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Extinction and self-organized criticality in a model of large-scale evolution

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A simple model of large-scale biological evolution is presented. This model involves an N-species system where interactions take place through a given connectivity matrix, which can change with time. True extinctions, with removal of less-fit species, occur followed by episodes of diversification. An order parameter may be naturally defined in the model. Through the dynamical equations, the system moves towards the critical threshold, which triggers the extinctions. The frequency distribution $N(s)$ of extinctions of size s follows a power law $N(s)\approx s^{-\alpha}$ with $\alpha\approx 2.3$, close to known palaeobiological evidence. [S1063-651X(96)50807-X]

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Extinction patterns are a key feature of biological large-scale evolution [1]. Extinction has been only slightly less important than diversification and an adequate understanding of the nature of extinction patterns is as important as an understanding of how species are originated. The existence of large (mass) extinctions, well documented from the fossil record, has generated strong controversy [1]. One of the most striking properties of the statistical distribution of extinction sizes (measured as the number of taxonomic units lost) is that it displays a highly skewed, decreasing distribution with a continuous drift from small to large events. This result is not trivial: if two different processes were operating at two different scales, a two-peaked distribution should be expected. At one extreme, the so-called background extinction events (linked with biological causes) and, at the other, mass extinctions (linked with external, physical causes). But the observed pattern, with a continuous connection between small, intermediate, and large extinctions, seems to be in agreement with a common process operating at different scales.

More specifically, the number of extinction events $N(s)$ of size s has been shown [2,3] to be compatible with a power-law fit, $N(s)\approx s^{-\alpha}$, with $\alpha=2.01\pm 0.12$. As is well known, power laws can be linked with critical phenomena. In this sense, it has been conjectured that such critical points could be reached through some kind of self-organization process. These types of dynamical patterns are generically known as self-organized critical phenomena (SOC) [4]. In recent years, some new models of large-scale evolution are trying to shed light on this problem [5–7]. The basic proposal is that the observed patterns are the result of a SOC process.

In the model that we present here, extinctions naturally appear under the actualization laws that will be described. Each species is defined through its interaction with itself and with the remaining species in the ecology. We believe that the biological interpretation of this model is easier than that of some other models already proposed (see [8] for a discussion about models of evolution).

A simple model of macroevolution can be built up involving true extinctions and further diversification. Let us start with a set $\Omega=\{S_i\}$, $i=1,2,\dots,N$, of N species. Each species is defined by means of a binary variable, i.e., $S_i\in\Sigma=\{0,1\}$. Here 0 stands for extinct and 1 for alive. At the beginning, all species are alive, $S_i=1\,\forall i$. For simplicity, we assume that the system is fully connected (although some connections may occasionally take a zero value), i.e., there is a connectivity matrix $\mathcal{L}(\Omega)=(J_{ij})$, where the coupling J_{ij} among the ith and the jth species is such that $J_{ij}\in(-1,1)$ and follows a probability density $P(J_{ij})$ [i.e., $\int_{-1}^{+1}dJ_{ij}P(J_{ij})=1$]. Independently of the initial distribution chosen (for simplicity, it will be taken as a uniform one), the stationary distribution $P(J_{ij})$ is reached after a transient period.

Now the interaction among species will be described by means of a dynamical system,

$$S_i(t+1)=\Theta\left[\sum_{j\in\mathcal{C}_i}J_{ji}(t)S_j(t)-\theta_i\right], \tag{1}$$

where $\Theta(x)=1$ if $x>0$ and zero otherwise. Here $\mathcal{C}_i$ stands for the set of nonzero input connections to species i. In our paper, we set the internal threshold (which can be a measure of internal resistance to perturbations) to zero (i.e., $\theta_i=0$, $\forall i$). As we can see, this neural-like rule gives a simple criterion for species connectivity. Negative connections make the ith species less fit and positive values give higher fitness. There is no implicit symmetry in the way we choose the connections among species. From the biological point of view, it should be clear that many different situations can arise between two species: a predator-prey relationship gives a positive connection for a predator and a negative connection for a prey; in the case of cooperation or coevolution, both connectivities shall be positive; if we are dealing with competition, both might be negative. This is the reason why no symmetry restriction should be *a priori* imposed on the connections of the system.

The dynamics proceeds in four steps:

(1) For each species, we choose at random one of its connections $J_{ji}\in\mathcal{C}(\Omega)$, and change it to a new value J_{ji} randomly chosen in the interval $(-1,1)$. By using this rule, we can see that $\mathcal{C}_i\rightarrow N$ as time proceeds (if no extinctions are involved). This rule can be modified in order to keep fixed (at any value below N) the total number of connections.

(2) We compute the *local field* $\mathcal{F}_i=-\Sigma_j J_{ji}(t)S_j(t)$ for each species. Then they are updated following Eq. (1).

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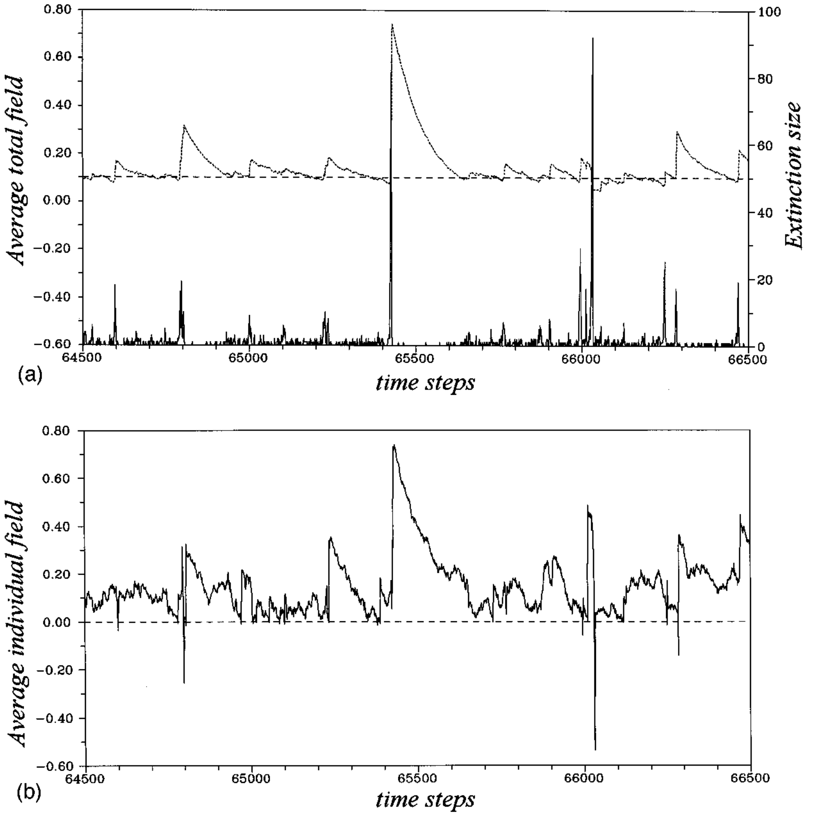

FIG. 1. (a) Number of species that become extinct through time. Long periods of stasis are punctuated by mass extinctions (right axis) and variation of the total field f_T in the same 2000 time steps (left axis). After a large event, the system goes back slowly to the critical threshold f^*. The dashed line at $f_T = 0.1 \approx f^*$ is only meant as a guide to the eye. (b) Individual field. Although the main features of the total field are reflected here, local fluctuations may lead the species to extinction when f_i falls below zero (dashed line). In all our simulations, $\epsilon = 0.01$ (see main text).

(3) If species i has become extinct [i.e., $S_i(t)=0$], the whole set of connections $C_i = \{J_{ij}, J_{ji}\}$, $\forall j$ is set to zero.

(4) Let us assume that M species have become extinct. Then $N-M$ alive species are present, and we have to fill the M vacant spaces. To do so, we choose a given alive species at random, say S_k, and M new species will be created by using the set C_k. The new connections for each new created species will be obtained from

$$J_{ij} = J_{kj} + \eta_{ij}, \tag{2a}$$

$$J_{ji} = J_{jk} + \eta_{ji}, \tag{2b}$$

where η_{ij} is taken from a uniform distribution $p(\eta)$ over the interval $(-\epsilon, \epsilon)$. In this way, the new species are the result of small modifications of the set C_k, and diversification has been introduced. Once N alive species are obtained, step (1) is repeated.

The random change in J_{ij} prevents the system from falling in a frozen state. It makes it possible to maintain the system in a nonequilibrium state. So the first rule works in a similar way as the grains of sand falling on a sandpile. This change can be a random mutation (leading to a change in fitness) or an external modification linked with the physical environment. As a consequence of this modification, the local fields will change over time.

Starting from a random initial condition, we let the system evolve. After $T \approx 10\,000$ transients, the statistical properties are analyzed. To begin with, let us consider the qualitative dynamics of our system, as shown in Fig. 1(a). The size of extinctions $S(t)$ is shown in the solid line in a system of $N=100$ species. As we can see, punctuated equilibrium can be observed. Long periods of little change (stasis) are followed by bursts of large extinction events (mass extinctions). This is consistent with paleontological evidence. The frequency distribution of extinctions of size s gives a power law $N(s) \propto s^{-\alpha}$, as shown in Fig. 2. The exponent is $\alpha = 2.3 \pm 0.1$, close to Raup's data [9]. Consider the way in which we replicate the species in our model. It is clear that the frequency distribution of extinctions is the same as the frequency distribution of the number of descendants of a given species (i.e., of subtaxas within a given taxa). The exponent α obtained is also consistent (within the error) with the one obtained by Burlando [10] in relation to the fractal geometry of philogenetic trees. In this context, the fractal structure of taxonomic relations (i.e., of the evolutionary tree) would be a consequence of criticality.

This power law is a first evidence of SOC dynamics. Additional information can be obtained from the study of waiting times. The waiting time t_s is defined as the number of

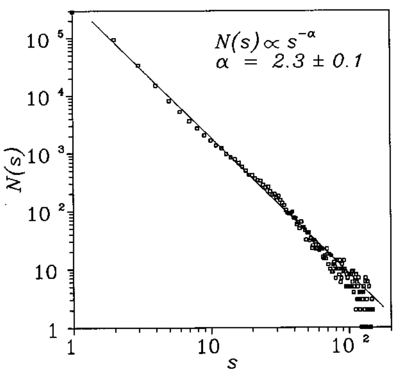

FIG. 2. Power-law distribution of extinctions in an $N=150$ system. The tail that does not fit the power law is always very short.

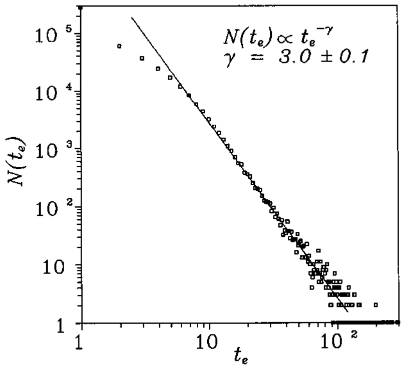

FIG. 3. Power-law distribution of lengths of intervals without activity (periods of stasis).

time units between two consecutive extinctions. If a SOC process is involved, we should expect another power-law relation in the frequency distribution of such waiting times, i.e., $N(t_s) \propto t_s^{-\gamma}$. As shown in Fig. 3, such a power law is also obtained in our system. Here we have $\gamma = 3.0 \pm 0.1$. This power law means that there is no temporal scale that would control the dynamics, and in this sense our model is clearly SOC. Some random systems may exhibit fractality, even $1/f$ noise, but the distribution of times of statis is found to follow an exponential distribution [3,11].

In order to further analyze the critical dynamical properties of the system, let us define the average individual field as

$$f_i = \frac{\mathcal{F}_i}{N} \tag{3}$$

and the average total field as

$$f_T = \frac{1}{N} \sum_i f_i . \tag{4}$$

Figures 1(a) and 1(b) show the dynamical evolution of both values. The average individual field f_i closely resembles the average total field, although the former is much noisier. Every time f_i falls below zero, the displayed species becomes extinct. The values f_T and f_i reflect a well-known process in the history of extinctions, a background of small ones (individual fluctuations that may lead to a single extinction) and a few big mass extinctions, during which almost every species becomes extinct. When the system reaches the stationary state, the value of f_T fluctuates around a self-organized threshold f^*. The comparison between Figs. 1(a) and 1(b) shows clearly how the evolution proceeds. Due to a diffusion process, the value of f_T tends to be slowly lowered. While f_T keeps above f^*, almost no extinction is found. But when $f_T \approx f^*$, large extinctions are triggered. Every time a species becomes extinct, new species appear through a copying process, as described by rule 4. The extinction of a single species may trigger a larger extinction event, in the following sense: this species probably supports others through its output connections, which may keep other local fields above zero. If those connections disappear, some other species will become extinct in the following time step. The precise value of the connections that are removed when a given species disappears may be viewed as a matter of ‘‘bad luck.’’ We can say that, in this model, two situations must coincide in order to have a mass extinction: on one hand, the total field needs to have a value close to the threshold, and on the other hand, a ‘‘negative’’ enough fluctuation has to appear. Both causes are responsible for large events.

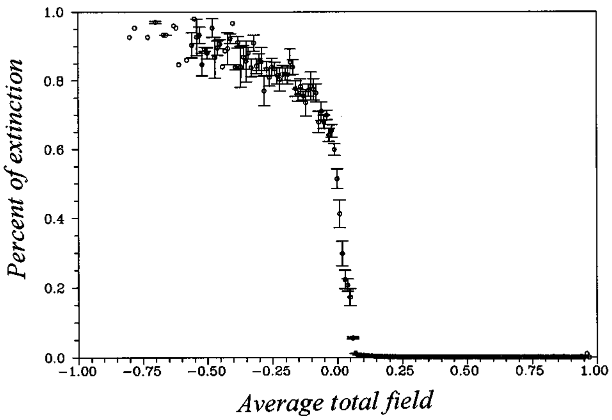

FIG. 4. Order parameter for this model. The normalized extinction size acts as an order parameter, and the total field f_T is the control parameter. The displayed result is an average over ten independent runs of 5×10^5 time steps after 2×10^4 transients were discarded in systems of size $N = 150$.

Keeping in mind that there is a critical threshold towards which the system moves but that is not stable, it is possible to define an order parameter for this system [12,13]. Let P be our dynamical order parameter, which is defined as the normalized extinction size (number of species that have disappeared over total number of species). Let also f_T be the control parameter (see Fig. 4). The critical threshold f^* that the system intends to achieve is the point where the correlation length ξ would diverge. It is in fact the single point where extinctions up to system’s size might be found. The limit $\xi \rightarrow \infty$ is an attracting point for the dynamics, but the system cannot reach and exactly maintain this value: any fluctuation would trigger an extinction and the copying process that follows would carry the system far from f^* again. In this sense, we have to talk about a marginally stable fixed point (as already stated in [13]).

This model will be further extended to incorporate the possibility of a variable number of connections which would account for a more realistic situation [14]. Many variations of this first model have been explored. In particular, the change in the threshold θ_i, the introduction of total connectivity ($C_i = N$), the nonmutation of the copied species ($\eta_{ij} = 0$, $\forall i,j$), and a discrete model with values ± 1 for the connections have been studied, and none of these modifications has been found to alter the critical exponents of the power-law distributions. It is our belief that this model catches some key features of large-scale evolution that had not been previously recovered [6,15] and its robustness against strong modifications with the maintenance of the reported exponents make a claim for it to be in a different universality class than that of other models, and probably closer to known field data.

Summing up, we have presented a model of macroevolution with explicit extinction and diversification. The obtained results can be easily interpreted from the biological point of view, and we have recovered some of the most relevant large-scale paleobiological data: power-law distributions of extinction and diversification, evolutionary bursts, periods of stasis, and mass extinctions. The model has been shown to display self-organized criticality in a new universality class, and an order parameter has been found, allowing a reinterpretation of the model in the light of classical critical transitions, a possibility that will be further explored.

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