$p_2(x) = \frac{f_2(x)}{(x+1)^{\tau_2}}, \quad (13)$$

where $f_1(x)$ and $f_2(x)$ are continuous, non-singular, and reasonably smooth functions which tend towards a positive constant for $x \rightarrow \infty$. The pdf $p_{\text{sum}}(x)$ of the sum $X = X_1 + X_2$ is the convolution of $p_1(x)$ and $p_2(x)$:

$$p_{\text{sum}}(x) = \int_0^x p_1(x') p_2(x-x') dx'$$

$$= \int_0^x \frac{f_1(x')}{(x'+1)^{\tau_1}} \frac{f_2(x-x')}{(x-x'+1)^{\tau_2}} dx'. \quad (14)$$

After a change of the integration variable to $z = x'/x$ we obtain

$$\begin{aligned} p_{\text{sum}}(x) &= \int_0^1 \frac{f_1(xz)}{(xz+1)^{\tau_1}} \frac{f_2(x(1-z))}{(x(1-z)+1)^{\tau_2}} x dx' \\ &= x^{1-\tau_1-\tau_2} \int_0^1 \frac{f_1(xz)}{(z+\frac{1}{x})^{\tau_1}} \frac{f_2(x(1-z))}{(1-z+\frac{1}{x})^{\tau_2}} dx'. \end{aligned} \quad (15)$$

For large x , there are two main contributions to this integral, at $z \approx 0$ and at $z \approx 1$, which stem from the first and from the second term in the denominator. Since the denominators will become arbitrarily large for large x , we can assume the other terms to be constant in the regions where the main contributions come from. Therefore, we find

$$p_{\text{sum}}(x) \approx x^{1-\tau_1-\tau_2} \left[C_1 x^{\tau_2-1} + C_2 x^{\tau_1-1} \right], \quad (16)$$

where C_1 and C_2 are positive constants. Obviously for large x the term with the largest exponent will dominate. Hence we have

$$p_{\text{sum}}(x) \sim x^{-\min\{\tau_1, \tau_2\}}. \quad (17)$$

This result can be easily extended to the case of an arbitrary finite number of random variables with power-law tail by iteration. Asymptotically, the tail of $p_{\text{sum}}(s)$ will always be dominated by the contribution from the term with the smallest exponent.

Back to the ensemble of infinitely large coherent-noise systems, we find that it will display power-law distributed event sizes, as its single constituents do. If the subsystems' stress-distributions are functionally different, the exponent of the compound system's event distribution will be the smallest of the subsystems' exponents.

The above result should also hold in the situation of finite coherent noise systems, as long as their total number is small compared to their typical size.

Trees with random stress distributions

We argue above that in the limit of large stresses the tree will break down into subsystems, virtually independent of each other. The behaviour of our model depends heavily on the size of the parts we find. If the different parts are all very small, the system will lose its coherent-noise characteristics. Instead of a power-law distribution the extinction events will then

follow a gaussian distribution because of the central-limit theorem. Therefore, in this section we will study the distribution of the subsystems' sizes that arises if we randomly assign stress distributions to the tree's nodes.

We assume that the probability for a certain stress distribution to be assigned to a certain node does not depend on the position of the node in the tree. In other words, we use the same set of stress distributions on all levels of the tree. Furthermore, we assume that for any two stress distributions we use we can identify one of the two that falls off faster than the other one. Under these conditions, we can study the structure of such trees by simply assigning integers to the nodes of the tree, where larger integers stand for distributions that are falling off slower. If the set of possible stress distributions is infinite, the probability of finding two nodes with the same distribution is zero. Consequently, in a tree with n nodes, we will assign every integer from $1 \dots n$ to exactly one node. This is displayed in Fig. 2 for a tree with 15 nodes. For every leaf i of the tree we can then define a characteristic number a_i . This number is the maximum of the nodes' numbers encountered on the way from the leaf up to the root. All the leaves with the same characteristic number belong to the same subsystem. In the example of Fig. 2, we have five subsystems in total. Three of them contain only one leaf, one contains two and one contains three leaves.

In general, we are interested in the distribution of subsystems arising in large trees. Therefore, we have done simulations in which we have several thousand times assigned random integers to the nodes of a large tree. For every single realization of the tree, we have computed a histogram of the frequency of the different parts' sizes. Finally, we have calculated the average of all the histograms. Fig. 3 shows the result of such simulations for two different trees with 10000 histograms each. We find the expected frequency $f(k)$ of large independent parts in the tree decreasing as a sawtooth function that follows approximately a power-law with exponent -2 , independent of l and n . The sharp peaks in the distribution arise whenever the size of a complete subtree is reached. Therefore, we observe in Fig. 3, e.g., the peaks in the distribution of the tree with $n = 10$ appearing at powers of 10.

The power-law can be explained easily if we assume the main contributions to come from complete subtrees. The expected frequency $f(k)$ to find an independent subtree with b layers, which corresponds to a subsystem of size $k = n^b$, can be written as the number of such subtrees in the whole system, $N(b)$, times the probability that any of these subtrees will be indepen-

dent of the rest, $P(b)$. Hence we write

$$f(n^b) = N(b)P(b). \quad (18)$$

The number of subtrees of size n^b is $N(b) = n^{l-b}$. For the probability $P(b)$ we find

$$P(b) = \left(l - b + \sum_{i=0}^{b-1} n^i \right)^{-1}, \quad (19)$$

which is simply the probability for the integer assigned to the node at the root of the subtree to be larger than all the other integers which are assigned to the remaining nodes of the subtree and to the nodes above the subtree. If we increase b by one, we get $N(b+1) = n^{l-b-1} = N(b)/n$. With slightly more effort, we find also

$$\begin{aligned} P(b+1) &= \left(l - b - 1 + \sum_{i=0}^b n^i \right)^{-1} \\ &= \left(l - b + n \sum_{i=0}^{b-1} n^i \right)^{-1} \approx \frac{1}{n} P(b). \end{aligned} \quad (20)$$

Therefore, we can write

$$f(nk) \approx \frac{N(k)}{n} \frac{P(k)}{n} = n^{-2} f(k), \quad (21)$$

which implies $f(k) \sim k^{-2}$.

The peaks in Fig. 3 appear whenever the size of a complete subtree is reached, as we have noted above. This means they are connected to the extremely regular structure of the trees we use in this work. Therefore, we are currently investigating trees with irregular structure. For these trees, the spikes disappear and, in log-log plot, the function $f(k)$ becomes almost a straight line with slope -2 . From the simulations we have done so far, we can say that this result is very general and seems to be independent of the special trees' properties.

Simulation results

Since we are interested in the typical behaviour of our model, we have to do many simulation runs with different tree sizes and different stress distributions at the tree's nodes. But the simulation of large trees is very slow, and therefore it is hard to get a good sample of the parameter-space. To overcome this difficulty we have also done simulations based on the arguments of the previous sections. As we have seen there, in the limit of large stresses it is possible to map the leaves of the tree onto a system consisting of several independent coherent-noise models, with the sizes k of these subsystems distributed according to k^{-2} .

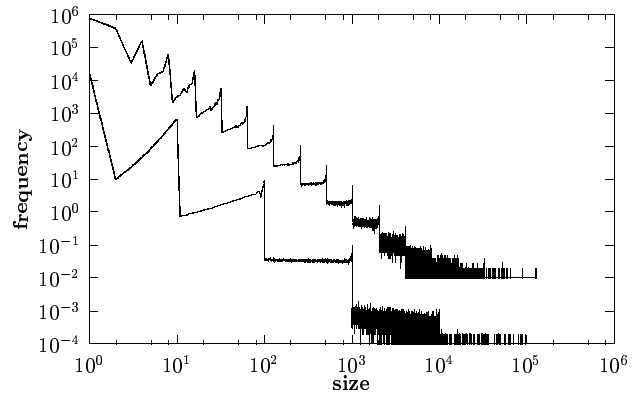


Figure 3: The expected frequency for the occurrence of large independent subsystems decreases as a sawtooth function that follows approximately a power-law with exponent -2 . The upper curve stems from a tree with $l = 18$ and $n = 2$. It has been rescaled by a factor of 100 so as not to overlap with the lower curve. The lower curve stems from a tree with $l = 6$ and $n = 10$.

In Fig. 4 we show a comparison between the full simulation and the approximation. To come as close as possible to the full simulation, we use the maximum of 5 independent, exponentially distributed random variables as stresses for the independent coherent-noise models, since for the tree we have likewise chosen $l = 5$ and exponential stress-distributions. Clearly the behaviour of the approximation is close to the one of the full simulation, which verifies the analytical reasoning of the previous sections. Both simulations display power-law distributed extinction events. For the full tree, we find an exponent $\tau_{\text{tree}} = 2.35 \pm 0.05$, while for the approximation, we find $\tau_{\text{approx}} = 2.30 \pm 0.05$. If we consider the high level of abstraction from the tree to an ensemble of coherent-noise systems, this agreement is excellent.

Note that in comparison to a normal coherent-noise model with only a single stress variable, the tree model produces a significantly larger exponent τ (If we run a normal coherent-noise model with the stress distribution of the approximation in Fig. 4, we get an exponent $\tau \approx 1.8$). The increased exponent τ has its origin in the distribution of the subsystems' sizes. The sizes scale themselves, thus modifying the scale-invariant behavior of the ensemble, compared to the one of a single coherent-noise system.

Discussion

We have presented a model of large-scale evolution and extinction that combines biotic and abiotic causes for extinction within a single mathematical framework.

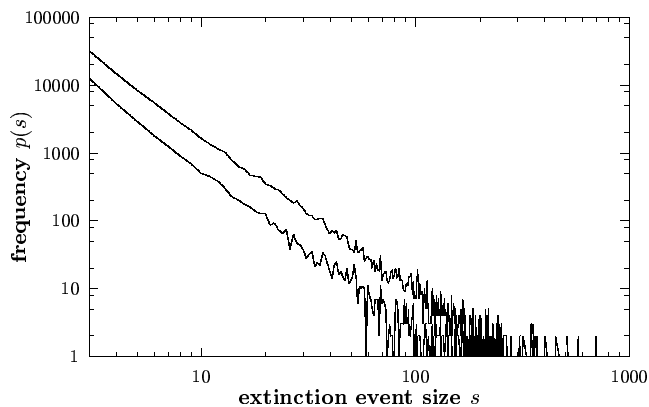


Figure 4: The frequency of extinction events in the tree model and in an ensemble of coherent-noise models. The lower curve stems from the simulation of a tree with $l = 5$, $n = 10$ and $m = 1$, which amounts to a total of 10^5 species. Stress distributions were assigned at random to the nodes of the tree. We used exponentially distributed stress with σ between 0.03 and 0.05. The upper curve corresponds to the simulation of an ensemble of coherent-noise models with a total of 10^5 species, and with the sizes k of the subsystems distributed according to k^{-2} . As stresses we used the maximum of 5 exponentially distributed random variables.

Furthermore, the model takes into account the hierarchical structure of the biosphere. To the best of our knowledge, the implications of environmental changes happening on different scales have not been studied previously in macroevolutionary models. Despite the choice of completely random environmental changes, the model has some interesting features. The distribution of extinction events follows a power-law with exponent in the region of 2 (note that the exponent depends on the choice of the stress distribution, as it is the case with coherent-noise models). From the fossil record, a power-law distribution with exponent $\tau \approx 2$ is reported for the extinction event sizes of taxonomical families (Solé & Bascompte 1996; Newman 1996). Moreover, it is interesting to observe the breakup of the tree into subsystems with sizes k distributed according to k^{-2} . The power-law distribution of the subsystem sizes implies that even in very large trees we will find large subsystems, governed mainly by only a single stress distribution. Intuitively, we would expect the subsystems to have roughly similar sizes, and to enter the dynamic of the whole system on an equal basis. But we observe exactly the opposite. The subsystems' sizes are scale-invariant, thus producing a scale-invariant distribution of contributions to the

overall system's behavior. In particular, only a small number of large subsystems produces events on large scales. This might be an explanation for the fact that in such large and complex systems like the biosphere we find usually smooth frequency distributions of typical objects or events.

The model we have studied in this work is certainly oversimplified. For that reason, we will close this paper with some remarks about extensions to the model that should be examined in a next step closer to biological reality. First of all, it is certainly a severe restriction to keep the number of species fixed throughout the simulation. Nevertheless, this is a restriction used very often in models of macroevolution (Peliti 1997). Only recently, work has been done where a change in biodiversity is considered (Head & Rodgers 1997; Wilke & Martinetz 1997). The behaviour of the model we study here is governed by the coherent-noise dynamic. For this dynamic, it has been shown that it can be generalized to include a variable system size without loss of its main features (Wilke & Martinetz 1997). Therefore, we believe a fixed system-size can be justified in the present work. It should be possible to extend our tree model to a model with variable system size. Another severe restriction is the usage of only one trait. But here a similar argument holds as in the case of the fixed number of species. A multi-trait version of the original coherent-noise model has already been studied (Newman in press). It behaves very similar to the single-trait version.

Finally, we want to discuss the way we compute the stress on a single species out of the multitude of stress values, generated at the different levels of the tree. Throughout this paper, we have used the maximum of the stress values. This allows for an easy and very general analytical investigation. Another natural choice, however, would be to sum up all the stresses. We have also done some simulations in this fashion. The behavior of the system remains roughly the same. This happens because in a finite sum of non-identically distributed random variables, we expect large values to be dominated by a single term of the sum, similar to the case of the maximum of several random variables. For the sum of exponentially distributed random variables, an easy calculation shows that this conjecture is indeed true. With some more effort, we can prove the same for the sum of power-law distributed random variables, as we have already done in this paper. Nevertheless, in the general case with arbitrary distributions, the conjecture is hard to demonstrate.

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