Self-organized criticality, evolution and
the fossil extinction record

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Abstract

Statistical analysis indicates that the fossil extinction record is compatible with a distribution of extinction events whose frequency is related to their size by a power law with exponent $\tau \approx 2$. This result is in agreement with predictions based on self-organized critical models of extinction, and might well be taken as evidence of critical behaviour in terrestrial evolution. We argue however that there is a much simpler explanation for the appearance of a power law in terms of extinctions caused by stresses (either biotic or abiotic) to which species are subjected by their environment. We give an explicit model of this process and discuss its properties and implications for the interpretation of the fossil record.
I. INTRODUCTION

There has in the last few years been much interest in the idea that coevolution in extended ecosystems could give rise to self-organized critical behaviour (Kauffman 1992, Bak and Paczuski 1996, Solé and Bascompte 1996). It has been suggested that as a result of competitive interactions between species, ecosystems drive themselves to a critical state in which the chance mutation of one species can spark a burst, or “avalanche”, of evolution that can touch an arbitrary number of other species, and potentially even the entire planet. The attraction of this theory is that it could provide a natural mechanism for the rapid turnover of species seen in the fossil record without the need to invoke environmental catastrophes to explain the extinction and replacement of apparently well-adapted species. Within this theory constant change is a natural feature of evolution, and stability merely an illusion brought about by the myopia of the observer; viewed on a sufficiently large scale in either time or space there is nothing remotely stable about evolution.

Intriguing though this theory is, it suffers at present from a lack of hard evidence in its favour. There has been much discussion, and some anecdotal evidence, of the processes which it is supposed are responsible for self-organization at the species level (see, for example, Maynard Smith 1989), and it has also been observed (Burlando 1990) that taxonomic trees appear to possess a self-similar structure which might be evidence of underlying critical processes. For the moment however, most of our quantitative data on terrestrial evolution come from the fossil record, a record whose coverage and temporal resolution is sufficiently poor as to make it difficult to distinguish between competing theories. One hint of an underlying complex dynamics may be the “punctuated equilibria” originally pointed out by Eldredge and Gould (1972), in which species evolve in bursts, separated by periods of stasis. Many theories of self-organization in evolution predict intermittent behaviour of precisely this kind. However the feature of the fossil record that has attracted the most attention to date, as far as self-organization is concerned, is the record of extinctions.

Extinction has played an important role in the evolution of life on Earth. Of the estimated
one billion or more species which have inhabited the planet since the beginning of the Cambrian, only a few million are still living today. All the rest became extinct, typically within about ten million years of their first appearance. A variety of explanations have been proposed for this high turnover rate. The most traditional are that extinction is a result of abiotic environmental stresses (Raup 1986, Hoffmann and Parsons 1991). For example, species can die out through inability to evolve fast enough to keep pace with a changing environment—a change in climate, for instance, or changes in the chemistry of the sea. More recently it has been suggested that some extinction events may have been the result of sudden planet-wide calamities, such as changes in sea-level (Hallam 1989), the impacts of meteors or comets (Alvarez et al. 1980), or large-scale volcanism (Courtillot et al. 1988, Duncan and Pyle 1988). The alternative explanation for extinctions is that they arise through a biotic mechanism; even though a species may coexist in apparent stability with its competitors for millions of years, it can still become extinct if one of those competitors evolves to a new form, or if a new competitor expands into its territory (Maynard Smith 1989). Since there is evidence in support of both biotic and abiotic mechanisms for extinction, it is probably reasonable to suppose that both have played a part in the history of terrestrial life.

The fossil data on extinction cover about 250 000 fossil species, which constitute a very small fraction of all the species that have ever lived, but still a statistically significant sample. Given a sufficiently large number of fossils from any one taxon, one can infer approximate dates of origination and extinction of that taxon, and hence, for example, measure the distribution of lifetimes of taxa, or of the sizes of extinction events. It has been suggested that these data could provide a test of the proposed self-organizing models of evolution, provided we can establish some connection between the dynamics of evolution and the extinction rate. The problem is that we are not even sure that such a connection exists, let alone what it is. A number of possibilities have been suggested recently, based on theories of extinction caused either by species interactions, or by environmental stress. Bak and Paczuski (1996) have argued that if an apparently well-adapted species can be driven to extinction by the sudden evolution of a competitor species, then one should expect to see
heightened extinction during periods of enhanced evolutionary activity. If evolution takes place in bursts, or avalanches, as predicted by self-organized critical models, then, they argue, so might extinction. By combining arguments such as these with explicit mathematical models of avalanche dynamics in evolution, like those of Kauffman and Johnsen (1991) and Bak and Sneppen (1993, Sneppen et al. 1995), it has been possible to make predictions about the expected frequency of extinction events. (See, for example, Kauffman (1995).)

Another possible connection between extinction and evolution has been investigated in modelling work by Solé (1996). In his model one takes a large number of interacting species and applies a specific criterion for deciding when the pressure placed on a species by those around it is sufficient to drive it to extinction. New species appear by speciation from the survivors at precisely the rate required to keep the total number constant. The model displays mass-extinction events of all sizes \( s \) up to the size of the entire ecosystem. Furthermore, if one constructs a histogram of the relative frequency \( p(s) \) of extinction events of different sizes, the resulting curve follows a power law:

\[
p(s) \propto s^{-\tau}.
\]

The power-law form is one of the most characteristic features of critical behaviour, and has been taken as evidence of self-organization in a wide variety of systems. The measured exponent of the power law is \( \tau \approx 2 \), a prediction which should be testable against the fossil data. Another approach has been taken by Newman and Roberts (1995, Roberts and Newman 1996), who made the contrasting assumption that all extinction events were the result of physical stresses coming from outside the ecosystem. In their model species underwent avalanches of coevolution but were also subjected to environmental stresses of varying severity, which tended to wipe out the less fit species. This model also predicts a power-law distribution of extinction sizes, again with exponent \( \tau \approx 2 \).

In fact, the power-law extinction distribution is a recurring theme of almost all of the recent models of self-organization in evolution. This suggests that one might test the veracity of these models by examining the fossil record for such power laws. In the next section we
conduct just such an examination. We present results which show that the data are in fact consistent with a power law, and furthermore that we can extract quite an accurate figure for the exponent $\tau$, which is in perfect agreement with the more quantitative theories of extinction. Given this satisfying result, the next question we ask, which is addressed in the third section of the paper, is whether this implies that terrestrial evolution is indeed a self-organized critical process. At the risk of giving away the punchline, it turns out that the answer to this question is no—it implies no such thing. There is a much simpler and very elegant explanation for the appearance of a power law in the extinction distribution. We will show that, given only the very simplest of assumptions about the causes of extinction, we can formulate a model of the extinction process which does not rely on coevolution for its results (although coevolution can certainly be present) and yet predicts a power-law distribution of extinction sizes. Our results appear to be quite independent of such niceties as the dynamics of evolution or the difference between biotic and abiotic extinctions, implying that we should expect to see power laws in the extinction record whether evolution is self-organized critical or not.

II. DOES THE EXTINCTION DISTRIBUTION FOLLOW A POWER LAW?

In this section we investigate the question of whether the available data on the extinction of fossil species are compatible with a frequency distribution of extinction sizes following a power law of the form given in Equation (1). The data we use come from the compilation by Sepkoski (unpublished), as do those employed by most others who have conducted statistical investigations of terrestrial extinction. The particular subset we use deals with Palaeozoic and Mesozoic marine species, mostly invertebrates; data on marine invertebrates are far more numerous than those for any other fossil biota. We further restrict ourselves to the reduced data set created by Raup (1991), which has been edited to remove some statistical bias (Raup and Boyajian 1988). The edited data are grouped into genera. Although this grouping has the effect of reducing the number of extinctions in the data set, it has the advantage
of increasing the precision with which we know the date of any particular extinction. A summary of the data set is given in Table A1 of Raup (1991).

The most straightforward thing to do with the data is to divide the time they span into intervals, count the number of species becoming extinct in each interval (which is a measure of extinction rate) and make a histogram of the results. As discussed by Raup (1986), the divisions of time chosen for such analyses are usually the stratigraphic stages. The results of the histogramming are shown both on linear and on logarithmic scales in Figure 1. (On the latter the power-law distribution should appear as a straight line.) This oft-reproduced plot has been used by a variety of commentators as evidence both of the existence and the non-existence of a power-law extinction distribution in the fossil record. However, the errors on the histogram, shown as bars in the logarithmic plot, are really too large to allow the question to be answered one way or the other. To get an answer we must resort to statistical analysis of a more sophisticated nature.

Although not originally intended to address this particular issue, a suitable method of analysis has been given by Raup (1991), who introduced the concept of the “kill curve” and a technique for deducing it from the fossil record by comparing Monte Carlo calculations of genus survivorship with fossil survivorship data. It turns out that the kill curve is closely related to the distribution of extinctions. Let us look first at the original calculations performed by Raup.

Consider Figure 2. The solid line shows Raup’s kill curve. The curve is a cumulative frequency distribution of extinctions. The horizontal axis of the plot tells you how long a time $T$ you should expect to wait on average between extinction events which kill a fraction $s$ or more of the species in the ecosystem, where $s$ is given on the vertical axis. Note that $s$ is measured as a fraction of the total number of species, not genera, in the system. Although genus-level data are used to calculate the curve, it is extrapolated down to the species level, since this is of more relevance to biological issues. The curve in the figure was found by assuming the functional form
\[ s(T) = \frac{[\log T]^a}{e^b + [\log T]^a}, \]  

(2)

and then fitting the parameters \( a \) and \( b \) to the fossil data using a method similar to the one described below. As Raup emphasizes, the form of Equation (2) is not based on any particular theory of extinction. It was merely chosen because it has the expected sigmoidal form and is reasonably flexible. Using Sepkoski’s data, Raup finds a best fit to the fossil record when \( a = 5 \) and \( b = 10.5 \). These figures give the solid curve in Figure 2, whilst the dotted ones give the estimated error.

We now ask, what is the connection between the kill curve and the distribution of extinctions? Let us denote by \( p(s) \, ds \) the number of extinctions with size between \( s \) and \( s + ds \) taking place per unit time. The function \( p(s) \) is precisely the probability distribution of extinctions that we wish to calculate. The number of extinctions \( P(s) \) of size greater than \( s \) per unit time is

\[ P(s) = \int_{s}^{1} p(s') \, ds'. \]  

(3)

The mean time \( T \) between events of size \( s \) or greater is just \( 1/P(s) \), and thus we establish a connection between \( s(T) \) and \( p(s) \). Making use of this connection, we have plotted in Figure 3 the extinction distribution \( p(s) \) corresponding to Raup’s kill curve, and on logarithmic scales the result is something approximating a straight line, although it falls off as the size of the extinctions approaches unity. (A similar fall-off is seen in most theoretical models of extinction, so this should not be regarded as a grave problem.) We can conclude therefore that the published results of Raup imply an extinction distribution which approximately follows a power law, and by fitting a straight line to Figure 3 we can extract a figure of \( \tau = 1.9 \pm 0.4 \) for the exponent of the power law.

Taking the analysis a step further, we can also ask what happens if we assume a power-law form for the extinction distribution, calculate the corresponding kill curve and fit that to the fossil data. Reversing the argument given above, it is not hard to show that the form for the kill curve corresponding to a power-law is
Like Raup's kill curve, this one has two free parameters: the exponent $\tau$, and a "typical waiting time" $T_0$. We fit these parameters to the fossil data as follows.

First we note that the two parameters are not independent. The mean extinction rate per species for the period covered by the data set is known to be about one species per 4 million years (Raup 1991), and this is related to the extinction distribution by

$$\text{mean extinction rate} = \int sp(s) \, ds.$$  \hspace{1cm} (5)

This gives us a constraint on the values of $\tau$ and $T_0$ such that if we know $\tau$, the value of $T_0$ is fixed. As a result there is essentially only one parameter in the problem to be fitted to the data, and that is the exponent $\tau$.

The fitting is done by Monte Carlo simulation of genus survivorship. In this simulation genera are founded by a single species and for each unit of succeeding time there is a constant probability of speciation for each species in the genus, and a random time-varying probability of extinction which is distributed according to the kill curve, Equation (4), or equivalently according to the extinction distribution, Equation (1). One performs the simulation many times, starting each time with a large number of genera, and continuing until all of them become extinct. Then one plots the fraction of surviving genera as a function of time for each simulation, giving a set of survivorship curves. For a model with stochastically constant extinction, one expects all these curves to be identical, except for statistical variation due to the finite number of genera taking part. However, with an extinction rate which varies over time, as we are here assuming, we expect to see an intrinsic dispersion in this set of curves, and it is this dispersion that we compare with the fossil data. It is by essentially this method that Raup extracted values for the parameters $a$ and $b$ appearing in Equation (2). We have performed the calculation using the kill curve described by Equation (4), and find that the survivorship curves extracted agree as well with the fossil data as those presented by Raup (1991), and hence we can conclude that the data are indeed compatible with a

$$s(T) = \left[ \frac{T_0}{T} + 1 \right]^{\frac{1}{1+\tau}}. \hspace{1cm} (4)$$
power law extinction distribution. Furthermore, under the assumption that the distribution is a power law, we can extract a value for the exponent $\tau$ of the power law. That value is:

$$\tau = 2.0 \pm 0.2.$$  \hfill (6)

This figure is in good agreement with figures for the same exponent from the models of Newman and Roberts (1995) and of Solé (1996). The corresponding kill curve is shown as the dashed line in Figure \[2\] and agrees with the curve given by Raup, within the quoted accuracy.

So, if the fossil extinction distribution does follow a power law, can we take this as evidence that the underlying evolutionary dynamics is of a self-organized critical nature? This is the question we address in the next section.

III. WHY DOES THE EXTINCTION DISTRIBUTION FOLLOW A POWER LAW?

We have shown that the fossil data for marine species compiled by Sepkoski are consistent with the existence of a power-law distribution of extinction sizes with an exponent close to 2. In the light of the arguments reviewed in Section I, would we then be justified in claiming, tentatively perhaps, to have found evidence that terrestrial evolution is a self-organized critical phenomenon? In this section we argue that this is not a justified assumption—that there is in fact a much simpler explanation for the appearance of a power law. Using a minimum of assumptions about the nature of evolution and extinction, we formulate a new model which predicts that the extinction distribution should follow a power law regardless of the nature of the underlying evolutionary processes, and indeed regardless of the precise causes of extinction. This model offers at once an elegant explanation of the observed extinction distribution, and at the same time a (perhaps slightly disheartening) demonstration that we cannot hope to learn much about the nature of the evolutionary process by examining this distribution.
The principal assumption of our new model is that the extinction of a species is caused by a change in its environment. Changes may take many forms, and in particular may be either biotic or abiotic in nature: they may be due either to changes in the other species with which a species interacts, or to environmental effects such as climate change. Let us call these causes of extinction “stresses”. During its lifetime, a species will in general experience a number of these stresses, and for any given stress each species will have a certain tolerance (or lack of it). We quantify this tolerance in our model by a species fitness measure which we denote $x$. When the stress occurs, species with higher values of $x$ are less likely to become extinct than those with lower values. The ability to withstand stress could depend on many factors, such as ability to adapt to a new environment (“generalists” vs. “specialists”), or possession of particular physical attributes. (Large body mass, for example, appears to have been a disadvantage during the extinction event which ended the Cretaceous.) For our purposes however, we will not need to know exactly what properties the fitness depends on; all that will matter for us is that such a fitness can be defined. For convenience, $x$ is assumed to take values between zero and one, though this is not a necessary condition for any of the results discussed later.

We also need to define a measure of the size or strength of our stresses, so as to distinguish between, for example, the impacts of large and small meteors on the Earth. In our model we therefore divide time up into short intervals, and define another number, denoted $\eta$, which measures the level of stress during a given interval. When the stress level is high we expect many species to become extinct in that time interval; when it is low, few will become extinct. We have chosen a simple rule for our model to achieve this result: if at any time the numerical value of $\eta$ exceeds that of the fitness $x$ of a species, that species becomes extinct. One may well worry about how we choose the values of the stress level $\eta$. However, as we will show, the result that the extinction distribution is a power law does not depend on what choice we make (though the precise exponent of the power law does). Our only assumptions will be that small stresses are more common than large ones, and that, based on the evidence of terrestrial prehistory, stresses large enough to wipe out every species on
the planet are uncommon.

In order to complete our model there are a couple of other components we need to add. First, we assume that the number of species our ecosystem can sustain is roughly constant over time. To satisfy this constraint, we introduce after every extinction event new species equal in number to those that have become extinct. We need to choose values for the fitnesses of these new species. The two obvious ways to choose them would be either by “inheriting” fitnesses from survivor species (from which they are assumed to have speciated), or by giving them purely random fitness values. Again, it turns out that the qualitative predictions of the model are independent of the exact choice we make.

Finally, we observe that, if this were all there was to our model, its dynamics would soon come to a standstill, when all the species with low fitnesses had been eliminated and all those remaining were susceptible only to very large stresses, which, as we have said, are rare. Clearly this does not happen in a real ecosystem, and the explanation is clear: evolution. In the intervals of time between large stresses on the ecosystem, the selection pressure of the stress is not felt and species evolve under other competing pressures, possibly at the expense of their ability to survive stress. Thus, over time, species’ fitnesses with respect to stress may increase or decrease. Again there are two contrasting views about how this might take place. The gradualist viewpoint would be that fitnesses wander slowly and continually over time. The alternative is the punctuated equilibrium viewpoint, under which, in any given interval of time, some small fraction $f$ of species would evolve to radically new forms, assuming completely different values for their fitnesses. Once more, it turns out that the fundamental predictions of our model do not depend on which choice we make.

We are led then to a new model of extinction which in its simplest form is as follows. We have an ecosystem consisting of some large number $N$ of species. With each species $i$ we associate a fitness $x_i$ which can take values between zero and one. We then execute the following steps repeatedly.

1. At each time-step, a small fraction $f$ of the species, selected at random, evolve, and
their fitnesses \( x_i \) are changed to new values chosen at random in the range \( 0 \leq x_i < 1 \).

2. We choose a stress level \( \eta \) randomly from some distribution \( p_{\text{stress}}(\eta) \), and all species whose fitnesses \( x_i \) lie below that value become extinct and are replaced by new species whose fitnesses are also chosen at random in the range \( 0 \leq x_i < 1 \).

Many variations are possible. We discuss some of the more important ones below, but for the moment let us examine the predictions of this version of the model. We have performed extensive simulations of the model using a wide variety of different choices for the form of the stress distribution \( p_{\text{stress}}(\eta) \), including forms with a power-law fall-off away from zero (such as a Lorentzian) which might be expected if the stresses were primarily due to coevolutionary avalanches, and forms with an exponential fall-off (such as an exponential or a Gaussian) which might be more appropriate for abiotic stresses. The results are shown in Figure 4.

In each case the distribution of extinctions closely follows a power law over a wide range of sizes \( s \), deviating only at very small values of \( s \). The exponent of the power law depends on the exact form of the stress, but its existence does not. There appear to be only two conditions for producing a power law, and they are (i) that the fraction \( f \) of species evolving in each time-step should be small \( f \ll 1 \), but non-zero (in order that the dynamics does not grind to a halt, as described above), and (ii) that the chances of getting a stress of sufficient magnitude to wipe out every species in the system should be very small. If these conditions are satisfied, then in every case we find a power-law distribution of extinction sizes.

In this simplest form, the model is in fact exactly the same as a model used by Newman and Sneppen (1996) to model the dynamics of earthquakes. Their paper gives a detailed mathematical analysis of the model, explaining the appearance of the power law within a time-averaged approximation and also giving an explanation of the conditions (i) and (ii) above. Rather than reproduce that discussion here, we refer the reader to that paper, and here discuss instead the connection of our model to real extinction, an issue which brings up a number of important questions. First, there are the questions of the form of the stress distribution \( p_{\text{stress}}(\eta) \), the choice of the fitness for newly appearing species, and the particular
dynamics we have chosen to represent the evolution process. Depending on which school of thought he or she adheres to, the reader might well have chosen these features of the model differently. However, as we have already mentioned, such changes have no effect on the appearance of a power law extinction distribution. This fact is depicted explicitly in Figure 4, in which the extinction distributions for various choices of $p_{\text{stress}}(\eta)$ are compared. A more important objection to the model is that we have assumed that every stress on the system affects every species. This is clearly not realistic. Some stresses will for example be localized in space, or will not reach under the sea, or will only reach under the sea, and so forth. This kind of situation can be accounted for by considering a different fitness function $x$ for such stresses, one for example which is much higher if you live under the sea, or in Africa, or whatever. But this now means that we have two (or more) fitness functions for each species. This brings us on to another important issue, which is that there are of course many types of stress. Not all stresses are equivalent, and some may affect certain species more than others. Thus it is inadequate to have just one fitness function for each species. We should instead have many such functions—one for each type of stress. This leads us to a more sophisticated “multi-trait” version of the model in which each species has a number $M$ of different fitness functions, or equivalently an $M$-component vector fitness $\mathbf{x}$, and $M$ corresponding different types of stress. The dynamics of the model are exactly as before, except that now a species becomes extinct if any one of the types of stress to which it is subject exceeds its threshold for withstanding that type of stress. For all values of $M$ which we have investigated (up to $M = 50$), this model too shows power-law distributions of extinction sizes.

It thus appears that for both the simplest version of our model, and for all reasonable variants, the power law distribution of extinction sizes is an inevitable result. The only required features are stresses, either biotic or abiotic to which species are subjected, and varying abilities of the species to withstand these stresses. Nothing about this model requires that we have a self-organized critical evolutionary dynamics taking place; coevolutionary avalanches, of the kind supposed by earlier authors to be responsible for power-law behaviour
in the extinction size distribution, are not a component of our model.

IV. CONCLUSIONS

Based on modelling work by a number of authors, the claim has been made that a self-organized critical evolutionary dynamics should give rise to a power-law distribution of extinction sizes. In this paper we have first investigated the nature of the fossil record and concluded that it is entirely compatible with such an extinction distribution. Second, we have asked whether this implies that evolution is indeed a critical process, a question which we have answered by proposing a new and simple model for extinction which makes no assumptions about the dynamics of the evolution process but which nonetheless predicts a power-law extinction distribution in every case we have investigated. We thus conclude that there is no evidence in the distribution of fossil extinction events to support the notion of self-organized critical behaviour in evolution. What we have instead, is a rather elegant picture of an empirical result—the power-law distribution of extinctions in the fossil record—and its explanation in terms of a theory of extinction caused by stresses on the ecosystem.

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FIG. 1. Histogram of the relative frequency of extinction events of various sizes on linear scales and (inset) on logarithmic ones.
FIG. 2. Kill curves for Phanerozoic marine species. The solid line is the curve given by Raup (1991) and the dotted lines are the associated errors. The dashed line is the best fit kill curve of the form given in Equation [4].
FIG. 3. The extinction distribution corresponding to the solid kill curve in Figure 2.
FIG. 4. The distribution of extinction sizes measured in simulations of the model for three different forms of the stress distribution $p_{\text{stress}}(\eta)$. The exponents of the power laws are $\tau = 2.02 \pm 0.02$ for the Gaussian, $\tau = 1.84 \pm 0.03$ for the exponential, and $\tau = 1.24 \pm 0.04$ for the Lorentzian.