A multiplicative multifractal model for originations and extinctions

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Abstract.—Recent works have suggested that the fossil record exhibits a fractal structure; i.e., that processes, such as extinction, follow a power-law size distribution and their time series show a 1/f power spectrum. This structure has been used as evidence that evolutionary dynamics are an example of a self-organized critical (SOC) process. We have reexamined this claim by analyzing a detailed record of marine genus-level extinctions and originations. Our results indicate that neither extinctions nor origination metrics show the power-law size distribution or a 1/f power spectrum characteristic of SOC and related models. We also believe that the underlying assumptions of SOC are incompatible with our understanding of the processes controlling macroevolutionary patterns.

Statistical analyses of the data sets are compatible, however, with the presence of multifractal self-similarity in both records, consistent with a hierarchical and multiplicative generating process. This model assumes that multiple causal mechanisms, acting over many spatial and temporal scales, interact to promote or inhibit originations and extinctions. In this view, the same event can have quite different impacts depending on the state of the biotic or physical system at the time that it occurs. This may at least partially explain such phenomena as the imperfect correlation between eustatic sea-level changes and macroevolutionary processes and the apparent nonlinear response of biotic systems to bolide impacts.

Introduction

Gould (1977) described three “eternal metaphors” or questions of evolutionary paleontology. One of these is what is the motor of organic change; i.e., to what extent is evolutionary change driven by internal biotic interactions as compared with external forcing by abiotic processes? In the past two decades, especially since the publication of the seminal Alvarez et al. (1980) paper on the K/T impact, the argument has swung strongly in favor of physical control (e.g., Raup 1992; Eldredge 1999). Recently, however, the role of biotic interactions has received new support from outside the paleontological community, particularly from physicists. In a series of papers and a book, Per Bak, Kim Sneppen, and their colleagues (Bak and Sneppen 1993; Bak et al. 1994; Sneppen et al. 1995; Bak 1996; Solé et al. 1997) have argued that empirical patterns are in accord with a simple dynamical model of system behavior termed self-organized criticality (SOC), in which large-scale patterns arise as a consequence of local, small-scale interactions (Bak et al. 1987, 1988). Specifically, they suggested that the major-scale patterns seen in the fossil record, including major radiations and extinctions, “may have taken place without being triggered by large cataclysmic events; they may be intrinsic consequences of the dynamics of biology; that is, they are self-organized” (Bak et al. 1994).

The SOC model, and parallel work by Kauffman and Johnsen (1991; Kauffman 1993), has produced a rapidly growing literature on “evolution models,” most of which is published in physics journals and thus may be unfamiliar to paleontologists (e.g., Grassberger 1995; Wilke and Martinetz 1997; Ausloos et al. 1998; Drossel 1998; Pelletier 1999; Staindish 1999; Pękalski 1999; cf. Plotnick and McKinney 1993; Newman 1996; Kaufman, et al. 1998). The empirical basis of these models tends to rely on a very limited subset of the paleobiological literature, most commonly that of Raup (1991a,b).

The last ten years have also seen a major growth in the concern with issues of scale and hierarchy in both paleontology and ecology (Allen and Hoekstra 1992; Enquist et al. 1995;
Aronson and Plotnick 1998; Cohen 1998; Martin 1998; Patzkowsky 1999). It remains unclear whether characteristic scales of behavior of ecological and evolutionary systems can be identified (Aronson and Plotnick 1998) and how these scales correspond to scales of external forcing. Self-organized criticality makes very specific predictions concerning the scaling of evolutionary dynamics. Specifically, it predicts that phenomena such as extinctions and originations should be fractal; i.e., that the statistical properties of each should not change across scales (Aronson 1994; Plotnick 1995).

In this paper we will describe new analyses of Phanerozoic patterns of extinction and origination at the genus level and show that they are not compatible with the SOC model. We also will describe why we believe that the canonical SOC model for evolution is conceptually flawed. We will then present an alternative conceptual and statistical model, based on hierarchical concepts, for these patterns. This new model closely matches many aspects of the empirical record and, we believe, is far more in accord with the current understanding of paleontologists concerning controls of macroevolutionary patterns (e.g., Bennett 1997; Allmon, et al. 1998; Aronson and Plotnick 1998; Miller and Mao 1998).

Self-Organized Criticality As a Model for Macromutation

The Model.—In the Bak–Sneppen SOC model for evolution, each species in the system is represented by a single value from a bounded range of numbers. This number denotes “fitness” of the species. The species are arrayed on a line with periodic boundary conditions (ends are connected), so that every species has two neighbors. Initially, the values are randomly assigned. It is now assumed that the least-fit species, i.e., the one with the lowest number, will be most subject to change. This change is accomplished by randomly changing the number assigned to the species. This change corresponds to either an extinction or a mutation. Which one of these it is seems to be somewhat arbitrary (Bak [1996] uses the term “pseudoextinction”). The total number of entities in the system remains constant. “External” perturbations in the model thus occur only at the smallest scale, that of the single species.

Biotic interactions are introduced by having the change of the least-fit species trigger similar random changes in each of its two neighbors. After the neighbors are changed, the simulation again locates and changes the species in the system with the lowest fitness and iterates the process.

Initially, the average value of fitness in the system is close to the midpoint of the range. In addition, since low values could occur anywhere along the line, the locations of successive least-fit species are independent. As the system develops, however, the average value increases well above the midpoint. As a result, it is far more likely that a change in a species fitness value will be negative. The upshot of this is that the change of the least-fit species will probably reduce the fitness of its neighbors, making it likely that the one of them will be the species found in the next iteration. The end product is that regions of the system undergo “avalanches” of change, which Bak (1996) compares to “mass extinctions” or “punctuated equilibrium.” The large-scale structure of the simulation is thus a consequence of small-scale processes and of the system’s tendency to self-organize.

Evidence for SOC in the Fossil Record.—SOC models were developed to explain two separate and widely observed phenomena in the natural sciences. First, that the size distribution of events follows a self-similar power-law or fractal distribution. A familiar example is the Gutenberg–Richter law of earthquake magnitude. Second, that many time series are also self-similar, in that they possess a “1/f” Fourier power spectrum (Montroll and Shlesinger 1982; Bak et al. 1987, 1988; Schroeder 1991; Plotnick 1995). The power (squared amplitude) of the sinusoidal components of these series decline proportional to 1/frequency$^\beta$, with $\beta$ being approximately 1 (see Fig. 4). In comparison, the $\beta$ value for a random sequence (“white noise”) is 0 and for a random walk (Brownian motion) is 2. The avalanches in the SOC evolution model exhibit both 1/f spectra and power-law size distributions. Self-organized criticality thus makes very specific...
statistical predictions concerning the scaling of evolutionary dynamics. If SOC is to be viewed as a valid model for macroevolution, the fossil record also should show these properties.

Bak (1996) compared a histogram of “extinctions” in his SOC model with a histogram of extinction-event magnitudes published earlier by Raup (1991a,b), based on data from Sepkoski, and found them to be visually similar. He also claimed to find evidence for SOC from a log-plot of durations of fossil genera, using a transformation of a previously published histogram drawn from the Sepkoski database. Raup (1997), in his review of Bak’s book, pointed out that the transformation was incorrect.

Newman (1996) presented a statistical analysis of the same data, which indicated that frequency of extinction events are compatible with a power law with an exponent of approximately 2 (it should be noted that Newman explicitly presented an alternative, non-SOC model for this phenomenon). Finally, Solé et al. (1997) published an analysis of various extinction time series that purported to show strong evidence for 1/f behavior. The numerous alternative models for macroevolution found in the physics literature have accepted the empirical reality of 1/f and size power spectrum for the fossil record.

Unfortunately, the results of Solé et al. (1997) have been shown to be artifacts of their methods (Kirchner and Weil 1998; Plotnick and Sepkoski 1998; Newman and Eble 1999). First, their power spectrum was based on the Fourier transform of the autocovariance function, rather than on the squared magnitude of the Fourier transform of the raw data. This latter approach is generally what is used in the fractal literature when determining whether a sequence shows 1/f structure (Schroeder 1991; Plotnick 1995; Newman and Eble 1999). When applied to a random walk, for example, the value of the slope coefficient $\beta$ will be 2 when the second method is used, but will be 1 when the first method is employed. As a result, the first method will lead to an erroneous interpretation of 1/f for a random walk.

Second, they attempted to correct for the uneven lengths of the geologic stages by using linear interpolation between their data points. This procedure automatically introduces high levels of autocorrelation into their analyses. Kirchner and Weil (1998) and Plotnick and Sepkoski (1998) showed that apparent 1/f noise can be produced by interpolating between randomly generated points.

Solé et al. (1998) attempted to address these objections by applying a different analysis method to noninterpolated data. Rescaled range analysis (also known as R/S or Hurst analysis) compares the range (maximum minus minimum value) of a cumulative record against the time period $T$ over which the range is measured (Feder 1988; Plotnick 1995). For example, a random walk, whose step sizes (increments) are an independent random Gaussian variable (white noise), has a range that scales proportional to $T^{0.5}$. The exponent 0.5 in this relationship is $H$, the Hurst exponent.

For many empirical data sequences, the Hurst exponent exceeds 0.5, being typically in the range 0.7–0.8. This implies that the range of the cumulative record is greater than would be expected if the increments were an uncorrelated white noise. This can occur if the increments themselves are autocorrelated; i.e., positive increments tend to be followed by positive increments and negative increments by negative increments, a property called persistence. Mandelbrot and Wallis (1969) showed that Hurst exponents greater than 0.5 can be generated by a self-similar (fractal) series known as fractional Brownian motions, whose increments are termed fractional Gaussian noises (Feder 1988; Plotnick 1995). Fractional Gaussian noises show very long-term persistence; i.e., their autocorrelation asymptotically declines to zero. In comparison with white noises, therefore, which are independent and thus have no “memory,” fractional noises have “infinite memory.”

Since fractional noises generate series with Hurst exponents greater than 0.5, it has frequently been assumed that the reverse is also true. Solé et al. (1998) obtained an average Hurst exponent of 0.80 for their origination and extinction data sets. They indicated that this supports their previous interpretation of the fractal nature of the fossil record.

Unfortunately, there are several difficulties
with R/S analysis, First, there are technical problems, such as over- and underestimation, which are especially severe with small data sets (Wallis and Matalas 1969; Bassingthwaighte and Raymond 1994). More importantly, although a Hurst exponent \( \geq 0.5 \) is consistent with a fractal sequence, it is not uniquely so (Beran 1992). Klemes (1974) and Mesa and Poveda (1993) suggested alternative mathematical models that don’t require the “infinite memory” assumptions of the fractal noise models. For example, Mesa and Poveda (p. 4001) said “the so-called Hurst effect and other anomalies in geophysical time series are probably the result of a mixture of scales more than infinite memory” (emphasis ours). The model we will suggest in this paper is based on such a mixture of scales.

Newman and Eble (1999) developed a different interpolation scheme for marine family-level extinction data, based on data from Sepkoski (1992) and from Benton (1993). The data are converted into a flat step-pattern, with its width being the length of the stage and its height the per-million-year rate of extinction during that interval. Their Fourier analyses, based on the squared magnitude of the Fourier transform, indicate two different regions of the spectra. At higher frequencies, corresponding to time periods less than about 10 m.y., the spectra are artifacts of the interpolation scheme. At longer time periods, however they indicated that the frequency falls off exponentially rather than following a power law. Newman and Eble suggested that autocorrelation in the record was related to the turnover time for families. They also interpreted their results as not requiring SOC.

Eble (1999) examined origination frequencies at the family level for selected terrestrial groups and at the genus level for various marine groups. Out of six groups considered, only two showed any indication of a power-law distribution.

It should also be pointed out, as discussed by Raup (1997), that presence of a power-law distributions (or 1/f spectra) does not automatically imply that SOC is the underlying mechanism. Other models, such as that of Newman (1996), generate similar behavior without biotic interactions.

**Conceptual Basis of SOC.**—There are numerous conceptual grounds for being critical of self-organized criticality. As pointed out by Aronson and Plotnick (1998), the Bak–Sneppen evolution model is highly abstract and is not based on properties of real ecological or evolutionary units. The SOC model is “bottom-up,” i.e., the large-scale structure in the model is a consequence solely of local, short-term interactions. Microevolutionary processes produce macroevolutionary phenomena in SOC; long-term or large-scale changes in the physical environment or taxonomic evolution play no role. External perturbations in the system are constant and of a single small scale, that of an individual “species.” These perturbations also affect only the “least-fit” species; species with high fitness are affected only because of biotic interactions. As a result, nearly all of the system’s behavior is a result of internal cascades resulting from self-organization in the system. The strength of biotic interactions is very high. Finally, system size is constant throughout the simulation.

We believe that virtually all paleontologists and evolutionary biologists, even those who do not recognize a phenomenological break between microevolution and macroevolution, would find SOC not only counterintuitive, but conceptually flawed. The more obvious conceptual objections to SOC include the following:

1. The number of components of biotic systems are not fixed, but can change dramatically over time.
2. External perturbations can range in scale from local to global and from short- to long-term and affect a wide range of numbers of taxa.
3. Extinctions of taxa may depend only marginally on some reified metric of fitness.
4. Biotic interactions range widely in strength; most are weak (Plotnick and McKinney 1993).
5. All species are not equal; they differ tremendously in their response to perturbations and their impact and dependence on each other.

Finally, stemming from the initial papers on SOC, the published literature on evolution models often misstates paleontological concepts. In the most glaring case, the concept of
punctuated equilibrium is conflated with both mass extinctions and evolutionary radiations and is used synonymously with rapid turnover (Aronson and Plotnick 1998).

Alternative models do exist that address some of the objections to SOC models. For example, the model of Plotnick and McKinney (1993) utilized variable magnitudes of perturbation and kept perturbations and biotic interactions independent. Newman (1996) introduced a non-SOC model largely driven by time-varying external perturbations and was able to produce the purported 1/f structure (see also Standish 1999). Wilke and Martinetz (1997) modified the Newman model to incorporate variable system sizes. The coupled logistic model of Sepkoski (1984), which incorporates both biotic interactions and perturbations, still retains great explanatory power.

Despite these objections, there is still a great deal of value in the Bak–Sneppen SOC model (Maddox 1994; Grassberger 1995; Aronson and Plotnick 1998). Most importantly, it has served to redirect the attention of paleontologists to the major roles that biotic interactions and internal ecosystem organization must still play in any general model of evolutionary phenomena (Plotnick and McKinney 1993; Patterson and Fowler 1996).

SOC and Phanerozoic Patterns of Origination and Extinction

Database.—We have reassessed the empirical support for SOC using a detailed unpublished compilation of marine genus-level originations and extinctions for the Phanerozoic (Sepkoski 1997). The database includes approximately 36,000 genera. Since most time-series analysis techniques require time units of equal duration, all metrics were determined in as near as possible to equal 5.0-m.y.-long intervals (x̄ = 5.0; SD = 1.7). This was done by subdividing some stratigraphic units and distributing low-resolution data (i.e., times of origination or extinction known only to series or system) among the intervals, in proportion to data whose age is definitely known. As a result, the data set includes fractional numbers. Unavoidably, as the case with any interpolation method, this introduces some autocorrelation into the analysis. There were 108 total intervals.

We analyzed four different metrics each for originations and extinctions (Gilinsky 1991; Foote 1994). These include
1. NE and NO: raw number of extinctions and originations per stratigraphic interval (Fig. 1);
2. PE and PO: proportional extinction and origination; per-taxon rate in percent (NE or NO divided by interval diversity * 100);
3. TE and TO: total extinction and origination rates or number per million years (NE or NO divided by interval length);
4. PTE and PTO: per-taxon extinction per million years (PE or PO divided by interval length).

Analyses.—The frequency distributions of the metrics are shown in Figure 2 and for log-transforms of the data in Figure 3. In contrast with the histogram given by Raup (1991a), the frequency distributions are non-monotonic (although they could be made to look monotonic if larger bins were used (Raup 1997)). They clearly do not match the expected SOC pattern of a power-law distribution, which would predict a preponderance of small values. One-way Kolmogorov–Smirnov tests show that only the NO distribution is distinguishable from a log-normal distribution at the 1% level.

A second disagreement with the predictions of SOC is found when examining the log power spectra of the NO and NE sequences, which was produced using a discrete Fourier transform (Fig. 4). The regression of the NO time-series power spectrum has a slope of −0.87, with an r of −0.54; whereas that of the NE series has a slope of −0.42, with r = 0.28. An ANOVA indicated that the regressions are significant at the 0.05 level. Although both the originations and extinctions time series show a power spectrum that appears to decline relative to frequency and thus to suggest the presence of at least some autocorrelation in the series, the correlations are low and the slopes are less than −1. It cannot be ruled out that at least part of the autocorrelation is an artifact of the methods used to generate the sequence (i.e., the treatment of low-resolution data).

Taken together, these analyses suggest that
MULTIPLICATIVE MULTIFRACTAL MODEL

FIGURE 1. Generic level biodiversity patterns over the past 600 m.y compared with a synthetic multifractal series. Data series composed of 111 time units approximately 5 m.y. long. A, Total number of originations per time interval (series NO). B, Total number of extinctions per time interval (series NE). C, A 120-point synthetic multifractal series, scaled to size of originations series.

FIGURE 2. Frequency histograms of eight metrics of originations and extinctions. One hundred eight time intervals over last 545 m.y. Top row: NO = raw number of originations per interval; PO = per-taxon rate of origination; TO = originations per million years; PTO = per-taxon originations per million years. Bottom row: NE = raw number of extinctions per interval; PE = per-taxon rate of extinction; TE = extinctions per million years; PTE = per-taxon extinctions per million years.
the empirical fossil record is not compatible with self-organized criticality. We find little compelling evidence for fractal self-similarity in the fossil record. As we will discuss in the next section, however, we do find evidence for multifractal self-similarity.

A Basic Hierarchical Model for Macroevolutionary Patterns

**Conceptual Model.**—As described earlier, nearly all of the origination and extinction metrics show a log-normal distribution. It has long been recognized that log-normal distributions can arise from the multiplicative effects of independent factors; i.e., that the products of random variables produce log-normal distributions (Montroll and Shlesinger 1982; May 1986). In this section we will present a hierarchical “top down” model for the empirical patterns in the fossil record, including the log-normal distributions. This model makes no specific assertions about which processes produce the observed patterns. Instead, it is based on several simple and defensible assumptions about the nature of these processes.

The first assumption is that there exists a large number of processes, both biotic and abiotic, that control the probabilities of extinction and origination of taxa during any given time interval and the appearance of these events in the fossil record. A vast number of processes, including (but not restricted to) sea-level change, climate change, bolide impact, oceanographic circulation changes, fluctuations in nutrient levels, evolution of predators, and competition, have been invoked as driving mechanisms. Similarly, a wide range of geological processes are responsible for the stratigraphic position of a last or first appearance in the record. There is also no a priori reason to suggest that any one of these processes is solely responsible for the observed variability.

The second is that these processes act over a wide range of temporal (and spatial) scales, up to and including the length of the Phanerozoic (Delcourt and Delcourt 1988; Miller 1997; Aronson and Plotnick 1998). Many processes, such as Milankovitch climatic forcing (Bennett 1997) have characteristic scales or ranges of scales. Other processes show evidence of scale independence (Aronson 1994; Aronson and Plotnick 1998).

The third assumption is that many of these processes act hierarchically, so that long-term and large-scale processes limit the variability produced by short-term and more local processes. In the language of complex systems theory (e.g., Werner 1999), processes at large spatial and temporal scales provide context for those at smaller scales. This structure imposes long-term correlations in the model. This idea is related philosophically to the three-tier hierarchical scheme suggested by Gould (1985), which was expanded to four tiers by Bennett (1990, 1997).

For instance, plate tectonics clearly provides...
the larger-scale context for nearly all smaller-scale geological and geophysical processes, such as eustatic sea-level changes and Milankovitch-associated climate changes (Brett 1995; Bennett 1997). A given amount of sea-level change, for example, would have very different environmental and ecological consequences given a Cretaceous as opposed to a Permian paleogeography. Similar long-term changes include changes in global nutrient levels (Bambach 1993), ocean carbonate chemistry (Stanley and Hardie 1998), and the turnover in Phanerozoic evolutionary faunas (Sepkoski 1984). Again, particular physical processes should have very different biotic impacts when they occur in relatively low-nutrient, brachiopod-dominated ecosystems in calcite seas than they would in high-nutrient, mollusk-dominated ecosystems in aragonite seas.

Conversely, short-term or local conditions that promote originations or extinctions in only one region may only minimally impact global rates (Miller and Mao 1998). Global peaks or valleys will occur only if either there is larger-scale global control (e.g., ocean-current changes leading to increased provinciality) or a fortuitous summing up of local changes (Miller 1997).

A similar argument can be made that the state of a biotic system at the time of a particular perturbation will strongly influence how it responds. Stanley (1990) has proposed that the magnitude of extinction due to cooling is dependent on the existence of temperature-sensitive species. If these species go extinct at one cooling event, they will not be available if another such episode occurs shortly afterward. Similarly, Plotnick and McKinney (1993) suggested that if ecological systems tend to self-organize, the degree of self-organization at the time of the disturbance will condition its response. Implicit in this concept is the idea that a system’s response to forcing...
Figure 5. A hierarchical multiplicative cascade model. First seven sequences represent probabilities varying at different characteristic scales. Each level varies at twice the rate of the one above it. All probabilities are independently drawn from a Gaussian distribution with a mean of 0.5 and standard deviation of 0.05. There are 128 total intervals. The sequence at the bottom is the product of the probabilities for each sequence across all seven levels. It has been rescaled to sum to one. The values can be thought of as the proportion of all "originations" that occur during each interval. Another example is shown in Figure 1C.

...can be nonlinear or can exhibit threshold effects.

The final, related assumption, is that these processes do not act independently. Instead, they often act multiplicatively or additively, so that they are have much greater impact in combination than they would separately. Erwin (1993) used the metaphor "Murder on the Orient Express" to refer to his model for a possible mechanism for the end-Permian extinction. He suggested that the extinction "cannot be traced to a single cause, but rather a multitude of events occurring together..." (p. 256). Under this view, a large number of extinctions occur only when a lot of things go wrong simultaneously, intermediate numbers occur when some things go wrong, and relatively few occur when only one or two things go wrong. In parallel, major pulses of origination, especially those that cut across taxonomic boundaries and/or are global in scope, should occur only when many things "go right" simultaneously.

Mathematical Model.—A simple mathematical model, one that is broadly consistent with the conceptual model and thus provides a initial approach to quantifying it, is a hierarchical multiplicative cascade process (Feder 1988; Mandelbrot 1989; Stanley 1991; Over and Gupta 1996). This iterative algorithm produces a log-normal size distribution and a self-similar multifractal distribution in time (Plotnick 1995; Cheng 1999). Multifractals are self-similar distributions of some property over a geometric surface, e.g., the distribution of extinction values over the time line. Plotnick (1995) proposed their use as a model for variations in fossil abundance patterns. A similar model was recently proposed by Harte et al. (1999) for spatial patterns of species abundance and distribution.

The basic structure of the cascade model is of multiple hierarchical levels that interact multiplicatively (Fig. 5). I will describe it in terms of originations, although the same concept also applies to extinctions. Each level is characterized by a process that affects the probability of originations, with the probability varying at a characteristic timescale at each level.

At hierarchical level one, the entire time period is initially divided into two equal-length
Three things should be noted about this process. First, it is explicitly self-similar. Each level in the hierarchy is identical to the one above it, but at half the temporal scale. Second, a very large number of originations can occur only if the probabilities at all levels of the hierarchy are high; likewise, very small numbers of originations can occur only if the values at all levels of the hierarchy are low. As a result, very high values and very low values are both uncommon; the vast majority of probabilities are of intermediate value. Finally, the hierarchical structure imposes autocorrelation in the series; e.g., a high probability for an interval at an upper level in the hierarchy increases originations over many time intervals.

The power spectra of sequences produced by this process are quite similar to that of the empirical sequences. For example, the sequence in Figure 1C yields a slope value of $-0.78$, with a correlation coefficient of $-0.53$; nearly identical to those for the actual data for originations (Fig. 4C).

We also calculated the Hurst statistics for several realizations of this process and obtained values in the range of 0.75–0.8. This compares with values of 0.68 for NE and 0.75 for the NO series.

Most importantly, consistent with this being a random multiplicative process, the expected size distribution of the values is log-normal. For example, the frequency distribution for the series in Figure 6 is shown in Figure 7; it is indistinguishable from log-normal at the 0.01 level. This can be directly compared with the results for the empirical series described above.

**Lacunarity Analysis.**—In addition to the log-normal frequency distribution, the self-similar and hierarchical structure of the model produces a characteristic multifractal temporal distribution, which can be revealed using lacunarity analysis (Plotnick et al. 1996; Cheng 1999). Lacunarity analysis is a simple statistical method for the analysis of spatial or temporal patterns over multiple scales. In the analysis of time series, a moving window or box of length $t$ is placed at the beginning of the sequence and the sum of the values (the box mass) within the box is determined. The box is now moved one time step along the se-
quence, overlapping with its previous position, and the box mass is again calculated. This process is repeated through the length $T$ of the series, resulting in an exhaustive resampling of the sequence at scale $t$. The mean $m_t$ and variance $s_t^2$ of the box mass are now determined. The lacunarity statistic, $\Lambda = s_t^2/m_t^2 + 1$ is calculated for this value of $t$. Since lacunarity is a function of the variance of the box masses, higher values of lacunarity indicate a greater degree of clustering at a particular scale. This process is repeated for a range of box sizes (usually 1 to $T/2$) and a log-log plot of the lacunarity versus the box size is produced.

The shape of the resulting lacunarity function reflects the distributions of the values over the range of scales (Plotnick et al. 1996; Cheng 1999). Self-similar multifractal distributions, such as that produced by the multiplicative cascade mode, yield straight lines with a negative slope (Fig. 7). Random series, in contrast, have a concave-upward lacunarity function. The random series analyzed in Figure 7 was produced by randomizing the multifractal sequence; i.e., both the random and multifractal series have identical log-normal frequency distributions. They differ in temporal arrangement of the values; it is this difference that is detected by the lacunarity analysis.

The lacunarity functions for the NO and NE series are shown in Figure 8. The origination series is closely approximates a straight line ($r = 0.992; n = 55$), strongly suggesting that it possesses a self-similar or multifractal structure. The extinction series, in contrast, appears to be made of two straight line segments, with an apparent break in slope at a log box size 0.7, corresponding to a box size of 5. The correlation coefficients for the two lines (above and below the break) are 0.995 and 0.980, respectively, compared with 0.967 for the entire set. As discussed by Plotnick et al. (1996), such changes in slope generally correspond to changes in scaling behavior in a multifractal. In this case, the upward break in slope at smaller box sizes indicates that there is a relatively greater clustering of extinctions at less than or equal to five time intervals.

Five time units are on average approximately 25 m.y. The break in slope thus roughly corresponds to the familiar extinction periodicity at 26 m.y. (Raup and Sepkoski 1986). This periodicity is also evident in an autocorrelogram of the data, which show a small but statistically significant peak at the same scale. No such peak is evident in the originations sequence. It should be pointed out that Raup and Sepkoski documented the periodicity only for the past 250 m.y., whereas the current analysis examines the entire Phanerozoic record.

What could produce such a pattern? Three possibilities should be investigated:

1. An ‘‘excess’’ of extinctions occurs in short intervals every 25 m.y. These represent an unusual recurrent event, such as might be produced by the suggested ‘‘death star.’’
2. A periodic function, with a period of
about 25 m.y., is imposed on the more random background; a signal of this kind might arise from a time lag built into the system (e.g., Stanley 1990; Plotnick and McKinney 1993).

3. Periods less than 25 m.y. are controlled by a different set of processes than those longer than 25 m.y. and the pattern of self-similarity changes.

Along with the frequency-distribution, Fourier, and autocorrelation analyses, these results suggest that the statistical properties of the extinction time series and the origination time series, although generally similar, have notable differences. Especially intriguing is the possibility that two scaling regimes exist in the extinction record, compared with one in the origination record.

We do not find this difference surprising. Originations of species should respond to a different, though perhaps overlapping, set of biotic and physical forcings than do extinctions (Foote 1994; Eble 1999; Kirchner and Weil 2000). For example, Allmon et al. (1998) suggested a model in which species origination was maximal at intermediate levels of environmental disturbance.

Discussion

Underlying the quest for development of SOC and other evolution models is the idea that the behavior of highly complex ecological and evolutionary systems can be reduced to a very small set of rules. Instead, it is far more likely that observed patterns result from the complex interplay of numerous biotic and abiotic factors occurring over a wide range of spatial and temporal scales and cannot be reduced to such a set of rules (O’Neill et al. 1986; Jablonski and Sepkoski 1996; Bennett 1997; Aronson and Plotnick 1998; Brett 1995; Miller and Mao 1998; Patzkowsky 1999).

We have proposed a conceptual and mathematical model that explicitly includes such multiscale forcing of macroevolutionary patterns and produces synthetic origination and extinction records that are extremely similar in their statistical properties to the empirical data. The most critical of these similarities are linear lacunarity functions and a log-normal, rather than a power-law, distribution of values.

The fundamental concept of this model is that the number of originations and extinctions occurring at a given time or place can only rarely be explained by a single isolated mechanism. Instead, the context in which an event occurs, which is controlled by processes acting at other scales, strongly influences the response of the system. We have been deliberately vague as to the precise processes involved at any scale and the mechanisms of their interactions. What we hope we have shown is that discussions of mechanisms for extinctions and originations that focus on single processes such as climate, sea-level change, or “mutations” (the SOC model) are far too simplistic. The empirical pattern is instead consistent with multiple causal mechanisms, acting over many spatial and temporal scales, that act synergistically to promote or inhibit originations and extinctions. In this view, it is the context within which a particular process or event occurs that is important. The same event can have quite different impacts depending on the state of the biotic system at the time that it occurs (Plotnick and McKinney 1993; Stanley 1990). This may at least partially explain the imperfect correlation between eustatic sea-level change and macroevolutionary process (Brett 1995), the apparent nonlinear response of biotic systems to bolide impacts (Poag 1997), and the differences in turnover patterns between Siluro-Devonian and Ordovician ecosystems (Patzkowsky 1999).

Although the quantification of response variables, such as number of extinctions or originations, has greatly improved, comparable quantitative descriptors of forcing parameters and numerical descriptions of their interactions with each other and the biotic system are still in a very early state (Patzkowsky 1999). We have no way, for example, of comparing the biotic impact of a 5°C temperature drop with a 100-m rise in sea level. Nor is it understood how either of these would interact with each other, or how their effects would differ as a function of such things as global sea level or continental positions or taxonomic composition. And clearly, any models that would be developed must explain not only global gamma diversity patterns, but the remainder of the empirical record as well. Fi-
nally, neither overall visual similarity nor even simple statistical agreement between models and data is sufficient to determine whether a model correctly describes the observed record. These are only the initial steps in model validation (Rykiel 1996).

As described in the report of a recent workshop on future research directions in paleontology (Flessa 2000: p. 8), “A well-concerted and broad based effort is needed now to test hypotheses on driving mechanisms and to develop the next generation of models that treat dynamics in terms of underlying components such as origination and extinction rates over a spectrum of spatial and temporal scales.” We echo the call in this document and of Patzkowsky (1999) for a “new agenda for evolutionary paleoecology” that addresses these issues.

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Literature Cited


