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THE ROYAL
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Evolutionary patterns from mass originations and mass extinctions

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The Fossil Record 2 database gives a stratigraphic range of most known animal and plant families. We have used it to plot the number of families extant through time and argue for an exponential fit, rather than a logistic one, on the basis of power spectra of the residuals from the exponential. The times of origins and extinctions, when plotted for all families of marine and terrestrial organisms over the last 600 Myr, reveal different origination and extinction peaks. This suggests that patterns of biological evolution are driven by its own internal dynamics as well as responding to upsets from external causes. Spectral analysis shows that the residuals from the exponential model of the marine system are more consistent with $1/f$ noise suggesting that self-organized criticality phenomena may be involved.

Keywords: evolution; origination; extinction; $1/f$ noise; fractal scaling

1. INTRODUCTION

Among the various models of the macrodiversification patterns of organisms (Benton 1997; Sepkoski 1984; Walker 1985), the models based on equilibria seem to be more easily accepted, because of the fact that they are widely accepted on ecological time-scales. Studies of island biogeography (MacArthur & Wilson 1967) suggested that diversification processes at the species level are controlled by equilibria determined by the structure of the ecological system. This leads to a theory suggesting that an ecological system has a fixed number of niches for the species to live in. The diversity increases exponentially if the current diversity is far less than the maximum number of species allowed in the system and other environmental factors affecting the diversity can be ignored. However, the effects of the equilibrium become stronger as the diversity gets closer to maximum diversity. When the diversity reaches the equilibrium, the diversification pattern fluctuates around the equilibrium and the system shows stationary behaviour.

The simplest approach based on a single equilibrium is the logistic model, in which the rate of increase is proportional to both the current diversity and its difference to the equilibrium level. However, major discrepancies exist between the nature of evolutionary patterns observed in the short-term and those that emerge over the geological time-scale (Sheldon 1996), and no single model can explain patterns on all scales. When a diversification process is observed at an ever-increasing macroscopic scale, the equilibrium is not sustained, and is harder to observe. Eventually it may become variable. Even on ecological time-scales, a model based on a single equilibrium may become unstable over longer time intervals, and models with multiple equilibria may be more suitable for these (Steele 1985). The idea of multiple equilibria is also introduced into the long-term diversification of organisms (Sepkoski 1984). According to the idea, the overall pattern is divided into several parts by some mass extinction events (Courtillot & Gaudemer 1996); this assumes that the events always changed the initial state of the model and the other parameters. A logistic expression is then fitted to the diversification curve between each event, which assumes that the diversification process is controlled by a fixed global equilibrium level until another mass extinction event upsets the equilibria conditions.

Here we present a different idea, in which the diversification of life shows a pattern that fluctuates around an exponential curve. There are fluctuations above and below the exponential curve, as a result of the positive or negative effects of the mass extinction events. These are treated as unpredictable noise in the global trend because they are all caused by random events. The power spectrum of residuals in the exponential model of the marine system is consistent with $1/f$ noise, suggesting that the fluctuations come from the internal dynamics of the system responding to external perturbations. When we exclude the unpredictable parts of the signal, we get an exponential pattern, which represents the predictable part of the biological diversification process. Further tests on distributions of extinctions and originations indicate that the mass extinctions are not qualitatively distinct from background extinctions. The $1/f$ power spectrum of the extinctions and the self-similarity of extinction statistics (Sole *et al*. 1997) indicate that the system demonstrates patterns similar to that generated by a self-organized criticality (SOC) mechanism.

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2. DIVERSIFICATION PATTERNS IN MACROEVOLUTION

The existence of biological and environmental equilibria in the historical record of living systems is widely accepted by ecologists, biologists and palaeontologists. It is also based on the idea that there are fixed numbers of niches and that life expands to fill those available adaptive slots (Rieppel 1984). The equilibrium model assumes that after the initial filling of ecospace, the newly evolved taxa with superior adaptations will always replace earlier taxa, or drive them to extinction, so that a general and constant total species diversity is always maintained. Theories of this equilibrium are based on the assumption that there is a fixed carrying capacity for islands and other limited habitats (MacArthur & Wilson 1967; Rosenzweig 1995). In 1969, MacArthur published a graph which indicates that the total rate of the arrival of new species to the island community rises at a decreasing rate with diversity, whereas its total extinction rate rises increasingly (MacArthur 1969). This means that a steady state, or equilibrium, will be attained at the point at which the curves intersect. These issues influence ecologists of modern environments, and they have also been extended to regional and global scales and to the long span of geological time (Whittaker 1977; Rosenzweig 1995).

The relationship between species and area (Simberloff 1974) may also be explained by this equilibrium theory: the larger the geographical area the higher the equilibrium of diversity, and species with more habitats can attain a higher equilibrium diversity. This species–area relationship has a theoretical foundation based on the assumption that the total number of individuals of a group on islands is roughly proportional to the area occupied (May *et al.* 1995; Preston 1962; MacArthur & Wilson 1967; May 1975). The islands concerned may be real ones in the sea, or virtual islands, such as freshwater lakes or isolated mountain tops. This idea can be extended to continental, marine or global ecological systems and the area involved in the theory may be extended to the ecospace occupied by the organisms in the system, although some issues arise with extensions to continental systems (Lawton & May 1994). Such ecospace represents not only the size of the three-dimensional space that the organisms live in, but also the life and richness in the habitats of the system. There may be similar relationships between the number of species and the size of the ecospace in a particular system so that in such a case the diversification may show a logistic pattern.

Sepkoski (1984) explicitly extended these ideas into arguments about macroevolution, suggesting that the macrodiversification of life also follows logistic patterns. More recently, using the data of family ranges from the Fossil Record 2 database (Benton 1993), Courtillot & Gaudemer (1996) modelled the diversification of marine organisms with logistic curves, showing strong changes taking place during mass extinctions at the Late Permian, Late Triassic and Cretaceous–Tertiary boundary. From this model, they came to the conclusion that mass extinctions increase the potential equilibrium diversity of the global ecological system. Mass extinctions are relatively short intervals of intense species death though there are different views about their causes (Raup 1995; Ward 1995). After a mass extinction the emptied ecospace may be responsible for the subsequent explosion of diversity. If a mass extinction is not strong enough to destroy all the organisms in an environmental system the survivors will diversify rapidly, freeing them from the effect of the equilibrium (Miller & Sepkoski 1988). But it cannot explain why the ecospace itself also increases. If we assume that only mass extinctions can offer the remaining organisms new habitats, we may ask why should the competition (which also endangers the existence of a group of organisms) not force them to find new habitats? Furthermore, it is also possible for the catastrophic events to reduce the total ecospace by destroying the organisms in particular habitats and thereby limiting the potential for closely dependent taxa to survive. It is difficult to imagine these kinds of catastrophic events always leading to an increase of the potential equilibrium level.

A key question is ‘how many times has life undergone major diversifications into new ecospace?’ Rosenzweig (1995) notes that diversity increased after life invaded major new sets of habitats, such as the colonization of muddy sea floors in the Ordovician, the movement of plants and animals on to land in the Silurian and Devonian, the diversification of marine communities in the Cretaceous, and the radiation of angiosperms in the Cretaceous. Benton (1987, 1997) suggests that diversity also increased after countless other invasions of new habitats, such as the development of the arborescent habit, flight, shell piercing and crunching in marine predators, tree climbing, tool use, etc. As more ecospace is occupied by these adapting organisms, the niches available in the ecological system also increase, which in turn increases the potential equilibrium diversity.

On ecological timescales, or at least those at which ecological measurements are made, organisms are unlikely to be observed to evolve into new ecological niches at a significant rate. As a result, species–area relationships observed over a few years may appear to remain constant, suggesting a logistic pattern for the diversification of such organisms. On the other hand, when we consider the evolutionary time-scale, the equilibrium may not be constant, because the total number of niches available may change as organisms continually adapt to new habitats. They are also influenced by other macroscopic changes such as continental drift, sea-level change and global temperature fluctuations, which are not obvious over relatively short time spans. Some palaeontologists suggest that there should be no limit in the diversification of organisms (Benton 1996; Whittaker 1977): with enough time, and with normal rates of origination (or immigration) and extinction, new species can surely migrate and adapt and thereby increase species diversity. The ultimate limits on this diversity should be unattainable in reality, since externally triggered mass extinctions will always ensure that this theoretical limit lies well above the level attained.

Furthermore the global ecosystem shows more complex patterns when geographical location is considered: the regional equilibrium in different locations may evolve in different directions, and may change the direction through geological time. However, a more regular

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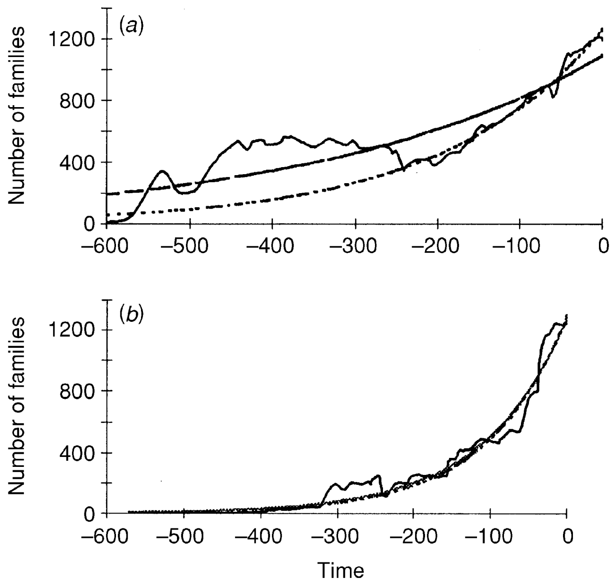

Figure 1. The exponential fits to macrodiversification patterns based on the number of families (*a*) marine organisms, (*b*) terrestrial organisms. The dashed line is the exponential fit for the data from 600 Myr ago to the present. The dotted line is the exponential fit from 250 Myr ago to the present. We used the earlier one throughout our analysis, although we are not against the idea of putting more weight on the later part of data.

pattern can be observed on the global scale. The idea leads to the conclusion that the larger the ecosystem is, the more obvious is its exponential trend in the diversification. We can see from the conclusion that the exponential trend may not be so obvious at the earlier stage of the evolution due to the smaller size of the ecospace occupied by the earlier organisms. A logistic character could be mistakenly perceived from the long-term stasis in the diversification pattern of marine organisms during the Palaeozoic era (see figure 1). Either the vulnerability of the system to the environmental fluctuations or the frequent and greater environmental changes during the Palaeozoic era may be responsible for long-term stasis. Sheldon (1996) suggests that greater environmental fluctuations during some geological age may lead to a long-term stasis in evolution, while rapid evolution takes place in more stable environments. His model can be better understood by the example of a forest in an area subject to fires (Allen & Hoekstra 1992, p. 272). The more frequent the fire, the smaller the accumulated fuel in the form of unburnt debris, and the smaller the next fire is likely to be, so that the stasis happens during the time when there are frequent fires.

One of us (Benton 1995) has suggested that the global macrodiversification of life has followed an exponential curve. If that is true, there may be two kinds of explanation in terms of classic equilibrium models. One is that the potential equilibrium is so high that its effects on diversification can be ignored. In mathematical terms, we can see that when an equilibrium approaches infinity, the curve of the equilibrium model during a particular interval of time approaches an exponential curve. Another possible explanation is that the equilibrium also changes with evolution. As organisms continually find new habitats, the potential capacity of the ecological system may also increase. If we assume the probability of finding new habitats for the organisms is proportional to the diversity, the rate of increase of equilibrium $N_f\ (t)$ should also be proportional to the diversity $N(t)$, such as

$$\frac{\mathrm{d}N_f(t)}{\mathrm{d}t} = (t). \tag{1}$$

According to the equilibrium idea, the effects of the $N_f\ (t)$ to the diversification rate can be expressed as

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = \alpha N(t)(N_f(t) - (t)). \tag{2}$$

By introducing equation (1) into equation (2), we derive the differential equation of $N(t)$:

$$\frac{1}{N(t)}\cdot\frac{\mathrm{d}^2N(t)}{\mathrm{d}^2t} - \frac{1}{N(t)^2}\left(\frac{\mathrm{d}N(t)}{\mathrm{d}t}\right)^2 + \alpha\frac{\mathrm{d}N(t)}{\mathrm{d}t} - \alpha(t) = 0. \tag{3}$$

Solving this equation, we can get the simplest solution of $N(t)$:

$$N(t) = N_0 \cdot \mathrm{e}^{\chi t} \tag{4}$$

From equations (4) and (2) we can derive the expression of $N_f\ (t)$:

$$N_f(t) = \frac{\chi}{\alpha} + N_0\mathrm{e}^{\alpha t}. \tag{5}$$

Here the parameter χ governs the changes of the equilibrium through geological time, and we assume it is relatively constant in the time interval considered. The changes in structure of the system should be much slower than in the diversity itself, and not so vulnerable to external perturbation as is the diversity. Therefore the parameter χ should also be more resistant to the changes. On the other hand the parameter α reflects the effects of the diversity to the diversification rate, and it is subjected to greater fluctuations due to the environmental noise. This leads to a diversification pattern fluctuating around an exponential curve. We can see that both the exponents in the diversification equation (4) and the equilibrium changes in equation (5) are determined by the parameter χ, therefore the diversification pattern is mainly determined by the patterns of the changes in the equilibrium level. The parameter N_0 is determined by the initial condition of the model.

If we are to use a single model to describe the evolutionary change at the family level, then the exponential model is more suitable than the logistic one, because of the great variance in the equilibrium parameter of the logistic model within a small confidence interval. Figure 1 shows the possible exponential fits of the stratigraphic ranges of families from the Fossil Record 2 database (Benton 1993). When we consider the data from 600 Myr ago to the present (dashed curve), most deviation comes from the Palaeozoic era. Most palaeontologists accept that the more ancient parts of the fossil records are, the more likely they are to diverge from reality than more recent parts (Raup 1972). From this idea, if we only model data from 250 Myr ago, the fit improves greatly (dotted line). Even so, we can see from figure 1 that there are still relatively strong deviations in the Cenozoic era. In this respect we cannot get a better fit using an exponential model than by using the logistic one, no matter how we divide the data. Therefore we have used the data from 600 Myr ago to the present throughout our analysis, although we are not against the idea of putting more weight to the later part of the data in extrapolating the future trends of the pattern. When we view the whole pattern in a more macroevolutionary way, both the Palaeozoic and Cenozoic eras can be treated as fluctuations of the diversification pattern around the exponential curve. If we accept this idea, the fluctuations above the exponential curve should be qualitatively indistinguishable from fluctuations below the exponential curve.

This does not mean that by analysing the previous behaviour of the pattern, we can predict the beginning of a fluctuation or its duration. Here the fluctuations are caused by ecological noise. And the power spectrum analysis of the noise (see § 3) shows that it holds a character that slow variations have much greater strength in per-unit frequency than the rapid ones, which are categorized as a reddened spectrum (Keshner 1982; Steele 1985; Arino & Pimm 1995). The reddened noise arises from various factors correlated on different timescales, and these are only revealed in longer time-series (Halley 1996). In this respect, we can see that the long-term greater fluctuation during the Palaeozoic era, which has been wrongly perceived as a clear evidence of logistic model (Courtillot & Gaudemer 1996) is not qualitatively distinct from other smaller fluctuations. The main signal in the diversification, which is left out in the logistic model is the global exponential trend. Both the upward fluctuations caused by rapid diversification and the downward fluctuations caused by mass extinction can be seen as the (positive or negative) effects of extinction perturbations.

From this point of view, the external perturbations such as meteorite impacts may have different effects during different geological ages. For example, although the mass extinction at the end-Permian appears to be much stronger than the K-T mass extinction in the extinction data (see figure 4), the external perturbation at the K-T may be much stronger. The mass extinction at the end-Perimian happened when the diversification pattern approached the exponential curve from above (see figure 1), while the K-T mass extinction happened when it approached the exponential curve from below. This indicates the important role of the internal dynamics of the ecological system during mass extinctions. Bak (Bak *et al*. 1988; Bak 1996) argues that the ecological system may also develop a SOC after a long evolutionary stage, and the fluctuations, as well as waiting-times between phase transitions, are distributed according to a $1/f$ power law. In such a state, a small local perturbation may cause a global chain effect, so that mass extinction is possible even without an external catastrophic event.

3. SPECTRA OF NOISE IN DIVERSIFICATION PATTERNS

Usually a time-series model is mainly composed of two components: one of them represents the deterministic trend, and it can be estimated by an analytic function; the other one describes the indeterministic fluctuations (Harvey 1993). The parameters of the analytic function can be estimated from the time series by least squares regression, while the residuals are considered to be generated by a stochastic process capable of generating different sets of observations over the same time period on rerunning the model. In most cases, each one in the residuals tends to have a value that is closer to that of the residuals immediately adjacent than to those that are further away. This type of structure is known as serial correlation, and is usually modelled by an autoregressive-moving average (ARMA) process, or an autoregressive-integrated-moving average (ARIMA) process (see Harvey (1993) for more details). The properties of the residuals can be either analysed in the time domain by drawing the autocorrelation function, or in the frequency domain by drawing the power spectrum.

However, when the power spectrum of the residuals is ever increasing towards the lower frequency, a stationary stochastic model may always become unstable whenever a longer time interval is included. This kind of phenomenon, described as 'the more data we include, the more variable the statistics become' is often seen in ecological time series (Halley 1996), so that the family of $1/f$-noise-fluctuations is introduced into the ecological time-series by some ecologists.

The family of $1/f$-noise is characterized by power-law spectra of the form: $S(f)\propto 1/f^{\Upsilon}$, where $0\leqslant \Upsilon \leqslant 2$ (see figures 2 and 3). Among the family of $1/f$-noise, those with an exponent Υ less than unity, such as white noise ($\Upsilon=0$) are said to be stationary, while those with an exponent greater than unity (for example brown noise with $\Upsilon=2$) are said to be non-stationary. The boundary between these two classes is pink noise with $\Upsilon=1$, which is itself classed as non-stationary (Halley 1996). These three kinds of noise are often used in analysing and modelling patterns in ecological systems (Steele 1985; Halley 1996). Furthermore, a sequence of uncorrelated random variables with constant mean and variance is called white noise and its spectrum is flat in the frequency domain (Harvey 1993). The other noises among the family of $1/f$-noise have a reddened spectrum, correlated on different time-scales. Brown noise is also called a random walk, and it satisfies the Markov property (Keshner 1982). Brown noise can be simulated by adding white noise to the previous value to get the next value. Among ecologists, the family of $1/f$-noise is receiving more and more attention (Keshner 1982), and is thought of as one of the ubiquitous phenomena in ecological systems and some other complex systems in nature (Lowen & Teich 1990). If environmental fluctuations are seen as having a 'reddened spectrum', it is easier to understand phenomena such as increasing variability of the ecological time-series over the longer time interval (Halley 1996).

The power spectrum of the residuals from the model of marine organisms is consistent with a power law suggesting that they are generated by $1/f$-noise (figure 2). Although we get greater fluctuations around the exponential in the marine system (figure 1), we get fewer fluctuations in power spectra of the residuals fitting to a power law. We get the opposite result from the terrestrial system: much smaller fluctuations in the exponential fit,

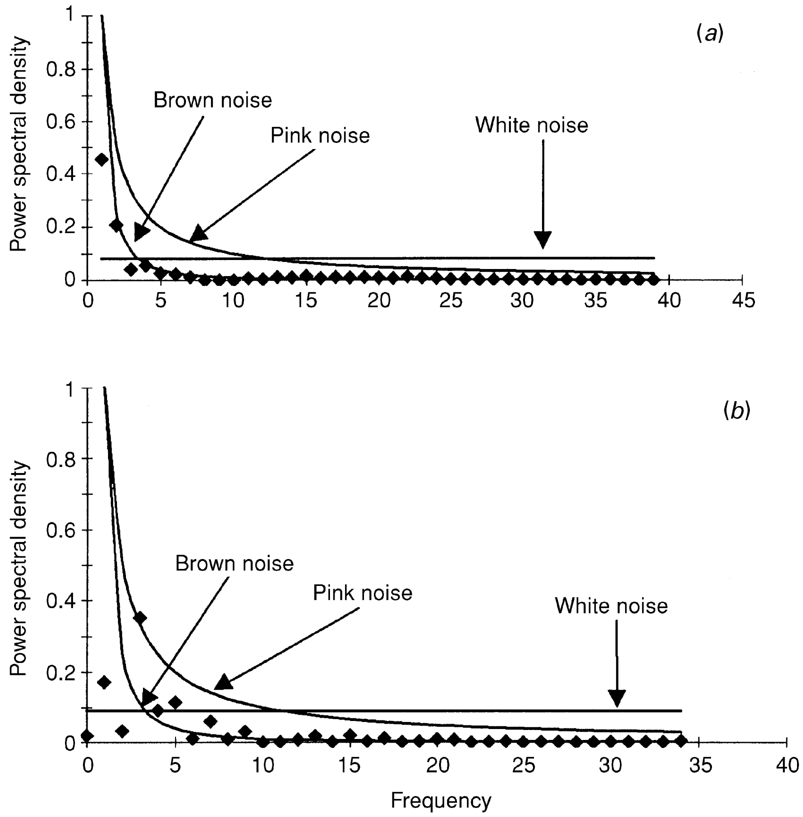

Figure 2. Power spectrum graphs of residuals from the exponential modelling of the diversification patterns (see figure 1) of (*a*) marine organisms, and (*b*) terrestrial organisms. The diamonds represent the power spectral densities of the residuals, and the curves represent in turn white noise, pink noise and brown noise. The power spectra shows that the noise in the marine system fits $1/f$ noise, while the noise in the terrestrial system has a power spectrum with more oscillations. We can see that the noise in the terrestrial system is closer to the stationary autoregressive process, except some oscillations in the power spectrum. The frequency unit in the graph is $1/N\Delta$, where N is the number of data points and Δ is the sampling period. We have used 7 Myr as the sampling period, based on the number of data points during the interval of time from 600 Myr ago to the present and the mean distance between the data points.

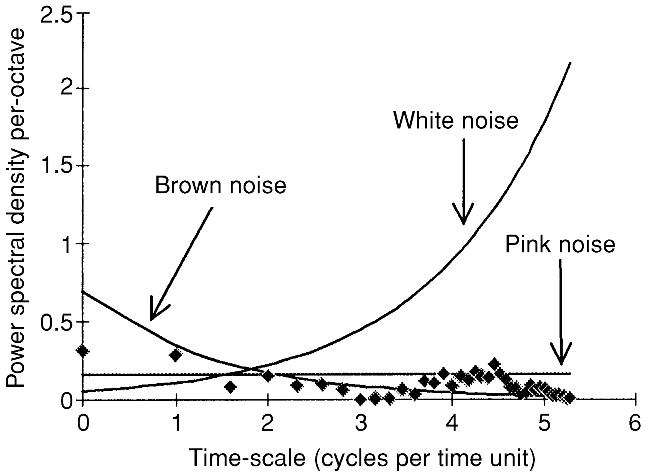

Figure 3. The spectral densities for marine organisms, per octave, of the residuals derived from figure 2, using the transformation formula $F(\phi) = \mathrm{d}f/\mathrm{d}\phi.S(f)$, where $S(f)$ is the spectral density shown in figure 2 and $\phi = \log_2(f)$. In the graphs, horizontal axis represents ϕ and the vertical axis represents the relative influence per unit time-scales represented by ϕ. Note how pink $1/f$-noise contains equal influences (areas under the curve) for all time-scales, while white noise emphasizes short time-scales and brown noise emphasizes long time-scales. It is clear that the residuals for marine organisms are generated by noise, which lies between brown noise and pink noise.

but greater fluctuations in the power spectrum of the residuals (figure 2). This means that the process of generating the residuals from the terrestrial system is affected much more by external factors than that in the marine system. However, except for some oscillations in the power spectrum, the noise from the terrestrial system is closer to the stationary autoregressive process (see chapter 6 of Harvey (1993) for more details). From figure 3, we can examine more clearly the influence of the noise on different time-scales. Pink noise, which lies mid-way between white noise and brown noise, contains disturbance equally on all time-scales, indicating that it has a fractal feature. The noise in the marine system lies between brown noise and pink noise. Steele (1985) analysed the power spectra of the temperature variance in terrestrial and marine ecological systems, and got the same shapes as those shown in figure 2.

The comparison of the power spectra of marine and terrestrial systems shows the major difference between their internal dynamics: the slower variations in marine systems have greater strength than in the terrestrial systems, perhaps because of the continuity of the geographical regions within the marine system. Steele (1985) noticed that the fluctuation in a marine ecological system is more reddened than the terrestrial one, and argued that at very long time-scales the system is inherently unpredictable and must be considered in the evolutionary, rather than the ecological, context.

4. EXTINCTION AND ORIGINATION EVENTS

Global mass extinction and origination patterns are shown in figure 4. If we regard the larger extinction peaks as mass extinction events, we should also name the larger origination peaks as mass origination events in the same way, so that we can use them to represent the events in which rapid origination takes place during a relatively short time. One of the possible causes of the events may be the internal dynamics of the system explained in terms of SOC models (Sole *et al.* 1997; Bak *et al.* 1988; Bak 1996). The system develops to a state in which some local, minor

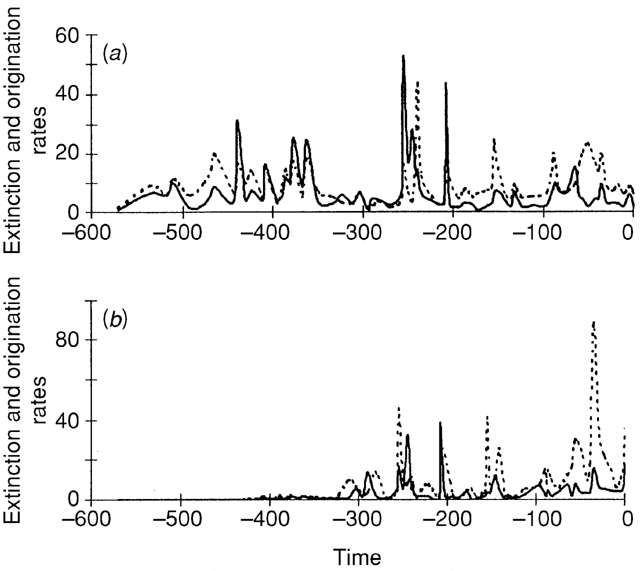

Figure 4. Patterns of the extinction rate and the origination rate through time of (*a*) marine organisms, and (*b*) terrestrial organisms. The solid line represents the extinction rate, the dashed line the origination rate. Each mass extinction event has an extremely large number of effects (positive and negative) subsequently, and it can be traced in all time-scales.

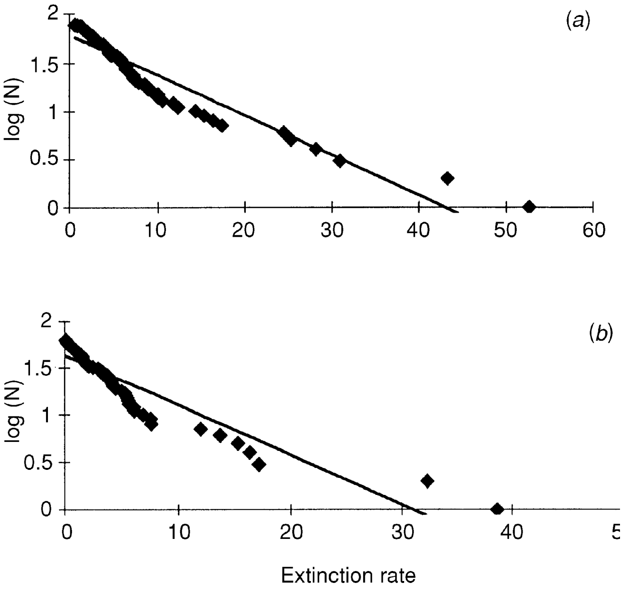

Figure 5. The distribution of extinction events (assumes one single extinction event averaging in each stratigraphic unit) with their size in terms of extinction rates of (*a*) marine organisms, and (*b*) terrestrial organisms. *N* represents the number of extinction events higher than the corresponding value. The curves are the best linear fit to the data in semi-log space.

perturbations within the system (or some external perturbation imposed on the system) can lead to a major, even global, chain effect causing a large number of mutations. They force a large number of organisms to find themselves in the valleys of the fitness landscape (Bak 1996; Wright 1982). If the current distribution of organisms favours most of them being in the valleys from where they can successfully reach the nearest available peak (otherwise they would become extinct), a mass

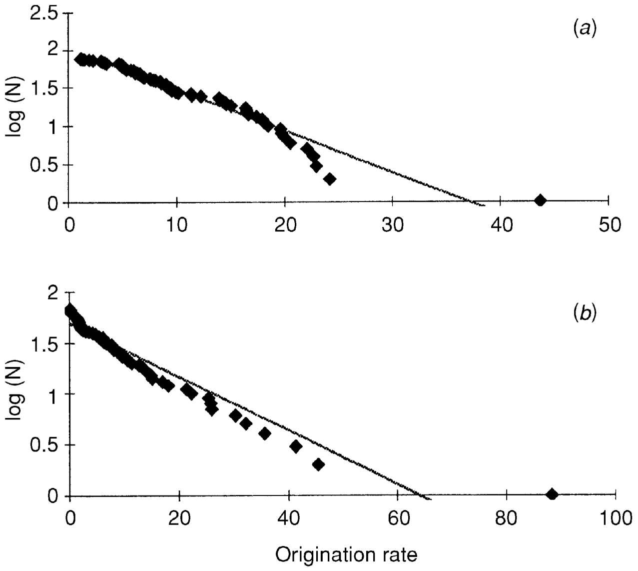

Figure 6. The distribution of origination events (assumes one single origination event averaging in each stratigraphic unit) with their size in terms of origination rates of (*a*) marine organisms, and (*b*) terrestrial organisms. *N* represents the number of origination events higher than the corresponding value. The curves are the best linear fit to the data in semi-log space.

origination may be triggered. On the other hand, if the distribution of organisms results in overcrowding in some area of the fitness landscape (which prevents the organisms from reaching the nearest available peak) a mass extinction may eventually be triggered. If we accept the SOC model as a valid model of the ecosystem, then we can easily understand the existence both of punctuated equilibria (Eldredge & Gould 1972) and of mass extinction–origination events.

From figure 4, we can see that the mass extinction events have some positive effects on the subsequent mass origination events, although they are independent events. If we think of a mass extinction as a random perturbation imposed on the system, it has an extremely large number of effects subsequently, and these effects (both positive and negative in this case) can be traced on all time-scales. This phenomenon generates partially correlated but random fluctuations in the diversification patterns (see figure 1). We can see that mass extinction events cause fluctuations below the exponential curve, while mass origination events cause fluctuations above the exponential curve. In any stratigraphic range, we can sum all of the extinction events to get a single overall extinction level, as well as for originations. Plots of these levels are shown in figures 5 and 6. We can see the linear fits are better in the marine system than in the terrestrial system. From the linear fits, we can see that the events show a similar pattern to the one caused by SOC systems.

5. CONCLUSIONS

Our analysis suggests that macrodiversification at the family level has followed a pattern fluctuating around an exponential curve, and that this trend will continue. The fluctuations (either downwards or upwards) that deviate from the exponential curve may be filtered out in the global trend. The perturbations imposed on the system may subsequently have an extremely large number of effects (either positive or negative). The effects of mass extinction events can be traced on all timescales. Although we get greater fluctuations in the exponential model of the marine system, the power spectrum of the residuals is consistent with $1/f$-noise. We get opposite results from the terrestrial system: smaller fluctuations in the exponential fit, but more oscillations in the power spectrum of the residuals. However, except for some oscillations in the power spectrum, the noise from the terrestrial system is closer to stationary autoregressive process.

In this picture we need not make any special distinction between the upward or downward fluctuations in the diversification patterns: they are the positive or negative effects of the extinction events. These interpretations of our data mean that the last 600 Myr of life on this planet has created patterns similar to those of a SOC system. Furthermore, the maximum carrying capacity has not been reached and may never be attainable because of future mass extinctions.

Note: we have used 7 Myr as the sampling period (see legend to figure 2) not the 1 Myr interpolation used by Sole *et al.* (1997), shown by Kirchner & Weil (1998) to give no evidence of fractal scaling.

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