Self-organized criticality, evolution, and extinction

M. E. J. Newman

Cornell Theory Center, Cornell University, Ithaca, NY 14853–3801

(June 25, 1996)

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 for self-organizing behavior 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.

This work was funded in part by the NSF under grant number ASC-9404936, and by the Cornell Theory Center.

I. INTRODUCTION

There has in the last few years been much interest in the idea that co-evolution in extended ecosystems could give rise to self-organized critical behavior (Kauffman 1992, Bak and Paczuski 1996, Solé and Bascompte 1996). On the basis primarily of evidence from computer modeling experiments, the suggestion has been made that, as a result of the interaction of species through mechanisms such as competition and predation, 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 and hence of the high current level of biodiversity, 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.

The idea of evolution as a self-organizing phenomenon is certainly an intriguing one, but at present it suffers from a lack of hard evidence either to prove or disprove it. Although a number of workers have cited examples of biological or paleontological data which appear to support the idea of self-organization, there is by no means a clear case in favor of it. A competent lawyer would have no difficulty in persuading a jury that life on Earth has arisen merely as the result of millions of years of gradual Darwinian evolution, with the occasional big rock falling from space to spice things up.[1] There *is* evidence of self-organized critical behavior in a number of other systems, notably in earthquakes (Christensen and Olami 1992)

---

[1]In fact, Raup (1992) has used statistical analyses to show that the rather fanciful hypothesis that *all* major extinction events in the Earth's history have been caused by meteor impacts is within the realm of possibility, given the quality of the fossil data.

and in avalanches in piles of sand or rice (Frette *et al.* 1996). And more importantly, there is evidence of it in computer experiments on the evolution of "artificial life". Using *Tierra* (Ray 1994), a simulation system in which self-reproducing computer programs evolve and compete for limited resources, Adami (1995) has observed a series of discontinuous "phase transitions" in the fitnesses of interacting species and measured the distribution of waiting times between these transitions. On the basis of these experiments, Adami suggests that one should see a spectrum of co-evolutionary avalanches which lacks any defining size scale, possessing a probability distribution $p(s)$ which follows a power law:

$$p(s) \propto s^{-\tau}. \tag{1}$$

The power-law form is one of the most characteristic features of critical behavior, and has been taken as evidence of self-organization in a wide variety of systems.

However, in the crucial case of biological evolution on the Earth—the one case that we are really interested in—evidence in favor of self-organization has been rather hard to pin down. There has been much discussion, and some anecdotal evidence, of the processes which, it is supposed, are responsible for self-organized critical behavior at the species level (see, for example, Maynard Smith 1989). It has also been observed (Burlando 1990, 1993) 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). They presented evidence of uneven rates of evolution of single species; periods of stasis (equilibria) separated by intervals of rapid change (punctuations). Theories of self-organization in evolution predict intermittent behavior of precisely this kind, although the punctuations are expected to affect whole groups of interacting species, rather than just one species at a time.

However the feature of the fossil record that has attracted the most attention, 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 that 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, Parsons 1993, Glen 1994). For example, species can die out through inability to evolve fast enough to keep pace with a changing environment—a change in climate, for example, 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. Oft-cited examples include changes in sea-level (Hallam 1989), the impacts of meteors or comets (Alvarez *et al.* 1980, Raup 1992), and large-scale volcanism (Duncan and Pyle 1988, Courtillot *et al.* 1988). More exotic examples include devastating disease, or ionizing radiation from supernovas (Ellis and Schramm 1995). The alternative explanation for extinctions is that they arise through a biotic mechanism—that even in the absence of external stresses on the ecosystem species would become extinct through the effects of competition and predation. The idea is that 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, 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 in fact 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 occurred to a number of authors 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) for instance, 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, one might then expect to see some signature of this behavior in the extinction record. Explicit mathematical models of avalanche behavior in evolution have been given by, for example, Kauffman and Johnsen (1991) and by Bak and Sneppen (1993, Sneppen *et al.* 1995). Under suitable conditions, the size distribution of avalanches in these models follows a power law, and it has been suggested that this might potentially give rise to a corresponding power law in the extinction distribution.[2]

Another possible connection between extinction and evolution has been investigated in modeling work by Solé (1996). In this 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. This model also gives a power-law distribution of extinction sizes. 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), who made the contrasting assumption that all extinction events were the result of physical stresses coming from outside the ecosystem.

---

[2]In more recent modeling work incorporating niche invasion by Kauffman (1995), the link between evolution and extinction has been made more explicit and the results do indeed seem to indicate a power-law distribution of extinction sizes.

In their model species coevolved in a self-organizing fashion similar to that of the model of Bak and Sneppen (1993), 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 addition to these models, quite a number of others have been suggested connecting the dynamics of evolution with the extinction rate. Many, though not all of them, predict power laws in the distribution of extinctions. Given the variety of theories, and given the similarities of their predictions, we should perhaps be asking ourselves whether we can really answer any questions about evolution by looking at the extinction distribution. That problem is the subject of this paper. In particular we will address two issues. First, we will ask whether the fossil extinction record does in fact show a power-law distribution of extinction sizes. If, as some commentators have suggested, it does not, then there is a clear disagreement between the data and the models which predict power laws, suggesting that these models should at the very least be regarded as suspect. However, we will present results of analyses using the "kill curve" techniques pioneered by Raup (1991a) to show that in fact the data *are* consistent with a power law, and furthermore that we can extract quite an accurate figure for the exponent of that power law, which is in good agreement with the more quantitative theories of extinction. Second, we will ask whether this result then 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. As we will demonstrate, there is a much simpler 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 will 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 will 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 Paleozoic and Mesozoic marine species, mostly invertebrates; data on marine invertebrates are far more numerous than those for any other class of fossil biota. We further restrict ourselves to the reduced data set created by Raup (1991a), 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 (1991a).

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 (1991a), 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 first look 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

$$s(T) = \frac{[\log T]^a}{\mathrm{e}^b + [\log T]^a}, \tag{2}$$

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, while 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 $p(s)\,\mathrm{d}s$ the number of extinctions with size between s and $s+\mathrm{d}s$ 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

$$P(s) = \int_s^1 p(s')\,\mathrm{d}s', \tag{3}$$

or alternatively,

$$p(s) = -\frac{\mathrm{d}P}{\mathrm{d}s}. \tag{4}$$

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 a logarithmic scale 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 is approximately a power law, and by fitting a straight line to Figure 3 we can extract a figure of $\tau = 1.9 \pm 0.3$ 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. Using the argument given above, it is not hard to show that the form for the kill curve corresponding to a power-law is

$$s(T) = \left[\frac{T_0}{T} + 1\right]^{\frac{1}{1-\tau}}. \tag{5}$$

Like Raup's kill curve, this one has two free parameters: the exponent τ, 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 for the period covered by the data set is known to be about one species per 4 million years (Raup 1991a), and this is related to the extinction distribution by

$$\text{mean extinction rate} = \int s\, p(s)\, \mathrm{d}s. \tag{6}$$

This gives us a constraint on the values of τ and T_0 such that if we know τ, 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 τ.

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 time-varying probability of extinction which is chosen according to the kill curve, Equation (5) (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 that 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). Repeating the calculation for the kill curve described by Equation (5), we find that the survivorship curves extracted agree as well with the fossil data as those presented by Raup (1991a), and hence we can conclude that the data are indeed compatible with a power law extinction distribution. Furthermore, under the assumption that the distribution is a power law, we can extract a value for the exponent τ of the power law. That value is:

$$\tau = 2.0 \pm 0.2. \tag{7}$$

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 all extinctions have a cause. That is, we assume that an extant species would never die out if it found itself in an environment that was completely unchanging in every respect. Only when its environment changes can a species become extinct. 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, changes in sea level, or bolide impact. There is at least one case in which this assumption breaks down—the case of extinctions arising through the mechanism known as "gambler's ruin" (see for example Raup 1991b). Extinctions of this kind occur when the total number of individuals in a species is very small, so that natural population fluctuations may cause the size of the population to fluctuate to zero. We assume that extinctions of this type make only a small contribution to the total extinction rate, and can therefore be ignored.

Let us call our 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 the size or strength of our stress, 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 η, 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 η 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 η. 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 assumption 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, in accordance with fossil data,[3] the number of species our ecosystem can sustain is roughly constant over time. In order 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 fitnesses (equivalent to the assumption that these species find themselves living in a niche sufficiently different from that of their ancestors, that the process of adaptation has to start all over again). 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 very uncommon. 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, random values for their fitnesses. Once more, it

[3] There is some evidence (Benton 1995, Courtillot and Gaudemer 1996) that diversity has, on average, increased during the Phanerozoic, but the typical timescale for this increase is very long compared to the timescale on which extinction events take place. For the purposes of modeling the extinction process therefore, it is reasonable to assume a constant number of species.

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 timestep, a small fraction f of the species, selected at random, evolve, and their fitnesses x_i change to new values chosen at random in the range $0 \leq x_i < 1$.

2. We choose a stress level η 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 an algorithm which calculates the fitness distribution and avalanche sizes in a formally exact way for a system with an infinite number of species. This eliminates the effect of statistical errors due to finite system size. We have performed simulations 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. 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 getting 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 the 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 $p_{\mathrm{stress}}(\eta)$, 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 $p_{\mathrm{stress}}(\eta)$ 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—one for each type of stress. This leads us to a slightly more sophisticated version of the model which is similar in spirit to the multi-trait evolution model of Boettcher and Paczuski (1996). In this version of the model 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 exceed 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, and co-evolutionary avalanches, of the kind supposed by earlier authors to be responsible for power-law behavior in the extinction size distribution, are not a component of our model.

IV. CONCLUSIONS

Based on the modeling work of a number of authors, the claim has been made that self-organized critical dynamics in evolution should give rise to a power-law distribution of extinction sizes. In this paper we have investigated first the nature of the fossil record and concluded that it is indeed compatible with such an extinction distribution. Furthermore we have extracted a value of $\tau = 2.0 \pm 0.2$ for the exponent associated with the distribution. Second, we have asked whether this does in fact imply that the dynamics of evolution is critical, a question which we have answered by proposing a simple and apparently quite reasonable 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 behavior in evolution. (Nor is there evidence to refute it; our statement is merely that the observed distribution of extinction events is the one we would expect, regardless of the detailed dynamics of the evolution process.) 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.

V. ACKNOWLEDGEMENTS

The author is very grateful to David Raup for his help with the calculations described in Section II, and to Kim Sneppen for many fruitful discussions concerning the model presented in Section III. This work was funded in part by the NSF under grant number ASC-9404936, and by the Cornell Theory Center.

Adami, C. 1995 Self-organized criticality in living systems. *Phys. Lett. A* **203**, 29.

Alvarez, L. W., Alvarez, W., Asara, F., and Michel, H. V. 1980 Extra-terrestrial cause for the Cretaceous/Tertiary extinction. *Science* **208**, 1095.

Bak, P. and Paczuski, M. 1996 Mass extinctions vs. uniformitarianism in biological evolution. Brookhaven National Laboratory preprint no. 62678.

Bak, P. and Sneppen, K. 1993 Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* **71**, 4083.

Benton, M. J. 1995 Diversification and extinction in the history of life. *Science* **268**, 52.

Boettcher, S. and Paczuski, M. 1996 Exact results for spatiotemporal correlations in a self-organized critical model of punctuated equilibrium. *Phys. Rev. Lett.* **76**, 348.

Burlando, B. 1990 The fractal dimension of taxonomic systems. *J. Theor. Biol.* **146**, 99.

Burlando, B. 1993 The fractal geometry of evolution. *J. Theor. Biol.* **163**, 161.

Christensen, K. and Olami, Z. 1992 Variation of the Gutenberg-Richter b values and non-trivial temporal correlations in a spring-block model for earthquakes. *J. Geophys. Res.* **97**, 8729.

Courtillot, V., Féraud, G., Maluski, H., Vandamme, D., Moreau, M. G. and Besse, J. 1988 Deccan flood basalts and the Cretaceous/Tertiary boundary. *Nature* **333**, 843.

Courtillot, V. and Gaudemer, Y. 1996 Effects of mass extinctions on biodiversity. *Nature* **381**, 146.

Duncan, R. A., and Pyle, D. G. 1988 Rapid eruption of the Deccan flood basalts at the Cretaceous/Tertiary boundary. *Nature* **333**, 841.

Eldredge, N. and Gould, S. J. 1972 Punctuated equilibria: an alternative to phyletic gradualism. In *Models in Paleobiology* T. J. M. Schopf (Ed.), Freeman, San Francisco.

Ellis, J. and Schramm, D. N. 1995 Could a nearby supernova have caused a mass extinction? *Proc. Natl. Acad. Sci.* **92**, 235.

Frette, V., Christensen, K., Malte-Sørensen, A., Feder, J., Jøssang, T., and Meakin, P. 1996 Avalanche dynamics in a pile of rice. *Nature* **379**, 49.

Glen, W. 1994 What the impact/volcanism/mass-extinction debates are about. In *Mass-extinction debates* W. Glen (Ed.), Stanford University Press.

Hallam, A. 1989 The case for sea-level change as a dominant causal factor in mass extinction of marine invertebrates. *Phil. Trans. Roy. Soc. B* **325**, 437.

Kauffman, S. A. 1992 *The Origins of Order,* OUP, Oxford.

Kauffman, S. A. 1995 *At Home in the Universe,* OUP, Oxford.

Kauffman, S. A. and Johnsen, S. 1991 Coevolution to the edge of chaos: Coupled fitness landscapes, poised states, and coevolutionary avalanches. *J. Theor. Biol.* **149**, 467.

Maynard Smith, J 1989 The causes of extinction. *Phil. Trans. Roy. Soc. B* **325**, 241.

Newman, M. E. J. and Roberts, B. W. 1995 Mass extinction: Evolution and the effects of external influences on unfit species. *Proc. Roy. Soc. B* **260**, 31.

Newman, M. E. J. and Sneppen, K. 1996 Avalanches, scaling, and coherent noise. Cornell Theory Center preprint no. 96TR237.

Parsons, P. A. 1993 Stress, extinctions and evolutionary change: from living organisms to fossils. *Biol. Rev.* **68**, 313.

Raup, D. M. 1986 Biological extinction in Earth history. *Science* **231**, 1528.

Raup, D. M. 1991*a* A kill curve for Phanerozoic marine species. *Paleobiology* **17**, 37.

Raup, D. M. 1991*b* *Extinction: Bad Genes or Bad Luck,* Norton, New York.

Raup, D. M. 1992 Large-body impact and extinction in the Phanerozoic. *Paleobiology* **18**, 80.

Raup, D. M. and Boyajian, G. E. 1988 Patterns of generic extinction in the fossil record. *Paleobiology* **14**, 109.

Ray, T. S. 1994 An evolutionary approach to synthetic biology: Zen and the art of creating life. *Artificial Life* **1**, 179. Reprinted in *Artificial Life, An Overview,* C. G. Langton (Ed.), The MIT Press (1995).

Sneppen, K., Bak, P., Flyvbjerg, H. and Jensen, M. H. 1995 Evolution as a self-organized critical phenomenon. *Proc. Nat. Acad. Sci.* **92**, 5209.

Solé, R. V. 1996 On macroevolution, extinctions and critical phenomena. *Complexity,* in press.

Solé, R. V. and Bascompte, J. 1996 Are critical phenomena relevant to large-scale evolution? *Proc. Roy. Soc. B* **263**, 161.

FIGURES

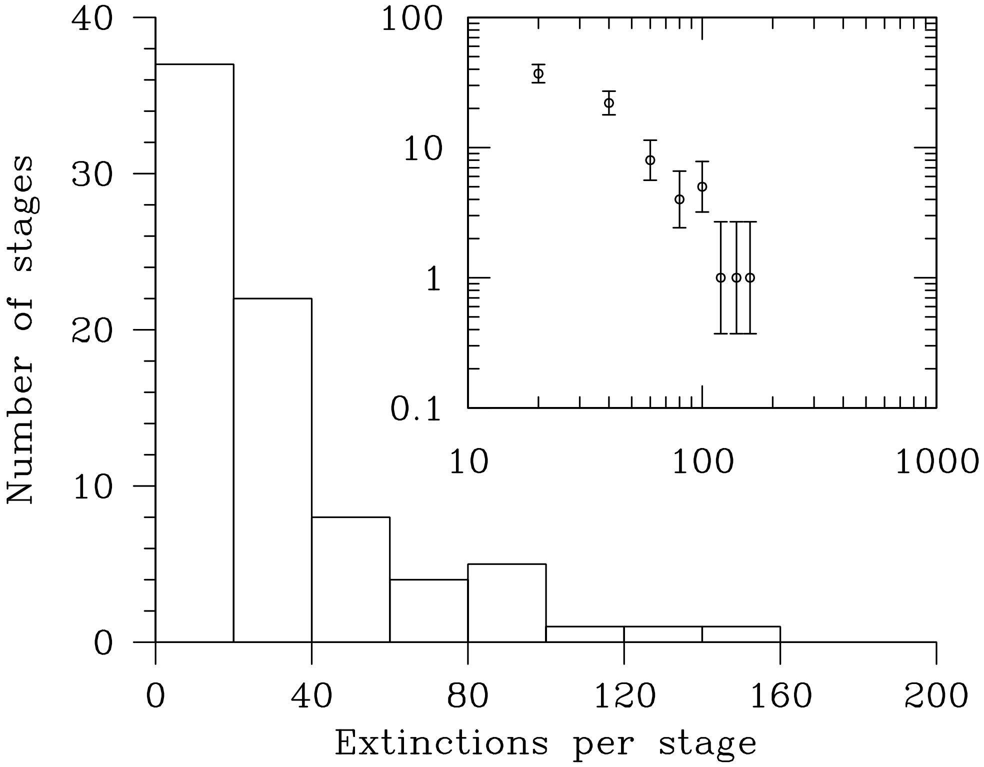

FIG. 1. Histogram of the relative frequency of extinction events of various sizes. Inset: the same data replotted on logarithmic scales with $\sqrt{N}$ error bars added. Given the size of the errors, it is hard to say whether these data indicate a power-law distribution of extinction sizes or not.

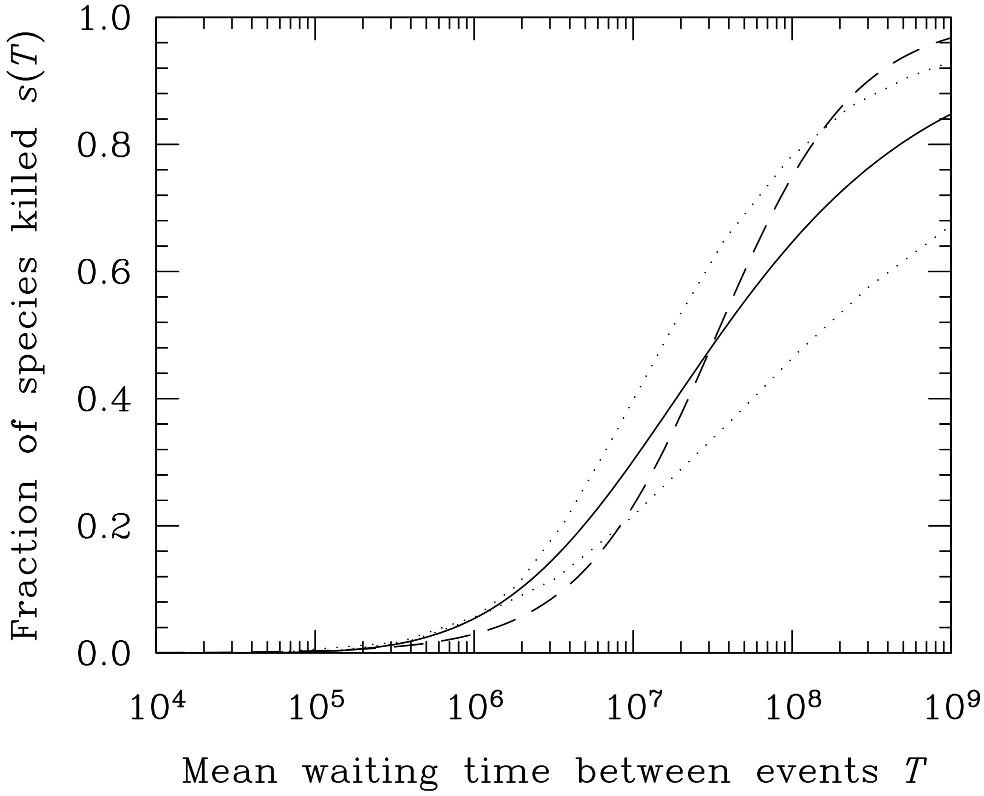

FIG. 2. Kill curves for Phanerozoic marine species. The solid line is the curve given by Raup (1991a) and the dotted lines are the associated errors. The dashed line is best fitting kill curve of the form given in Equation (5), which agrees reasonably with Raup's result within the given errors.

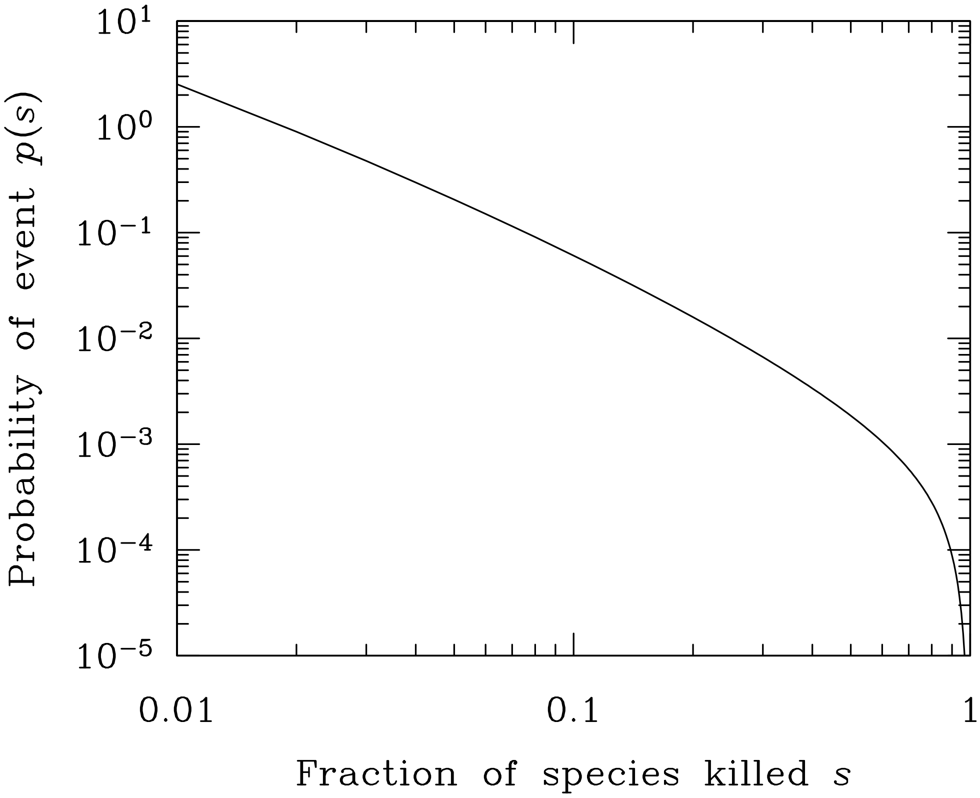

FIG. 3. The extinction distribution corresponding to the solid kill curve in Figure 2.

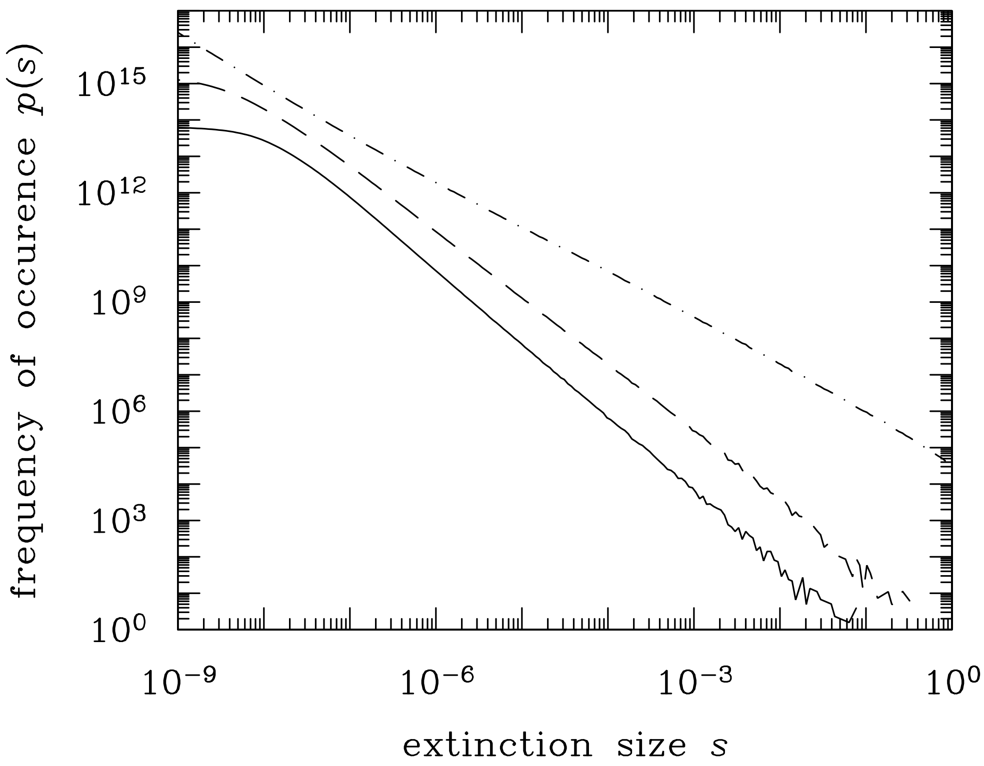

FIG. 4. Plots of the distribution of extinction sizes measured in simulations of the model described in the text. The solid line corresponds to stresses with a Gaussian distribution centered at zero, the dashed one to exponentially-distributed stresses, and the dot-dashed one to Lorentzianly-distributed ones. In each case the distribution is a power law over most of the range shown on the graph (i.e., a straight line on this log-log plot), falling off only for very small extinction sizes. The values of the exponents describing the power laws are: for the Gaussian $\tau = 2.02 \pm 0.02$, for the exponential $\tau = 1.84 \pm 0.03$, and for the Lorentzian $\tau = 1.24 \pm 0.04$.