

Long-range Correlations in the Fossil Record and the Fractal Nature of Macroevolution

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Summary

Recent studies on the fossil record time series has shown that there is consistent evidence for self-similarity i.e. long-range correlations with power-law behavior. The existence of such fractal structures means that, when looking at a given time frame, some basic properties remain the same if a change of scale is performed. To sum up: there is no characteristic time scale, as we could expect if some type of periodic or other low-dimensional dynamics were present. A possible explanation for such long-range order is a dynamical process operating at all scales, as it is the case for systems in the neighborhood of critical points. In this paper these results are further explored by extending previous data analysis and examining the relevance of recent theoretical approaches to the statistical features of the fossil record.

1 Introduction

Macroevolution is a complex process where different relevant factors interact in unfolding ways (Raup, 1991; Briggs and Crowther 1990; Jablonski, 1994). In recent years, it has been suggested that some statistical features of the fossil record (FR) could be interpreted as the result of the dynamics of complex ecosystems close to instability points (Kauffman and Johnsen, 1990; Bak and Sneppen, 1993; Solé et al. 1996; Amaral and Meyer, 1998). Specifically, it has been suggested that evolution in complex communities leads to a self-organized critical (SOC) state (Bak, 1997; Jensen, 1998) where small and large extinctions are caused by avalanches in the ecology. A small event, like the random extinction of a single species, can generate a set of extinctions propagating through the network structure.

The implications of this scenario for macroevolution are enormous. These models suggest that multispecies interactions are the relevant ingredient in shaping the structure of evolving ecosystems. As a consequence of the critical state, the fate of individual species would be the result of collective phenomena, not reducible to a list of individual fitnesses. In this context, it has been suggested that long-term, ecological-level network dynamics provides the natural decoupling between micro- and macroevolutionary dynamics (Solé et al., 1996; 1998).

The SOC hypothesis emerged of several observations from the fossil record. Some relevant features of the FR display fractal behavior, characterized by the presence of power law distributions. The main features are: (a) the number of extinction events $N(E)$ of size E follow a power law $N(E) \approx E^{-\alpha}$ with $\alpha \approx 2$ (Newman, 1997); (b) the power spectrum $P(f)$ of family fluctuations through the Phanerozoic displays self-similar, "1/f" dynamics, i. e. $P(f) \approx f^{-\beta}$ with $\beta \approx 1$ (Solé et al., 1997; Amaral and Nunez, 1998); (c) the lifetime distribution $N(T)$ of genera is a power law $N(T) \approx T^{-\gamma}$ where $\gamma \approx 2$ (Sneppen et al., 1995; Solé and Bascompte,

1996) and (d) the number of genera $N_g(S)$ formed by S species is also a power law $N_g(S) \approx S^{-\tau}$ with $\tau \approx 2$ (Burlando, 1990; 1993).

The obvious alternative to these models is an external scenario where meteorite impacts, volcanoes or changes in the magnetic field of Earth are the main actors (Raup, 1993; Raup and Sepkoski, 1994). This view has an obvious interest and relevance. There is clear evidence for external perturbations of the biosphere throughout the Phanerozoic and any theory of macroevolution should incorporate such random events (as done in Newman and Roberts, 1995; see also Newman, 1997). However, one should ask if these external events are the causal explanation of the previously mentioned features or the triggers of a cooperative biotic response. Which kind of process is at work?

To answer this question, careful data analyses have to be performed and adequate theories able to provide quantitative predictions must be constructed. In this paper we first further explore previous data analyses showing that self-similarity is a characteristic, nontrivial property of the fossil record. Finally, a model of macroevolution exhibiting SOC dynamics is analysed, showing that *all* the statistical features of the FR are reproduced in a quantitative fashion.

2 Spectral analysis and the Hurst effect

The presence of fractal properties in the FR time series has been widely analysed by many authors (general reference). The most popular tool is spectral analysis, based on Fourier Transform techniques. If self-affine structures are present a power spectrum $P(f) \approx f^{-\beta}$ is obtained (Solé et al., 1997). But fractal properties can also be analysed by means of another well-known method: the Hurst's *Rescaled Range Analysis* (RRA) (Feder, 1988; Mandelbrot, 1983; Korvin, 1992; Sugihara and May, 1990).

Let us consider a given time series $\{X_t\}$ with $t = 1, 2, \dots, T$. This can be the records of discharges from a river, the number of sunspots or the extinction size for a given group of organisms. The average of X_t over N time steps will be $\langle X \rangle_T = (\sum_t X_t)/T$. The departure from the average over a t -year time-horizon is given by

$$X(t, T) = \sum_{i=1}^t [X_i - \langle X \rangle_T] = \left\{ \sum_{i=1}^t X_i \right\} - t \langle X \rangle_T \quad (1)$$

Obviously at the end of the period, we get $X(N, N) = 0$. In this paper $X(t, T)$ is calculated by dividing the time series into $M(T)$ adjacent, non/overlapping segments of size T .

Two key quantities are computed from the previous time series. The first is the standard deviation, defined as $S(T) = T^{-1} \sum_{t=1}^T [X_t - \langle X \rangle_T]^2$ and the so called

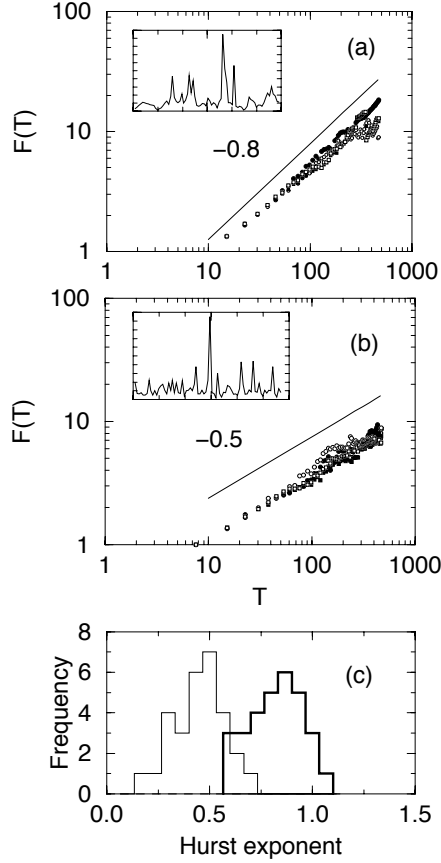


Figure 1

Figure 1: Hurst exponent analysis of (non-interpolated) time series (family level) and for the corresponding shuffled data sets (these and other data are available from <http://ibs.ucl.ac.uk/benton/foss2.html>). (a) two examples of scaling in the $F(T)$ -plot for total origination (circles) and total extinction rate (squares). Here black and white symbols indicate maximum and minimum estimates, respectively. The inset shows the time series for total extinction rate for all organisms; (b) the same as in figure 1a, but for the shuffled data sets (inset: the previous inset is shown, after shuffling the time series). Now the Hurst exponent decreases towards a characteristic value $H = 1/2$, as expected for random time series; (c) histogram for all computed Hurst exponents for the family-level FR time series (thick line) including both origination and extinction data (here 30 data sets are used). The thin line shows the corresponding histogram for shuffled data, which are clustered around $H = 1/2$

range of the time series, given by the difference between the maximum and the minimum over the period T :

$$R(T) = \max_{1 \leq t \leq T} X(t, T) - \min_{1 \leq t \leq T} X(t, T) \quad (2)$$

Using these quantities, the rescaled range $F(T)$ is defined as:

$$F(T) = \frac{R(T)}{S(T)} \quad (3)$$

In this way we have a measure which scales the range by taking the standard deviation as the unit of measurement.

Ordinary Brownian motion corresponds to the case $F(T) \propto T^{1/2}$ where the values of the time series are uncorrelated with each other. In terms of forecasting, the best prediction is the last measured value. However, when Hurst analysed the scaling in different natural systems he found that, instead of the previous relationship, a more general scaling was present, i. e.

$$F(T) \propto T^H \quad (5)$$

where H was shown to be differing greatly from $1/2$. Here H is very often larger than $1/2$ for systems as diverse as market price fluctuations, light intensity curves from quasars or precipitation data (Mandelbrot 1963, 1982; Korvin, 1992).

When the Hurst exponent is greater than $1/2$ the system shows *persistence* on all time scales: on the average, an increasing trend in the past implies an increasing trend in the future. If $H < 0.5$ then we will see an opposite effect: an increase in the past implies a decrease in the future; the local trend will be reversed and the predicted value tends to the mean value over the interval (antipersistence).

In the next section the Hurst exponent for several paleontological data sets is calculated. The Hurst exponent is closely related with the β exponent of the PS. In fact, it can be shown that $2H = 1 + \beta$ (see for example Stanley et al., 1996) and for simplicity we restrict our analysis to the Hurst approach.

3 Diversification, extinction and self-similarity

In a previous study, Solé et al. examined a well-known data set of family records from the Fossil Record 2 compilation (Benton, 1993). Both β and H were measured and a consistent evidence for $1/f$ dynamics found. Other authors have confirmed these results (Amaral and Meyer, 1998; Briggs et al, 1998; Newman and Eble, 1998) although some differences were reported. A rather important issue emerges from the interpolation methods and another from the presence of trends in the FR data.

Although interpolation of data points has been a common practice in time series analysis in paleobiology, one should always take care of the spurious results created by artificial correlations. This was also mentioned in Solé's et al. analysis and recently explored by some authors (Kirchner and Weil, 1998). The generation of spurious correlations is well known in nonlinear dynamics. Early studies on low-dimensional chaos in paleoclimatic records suggested the presence of a chaotic dynamical pattern with a small number of degrees of freedom (Nicolis and Nicolis, 1984). But it was shown that such a result was not completely supported by data because of the introduced interpolations. In this context, Kirchner and Weil have observed that random time series numbers together with interpolated points can also lead to scaling behavior. From a rather different perspective, Newman and Eble have suggested that the trends in the time series are responsible for the scaling behavior in extinction sizes and in the power spectrum (Newman and Eble, 1997, 1998).

These observations are relevant in our context but, instead of using interpolated data, we can proceed to analyse the available data sets with no interpolations. In the absence of interpolations, we have time series of short length ($N \approx 77$) but interestingly similar results are obtained, although some variability is also observed. In figure (1.a) we show some examples of scaling behavior for some data sets. Specifically we show total extinction and total origination rates for all organisms (Benton, 1995). Both maximum and minimum estimates are shown (In the insets of figure 1(a-b), the time fluctuations in total extinction rate is also shown). We can clearly appreciate a linear behavior in this log-log plot, spanning hundreds of Myr. The complete data set (30 time series) involving both origination and extinction, using different metrics, gives a Hurst exponent $\langle H \rangle = 0.80 \pm 0.06$ and the same result, with very small deviations is obtained for total, marine and continental organisms computed separately. The validity and robustness of this result is confirmed by shuffling the data sets in such a way that correlations are destroyed. This is shown in figure (1.b), where the previous inset is shown again for shuffled data. We can see that the slope of the previous data is now shifted to a lower value, close to $\langle H \rangle = 1/2$. This is in fact what we should expect when no long-range correlations are present. These results fully confirm the previous studies and do not give support to the artefactual origin of power law behaviour associated with interpolations (as claimed by Kirchner and Weil, 1998) although the presence of interpolated points gave larger Hurst exponents. Our results are summarized in fig. (1c) where the histograms with the frequency of both Hurst exponents from FR data and from a sample of shuffled data are shown. We can appreciate the weak overlap between both sets.

In relation with the presence of trends, such as the decrease of extinction rate (Newman and Eble, 1997, 1998) it must be mentioned that such trends are not present in most time series. Although a power-law decay in extinction rates $r(t) \approx$

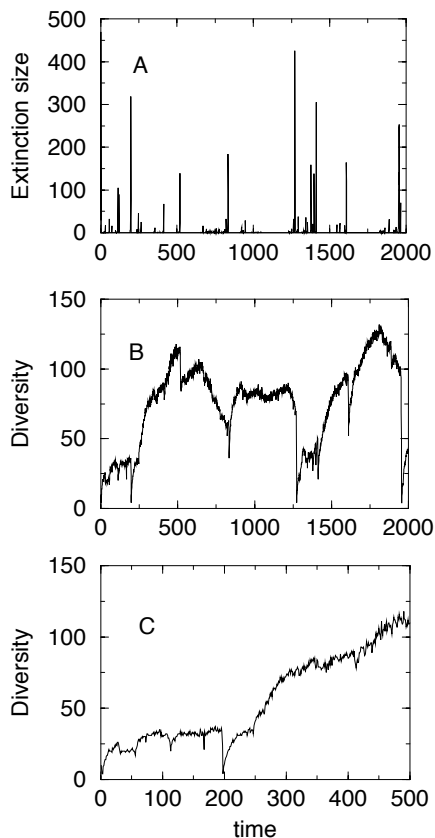


Figure 2: Extinction and diversification patterns for the simplified network model (Manrubia and Paczuski, 1998) for $N = 500$ species. (a) extinction dynamics: small and large (mass-extinction) events are observable, with a characteristic punctuated behaviour; (b) the time evolution of diversity, as defined through the number of genera, shows a complex pattern of fluctuations involving periods of stasis (with nearly constant numbers of genera) and sudden drops of diversity due to mass extinction events; (c) a close view of the previous plot, only involving the first 500 steps shows a well-defined, but transient, trend towards higher diversity levels. A first phase looks like a logistic growth process, interrupted by an extinction event at $t = 198$. Afterwards, a new, faster increase is observed. This plot is not different from the ones reported from real data sets This plot is characteristic of our model, but other runs of the simulation lead to different shapes involving more and less extinction events and as a consequence different shapes for the diversification curve.

$t^{-\eta}$ can be roughly fitted to the data (with a value close to one for accumulated data sets for extinction rate) the same interpolation in other time series gives η -exponents over a wide range of (positive and negative) values.

Power laws are a fingerprint of SOC dynamics but, as discussed by several authors (Solé and Bascompte, 1996; Newman, 1997) other mechanisms can lead to scaling in nature. At this point, either a very good knowledge of the system under consideration or an appropriate model (or both) are required. In the next section we use a previously introduced model to reinforce our hypothesis that the scaling in the FR is linked to complex, self-organized behaviour.

4 A network model of macroevolution

A simple model of macroevolution can be used to account for all the previous observations and most of the statistical features of the FR. The model has been already presented by Solé and co-workers (Solé, 1996; Solé, Bascompte and Manrubia, 1996; Solé and Manrubia, 1997) and it is inspired on previous theoretical approaches to evolution in terms of self-organized critical systems (Kauffman and Johnsen, 1990; Bak and Sneppen, 1995; however, strictly speaking the Kauffman-Johnsen model is not SOC, and parameters have to be fine tuned to get power-law behaviour).

Let us consider a set of N “species” S_1, S_2, \dots, S_N . Species are just numbers and no population structure is assumed. Species are connected through a matrix $\mathbf{W} = (W_{ij})$ where $\{W_{ij}\} (j = 1, 2, \dots, N)$ are the connections $W_{ij} \in [-1, +1]$ among species. Positive inputs mean interactions which facilitate survival and negative ones means predation, parasitism and other negative influences. In this approach species are basically defined by their sets of connectins i. e. by their trophic relationships. If the sum of connections is positive, i. e. $\sum_{j=1}^N W_{ij} > 0$, then species S_i will survive. If not, it is extinct and must be replaced by some of the surviving species. In the original formulation, the first rule was the randomization, at each step in the simulation, of one connection per species, i.e. $W_{ij} \rightarrow W'_{ij} \in [-1, +1]$. This rule involves changes due to external or internal events. Eventually, small changes can lead to the extinction of a cornerstone species which triggers an avalanche leading to a large extinction event (Solé et al., 1996).

Using this basic approach, several features of the fossil record were shown to be reproduced. Here we will extend our study and show that in fact all the reported statistical features are reproduced by a simplified model. A simplified model, based on the previous scheme, was proposed by Manrubia and Paczuski and it will be followed here (Manrubia and Paczuski, 1998). Each species is now represented by a single integer number $\phi_i \in \{-N, -N + 1, \dots, -1, 0, 1, \dots, N - 1, N\}$ which represents the sum of inputs from other species. The dynamics consists in three steps: (a) with probability $P = 1/2$, $\phi_i \rightarrow \phi_i - 1$, otherwise no change occurs; (b) all species

with $\phi_i < \phi_c$ (below a given threshold) are extinct. Here we use $\phi_c = 0$ but other choices give the same results. The number of extinct species, $0 < E < N$, defines the extinction size. All E extinct species are replaced by survivors. Specifically, for each extinct site (i. e. when $\phi_j < \phi_c$) we choose one of the $N - E$ survivors ϕ_k and $\phi_j = \phi_k$; (c) after an extinction event, a wide reorganization of the web structure occurs (Solé and Manrubia, 1998). In this simplified model this is introduced as a coherent shock. Each of the survivors are updated as $\phi_k = \phi_k + q(E)$, where $q(E)$ is a random integer between $-E$ and $+E$.

This model (like the original network model) has been shown to generate a pattern of power-law distributed events. It also generates a self-organized taxonomy with a scaling distribution of species within genus. The lifetime distribution of such genus is also a power law and all these distributions are in agreement with the observations (see table I). The extinction of individual species follows an exponential decay in agreement with Van Valen’s observation of the Red Queen effect (Van Valen, 1973).

Two additional aspects can be tested with this model. One is the presence of persistence as measured by the Hurst exponent. Another feature, this time a qualitative one, concerns with the patterns of diversification and the presence of trends in the fossil record.

Property	Observed	SOC Model
Dynamics	Punctuated	Punctuated
Mass extinctions	Few events	Expected
Diversity	Increasing	Transiently increasing
Species decay	Exponential	Exponential
Extinction pattern, $N(E)$	Power law ($\alpha \approx 2$)	Power-law ($\alpha \approx 2$)
Hurst exponent, H	persistence, $H > 1/2$	persistence $H > 1/2$
Genera lifetimes $N(T)$	Power law ($\gamma \approx 2$)	Power law ($\gamma \approx 2$)
Genera-species $N_g(S)$	Self-similar, ($\tau \approx 2$)	Self-similar, ($\tau \approx 2$)

Table I : some basic trends of macroevolutionary patterns. Observed and predicted by the SOC model (see text). All the quantitative reported exponents from the FR are reproduced by the SOC model as well as the qualitative features like the diversification curves.

We can count the number of genus in the model and follow their fluctuations in time. This is shown in figures (2. a-c) and (3. a-c) where both the extinction time series (a) and the diversity fluctuations (b) (number of genera over time) are shown. The initial condition is $\phi < 10$ for all species. In fig. (2) a relatively large system is used An interesting feature is that if we look at the first 500 steps, an

apparently increasing trend in diversity is found. This curve strongly resembles to the ones obtained for origination data (Benton, 1993; Courtillot and Gaudemer, 1996). But here, instead of deterministic models assuming a logistic growth of diversity, we have a highly nonlinear dynamics leading to large extinction events and strong changes in diversity at the (very) large time scale. This result should prevent us from conclusions about specific trends in the fossil record.

If a smaller number of species is considered ($N = 100$, fig. (3)) we can see that the fluctuations are of higher frequency. This pattern strongly resembles the one observed in some groups, like Ammonoidea (House, 1988). Now we can compute the Hurst exponent for these time series to check if the observed persistent behavior in the record also takes place in the model. And the answer is yes: in figure (3.c) we show an example of the scaling behavior exhibited by the fluctuations, and the Hurst exponent is typically found to be in the range $0.9 < H < 1.0$. Interestingly, if small data sets are used ($T = 100$, in the range of the ones used from the FR) smaller values are obtained, within the range $0.7 < H < 0.9$.

5 Summary and discussion

In this paper we have analysed the presence of long-range correlations in the Phanerozoic record of life. The basic measure is the Hurst exponent H , estimated through rescaled range analysis. Our study fully confirms that fractal, long-range correlations spanning hundreds of millions of years are present in both the extinction and origination time series. No interpolations are used, and in this sense our positive results suggest that scaling in the fossil record is not an artifact of the methods used for analysis. A characteristic persistent behavior is thus present in the large-scale dynamics of the biosphere, suggesting that biotic mechanisms of some kind could be at work.

A simple model of ecosystem dynamics showing self-organized critical behavior has been shown to fit very well both the available power laws from extinction data and species/genus distributions, with the correct exponents for all of them. The model also reproduces the diversification curves displayed by the FR data, with a transient increase in diversity punctuated by some drops associated with large extinction events. The Hurst exponent for the extinction fluctuations gives persistent behavior as in the fossil data and are in the same range when small, comparable data sets are used.

As far as we know, no other model has been shown to predict all these observations in such an accurate quantitative way. Although a variety of non-SOC models can explain the presence of scaling in the extinction statistics with the appropriate exponent (Sibani, 1996; Newman, 1997; Engelhardt, 1998) none of them provide appropriate taxonomy nor lifetime distributions (in Newman's stress model, for ex-

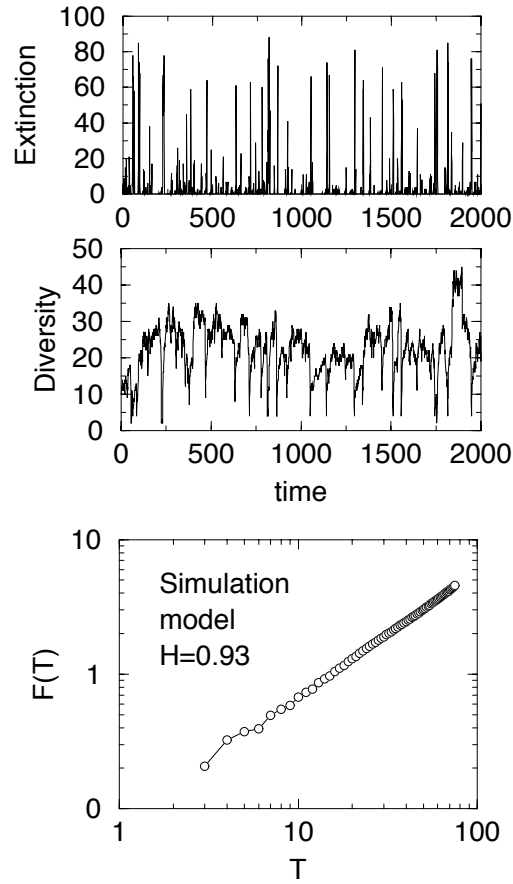


Figure 3: As in figure (2) but now a smaller number of species is used ($N = 100$). Again punctuated behaviour is observed (a) but the diversity pattern is much more fluctuating (b); (c) the Hurst analysis for the extinction time series (as shown in (a), calculated for the first $T = 100$ data points) gives a well-defined scaling $F(T) \approx T^H$ with $H = 0.93$, in agreement with real data.

ample, we get $\gamma = 1.0$ and $\tau = 1.5$, although it should be noted that some groups -like flowering plants- certainly show a different scaling exponent, in agreement with Newman's model).

The agreement reported between model and data strongly suggests that biotic responses play a prominent role in macroevolution. Other observations from the FR support this view (Maynard Smith, 1989). Further data analysis and theory will be required in order to explore these results. The relevance of the problem under consideration - how does life evolves on Earth - and the consequences for evolutionary theory are worth the effort.

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