Evidence for self-organized criticality in evolution

M. E. J. Newman

Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501. U.S.A.
Telephone: +1 (505) 984–8800   Fax: +1 (505) 982–0565
Email: `mark@santafe.edu`

Data of a number of different types have been put forward as evidence for self-organized critical behavior in evolution. These include fossil data on extinction rates and taxon lifetimes, evidence of fractal structure in taxonomic trees, and simulation data from experiments on artificial life. Here we present a new and very simple model of species origination and extinction which, although not critical, reproduces all of these data well. We suggest therefore, that data of these kinds should not be taken as evidence of self-organized criticality.

Key words: coevolution, extinction, self-organized criticality, power laws

There has in recent years been considerable interest in the idea that evolution might be a self-organized critical (SOC) process [1–3]. Although this suggestion has been made primarily on the basis of modeling studies, it is important also to consider the empirical evidence in its favor. In this paper we discuss a number of different forms of evidence which have been presented and ask whether they really show what they claim to.

The most direct form of evidence for SOC behavior in evolution comes from experiments on artificial life. Using the *Tierra* system, Adami [4] has measured the lifetimes of competing species and finds that their distribution is well approximated by a power law, which is a common signature of systems at or close to criticality. In biological evolution a similar power-law distribution has been pointed out by Sneppen *et al.* [5] in data on the lifetimes of genera drawn from the fossil record.

Burlando [6] has shown that taxonomic trees have a self-similar hierarchical structure which may taken as evidence of SOC behavior (see Ref. [3] for a discussion). For example, Burlando finds that the frequency distribution of the number of species per genus follows a power law over two or three decades. If we make certain assumptions about speciation, we can demonstrate that this is equivalent to the power-law distribution of genus lifetimes, since the longer-lived genera give rise on average to larger numbers of species.

Another form of evidence for SOC behavior comes from the fossil record of species extinction. A number of authors have suggested models connecting the dynamics of evolution to the extinction process [7–9], and although the exact dynamics of these models differs, they all concur on the prediction that, given an underlying evolutionary dynamics that is critical, the distribution of the sizes of extinction events should follow a power law. Newman [10] has demonstrated that the fossil data on extinctions are indeed compatible with a power law, and furthermore that the exponent of this power law is in good agreement with the predictions of some of the proposed models.

Given the evidence then, are we justified in concluding, at least tentatively, that evolution is indeed a self-organized critical phenomenon? In this paper we argue that this is, in fact, not a justified conclusion. We introduce a new and very simple model of evolution and extinction which contains no element which mimics the co-evolutionary avalanches which are considered responsible for critical behavior, and yet it reproduces accurately all of the results described above. If the experimental data can be reproduced reliably by a non-critical theory, then clearly those data do not constitute evidence of criticality.

Our model is one in which species become extinct because of stresses placed upon them by their environment. It is defined as follows. We take N species and give each one a fitness $0 \leq x < 1$, which measures its ability to withstand stress. We then divide time into short intervals and in each interval choose at random a number η, which represents the level of stress during that interval. All species feel the same stress. We now apply the following rule: if at any time the level of stress η exceeds the numerical value x of the fitness of a particular species, that species becomes extinct. In order to keep the number of species constant, we then repopulate the ecosystem at each step with new species equal in number to those that have just been wiped out, assigning them fitnesses chosen randomly in the interval $0 \leq x < 1$. The stresses η are chosen from some distribution $p_{\text{stress}}(\eta)$, and one of the most important features of the model is that its fundamental predictions do not depend on the particular functional form we choose for p_{stress}.

There is one further crucial element to our model: evolution. In the intervals between stresses, species evolve under other selection pressures and their fitness with respect to stress may either increase or decrease. We model this by choosing in each time interval a small fraction f of the species and changing their fitnesses to new values chosen at random. With this, the definition of the model is complete. Giving each species an initial random fitness, one now simply repeats the steps of applying the stress, wiping out species with low fitness, and then evolving a small fraction to new forms. We have studied the model both numerically and analytically. Here we summarize the main results.

First, in Figure 1 we show a histogram of the sizes of extinction events in the model, measured as a fraction of the total number of species in the system. The different lines represent the extinction distribution for different applied stresses $p_{\text{stress}}(\eta)$. As the plot shows, the distribution follows a power law closely over many decades, except at very small extinction sizes. Furthermore, although the exponent of the power law varies with the different types of applied stress, the existence of the power law appears to be robust. As shown by Newman and Sneppen [11], it is possible to demonstrate the power-law form of the extinction distribution analytically as well.

Next, in Figure 2 we show a histogram of species lifetimes for the model. Again the distribution has a power-law form, which agrees with the observations of Adami [4] and Sneppen *et al.* [5].

The model as described does not contain any information about taxonomic relationships, but it is not difficult to introduce these. If, for example, we are interested in the number of species per genus, we can proceed as follows. Initially we assign species at random to different genera and then, each time we add a new species to the model, we consider it to have speciated from one of the others, which we choose at random. Most of the time, the new species simply inherits its genus from the parent species. But in a small fraction g of cases (also chosen at random), we consider the species instead to be the founding member of a new genus. Using this prescription, we can construct a histogram of the number of species per genus similar to those constructed by Burlando [6]. An example of such a histogram is shown in Figure 3. Again, the scales are logarithmic, and the approximately straight-line form of the histogram indicates a power-law distribution, as seen in Burlando's data.

The model possesses a number of other interesting features, such as the "aftershocks" discussed by Newman and Sneppen [11]. These are extinctions which occur in the aftermath of a large extinction event, when a large number of new species have appeared to fill the niches vacated by the species which recently died out. These new species may be regarded as "opportunists", taking advantage of the underpopulated ecosystem to get a toehold in a new environment. They may or may not be well-adapted to survive stress, and those that are not will be susceptible to extinction the next time a stress of moderate size occurs. The extinction of these species is visible as smaller extinction peaks in the wake of the larger event. As well as predicting their existence, our model suggests that these aftershock extinctions should die off with time t as t^{-1}, a result which should, in theory, be testable against the fossil record.

Many variations on the model are possible. In general variations in the details of the dynamics (such as changing the way in which fitnesses are assigned, or the value of the evolution parameter f) appear to make little difference to the qualitative predictions of the model. One variation which is of interest however is the "multi-trait" model, which answers some of the most obvious objections to the model in its present form. This version of the model is discussed in Ref. [10].

To conclude, we have presented a new model of extinction caused by the interplay of stresses on the ecosystem with the evolution process. Although the model is very simple, and contains no elements which mimic the proposed self-organized critical evolutionary dynamics, it appears to reproduce well the power-law distributions which have been cited as evidence for SOC behavior. We conclude therefore that criticality is not necessary to produce these power laws, and hence that they should not be taken as evidence of it.

References

[1] S. A. Kauffman, *The Origins of Order*, OUP, Oxford (1992).

[2] P. Bak and M. Paczuski, Brookhaven National Laboratory preprint no. 62678 (1996).

[3] R. V. Solé and J. Bascompte, Proc. Roy. Soc. B **263**, 161 (1996).

[4] C. Adami, Phys. Lett. A **203**, 29 (1995).

[5] K. Sneppen, P. Bak, H. Flyvbjerg and M. H. Jensen, Proc. Nat. Acad. Sci. **92**, 5209 (1995).

[6] B. Burlando, J. Theor. Biol. **146**, 99 (1990).

[7] S. A. Kauffman, *At Home in the Universe*, OUP, Oxford (1995).

[8] M. E. J. Newman and B. W. Roberts, Proc. R. Soc. London B **260**, 31 (1995).

[9] R. V. Solé, Complexity **1**, 40 (1996).

[10] M. E. J. Newman, Proc. R. Soc. London B **263**, 1605 (1996).

[11] M. E. J. Newman and K. Sneppen, Phys. Rev. E **54**, 6226 (1996).

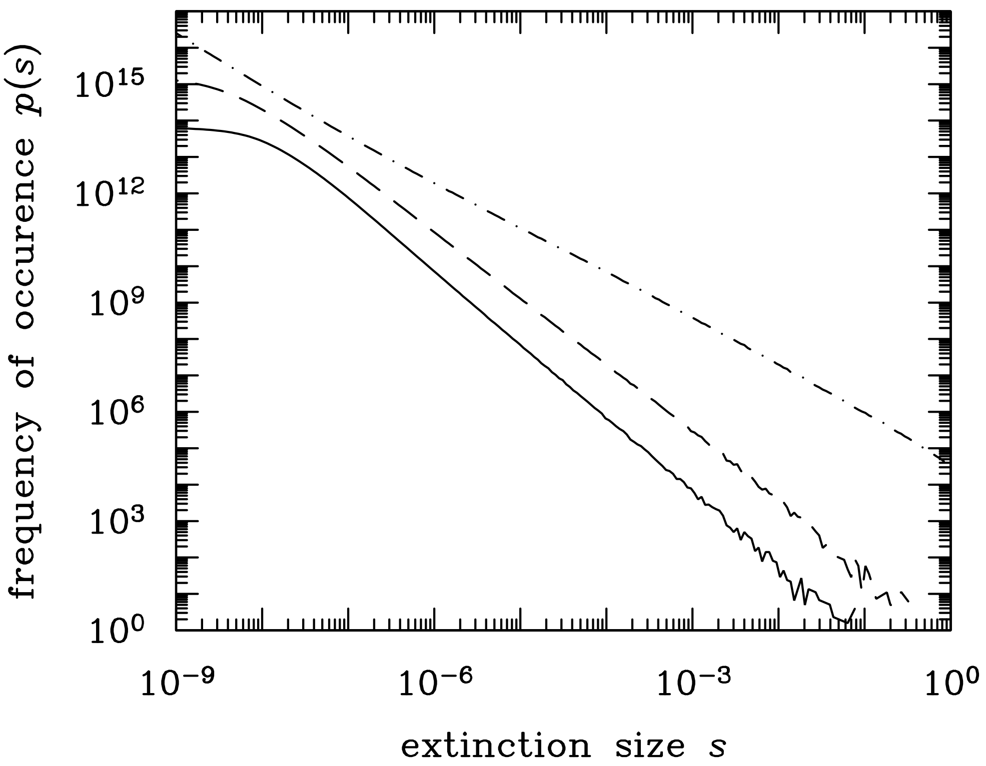

Fig. 1. Plots of the distribution of extinction sizes in simulations of the model. The solid line corresponds to stresses with a Gaussian distribution centered at zero, the dashed one to exponentially-distributed stresses, and the dot-dashed one to Lorentzianly-distributed ones.

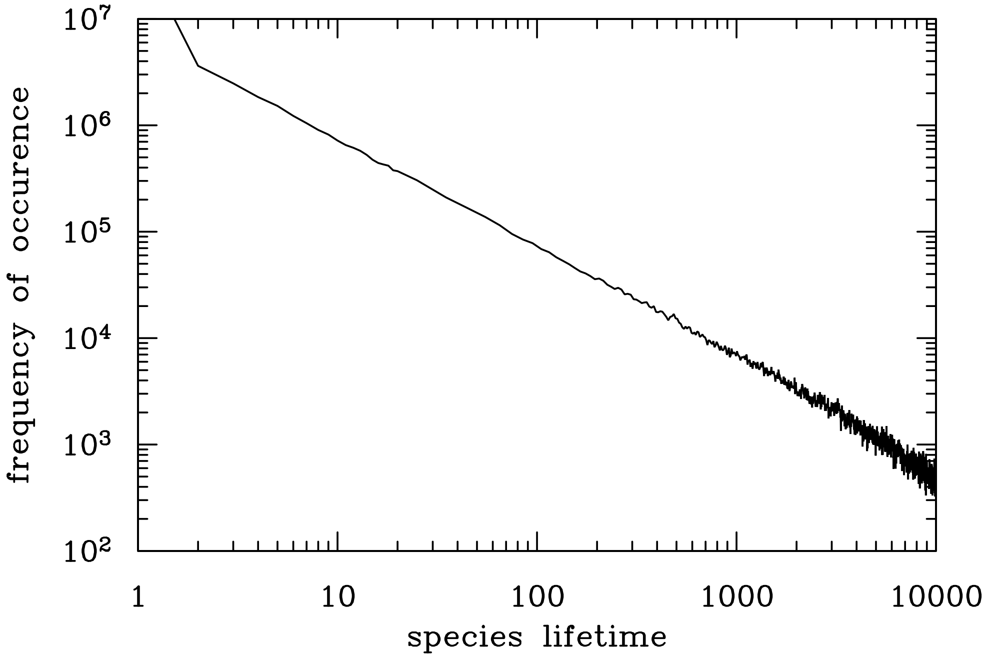

Fig. 2. Histogram of the distribution of species lifetimes from simulations of the model. Again, the distribution follows a power law.

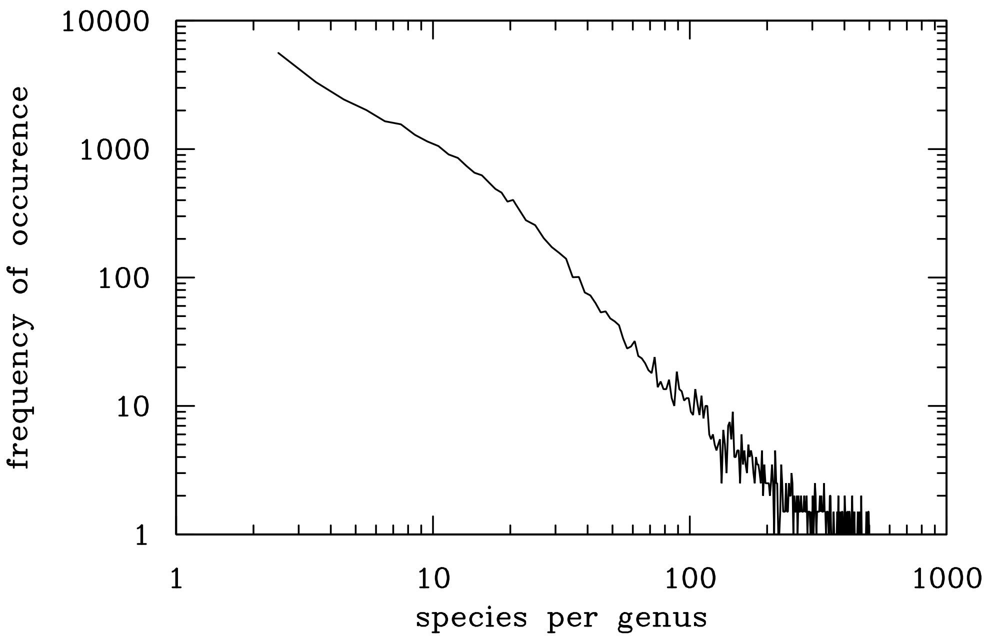

Fig. 3. Histogram of the number of species per genus in simulations of the model, calculated according to the method outlined in the text.