Decline in extinction rates and scale invariance in the fossil record

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Abstract.—We show that the decline in the extinction rate during the Phanerozoic can be accurately described by a logarithmic fit to the cumulative total extinction. This implies that extinction intensity is falling off approximately as the reciprocal of time. We demonstrate that this observation alone is sufficient to explain the existence of the proposed power-law forms in the distribution of the sizes of extinction events and in the power spectrum of Phanerozoic extinction, results that previously have been explained by appealing to self-organized critical theories of evolutionary dynamics.

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Introduction

It has been widely accepted for some time now that the mean rate of extinction, either of genera or of families, in the fossil record, appears to decline throughout the Phanerozoic (Raup and Sepkoski 1982; Sepkoski 1984, 1991, 1993, 1996; Van Valen 1984; Flessa and Jablonski 1985; Gilinsky and Bambach 1987; Raup 1988; Gilinsky 1994). This decline is illustrated in Figure 1, where we show the number of marine families becoming extinct per unit time in each stage since the beginning of the Cambrian, using data drawn from Sepkoski 1992. The decline is only an average trend. Certainly there are deviations from it; two of the largest extinctions in the plot, for example, occur in the second half of the data set. Overall, however, the decline in extinction is clear in the figure.

The same decline is visible in other extinction metrics as well. For example, it has become increasingly common in recent years to quote extinction figures in terms of the percentage of taxa becoming extinct in a given interval, i.e., the ratio of the number of taxa becoming extinct to the number in existence. This metric shows an even more dramatic decline than the simple extinction rate (see the inset to Fig. 1) because of the steady increase in diversity throughout the Phanerozoic (Sepkoski 1993, 1996; Benton 1995).

The origin of the decline in extinction rate has been much debated. Some authors have argued that it is a real biological phenomenon arising from a slow increase in the average fitness of species (Raup and Sepkoski 1982), from taxon sorting (Sepkoski 1984; Gilinsky 1994), from changes in taxonomic structure (Flessa and Jablonski 1985), or from taxon-aging effects (Boyajian 1986). Others have suggested that it may be an artifact of sampling biases (Pease 1992). In this paper, however, we are concerned not with the causes but with the implications of extinction decline.

In recent years there has been considerable interest in the so-called self-organized critical theories of evolution and extinction. Theories of this type contend that patterns of connectivity in ecosystems have a tendency to evolve to a “critical” state in which small perturbations can trigger disturbances of arbitrary magnitude. Starting with Kauffman and Johnsen (1991), a number of authors have suggested that the fossil record of extinction shows evidence of processes of this kind (Kauffman 1993; Sneppen et al. 1995; Solé and Bascompte 1996; Bak and Paczuski 1997), principally because of the existence of apparently scale-free distributions in the fossil data, particularly in
the sizes of extinction events and in the power spectrum of extinction. Kauffman (1993), for instance, has suggested that a histogram of the number of families becoming extinct per stage has a power-law form. Solé et al. (1997) have suggested that the power spectrum of fossil extinction intensity—the square of the Fourier transform—also appears to follow a power law. Distributions following power laws are often taken as indicative of critical behavior (Bak 1996), although there are also many other ways in which power laws can be generated (Montroll and Shlesinger 1982; Sibani and Littlewood 1993; Raup 1997; Spen- pen and Newman 1997; Somer ette and Cont 1997).

In this paper we make a number of observations. First, we note that the decline in extinction rate during the Phanerozoic can be accurately parameterized if we consider the cumulative total extinction, i.e., the total number of species that become extinct over a period of time, as the length of that period is increased. We show that this quantity can be well fit by a logarithmic function. We then use this parameterization to calculate the expected distribution of the sizes of extinction events in the fossil record, and show that the results are in precise agreement with the power-law form found by other authors. Thus there is no need to invoke self-organized critical theories to explain this form. Finally, we calculate the power spectrum of our declining extinction rate and show that it too takes a power-law form similar to that found by Solé et al. (1997).

Parameterization of Extinction Decline

Sepkoski’s database of marine families gives us an estimate of the total number of families becoming extinct in each of 77 intervals (usually stages but in some cases groups of stages) dating from the Vendian/Cambrian boundary at about 544 Ma. (The timescale used in this paper is that of Harland et al. (1990), updated with corrections kindly supplied by J. J. Sepkoski, Jr. and D. H. Erwin.) We define the cumulative total extinction $c(t)$ at time $t$ to be the total number of families in the database that became extinct at or before that time. If we denote by $x(t)$ the average extinction rate at time $t$ (i.e., number of families becoming extinct in the corresponding interval divided by the interval length) then we can write the cumulative extinction as

$$c(t) = \int_0^t x(t') \, dt',$$

where the integral runs from the start of the data set up to time $t$. This cumulative extinction metric was first proposed and studied by Sibani et al. (1995, 1998). It is useful for two reasons. First, it is much less susceptible than raw extinction metrics to noise in the data. As we will see, the plot of $c(t)$ as a function of $t$ is quite smooth, making it much easier to interpret than most other metrics. (This immunity to noise is a general characteristic of integrated metrics, and the use of such metrics is common in many branches of science and engineering where noise levels are high enough to be problematic.) Second, the cumulative extinction does not depend on how time is partitioned in the data set. In our study the data are divided, by and large, into stratigraphic stages, but the numerical value of $c(t)$ would be the same if we were to choose any other...
partitioning. To see this, we need only notice that the number of taxa becoming extinct before a certain time is not dependent on how we divide the time into intervals.

In Figure 2 we show the cumulative total extinction of marine families, calculated from Sepkoski’s data, as a function of time. Note how the data are plotted; we have found that for a certain choice of the axes the data take a particularly simple form. First, we have made the horizontal axis in the figure logarithmic and the vertical one linear, and second, we have shifted the origin of time from the start of the Cambrian to an earlier point. When plotted in this way, the cumulative extinction appears as a straight line. This implies that \( c(t) \) increases logarithmically in time and can be written in the form

\[
c(t) = A + B \log(t - t_0). \tag{2}
\]

The best fit is obtained by choosing values for the constants \( A = -17,700, B = 3130 \), and \( t_0 = -262 \) m.y. In other words, the data take a straight-line form on a linear-log plot when time is measured from a point about 260 m.y. before the start of the Cambrian. It is interesting to speculate why this might be the case (although we will not do so here). Similar results apply for other extinction metrics as well. The cumulated per-taxon extinction, for instance, also closely follows a logarithmic growth law.

The straight-line fit in Figure 2 has an excellent \( r^2 \) of 0.996, but this is common with cumulative statistics. A more informative goodness-of-fit indicator is obtained by looking at the statistical significance of corrections to the straight-line form. Do the data support alternative hypotheses to the one given here? In this case, the leading correction to test for is the next term in the polynomial expansion of \( c(t) \) in terms of \( \log t \), which is the quadratic term. Using an \( F \)-test (Sokal and Rohlf 1995), we find that the \( p \)-value for the improvement of fit when we include the quadratic term is 0.42. This indicates that there is no statistically significant quadratic correction to the straight-line form (a fact that is also clear to the eye from the figure).

Sibani et al. (1995, 1998) proposed that the curve of cumulative extinction increases as a power law in time, meaning that it should appear straight on dual logarithmic scales. We have replotted the data in this way in the inset to Figure 2 but the fit in this case is considerably poorer than our logarithmic one \( (r^2 = 0.90) \). Interestingly, Sibani et al. were studying cumulative extinction metrics in the context of a quantitative model of extinction decline based on the idea of increasing mean species fitness. As it turns out, the predictions of their model are precisely in agreement with the form found here \( (eq. 2) \), rather than with their power-law form.

Combining equations (1) and (2) and differentiating, we now deduce the following form for the actual (noncumulative) total extinction rate:

\[
x(t) = \frac{B}{t - t_0}. \tag{3}
\]

In other words, the extinction rate falls off during the Phanerozoic as the reciprocal of time. This functional form is shown as the dotted line in Figure 1.

In the next two sections we study the consequences of the decline in extinction rate for the distributions of the sizes of extinction events and for the power spectrum of extinction.
Distribution of the Sizes of Extinction Events

One quantity that has received a lot of attention from the proponents of self-organized critical theories of evolution is the distribution of the sizes of extinction events in the fossil record. In fact, the temporal resolution of most current data sets is insufficient to distinguish individual extinction events, and so attention has usually focused on the number of taxa becoming extinct per stratigraphic stage. As Newman (1996) has pointed out, it is not clear that the distribution of this quantity obeys a power law, but the data are compatible with the power-law form, with an exponent of \(-2.0 \pm 0.2\). We now show that this is exactly what one should expect from an extinction profile which decays over time according to equation (3).

Sibani et al. (1995) demonstrated that given a declining extinction rate one can extract an estimate of the expected distribution of number of taxa becoming extinct per unit time. Here we use their methods to calculate this distribution for our data. The number \(dt\) of unit time intervals in which the number of families becoming extinct lies in the range \(x\) to \(x + dx\) is proportional to the derivative

\[
\frac{dt}{dx} = \frac{(t - t_0)^2}{B} = \frac{B}{x^2} 
\]

where we have made use of equation (3) twice. In other words, the probability \(p(x)\) of a number \(x\) of families becoming extinct in any randomly chosen stage should vary as

\[
p(x) \sim x^{-2}. \tag{5}
\]

This is precisely the power-law form with an exponent \(-2\) observed in the fossil data. Given the form of the decline in extinction intensity, therefore, no further assumptions are needed to explain this power-law form. In particular, it is not necessary to assume a self-organized critical dynamics.

The argument above is not perfect. In particular, it neglects variation in stage lengths, which could contribute significantly to variation in the number of taxa becoming extinct per stage. It also assumes equation (3) to be an exact representation of the decline in extinction rate, whereas it is of course only an approximation, since the real extinction rate contains fluctuations about the average form, of which the most important are the large mass extinction events. Nonetheless, the crucial point is that the distribution of the sizes of extinction events need not have anything to do with the proposed critical processes. A declining extinction rate is all that is needed to explain the observed data.

The Power Spectrum of Extinction

Solé et al. (1997) have analyzed the Phanerozoic extinction record using Fourier transform techniques and proposed that the power spectrum \(P(f)\) of extinction falls off with frequency \(f\) according, once more, to a power law:

\[
P(f) \sim f^{-\beta}, \tag{6}
\]

with values of the exponent \(\beta\) in the vicinity of 1. They suggested that this too could be a sign of critical dynamics in the processes giving rise to extinction (although they conceded that other explanations are also possible). In this section we demonstrate that a mean extinction rate that declines according to equation (3) is also sufficient to explain the observed power spectrum, without resorting to theories involving critical phenomena.

The power spectrum for an extinction rate declining as \((t - t_0)^{-1}\) is given by

\[
P(f) = \left| \int_0^{t_1} (t - t_0)^{-1} e^{i2\pi ft} dt \right|^2, \tag{7}
\]

where we measure time again from the beginning of the Phanerozoic and \(t_1\) is the latest time for which we have data, in this case the end of the Pleistocene. This integral is unfortunately not analytically tractable, but it is trivial to perform numerically. We have done this and the results are shown in Figure 3 for the value of \(t_0\) extracted from our fit to the fossil data. As the figure shows, the results follow a power-law form (i.e., a straight line on the logarithmic scales used in the figure) closely over the range of frequencies of interest, with an exponent \(\beta = 1.96 \pm 0.01\). Although, as we mentioned above, Solé et al. found values of \(\beta\) in the region of 1, in our own calculations we have found values closer to 2 (Newman and
Eble 1999), so the form found here is not implausible. (There may also be some differences introduced by the use of different data sets; the results of Solé et al. were based on analysis of the data of Benton (1993), rather than that of Sepkoski.)

It is worth mentioning that this is not the only alternative explanation that has been proposed for the form of the fossil power spectrum. Kirchner and Weil (1998) have suggested that it may be an artifact of the method of analysis used by Solé et al.; by contrast with the direct Fourier transform method we have used here, Solé and coworkers used an autocorrelation method to calculate the power spectrum, which may have inadvertently produced a $1/f$ form where there was none in the data. Another possibility is that the form of the spectrum is primarily a result of the division of the data into stages (Newman and Eble 1999).

**Conclusions**

In this paper we have studied the cumulative total extinction for fossil marine families during the Phanerozoic and shown that it can be well approximated by a logarithmic growth law. This in turn implies that the extinction intensity itself falls off as the reciprocal of time. We have made use of this observation to demonstrate possible explanations of two previously published results: the power-law form of the distribution of the sizes of extinction events and the power-law form of the power spectrum of the fossil extinction record. In both cases we show that the decline in extinction intensity is all that is necessary to explain the observed results; we do not need to appeal to an underlying self-organized critical dynamics as other authors have done.

The results presented in this paper are only one step in an argument. We have shown that a declining extinction rate can account for a number of earlier observations. The other step in the argument is to explain what gives rise to the decline. This is a question of great interest and one about which arguments will no doubt continue for many years.

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