

Self-organized criticality in coevolving interacting systems

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A simple physical model of biological evolution of an ecology of interacting species is introduced. The model self-organizes into a critical steady state with intermittent coevolutionary explosions and exhibits the “punctuated equilibrium” phenomenon. The dynamics of the model markedly differs from that of an earlier (and simpler) one of Bak and Sneppen [Phys. Rev. Lett. **71**, 4083 (1993)], but allows for similar conclusions, which allows one to speculate about their universality.

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Gould [1] has conjectured that biological evolution takes place in terms of intermittent bursts of activity separating relatively long periods of quiescence rather than in a gradual fashion. Such an intermittent pattern has been observed by Raup, Sepkosky, and Bayonian [2–5] by studying fossil records. When referring to this intermittent behavior of the evolution of single species, Gould speaks of “punctuated equilibrium.” It has been suggested that extinction events (at least the larger ones) are caused by external forces [6–8].

Plausible as this sounds, punctuated equilibrium may well be the natural consequence of the intrinsic biological dynamics, with no need for external triggering mechanisms. The ecology of interacting species may have evolved to a self-organized critical state [9,10]. Self-organized criticality (SOC), a concept introduced by Bak, Tang, and Wiesenfeld and best illustrated by the celebrated Bak sandpiles [11,12,14–16], refers to the tendency of some dynamical systems to organize themselves into a “poised,” far off equilibrium state.

However, theoretical investigations have been thwarted by the difficulty of constructing realistic yet tractable mathematical models. First, punctuated equilibria were observed by Bak, Chen, and Creutz [9] in the “Game of Life,” a simple computer model of a society of living and dying individuals living on a two-dimensional lattice, that, however, *is not robust against small changes in the rules*, as it should be in order to represent “real” evolution. Later, Kauffman and Johnsen [10] studied elaborate “*NKC* models” of species coevolving at the edge of criticality, with periods of stasis interrupted by avalanches. However, these models do not self-organize: *some external tuning of the system is needed to obtain critical behavior* [13,14]. Bak *et al.* [15,16] have investigated an evolving biological model that self-organizes to a critical steady state, although it is too simple to allow for reasonable conjectures concerning terrestrial biology. This model does exhibit punctuated equilibrium and is to be regarded as a major advance in our understanding of evolutionary phenomena.

We see that, on the one hand, “realistic” models re-

quire external tuning in order to exhibit SOC, while, on the other, one reaches it in a robust fashion only in rather simple models. Such a state of affairs should motivate the search for somewhat more realistic biological models that self-organize without external intervention. We can regard the well-known Lotka-Volterra equations for the oscillations of a predator-prey pair of biospecies [17] as the archetype of a biologically inspired dynamical system [18] and it is our intention to look to it for guidance in such a search.

We thus introduce in the present effort a model that deals with several interacting species. The dynamics of the model, inspired in [17], will be seen to evolve naturally towards a critical state that clearly exhibits the punctuated equilibrium phenomenon without external tuning. Of course, this is also a simple model, but it does contain features associated with actual biological evolution. Moreover, it is of a rather general character, as it can be easily modified in order to introduce more realistic ingredients. Finally, the level of description is conceptually different from that of the above cited pioneering efforts.

We deal with M distinct, interacting biological species, each of which is represented by a vector in \mathbb{R}^N . The components V_α^i of \vec{V}^i represent different phenotypic features (α, β, \dots) that are to be affected and modified by the evolutionary process. The degree to which the i th species is “adapted” to the environment is represented by a quantity F_i , to be called its “fitness”:

$$F_i = \sum_j^M \sum_{\alpha, \beta}^N g_{\alpha\beta}^{ij} V_\alpha^i V_\beta^j + \sum_\gamma^N V_\gamma^i A_\gamma^i, \quad i = 1, \dots, M, \quad (1)$$

where the hypermatrix $g_{\alpha\beta}^{ij}$ provides the details of the interspecies interaction and the second summand on the right-hand side is an “environmental” one (see below). We assume $g_{\alpha\beta}^{ij} = -g_{\beta\alpha}^{ji}$. This is a reasonable assumption, because if the α feature of the species i gives it a competitive edge against the β feature of the j species, the latter gives it, of course, a competitive disadvantage against the former (symbiosis is excluded). The A_γ^i matrix mimics the environmental influence (such as climate and geography) over the γ feature of the i th species. Notice the strong similarity of the right-hand side of (1) to that of Volterra’s dynamics for the populations N_i of M

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interacting species [17]

$$\frac{dN_i}{dt} = \sum_{j=1}^M A^i N_i + g^{ij} N_i N_j, \quad (2)$$

where, of course, the symbols have different meanings, which we do not need to explicate here.

Of course, the components of \vec{V}^i must necessarily exhibit some degree of correlation, as genes are simultaneously involved in several phenotypic features. We shall represent this correlation by recourse to mappings between a set of $k + 1$ real parameters and each of these components, i.e.,

$$f_\beta: a_0^i, \dots, a_k^i \longrightarrow V_\beta^i, \quad (3)$$

where

$$V_\beta^i = f_\beta(a_0^i, \dots, a_k^i), \quad (4)$$

with f_β an arbitrary function. The set a_0^i, \dots, a_k^i defines in fact the i species. As a result of biological mutations, these parameters are allowed to vary with time. The family of all these (M) sets can be called the *configuration* of the system.

The conceptual difference between the a 's and the V 's should be emphasized here. The components of V denote different phenotypic features of the species that this vector represents. These features are correlated, via the a 's, in the manner just described. Genetic changes, here mimicked by modifications in the a values, drive the evolutionary process. The correlations just mentioned constitute an essential aspect of our model.

Our system evolves as follows. We start with an arbitrary initial configuration (the a_i are randomly chosen within $[-1, 1]$) and, in each of a series of time steps, mutation effects are mimicked by slightly modifying the a_i for the l th species. Both the selection of l and the nature of the changes are random. The condition $|\vec{V}^i| = 1$ is enforced so as to avoid unrestricted growth (with time) of $|\vec{V}^i|$.

A particular mutation (change in a given a) is "accepted" if it increases the corresponding fitness (as a consequence of such a mutation F_i grows). The a change in this case is retained. Otherwise it is discarded and the a_i end up with their previous values.

Extensive numerical studies suggest that such a system never reaches an equilibrium situation, a fact that could be guessed from the skewed symmetry of g^{ij} [19]. The number of species M is kept constant for the sake of simplicity. However, as the features of each species are in a state of continuous change, there is a considerable amount of "evolutionary activity," which we shall quantify with reference to the motion of a "center of mass"

$$\vec{X}_{\text{c.m.}} = \sum_{i=1}^M \vec{V}^i, \quad (5)$$

whose value is to be ascertained at a series of regularly spaced times. A species becomes extinct when it accumulates a succession of changes of a certain magnitude, more specifically, whenever the vector \vec{V}^i traverses in \mathbb{R}^N a distance larger than (a threshold) D_t .

For the sake of simplicity we choose (i) our hypermatrix in the form

$$g_{\alpha\beta}^{ij} = k_{ij} \delta_{\alpha\beta} \quad (6)$$

and (ii) $A_\gamma^i = 0$. Thus (1) reduces itself to

$$F_i = \sum_{j=1}^M k_{ij} \vec{V}^i \cdot \vec{V}^j, \quad i = 1, \dots, M, \quad (7)$$

where $k_{ij} = -k_{ji}$. The k_{ij} are randomly chosen within $[-1, 1]$ (for $i < j$) and are kept constant throughout. These simplifications notwithstanding, a complex enough dynamics ensues that can account for important details of fossil records.

As polynomials are the basis in any reasonable function space, the "correlation functions" discussed above can be chosen in a simple, and at the same time general, fashion as k -degree polynomials [cf. (4)]

$$f_\beta = \sum_{n=0}^k a_n x^n, \quad x = \beta/N, \quad (8)$$

so that

$$V_\beta^i = \sum_{n=0}^k a_n^i (\beta/N)^n.$$

Figure 1 displays "activity" as represented by the distance traversed by $X_{\text{c.m.}}$ in regular time intervals. Here we take $M = 17$ and $N = 7$ and $f(x)$ is a polynomial of second degree. We considered 1000 time steps (arbitrary size). Figure 1 strikingly resembles Sepkoski's extinction curve [5], obtained by recourse to a careful study of fossil records.

A suggestive, more quantitative result is obtained by constructing a histogram with the data of Fig. 1 (Fig. 2). By studying extinction patterns in 106 intervals of about 5×10^6 yr each, Raup has concluded that the corresponding distribution follows a power law [3]. We see in Fig. 2 that the data of our model are well fitted by a power law. The concomitant slope β cannot be directly

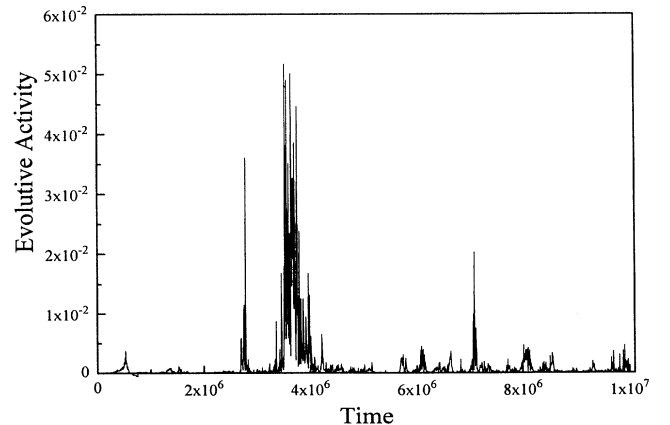


FIG. 1. Global evolution rate (arbitrary units) for $M = 17$ and $N = 7$. Each point represents the distance traversed by the center of mass of the system in 1000 time intervals of arbitrary size.

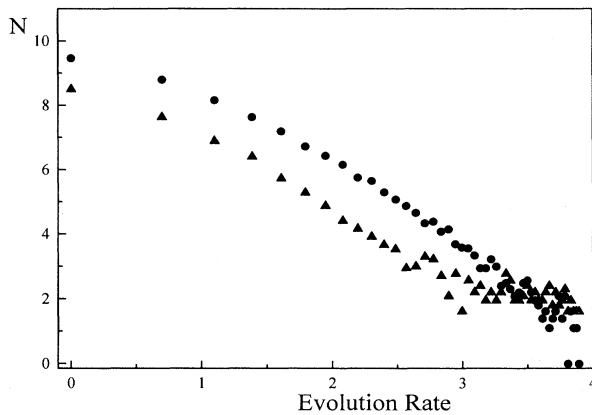


FIG. 2. Histogram constructed with the data depicted in Fig. 1 (lower curve). The log-log graph clearly shows that a power law is obeyed. The corresponding curve obtained with $M = 50$ and $N = 10$ is also exhibited (upper region).

compared to the one of Raup because ours is a continuous distribution [of the form $P(D)dD \propto D^{-\alpha}$] and not a discrete one (number of extinguished species). Our β is a function of both α and n , the number of intervals in the bar chart. This interrelation of α , β , and n is the cause of large errors in the estimation of α . In the case of Fig. 2 we have $\alpha \simeq 0.6$.

We portray evolutive activity vs time, but for a single species, in Fig. 3. Punctuated equilibrium is indeed observed: long periods of “passivity” are interrupted by sudden activity outbursts, which play here the role of Bak’s avalanches [15]. We find the same results independently of the particular values chosen for M and N .

The species in our model eventually become extinct as changes due to mutations accumulate. As stated above, a species is to be regarded as extinct whenever the vector \vec{V}^i traverses in \mathbb{R}^N a distance larger than a threshold D_t . This threshold can be, in principle, arbitrarily chosen. A sensible choice, however, is to select it to be of the order of the greatest length traversed by any of the vectors

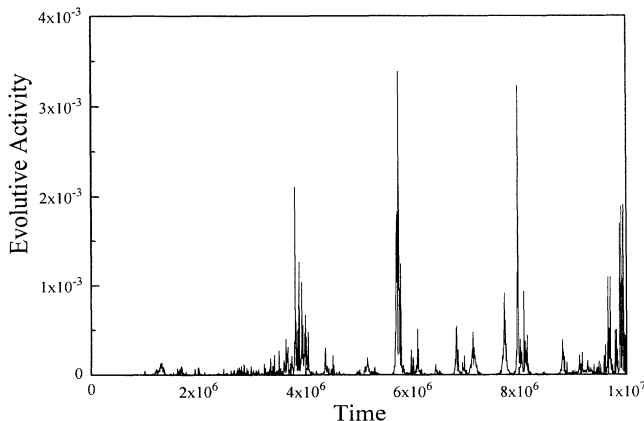


FIG. 3. Single-species evolutive activity (arbitrary units). The data are those of Fig. 1. Punctuated equilibrium is clearly observed.

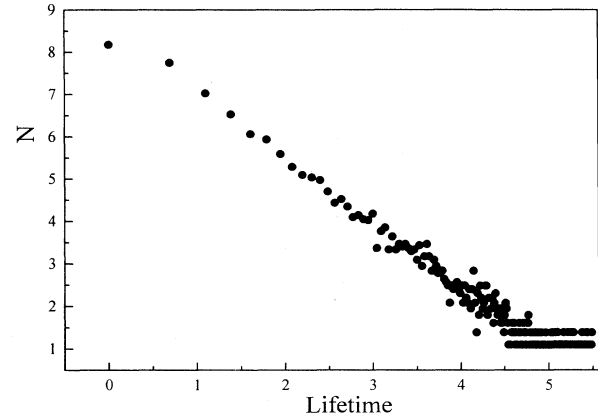


FIG. 4. Lifetime distribution (arbitrary temporal units) for $M=25$ and $N=7$. The log-log graph allows one to easily appreciate that a power law is fairly well adjusted.

\vec{V}^i in a single time step. D_t be neither very small (all species become rapidly extinct) nor very large (too few species will become extinct during the whole simulation process). We have made sure that our results are robust against changes in D_t around the chosen value. When a species becomes extinct, the vector that represented it is kept as the representative of a newborn species.

The concomitant distribution of lifetimes deserves then to be studied (Fig. 4). We see that lifetime distributions do adjust a power law, in agreement with the findings (fossil records) of Raup *et al.* [2–5].

Suppose now that all “mutations” are retained, whether or not they are “beneficial.” Darwinian competition is thus ignored. Figures 5–7 depict the associated results. Punctuated equilibrium no longer obtains. No power laws are obeyed. The associated dynamics can be regarded as considerably “poorer.”

An extremely simple model of biological, competitive coevolution has been presented that is able to exhibit a rich, complicated dynamics, complex enough so as to mimic (even if superficially) *some* facets of actual bio-

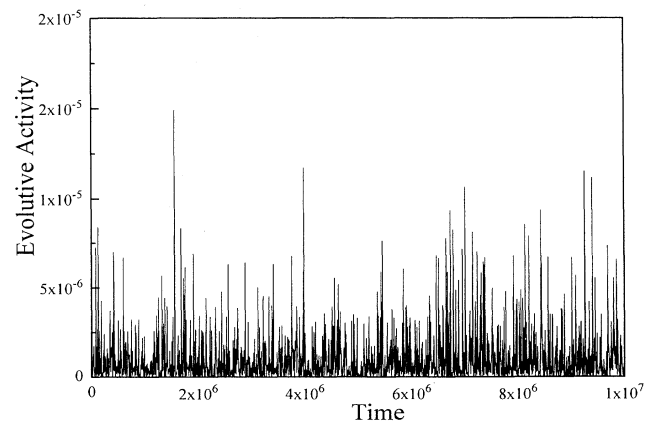


FIG. 5. Global evolution rate (arbitrary units) for random motion without Darwinian competition (see the text) for the case $M = 17$ and $N = 7$. Additional details are as in Fig. 1.

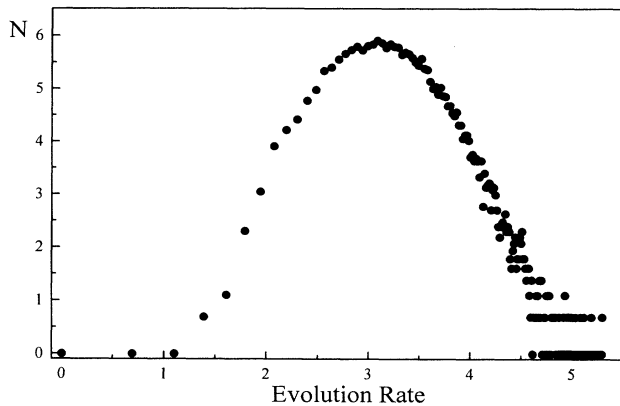


FIG. 6. Histogram constructed with the data of Fig. 5. Additional details are as in Fig. 2. No power law is seen to be obeyed.

logical evolution. On the basis of this model one can conclude that *these* facets can be explained without recourse to catastrophic events. It is shown in Fig. 1 that evolution towards a critical state proceeds rather rapidly.

Our model can be regarded as more realistic than that of [15]. Its main advantage *vis-à-vis* the model of Bak and Sneppen [15] resides in the fact that the interaction among species receives a much more detailed treatment: species *A* is here able to respond gradually to changes affecting species *B* and second-order effects arising out of this interaction and affecting *other* species (*C, D, ...*) are also taken into account. A chain of changes thus ensue that takes place within the time scale in which *B* is changing. In other words, in our model “actions” (modifications in the features of a given species due to biological evolution) and “reactions” (concomitant changes in the remaining species) take place almost simultaneously, which is not the case in [15]. This difference between the models is to be attributed to the diverse temporal scales (TS’s) they encompass. In [15] the TS’s are those for which a given species suffers drastic modifications, while ours allow for the description of very small ones.

Our model differs in a fundamental manner from previous ones that predict extinction curves (ECs), e.g., Game of Life [9], *NKC* Kauffman-Johnsen models [10], asym-

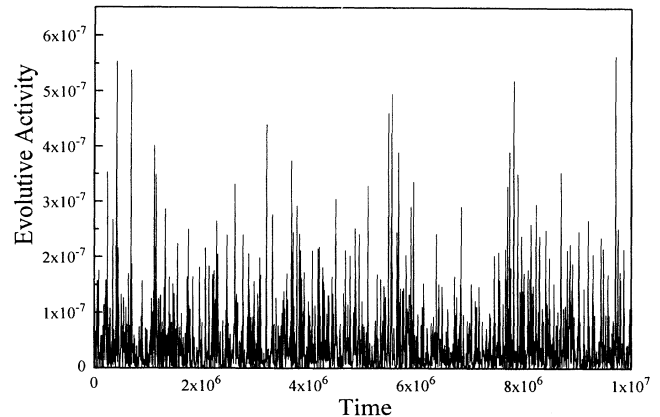


FIG. 7. Single-species evulsive activity (arbitrary units). The data are those of Fig. 5. Punctuated equilibrium is no longer observed.

metric spin glass models [13], or the Bak *et al.* model [15,16]. The ECs in these models respond basically to an identical procedure. (i) Let the system evolve until it reaches a frozen state. (ii) After it comes to rest, perturb it by a single random mutation that does not increase the fitness of the corresponding species. This induces a coevolutionary avalanche, rather small in the beginning. When the system comes again to a stop repeat (ii). After a while, the system is pumped up to a “poised” state, where yet another mutation may induce an avalanche of any size.

In our case we cannot properly speak of avalanches but rather of sudden activity explosions. But in this case, however, these activity outbursts *are not the product of perturbations of an equilibrium state*. Instead, they arise out of the intrinsic dynamics of the system.

Summing up, our model markedly differs from that of Bak, Sneppen and Flyvbjerg [15,16] in its dynamic aspects. However, “evolution” proceeds in a rather similar manner in both models, which tends to support the notable ideas put forth by those authors concerning the possibility of understanding, on the basis of simple models, the phenomenon of self-organization into a critical steady state.

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