PHYSICAL REVIEW E VOLUME 55, NUMBER 4 APRIL 1997

Criticality and unpredictability in macroevolution

Ricard V. Solé[1,2] and Susanna C. Manrubia[1]
[1]*Complex Systems Research Group, Departament de Física i Enginyeria Nuclear, Campus Nord, Mòdul B4,*
Universitat Politècnica de Catalunya. c/Sor Eulàlia d'Anzizu s/n, 08034 Barcelona, Spain
[2]*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501*

(Received 11 October 1996; revised manuscript received 2 December 1996)

A recently presented model of large-scale evolution exhibiting self-organized criticality is explored from the dynamical point of view. It is shown that the system approaches the critical state in an anomalous way, with a dynamical exponent $z=0$. At the same time, the complexity of the interactions among species increases, leading to higher unpredictability. The dynamic evolution is able to generate phylogenetic fractal trees with dimension close to the one obtained from real taxonomy. Some analytic results are presented and an interesting interpretation of the macroevolutionary process is suggested. [S1063-651X(97)15503-9]

PACS number(s): 87.10.+e, 05.40.+j, 64.60.Lx

I. INTRODUCTION

Macroevolution, as a nonequilibrium dynamical process, has received considerable attention in recent studies [1–4]. Based on simple models, the overall pattern of evolution has been suggested to be the result of a self-organized critical process [5]. Recent results based on the analysis of the fossil record seem to be consistent with this conjecture [6]. The underlying problem comes from the interaction of species (or other taxonomic units) in a complex ecosystem. Classically, ecological theory has been based on the well-known Lotka-Volterra equations [7,8]

$$\frac{dn_i}{dt}=f_i(\mathbf{n})=n_i\left(\epsilon_i-\sum_{j=1}^{N}\gamma_{ij}(t)n_j(t)\right),\quad i=1,\ldots,N, \tag{1}$$

with $\mathbf{n}\equiv(n_1,\ldots,n_N)$. The main properties of the system are determined by the so-called *community matrix*, $\Gamma=(\gamma_{ij})$, whose elements give the strength and type of the interactions. Ecological theory deals with constant Γ matrices, but evolution implies changes in the interactions, so the previous approach becomes more complicated. A quantitative approach to a general, arbitrarily wired many-species community is a challenge for theoretical ecology [8]. Though many particular cases have been solved, involving special matrix symmetries and/or directional trophic links (i.e., food chains) no general treatment has been obtained. For low-N communities, many relevant examples (as the so-called replicator networks [7]) have been solved.

A classical result involving large-N, randomly wired ecosystems, was obtained by May in 1972 [8,9]. This study involved a statistical approach to dynamical systems, based on the Wigner's semicircle law. Specifically, let us consider the linearized set of equations

$$\frac{dy_i}{dt}=\sum_{j=1}^{N}\partial_{x_j}f_i(\mathbf{n})_{P*}y_j \tag{2}$$

close to the equilibrium point $P^*\equiv(n_1^*,\ldots,n_N^*)$. Here, as usual, y_j represents the perturbation from the equilibrium value n_j^* in the neighborhood of P^*. If C is the fraction of nonzero entries in the matrix $(a_{ij}=\partial_j f_i)$, and if σ^2 is the variance of such matrix elements, it can be shown [8] that the probability $P(N,C,\sigma)$ that the system is stable will be such that

$$P(N,C,\sigma)\to 1 \quad \text{if } \sigma\sqrt{NC}<1,$$

$$P(N,C,\sigma)\to 0 \quad \text{if } \sigma\sqrt{NC}>1, \tag{3}$$

i.e., we have a sharp phase transition for $N\to\infty$. This is an interesting example of a sudden qualitative change of behavior in complex ecosystems when a given parameter is varied.

Though total randomness in the choice of the couplings neglects those links which are intrinsic to the system as a realistic model ecosystem, other recent approaches based on the simulation of multispecies communities also show striking, sharp limits to diversity and stability [10,11].

Now a step must be introduced in order to move from ecology to evolution. In a real ecosystem, changes in the species phenotype are allowed and so the matrix of interactions is in fact an evolving, time-dependent matrix. Most theoretical studies dealing with coevolution usually only consider two-species relations, where a prey and the corresponding predator (or parasite) evolve together. It is assumed that some kind of ''fitness'' function can be defined which, in the ideal case, is described by a single number. More generally, we have to use the metaphor of ''fitness landscape,'' where many different traits are considered [1]. Then, in order to improve their fitness, the two species evolve in time and their connections become modified.

It is also assumed that those individuals with lower fitness (in relation with the mean population fitness) are less able to survive and/or give offspring, and then natural selection removes them from the system. This is, roughly speaking, consistent with the Darwinian theory. If true, then the extrapolation of the microscale (involving coevolution in populations) to macroevolution would be a straightforward step.

There is, however, a considerable debate about whether microevolution is able to fully describe macroevolution [12,13]. There are several problems, which involve, for example, the existence of external stresses [14,15] linked with

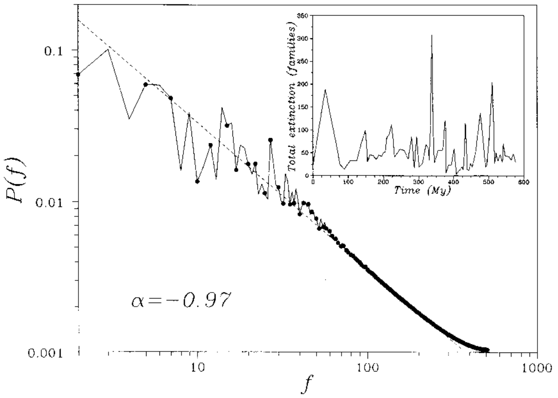

FIG. 1. Total number of families that went extinct from the Cambrian (about 600 milion years ago) to the present. The main figure represents the power spectrum (here calculated as the Fourier transform of the autocorrelation function) of the series in the inset. It is of the form $P(f) \propto f^{-\alpha}$.

abiotic causes. But other intrinsic phenomena can play a very important role, as the existence of unavoidable higher-order interactions (i.e., trophic relations involving several levels) which make network ecosystems highly unpredictable on large time scales. Though direct two-species interactions can be sometimes analytically explored, eventually leading to predictions consistent with natural selection, many examples from real ecosystems show us that this is not the case. As N-species interactions are taken into account, the existence of multiple attractors and the unpredictable nature of higher-order interactions makes intrinsic dynamics much more relevant than natural selection in the long run [16].

Additionally, theories on macroevolution must be able to say something quantitative (and so testable) concerning the statistical properties observed in the fossil record. Roughly, the following observations have been made.

(1) The extinction pattern of species (or families or other taxonomic units) is clearly punctuated. Long intervals of time show low extinction rates, but from time to time a sharp rise in extinction levels is observed [14]. An example is shown in Fig. 1. The corresponding power spectrum $P(f)$ is also shown, with a power-law behavior, i.e., $P(f) \propto f^{-\beta}$. In this example and others analyzed in the fossil record [6] it has been found that very often $\beta \approx 1$.

(2) The distribution of extinctions $N(m)$ of size m follows a power-law decay with $N(m) \propto m^{-\alpha}$ with $\alpha \approx 2$ [6,15].

(3) The lifetime distribution of family and genera durations $N(t)$ follows a power-law decay $N(t) \propto t^{-\kappa}$ of $\kappa \approx 2$ [17].

(4) The statistic structure of taxonomic systems also shows fractal properties. For example, the number of genera formed by S species, $N_g(S)$, follow a power-law distribution with $N_g(S) \propto S^{-\alpha_b}$ with $\alpha_b \approx 2$ [18].

(5) A study of the rates at which different groups of organisms go extinct through time shows that a species might disappear at any time, irrespective of how long it has already existed. This result, first reported by Leigh Van Valen [19] strongly modified the ecological view of macroevolution.

These five observations should be explained by any consistent theory of macroevolution. As far as we know, there is no theory, based on classical population genetics (i.e., on microevolution) able to reproduce and interpret these properties. This obviously does not mean that such a theory would not be possible. But, in principle, it would be extremely complicated, as far as a large set of equations involving populations together with equations for parameter selection would be necessary.

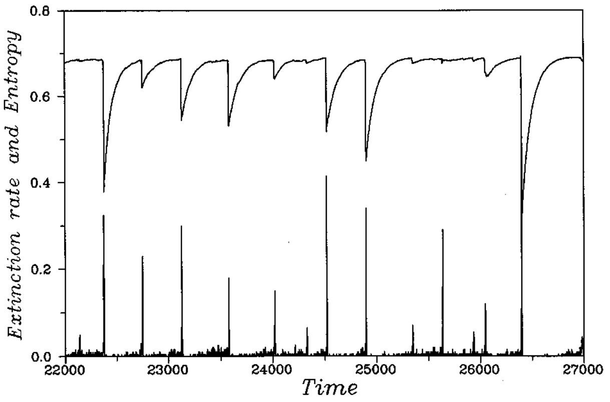

FIG. 2. Temporal variation of the Boltzmann entropy $H(t)$. When $H(t) \rightarrow H_{\max} = \ln(2)$, extinctions are triggered. The displayed system has a size $N=200$.

There is, however, an alternative approach based on the so-called self-organized critical phenomena [5]. Self-organized criticality (SOC) refers to the tendency of large dynamical systems to evolve *spontaneously* toward a critical state typically characterized by spatial and temporal self-similarity. One of the conjectured applications of SOC theory was precisely the dynamics of large-scale evolution [1–4]. The underlying idea is to identify simple, but biologically consistent mechanisms able to drive the system toward a critical state. At such a state, some of the observed scale-free properties would be naturally obtained (the opposite, however, is not true: power laws can be obtained in noncritical systems [15]). Additionally, universal behavior is expected, and so no detailed set of rules is necessary.

In this paper we explore a previously introduced [3,4,16], simple model of macroevolution which poises itself to a critical state. In Sec. II the model is briefly introduced, and a first important property, i.e., the evolution toward highly unpredictable states, is described. It is conjectured that such an unpredictable state makes macroevolution essentially decouple from microevolution, as early suggested by some paleontologists [13]. In Sec. III some analytic results are derived, and in Sec. IV the existence of a fractal taxonomy, an emergent property of our system, is described. In Sec. V we outline some of the implications. An interesting interpretation of macroevolution, as a dynamical process, is introduced.

II. EVOLUTION MODEL

Recently, the authors introduced a simple self-organized model of macroevolution [3,4,16]. In that model, the interaction among species is introduced by means of a connectivity matrix $\mathbf{J}=(J_{ij})$, and evolution is represented through changes in its elements. A set of N species which can be found in a state $S_i \in \{0,1\}$ is considered. The elements J_{ij} are allowed to take real values in the interval $[-1,1]$, and the

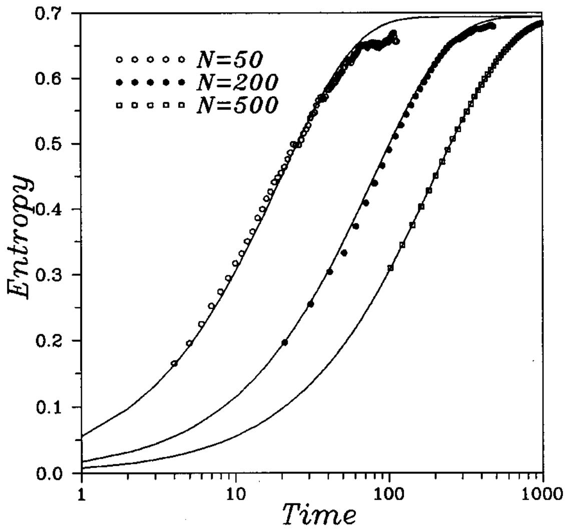

FIG. 3. Numerical (symbols) and analytical (continuous line) values of the entropy $H(t)$ for three different system sizes. The initial condition has been numerically fixed.

state of each species is updated according to

$$S_i(t+1)=\Phi\left(\sum_{j=1}^{N} J_{ij}(t)S_j(t)\right) \tag{4}$$

where the function $\Phi(z)=1$ if $z>0$ and zero otherwise. This last equation can be understood as the discrete counterpart of Eq. (1), but involving a much larger time scale. The model is updated in three steps, as follows.

(i) Random changes in the connectivity matrix. Each time step we pick up one input connection for each species and assign to it a value drawn from the uniform distribution $p_u(w)=\frac{1}{2}$ in the interval $[-1,1]$, without regard to the previous state of the connection.

(ii) The local fields are computed, $\mathcal{F}_i(t)=\Sigma_j J_{ij}(t)S_j(t)$. If some of these fields fall below zero, let us say for $e=1,\ldots m$, the set of connections $J_{ej}=J_{je}=0$ $(\forall j,\ e=1,\ldots m)$, synchronously. An extinction of size m has taken place.

(iii) Diversification. One of the alive species, $a \in \{m+1,\ldots,N\}$ is chosen at random, and its connections are copied to the extinct ones: $J_{ej}=J_{aj}$, $J_{je}=J_{ja}$, and $\forall j$.

In our previous paper [4], it was shown that the system evolves to a critical state with power laws in the extinction sizes $[N(m)\propto m^{-\alpha}$, with $\alpha\approx 2]$ [20], and waiting times until extinction, which reflect the well-known punctuated equilibium behavior displayed by real macroevolution [12]. In this paper we have analyzed the model in order to (1) have a better characterization of the intrinsic dynamics, and (2) interpret the observed behavior in evolutionary terms. All our extinction events start with a single or a few extinct species in the first time step. In following instants of time, the removal of connections and the replacement of the extinct species may have two very different effects on the remaining species of the system. Sometimes, if the species that we choose to replace the extinct ones has an average value of connections above the average of the system, we will obtain a situation where the local field of the species has increased, and thus becomes situated further from the extinction threshold, leading to a more stable state. In this case, a close extinction event is not very likely. On the other hand, simply by chance, we could have chosen an ancestor with a low local field (even negative). In this second case, the new species and the remaining ones will be proner to extinction, and a larger event may take place. This might start a chain of avalanches, a domino effect that eventually may lead to a large mass extinction.

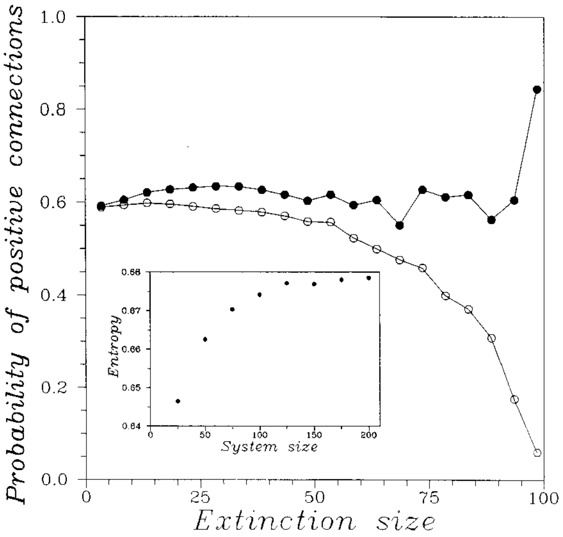

FIG. 4. Variation of the average probability of finding a positive connection just before and just after an event of size m takes place. The entropy always decreases after the extinction event and the replacement have taken place. The plots were calculated for a system of size $N=100$ and have been averaged for $t=10^6$ time steps after a transient was discarded. In the inset, we show the dependence of the entropy on system size for the minimal extinction, that is $m=1$. This minimal extinction is considered to be the one that may trigger an avalanche of extinctions. As can be seen, the unstable maximal value $H_{\max}=\ln(2)$ has to be reached in the limit $N\to\infty$ in order to start a chain of extinctions.

The described effect can be quantitatively measured in the following way. The random changes in the connectivity matrix [rule (i)] make the trophic links among species more and more complex. This complexity can be simply quantified by means of a statistical measure. We will first consider the time evolution of connections. In the most general case, we can consider the (time dependent) continuous distribution $f(\mathbf{J},t)$ of connections. For simplicity, however, we will restrict ourselves to a more simple formal approach according to which we just keep track of the sign of the connections. Most of the results are basically equivalent in both approaches. Besides, in many real situations, the structure of the connectivity matrix in a given ecosystem is limited to the knowledge of the signs of the cross interactions [21]. Let $P(J^+,t)$ and $P(J^-,t)=1-P(J^+,t)$ be the probability of positive and negative connections at time t, respectively. The time evolution of $P(J^+,t)$ is defined by the master equation

$$\frac{\partial P(J^+,t)}{\partial t}=P(J^-,t)p(J^-\to J^+)-P(J^+,t)p(J^+\to J^-). \tag{5}$$

From rule (i), we have a transition rate per unit time given by $p(J^- \rightarrow J^+)=p(J^+ \rightarrow J^-)=(2N)^{-1}$, and we obtain an exponential relaxation

$$P(J^+,t)=\tfrac{1}{2}\{1+(2p_0-1)e^{-t/N}\}, \qquad (6)$$

where we have the initial condition $P(J^+,0)=p_0$. This result leads immediately to an exponential decay in the average value $f_T=(\Sigma_i \mathcal{F}_i)/N$ of the local fields, $f_T \propto \exp(-t/N)$. The temporal variable f_T acts as a control parameter in our system [4]. This exponential time dependence gives a constant largest decay mode $\tau=1$ instead of the usual critical slowing down approach where $\tau=\xi^z$ (ξ is the correlation length of the system and z is the dynamical exponent associated to the critical slowing down; see [22] for more details). We find $z=0$, which indicates an anomalous approach to the critical state that has also been observed in a mean-field approximation of the Bak-Sneppen (BS) model [23]. We can compute the entropy of the connections, i.e., the Boltzmann entropy $H(t)=-P(J^+,t)\ln[P(J^+,t)]-[1-P(J^+,t)]\ln[1-P(J^+,t)]$. In Fig. 2, we represent the temporal evolution of the entropy together with the extinction pattern, and in Fig. 3 the numerical and the analytical variations of the entropy are shown. Recall that in the analytical calculation the zeros that might be found after the extinction event are not taken into account. This temporal evolution of the entropy has also been observed in Ray's model tierra of artificial life evolution [24]. The system slowly evolves to an "attractor" characterized by a randomly connected network. In this state, small changes of strengh $1/N$ can modify the sign of f_T, and an extinction event may take place. In the limit $N \rightarrow \infty$, only when the entropy is maximal $[H_{\max}=-\ln(\frac{1}{2})]$ is it possible to find the triggering extinction. The process of replacement works against the increase of entropy, and introduces order in the system by means of similar trophic links. A very informative measure of the strength of the fluctuations in the system is given by the representation of the average probability of positive (or negative) connections in the system just before and just after an event of size m takes place. Our results are represented in Fig. 4, together with the average entropy when an extinction of size $m=1$ takes place as a function of system size. The maximum value of the entropy is required to start an extinction event, and this maximum value is usually responsible for the extinction of one or just a few species. When this triggering extinction event takes place, the system has to reorganize to a more ordered structure far from the instability, and in some cases several consecutive extinctions are required before the avalanche stops and the system starts again to relax towards the critical threshold. These results are depicted in Fig. 5. As can be seen, large extinctions can only be obtained after some steps of "bad luck," initiated by a small event. This first event can only be obtained when the entropy is $\approx \ln(2)$, and this value is further approached as $N \rightarrow \infty$. The usual average output of an extinction event is a more ordered system, with a decreased value of the entropy.

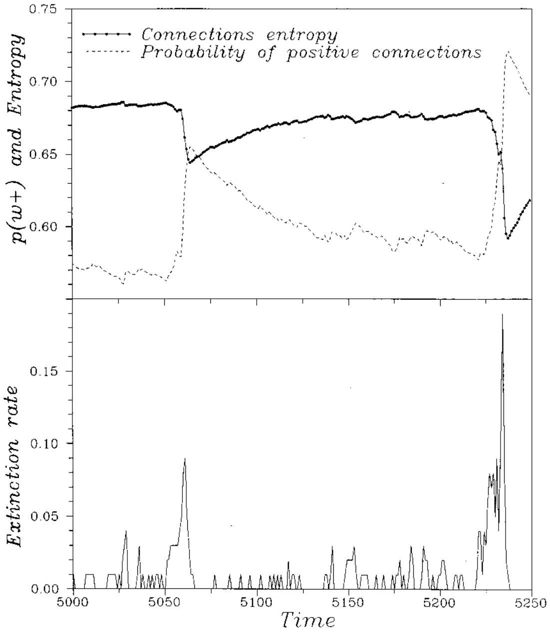

FIG. 5. Enlargement of the variation of entropy and probability of positive connections when a burst of extinction events takes place. The avalanche starts with a small extinction when the entropy is close to its unstable value and in some cases it is followed by larger events. Here we can talk about "bad luck" because the temporal extent and the total amount of species that go extinct depend on the chance in the election of the species that is going to replace the extinct ones. In our system, we can observe preshocks to large mass extinctions. The system always becomes more ordered after one such burst, as can be observed in the decrease of the entropy. The simulated system has size $N=100$.

The overall effect of the relaxation toward a random network is a highly survival of species. As a consequence, in the long run all species are equally likely to become extinct, as observed in the analysis of the fossil record. Let us mention, however, that a careful inspection of our simulations points out a power-law behavior of this quantity for small times (consistent with the observed lifetime distribution) together with a well-defined and wide exponential cutoff. This result suggests that perhaps the statistics available from the fossil record are not, at this level, complete enough to detect the power-law component, which nevertheless shall be present in the essentially exponential functions supporting the Red Queen effect in order to make both results compatible (field observations 3 and 5).

III. ANALYTIC RESULTS

The stationary solution of the system can be characterized by the distribution of connections $p(w)$in the **J** matrix. Let us call $p(w,t)$ the probability of finding a connection of value w at time t. Using a mean-field approximation, we can write in two steps the following master equation for this probability:

$$p(w,t+\tfrac{1}{2})=p(w,t)-\frac{1}{N}p(w,t)+\frac{1}{2N},$$

$$p(w,t+1)=p(w,t+\tfrac{1}{2})-\overline{k}q(w,t+\tfrac{1}{2})$$

$$+\frac{1}{1-\overline{k}}[p(w,t+\tfrac{1}{2})-\overline{k}q(w,t+\tfrac{1}{2})], \qquad (7)$$

where $\overline{k}$ is the average probability of extinction, and we have

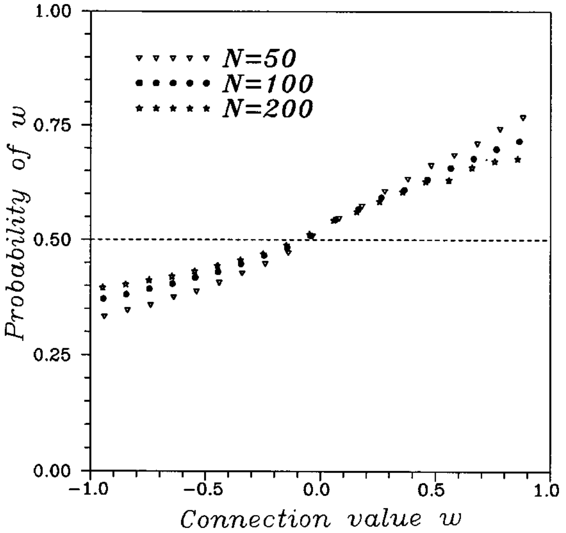

FIG. 6. Distribution $p(w)$ for different system sizes. These have been obtained by averaging over 10^6 time steps snapshots taken every 100 time steps. The connections with zero value are not taken into account. As can be seen, these distributions assymptotically approach the mean-field solution $p(w)=\frac{1}{2}$ for $N\rightarrow\infty$.

defined $q(w,t+\frac{1}{2})$ to be the probability of removing a connection of value w from the matrix when an extinction of average size $\overline{m}=N\overline{k}$ takes place. The first equation simply considers the random change in the interactions [rule (i)]: a value w will disappear with probability $p(w,t)/N$ and will appear with probability $1/2N$. The second equation takes into account the removal of connections due to extinction (second term) and the introduction of additional connections through diversification (third term). The fact that we cannot directly evaluate the probability distribution of removed connections makes the analytical treatement of the model slightly different from other mean-field approximations to evolutionary models [23,25]. Our mean-field approximation consists in removing $\overline{m}N$ connections at random from the matrix, and adding the new ones just by picking up randomly the same number of connections from the remaining ones, without considering that in rule (iii) the copied connections all belong to the same species: we get rid of the correlations. We further consider the average extinction rate $\overline{k}$ instead of k, which would be time dependent. The stationary solution of Eq. (7) reads

$$(N\overline{k}-1)p(w)-N\overline{k}q(w)+\tfrac{1}{2}=0. \tag{8}$$

This equation is formally identical to the one obtained for the stationary probability distribution of fitnesses in the BS model [see Eq. (5) in Ref. [23]]. Equation (8) has the solution $p(w)\equiv q(w)\equiv\frac{1}{2}$. In Fig. 6, we represent the numerically obtained distribution $p(w)$ for different system sizes N. As can be seen, the mean-field solution $p(w)=1/2$ is asymptotically approached as $N\rightarrow\infty$. The BS model, or the variation introduced by Roberts and Newman [25], both have uniform distributions for fitnesses above a certain self-organized threshold. This threshold comes from the explicit definition of extremal dynamics. In our case, although in some sense the dynamical rules lead to the removal of the species with the lowest local field, no extremal principle holds for the connections, for which the master equations are written [26].

The solution of Eq. (8) can be obtained exactly if we consider just two values for the connections: $J_{ij}=\pm 1$ (see [4]). In this case, both $q\equiv q(1)$ and $\overline{k}$ can be computed as follows: in the mean-field approximation, $\overline{k}$ is simply the probability of choosing N numbers from the matrix such that their sum (the local field) is negative or zero. This means that we have to find a maximum quantity of $N/2$ 1's in the set, so

$$\overline{k}=\sum_{M=0}^{N/2}\binom{N}{M}p^{M}(1-p)^{N-M}, \tag{9}$$

where we have defined $p\equiv p(1)$, and q can be written as

$$q=\tfrac{1}{2}+\frac{\langle\mathcal{F}_{-}\rangle}{2N}, \tag{10}$$

where we have defined

$$\langle\mathcal{F}_{-}\rangle=\sum_{M=0}^{N/2}(2M-N)\binom{N}{M}p^{M}(1-p)^{N-M} \tag{11}$$

as the average value of the removed local fields. Substitution of the last two expressions into the stationary solution (8) gives the following equation for p:

$$p=\frac{N\left[\sum_{M=0}^{N/2}\binom{N}{M}p^{M}(1-p)^{N-M}\right]\left[\frac{1}{2}+\frac{1}{2N}\langle\mathcal{F}_{-}\rangle\right]-\frac{1}{2}}{N\sum_{M=0}^{N/2}\binom{N}{M}p^{M}(1-p)^{N-M}-1}, \tag{12}$$

which has the mean-field solution $p=\frac{1}{2}$. As can be seen, the exact solution for the master equation requires the evaluation of the distribution displayed by the removed connections, taking into account the criterium over its sum. It could be calculated explicitly in the discrete case, and the continuum case has been extrapolated from that one, and verified to fulfill the equations and to approach the theoretical solution numerically.

IV. FRACTAL TAXONOMY

In the history of evolution, natural parental links among different species naturally appear as a result of mutation and diversification from an ancestral group. The relationship among species is usually represented by means of a phylogenetic tree, where the moment of splitting of a new species from an old one is represented in an axis of a two-dimensional plot, together (usually) with a "distance" to this species in another axis, which intends to account for the degree of initial taxonomic separation. There is some controversy about the goodness of the classification of species into genera, genera into families, and so on (the so-called taxonomy). Nevertheless, recent studies about phylogenetic trees at different taxonomic levels (generation of new species, new genera, new families, new clades, etc.) suggest that there might be some kind of universality in those trees independent from the taxonomers point of view [18]. That is, it

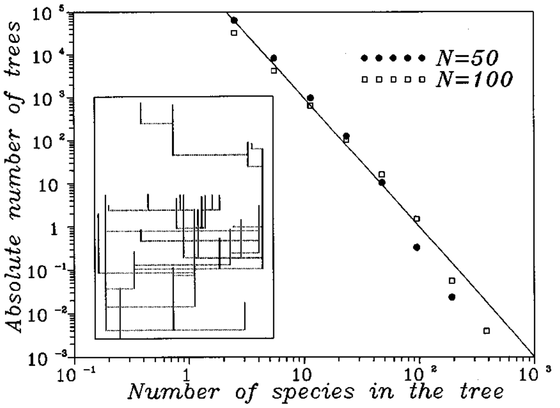

FIG. 7. Distribution of phylogenetic tree sizes. The size of a tree is defined as the total number of branches it possesses or the total number of species that originate from the first ancestor. About 10^7 time steps are required to give the shown distributions. The continous line has a slope of -3. In the inset, a tree from a system of size $N=50$ is shown. The vertical axes represent time and the horizontal axes the species. When a speciation event takes place, the new born species is linked to the ancestor with a dotted line. The length of the vertical lines represents the lifetime of each of the species.

may be that the grouping of subtaxa within a higher taxa is not an artificial human ordering, but the result of the very process of evolution. On the other hand, if self-similarity in taxonomy holds, this would be an independent support to the conjecture that real macroevolution is operating close to a self-organized critical point.

The dynamical rules that define our model naturally poise the system to a critical state. In this critical state, a property of real taxonomy is recovered: the system generates fractal phylogenetic trees, as has been observed by Burlando [18]. The value of the critical exponent α_b that defines the ‘‘branching’’ of species into others is the same as our exponent for the extinction sizes, $\alpha=\alpha_b\approx 2$, and is very close to the exponent obtained from real data [18]. This result is a direct output of our third rule, replacement of extinct species, provided we chose a single species to act as the ancestor of all the new ones. This result, however, can be extended to the case of choosing species at random to replace the extinct ones, and the value of the exponent remains unchanged.

We have also measured the distribution of the number of species that at any time have belonged to a given tree. This means that we sum over all the time that at least one species phylogenetically linked to the first ancestor is alive. In order to do so, we pick at random one species from the system and count the total number of species that have appeared as descendents from this first one. This is the size of our tree s. The distribution is $D(s)\propto^{-\beta}$, with $\beta\approx 3$. In Fig. 7 we display the distribution $D(s)$ for different system sizes and an example of a phylogenetic tree. Some other models have also considered this generation of trees. In this context, Vandewalle and Ausloos [27] have obtained phylogenetic trees with a fractal dimension depending on a certain parameter of their model, and Newman [15] was also able to define a taxonomy in a system driven by random external outputs and obtain an exponent compatible with a power-law distribution of exponent 2.

V. SUMMARY AND DISCUSSION

We have analyzed a model of large-scale evolution that, though simple, keeps some relevant traits of the real process, and is able to quantitatively recover the main observations of macroevolution. These include punctuated equilibrium, power laws in the distribution of extinction events, and lifetimes of species, fractal taxonomy, and a rate of disappearance independent of species age. In particular, the obtained value for the distribution of extinctions, $\tau\approx 2$, is very close to the exponent extracted from the fossil record [17] and also near the value obtained by Roberts and Newman [25]. In their paper, these authors modify the BS model in order to take into acount the influence of environmental factors. They introduce an external coherent noise that forces the simultaneous extinction of all the species below some randomly chosen threshold. A different model that simply relies on external stresses, without any mechanism to make the species interact directly, was introduced later by Newman [15]. The approach is, however, the same: it is the external influence and not the self-organization that causes the extinction. In this last model, the coherent effect that makes a certain fraction of species become simultaneously extinct is even clearer than in the model with the BS mechanism. In our model we also have a large coherent effect due to the process of species replacement, which is able to generate a large mass extinction when a species with a low local field is chosen to replace the extinct ones: it is very likely to have large domains in the **J** matrix with essentially the same number (which also justifies the one-dimensional approach to the problem; see [28]). It is quite clear that Roberts and Newman's model, Newman's model, and ours all include a feature, coherence, that seems to be essential to recover the right exponent for extinction sizes. In our case, all the exponents are clearly robust under many different definitions of the precise rules of the model, as far as the effects of drift toward the extinction threshold and coherence are maintained. These two characteristics might define a universality class, probably able to describe real macroevolution. The main theoretical consequence of our model is that macroevolution can be interpreted in an interesting way. Species interact through changing couplings. Though two given species directly connected can be understood in terms of classical two-species coevolution, higher-order (indirect) couplings can trigger small extinction events which, eventually, may lead to mass extinctions. In this context, the unpredictable nature of these interactions cannot fit into the classical theory. This model could be used as a theoretical framework for the old conjecture of an intrinsic separation between microevolution and macroevolution [12,13].

Finally, we should mention that our model could be an interesting approach to other complex systems with an evolving network structure. Economic networks, in particular, have been widely explored as complex adaptive systems [29,30]. In these networks, agents are coupled through evolving interactions. Noise in their couplings arises in several ways. In real life, agents are not always able to process perfectly information about the system (the network) in which they are embedded. Adaptive agents continuously switch their behavior as a consequence of changes in their expectations [30]. At the same time that agents are continuously evolving, the couplings among them evolve in rather complicated ways. The consideration of agents (or whole markets) with limited rationality will introduce changes in the couplings that may not always represent the best management of the resources. This situation leads to small, random changes similar to those introduced by our rule (i). Several models of market dynamics have shown that (as in the real economy) punctuated equilibrium is often observed [31]. Additionally, theoretical studies of generic mathematical models of market dynamics clearly show that, as couplings among stable markets grow, the likelihood of instabilities also increases, leading to a loss of the general equilibrium, as the system becomes increasingly diverse. The stability properties of these generic market models have been shown to apply not only to this specific case, but also to complex ecosystems [32]. In our model, the system spontaneously evolves to a highly diverse network of connections, linked with the onset of instabilities. Finally, recent studies [33] have revealed that markets display fractal structures in their internal organization. Interestingly, our fractal taxonomy is the outcome of a self-organized critical system with no characteristic time scales. Perhaps the observed fractal properties of markets can be generated through a similar process.

ACKNOWLEDGMENTS

The authors would like to thank S. Kauffman, P. Bak, J. Bascompte, M. Benton, B. Goodwin, S. Maslov, and M. Paczuski for useful comments. This work was supported by Grant No. DGYCIT PB94-1195. R.V.S. thanks the Santa Fe Institute for economic support.

---

[1] S. Kauffman and J. Johnsen, J. Theor. Biol. **149**, 463 (1991).

[2] P. Bak and K. Sneppen, Phys. Rev. Lett. **71**, 4083 (1993).

[3] R. V. Solé, Complexity **1**, 40 (1996).

[4] R. V. Solé and S. C. Manrubia, Phys. Rev. E **54**, R42 (1996).

[5] P. Bak, C. Tang, and K. Wiesenfeld, Phys. Rev. Lett. **59**, 381 (1987).

[6] R. V. Solé and J. Bascompte, Proc. R. Soc. London Ser. B **263**, 161 (1996); R. V. Solé, S. C. Manrubia, M. Benton, and P. Bak (unpublished).

[7] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, 1991).

[8] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1974).

[9] Yu. M. Svirezhev and D. O. Logofet, *Stability of Biological Communities* (Mir, Moscow, 1983).

[10] S. L. Pimm, *The Balance of Nature?* (Chicago Press, Chicago, 1991).

[11] J. A. Drake, Trends Ecol. Evol. **5**, 159 (1989).

[12] S. Gould and N. Eldredge, Paleobiology **3**, 114 (1977).

[13] N. Eldredge, *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought* (Oxford University Press, New York, 1985).

[14] D. M. Raup, Phys. Trans. R. Soc. London Ser. B **325**, 421 (1989); Science **231**, 1528 (1986).

[15] M. E. J. Newman, Proc. R. Soc. London Ser. B **263**, 1605 (1996).

[16] R. V. Solé, J. Bascompte, and S. C. Manrubia, Proc. R. Soc. London Ser. B (to be published).

[17] D. M. Raup, *Extinction, Bad Genes or Bad Luck?* (Oxford University Press, Oxford 1991).

[18] B. Burlando, J. Theor. Biol. **146**, 99 (1990); **163**, 161 (1993). The observed exponent $\alpha_b \approx 2$ is quite different from what should be expected from a simple statistical argument. A power law relation for taxonomy has been derived by some authors [see S. Nee, Proc. Natl. Acad. Sci. U.S.A. **89**, 8322 (1992)]. Assuming a branching process, where species are generated from a given ancestor, a power law with $\alpha = 3/2$ is obtained, rather far from the one observed in the fossil record.

[19] L. Van Valen, Evol. Theory **1**, 1 (1973).

[20] While this work was carried out, a simpler model was performed, where it was possible to get rid of the connectivity matrix [28]. The authors obtained an exponent $\alpha = 2$ analytically. Our first model and this one-dimensional simplification are believed to belong to the same universality class.

[21] In fact, many field studies provide a matrix where only the signs $(+,-)$ are indicated. Beyond the apparent limitations of this partial information, an important body of theory of ecological systems deals with the so-called qualitative stability (see [8,9]). Although the magnitudes of the mutual effects are seldom known accurately, a graph analysis of the network is a powerful tool in order to define the stability of a given graph. Additionally, the symmetry of the distribution of changes used in rule (i) is justified in terms of the origin of randomness. Changes in the connections can be generated through a multiple phenomena, both biotic and abiotic. Any asymmetry must be justified by means of a macroscopic argument, which (at this stage of our study) seems unjustified. A recent analysis of real network ecosystems has shown, on the other hand, that the random-graph approach used by May [8] seems totally justified [see D. Kenny and G. Loehle, Ecology **72**, 1794 (1991)].

[22] J. J. Binney, N. J. Dowrick, A. J. Fisher, and M. E. J. Newman, *The Theory of Critical Phenomena* (Oxford University Press, Oxford, 1995); N. Goldenfeld, *Lectures on Phase Transitions and the Renormalization Group* (Addison-Wesley, Reading, MA, 1992).

[23] H. Flyvbjerg, K. Sneppen and P. Bak, Phys. Rev. Lett. **71**, 4087 (1993).

[24] T. S. Ray and N. Jan, Phys. Rev. Lett. **72**, 4045 (1994); T. S. Ray, Physica D **75**, 239 (1994).

[25] M. E. J. Newman and B. W. Roberts, Proc. R. Soc. London Ser. B **260**, 31 (1995); B. W. Roberts and M. E. J. Newman, J. Theor. Biol. (to be published).

[26] For a review of extremal models, see M. Paczuski, S. Maslov, and P. Bak, Phys. Rev. E **53**, 414 (1996).

[27] N. Vandewalle and M. Ausloos, Europhys. Lett. **32**, 613 (1995).

[28] In this model, the continuous decay of fields is treated in a mean-field manner. Instead of a J matrix where single connections are randomly updated, a simple rule of field decay is used. Specifically, each species is represented by a number (its

local field), and at each time step it is on the average lowered by a certain amount. When the local field falls below the critical extinction threshold, the species dies out, and a set of replacement rules similar to the one used here is applied, together with a certain effect acting over the survivors and due to the extinction event. The statistical behavior of this simpler model is the same, but the removal of the matrix structure makes a derivation of the master equation and scaling laws tractable. See S. C. Manrubia and M. Paczuski (unpublished).

[29] *The Economy as an Evolving Complex System*, edited by P. W. Anderson, K. J. Arrow, and D. Pines (Addison-Wesley, Redwood City, CA, 1988).

[30] T. Hogg, B. A. Huberman, and M. Youssefmir (unpublished). These authors explored the theoretical implications of an international market system by means of strongly coupled local markets.

[31] This observation was first reported by Huberman in his studies about cooperations and dynamics with expectations in simple economic models. See, for example, J. Kephart, T. Hogg, and B. Huberman, Phys. Rev. A **40**, 404 (1989).

[32] T. Hogg, B. Huberman, and J. M. McGlade, Proc. R. Soc. London Ser. B **237**, 43 (1989).

[33] E. E. Peters, *Fractal Market Analysis* (Wiley, New York, 1994).