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Extinction: bad genes or weak chaos?

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SUMMARY

The dynamics of extinction and diversification of life is not a simple random process, driven by arbitrary inputs. Biotic interactions are known to play a very important role in the population response to physical factors. In spite of this fact, it is not clear how the ecological scale is related with the macroevolutionary one. In this paper we suggest that both levels are, at least to some extent, decoupled. Using a simple model of large-scale evolution, we show how an n -species ecosystem evolves towards a critical state where extinctions of all sizes are generated. This state involves a situation where high unpredictability is present. The basic properties of the overall macroevolutionary pattern are well reproduced and a new interpretation for this process is suggested.

1. INTRODUCTION

Populations change in time, often in rather complex ways (May 1974; Bascompte & Solé 1995). Sometimes, they go extinct. Extinctions can be associated with external factors as changes in sea level or the fall of an asteroid. However, biotic interactions play at least an equally important role: epidemics or the introduction or disappearance of a single species can trigger changes in population densities in other species. Eventually, the players in a community can be associated in an unlikely chain of events. Interactions can be extremely complex and involve apparently unrelated species. A very interesting example is the effect of the introduction of a mammalian virus to Southern England on the large blue butterfly (*Maculina arion*) (Ratcliffe 1979). The chain involved rabbits, certain type of grasses, a species of ants and the caterpillars of the blue butterfly.

Population fluctuations are a classical problem in the theoretical ecology. The standard mathematical approach is the Lotka–Volterra (LV) n -species model,

$$\frac{dN_i}{dt} = N_i \left(\epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j(t) \right), \quad (1)$$

where (N_i) , $i = 1, \dots, n$ are the populations of each species. These models have been explored in deep. Two main qualitative problems have been considered: (i) small- n problems, involving two or three species; and (ii) large- n models, involving a full network of interacting species. In the last case, the problem of stability versus complexity (May 1974) remains still open. The so-called community matrix $F = (\gamma_{ij})$ is the basic subject of all these studies.

Many interesting theoretical results have been obtained when certain assumptions over F hold (May

1974; Svirzhev & Logofet 1983). The following, and already classical result was obtained by May in randomly connected food webs (May 1972). Let C be the fraction of non-zero elements in F and let σ^2 be the variance of the set (γ_{ij}) . It was shown that the system will be stable if $\sigma\sqrt{nC} < 1$ and unstable otherwise. This transition is sharply defined for large n . This result, though may not be directly applicable to real ecosystems (Pimm 1991; see however Kenny & Loehle 1991) shows us that thresholds to complexity and stability can exist in generic ecosystem models.

Nevertheless, the stability of a given ecosystem is not a rigid property. Long-term changes are always threatening stability and the community structure and species competition change over time. Extinction can occur and many examples are available (Keitt & Market 1996; for a review, see Pimm 1991, and references therein). These extinctions only involve one or a few species, but on a larger timescale larger events can occur. In fact, the study of the available evidence from the fossil record (Benton 1995a) shows events of all sizes, from small to mass extinctions (Jablonski 1987).

As an example, in figure 1 we show the time fluctuations in the extinction rate (for genera) of marine animals. We see a wide range of fluctuations and the computation of the power spectrum $P(f)$, also shown, gives us a continuous, power-law decay $P(f) \propto f^{-\beta}$ with $\beta = 0.83 \pm 0.02$. This result is consistent with a recent hypothesis which tries to explain the ubiquity of scale-free laws in nature: the theory of self-organized critical phenomena (Bak *et al.* 1987; Bak & Sneppen 1993). Self-organized criticality (soc) is present in a wide set of systems far from equilibrium, from sandpiles and earthquakes to astrophysics and it has been

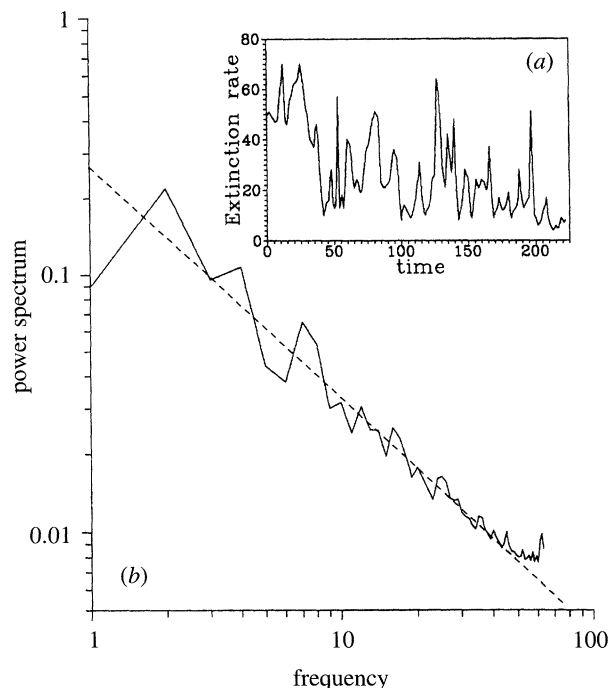


Figure 1. (a) Proportional rate of extinction as a function of the geologic time (here each time unit = 2 Ma) for genera of marine animals during the Phanerozoic (adapted from Allen & Briggs 1989); (b) Power spectrum $P(f)$ obtained from the previous time series. It gives a scaling relation $P(f) \propto f^{-\beta}$ with $\beta = 0.83 \pm 0.02$. Such a result is consistent with a scale-free phenomenon (see text).

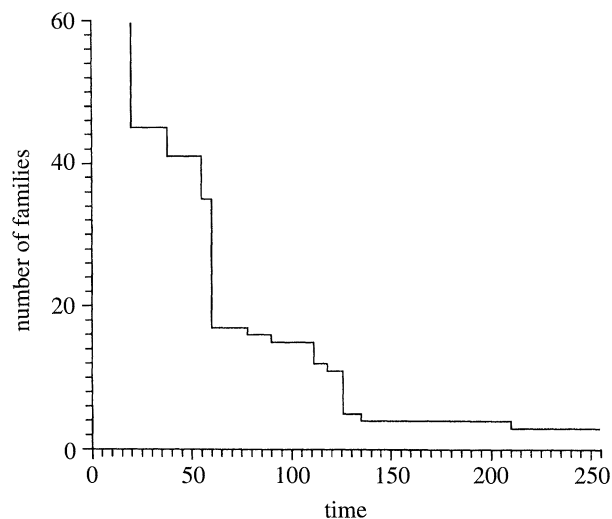


Figure 2. Decay of families of Trilobita from the early Ordovician to the late Permian, when they went extinct. We can see a wide set of changes from small extinctions to very large, as the one occurred at the end of the Ordovician period.

suggested to be present in biological evolution (Sneppen *et al.* 1995; Solé & Bascompte 1996). Such systems tend to organize themselves, after a transient period, in a state with no characteristic time- or length scale other than the system size. Small, basically random changes (the fall of a sand grain or the appearance of a new species) can be enough to trigger large events. In figure 2 a different picture of the discontinuous nature of extinction events is shown.

Here the total number of Trilobita families is shown from the early Ordovician to the late Permian. The number of families falls several times, but the height of this steps shows a very wide range of values.

David Raup (Raup 1993) used this example to ask the key question: did the trilobites do something wrong? Were they genetically inferior? Or had they simply bad luck? Ideally, the answer to this question, which involves the large scale, should be the result of the rules working at the shorter scale. In such a case, we could find a generalization of the previous equations, perhaps involving noise, and the observed extinction pattern would be obtained. But can such large-scale events be included in a generalized version of Lotka–Volterra equations? An affirmative answer to this question implies that macroevolution is correctly described from the lower-scale population dynamics and a reductionist approach would be justified. In some sense, large-scale evolution (and extinction) could be reduced to the microscale (Maynard Smith 1989). This view, however, is not shared by all evolutionary biologists (Eldredge 1985).

An important contribution to this problem came from theoretical ecology and is known as the Red Queen Hypothesis (van Valen 1973; Stenseth & Maynard Smith 1984; Benton 1995*b*). This hypothesis maintains that the different species within a community keep constant ecological relationships to each other, and that these interactions are themselves evolving. This theory predicts a constant extinction rate of species (or other taxa) in agreement with available data. This picture of evolution implies that bursts of extinction and speciation will happen only in response to changes in the physical environment.

A key ingredient of macroevolution is, in our view, absent in the LV approximation: the essentially discrete nature of extinction and diversification and the contingent nature of both processes. Once a species is gone, diversification of the surviving species will occur. This process will generate new arrangements in the community structure, which might lead to new extinctions.

In this paper we want to analyse this problem by means of a simple model of macroevolution. The basic ingredients (extinction, diversification and networks dynamics) will be included. In particular, we want to stress the existence of higher-level mechanisms explaining some of the patterns observed in the fossil record. As we will see, a new interpretation for the extinction pattern is obtained.

2. EVOLUTION MODEL

Previous models of evolution leading to critical states have been based in the so called Bak–Sneppen (BS), (Bak & Sneppen 1993) or the Kauffman–Johnsen model (Kauffman & Johnsen 1991). These are oversimplified pictures of evolving ecosystems leading to power laws. However, none of them involve real extinctions nor diversification, although some alternatives to these models have been explored. See for instance the niche invasion model of Kauffman

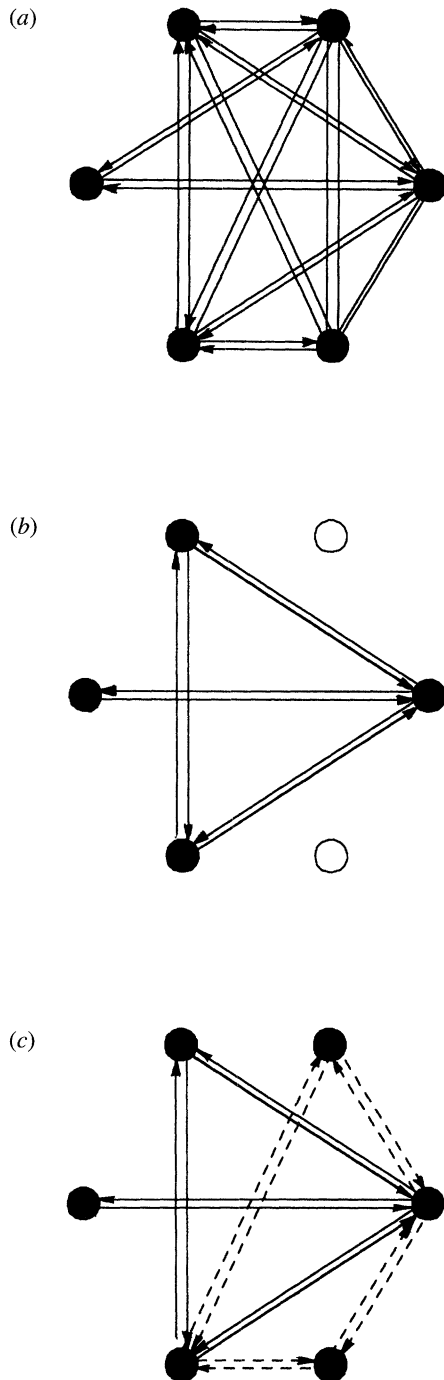


Figure 3. An example of the rules used in the evolution model. Here an $N=6$ network is shown, with a given connectivity (a). In (b), two extinct species are shown as empty circles. At (c), the last rule (diversification) is applied. The empty sites are occupied by the species marked by an arrow.

(Kauffman 1995) or the modified bs model introduced by Newman & Roberts (Roberts & Newman 1996). Recently (Solé 1996; Solé & Manrubia 1996) such ingredients have been explicitly taken into account in a new model of species interaction. Here we follow this last approximation.

The Lotka–Volterra equations (1) are too difficult to manage if F is formed by time-dependent terms. We want to retain the basic qualitative approach, but our interest is shifted from population sizes to the ap-

pearance and extinction of species. Here species are assumed to be a binary variable: $S_i = 0$ (extinct) or $S_i = 1$ (alive). The state of such species evolves in time (new assumed discrete) according to

$$S_i(t+1) = \Phi\left(\sum_{j=1}^n \gamma_{ij}(t) S_j(t)\right), \quad (2)$$

with $i = 1, \dots, N$. Here $\Phi(z) = 1$ if $z > 0$ and zero otherwise. Equation (2) can be understood as the discrete counterpart of (1), but involving a much larger timescale. In our model (Solé 1996; Solé & Manrubia 1996), the i th species is in fact represented by the set of connections $(\gamma_{ij}, \gamma_{ji}), \forall j$. The elements γ_{ij} are the inputs and define the state of the species. The symmetric elements γ_{ij} are the outputs and represent the influence of this species over the remaining ones in the system.

The dynamics is defined in three steps.

1. Changes in connectivity. Each time step we change one connection γ_{ij} , which takes a new, random value $\gamma_{ij}(t+1) \in (-1, 1)$, for each $i = 1, \dots, N$, with $j \in (1, \dots, N)$ chosen at random. This rule is linked with the internal changes that account for species interactions. They could be associated with external causes or simply be the result of small changes as a consequence of coevolution. This rule introduces random, small changes into the network.

2. Extinction. The local inputs $\mathcal{F}_i = \sum_j \gamma_{ij}(t) S_j(t)$ are computed, and all species are synchronously updated following (2). If the k th species goes extinct, then all the connections that define it are set to zero, that is $\gamma_{kj} = \gamma_{jk} \equiv 0, \forall j$. This updating introduces extinction and selection of species. Those sets of connections which make a species stable will remain. But in removing a given species, some positive connections, with a stabilizing effect on other species can also disappear, and the system can become more unstable.

3. Replacement. Some species are now extinct (i.e. $S_k = 0$) and empty sites are then available for colonization. Diversification then is introduced. A living species is picked up at random and ‘copied’ in the vacant spaces. The new species are basically identical to the one randomly chosen, except for a small random change in all their connections. Specifically, let S_c the copied species. For each extinct S_j (vacant spaces), the old connections are set to zero, and the new connections γ_{ij} and γ_{ji} are given by $\gamma_{kj} = \gamma_{cj} + \eta_{kj}$ and $\gamma_{jk} = \gamma_{jc} + \eta_{jk}, \forall j$. Here η is a small random variation (we take $\eta = 0.05$). In this way, the new species are the result of the diversification of one of the survivors.

The previous rules can be summarized in figure 3, where a small ecosystem is shown. In our previous study, it was shown that the system evolves to a critical state with power laws in the extinction sizes (i.e. $N(s) \propto s^{-\tau}$, with $\tau \approx 2$) and waiting times until extinction. The model shows punctuated equilibrium, as found in the real fossil record (Gould & Eldredge 1993). But here there is no separation between ‘mass’ and ‘background’ extinctions. All of them are generated by the same dynamical process, and no particular extinction size is privileged.

3. CRITICALITY AND UNPREDICTABILITY

In this section we want to analyse in which way the critical state is reached and the interpretation of the resulting dynamical pattern. The random changes in the network connections make the trophic links between species more and more complex. We can quantify their complexity by means of an adequate statistical measure. Let us first consider the time evolution of connections. Let $P(\gamma^+)$ and $P(\gamma^-) = 1 - P(\gamma^+)$ be the probability of positive and negative connections, respectively. The time evolution of $P(\gamma^+, t)$ is defined by the master equation

$$\frac{\partial P(\gamma^+, t)}{\partial t} = P(\gamma^-, t) P(\gamma^- \rightarrow \gamma^+) - P(\gamma^+, t) P(\gamma^+ \rightarrow \gamma^-). \quad (3)$$

From the definition of the model, we have a transition rate per unit time given by $P(\gamma^+ \rightarrow \gamma^-) = P(\gamma^- \rightarrow \gamma^+) = 1/(2N)$ and so we have an exponential relaxation $P(\gamma^+, t) = (1 + (2P_0 - 1) \exp(-t/N))/2$, where $P_0 = P(\gamma^+, 0)$. This result leads immediately to an exponential decay in the local inputs, $\mathcal{F}_i(t) \propto \exp(-t/N)$. As a result, the system evolves towards a critical state where the inputs introduced by the coevolving partners are small and so small changes involving single connections can generate extinctions.

We can use the entropy of connections per species, i.e. the Boltzmann entropy

$$H(P(\gamma^+, t)) = -P(\gamma^+, t) \log(P(\gamma^+, t)) - (1 - P(\gamma^+, t)) \log(1 - P(\gamma^+, t)), \quad (4)$$

as a quantitative characterization of our dynamics. The Boltzmann entropy (also known as the Shannon entropy) gives us a measure of disorder but also a measure of uncertainty (Ash 1965). It is bounded by

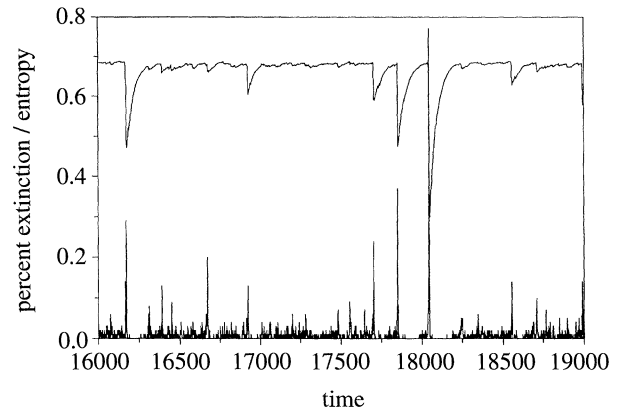


Figure 4. Extinction pattern in the model. Here $N = 100$ species are used, and a small time series is shown, together with the entropy. We see that large extinctions take place close to higher entropies (see text).

the following limits: $0 \leq H(P(\gamma^+, t)) \leq \log(2)$. These limits correspond to a completely uniform distribution of connections (i.e. $P(\gamma^+, t) = 1$ and $P(\gamma^-, t) = 0$) with zero entropy and to a random distribution with $P(\gamma^\pm, t) = 1/2$ which has the maximum entropy. Our rules make possible the evolution to the maximum network complexity, here characterized by the upper limit of the entropy.

As we can see in figure 4, $H(P(\gamma^+, t))$ grows, after a large extinction event, towards its maximum value $H^* = \log(2)$, with sudden drops near large extinctions. So our system slowly evolves towards an ‘attractor’ characterized by a randomly connected network. At such state, small changes of strength $1/N$ can modify the sign of \mathcal{F}_i and extinction may take place. At this point, one clearly sees what is the role that external perturbations play: for them to trigger a large extinction, it is necessary that they act on a system

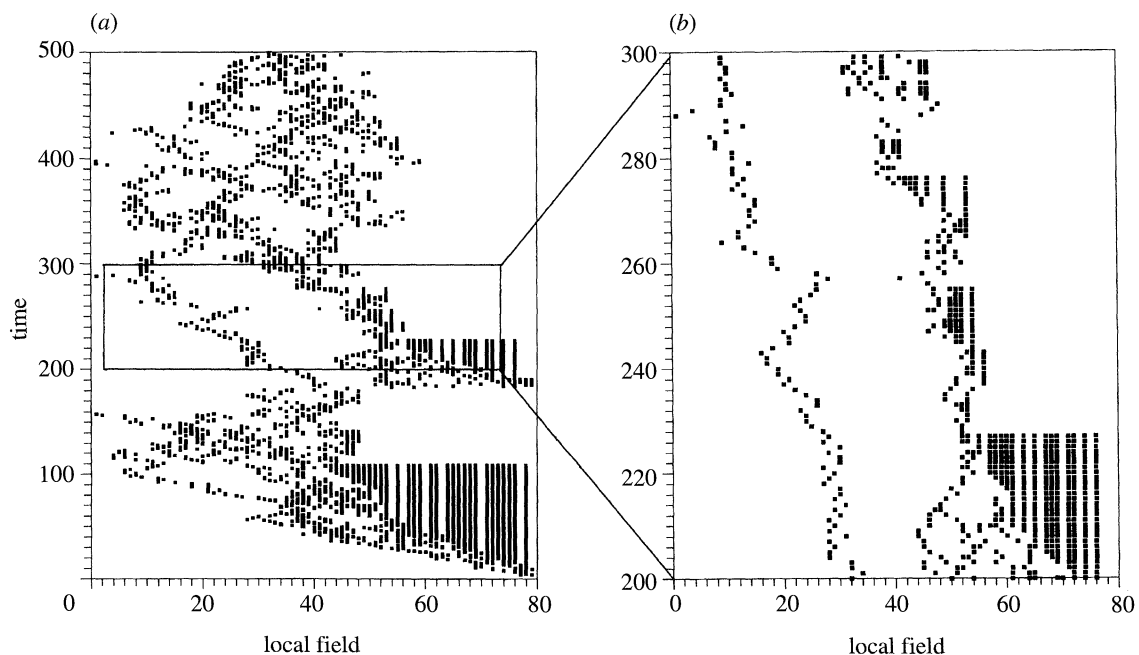


Figure 5. Fluctuations in the distribution of inputs \mathcal{F}_i (see text). After a large extinction ($t = 0$ in the figure) diversification occurs (a). As can be seen, the ordered pattern is replaced by a more random one. A detail of the fluctuations is shown in (b).

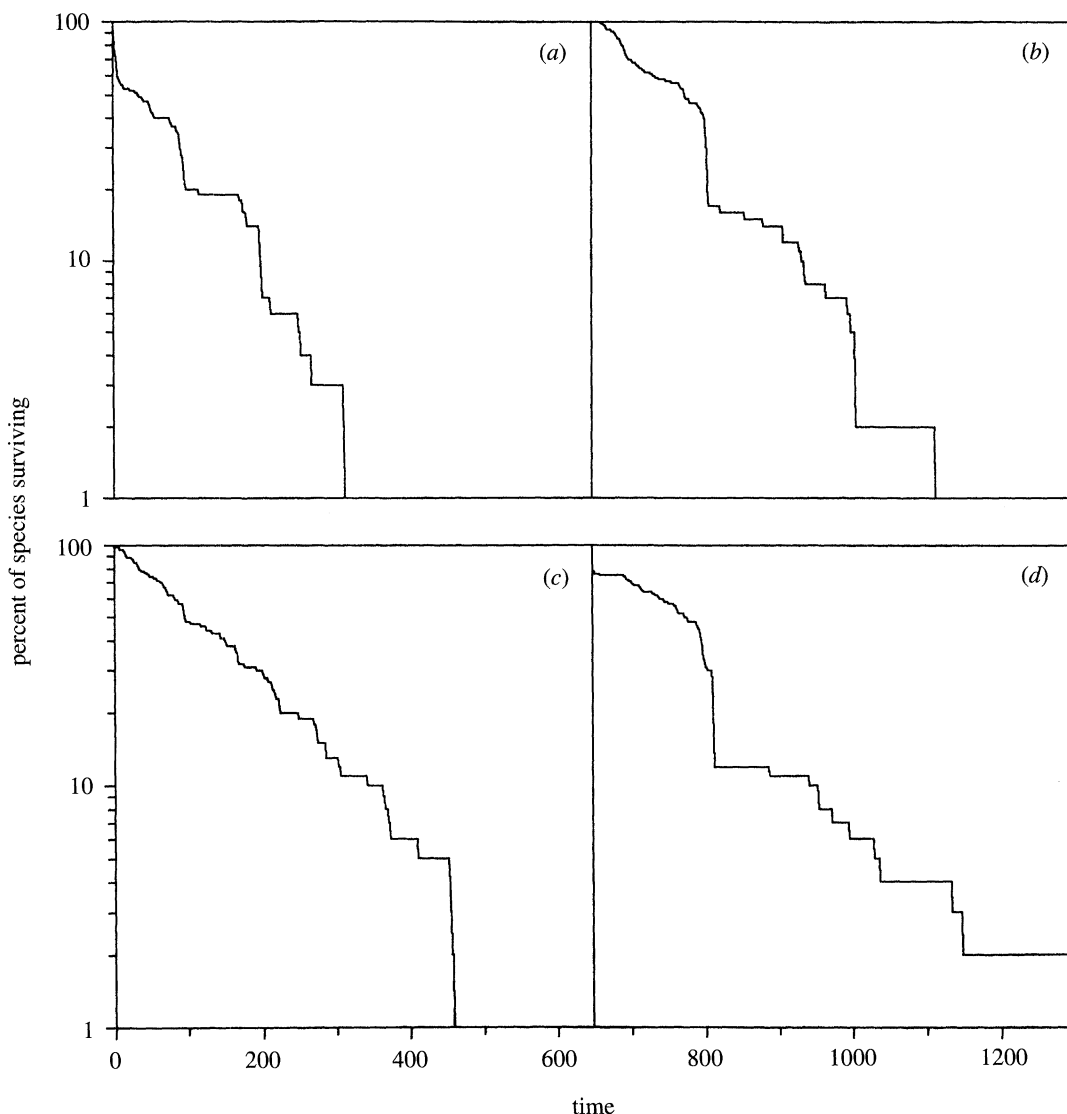


Figure 6. Extinction pattern of species over time. The decay of a given initial set of species (here $N = 100$) in four different situations is shown (see text). Both continuous and episodic decay are observed.

located close to the critical state (here, the network close to the maximum entropy). A large extinction will never be found in a system with a low entropy of connections even with a reasonably large external perturbation. This is a key property of soc systems. More specifically, a soc system has an order parameter that defines the transition displayed by the system (in our case the change from no-extinctions to extinctions) as a second order (or continuous) phase transition. This order parameter has been shown to be the extinction rate, while the control parameter is the average value of the connections $\langle \gamma_{ij} \rangle$ (Solé & Manrubia 1996). For $\langle \gamma_{ij} \rangle > 0$ no extinction will be found for a large enough system, while for $\langle \gamma_{ij} \rangle < 0$ extinctions of all sizes (up to system size) can be found.

We can see that a wide distribution of extinctions is obtained: it is a power-law distribution, $N(s) \propto s^{-\tau}$ with $\tau = 2.05 \pm 0.06$, consistent with the information available from the fossil record (Raup 1986, 1993; Solé & Bascompte 1996). This result also agrees with the Newman–Roberts model, who also obtained the same exponent within the error (Newman & Roberts 1995;

Roberts & Newman 1996; Newman 1996), while other models give values clearly different: $\tau \approx 1.1$ for the BS model and $\tau = 1$ for Kauffman–Johnsen’s.

Other properties can be explored. In particular, we could ask which type of diversification patterns are present. A direct consequence of criticality, as defined by the previous rules, is the existence of a power law in the taxonomy. If we look at a given species, it can generate, after an extinction event, one, two or many new species and the statistical distribution will be a power law with the same exponent than before (recall that rule 3, replacement of extinct species, copies all extinct species in a single alive one). It is interesting to see that available evidence from the fossil record shows precisely this range of values (Burlando 1990, 1993). In our case, every time that replacement takes place, we define the new elements to be a subtaxa of the parent species chosen to be copied.

As an example, we have considered the values of the local fields at each time step. Provided that the connections take values between -1 and $+1$, the internal fields can theoretically range from $-N$ to

+ N , though large negative values will be seldom observed. We divide this interval in N pieces and at each time step we look at all the species in the system and find all the intervals that are occupied at least by one of them. The time evolution of this is shown in figure 5 just after a mass extinction (where we chose $t = 0$). Black dots mean occupied sites. As we can see the previous rules generate a very complex pattern of diversification followed by extinctions. Random and ordered domains are observed.

4. THE RED QUEEN REVISITED

Finally, let us consider the law of constant mean extinction rate, van Valen's law (van Valen 1973). As mentioned in §1, this law maintains that the probability of extinction within any group remains essentially constant through time. This is a consequence of the Red Queen theory and an observational result. This is, however, an average: on average, extinction rates are constant but a close inspection of the decay curves shows both continuous and episodic decays (Raup 1986). The sudden, episodic drops are often associated with mass extinctions and are usually assumed to be the result of external perturbations.

The Red Queen model gives a striking, counter-intuitive explanation of the constant rate of extinction. If organisms are continuously evolving and adapting, why do they not get any better, on average, to avoid extinction?

The episodic (and apparently external) nature of the species decay is easily explained by our model. Though long periods of stasis and low extinction rates give a constant decay, it is the intrinsic dynamics that generates the episodes of extinction involving several (some times many) species. These survivorship curves are shown in figure 6 where four runs of our model are displayed. Each graphic is generated by starting at a given (arbitrary) time step in the simulation and following all the species present at this time step. The exponential decay in the number of survivors is closely related to the monotonous drift that the system experiences towards the extinction threshold, because of the constant change of connections to random values. As we can see (and this is rather typical) both constant and episodic decays are observed. We do not need to seek for a special external explanation for the episodic decay. Obviously, an external cause might trigger a large extinction event by altering the network dynamics at the critical state.

In our approach, the theoretical problems derived from the Red Queen interpretation simply do not arise. Extinctions are an unavoidable outcome of network dynamics. Though some selection of connections is present after each extinction event, unpredictability always increases. As with the example of the large blue butterfly, a given species cannot predict how the other players will modify their intrinsic properties and in particular how the network will be rearranged after a new extinction. This situation is basically shared by all the players, and so all of them are, on average, equally prone to disappear in the long run.

5. DISCUSSION

In this paper we have analysed the consequences of a simple self-organized model of large-scale evolution involving extinction and diversification. The model is inspired in the standard Lotka–Volterra approach but we move from the ecological timescale (where population changes are relevant) to the paleontological one (where changes in species composition occur). In the small scale, deterministic factors are usually dominant, though some types of unpredictable behaviour are present, for instance when deterministic chaos is involved. In the large scale, however, continuous, random changes in the trophic links move the system towards a critical state characterized by a high unpredictability and sensitivity to small perturbations. Here is worth emphasizing that spatial degrees of freedom can play a very important role. Actually, it is well known that space can stabilize species interactions which, otherwise would not persist (Hassell *et al.* 1991; Solé *et al.* 1992; Bascompte & Solé 1995). This situation allows a given ecosystem to explore a wide range of interactions and, in the long run, eventually triggered by external causes, extinction can occur. In fact, some authors claim that these external causes might be the generating mechanism of the observed power-law in real extinction events, and from this other point of view, a self-organizing system would not be necessary to account for the observed self-similar distributions (Newman 1996).

Because of the intricate network of couplings obtained at the critical state, the problem of which species will be gone is essentially unpredictable. Contingency has been recently aduced as one of the more relevant properties of the evolutionary process (Gould 1989) and in this paper we give a dynamical origin to this unpredictability. But in spite of the intrinsic contingency of this process, the critical state is characterized by some well defined properties: punctuated equilibrium and power laws. The first (qualitative) property is observed both in the model and in real data. Punctuated equilibrium is in fact a characteristic feature of the fossil record but it is also a typical, perhaps generic characteristic of complex systems poised at critical points (Solé *et al.* 1996). Power laws are the statistical counterpart of punctuated equilibrium. The fossil record shows several evidences of scale-free distributions (Raup 1993; Solé & Bascompte 1996; Solé *et al.* 1996). Such data sets have not been interpreted (nor reproduced) by means of classical models of population dynamics. The global pattern is emergent, resulting from the generation of complex correlations among species. This is in total agreement with the conclusions of other authors, as Gould points out: 'paleontologists should conciously explore the ways in which uncritical extrapolationism limit and channel thought. Evolution works on a hierarchy of levels, and some causes at higher levels are emergent'.

To sum up, we have shown that our model of large-scale evolution is able to recover the observed evolutionary patterns. The main consequence of our study is that the network complexity of a given ecosystem always grows in time leading to essentially

random nets of connections. Trophic links become very intricate in such a way that the sensitivity of the system to further changes (both biotic and physical) becomes maximum. In this sense, the Red Queen picture, where changes are made to adapt the system to the biotic environment, should be replaced by an always changing system where species are gone as a consequence of the unpredictable web of biotic relations. The observed fractal properties of the fossil record would be a direct result of this unpredictability in the critical state.

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