Punctuated Equilibrium and Criticality in a Simple Model of Evolution

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A simple and robust model of biological evolution of an ecology of interacting species is introduced. The model self-organizes into a critical steady state with intermittent coevolutionary avalanches of all sizes; i.e., it exhibits "punctuated equilibrium" behavior. This collaborative evolution is much faster than noncooperative scenarios since no large and coordinated, and hence prohibitively unlikely, mutations are involved.

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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 manner. Raup [2] has noted that extinctions are indeed episodic at all scales. There are a few large events such as the extinction of dinosaurs and the Cambrian explosion, but there is also a spectrum of smaller events. It has been suggested that this behavior indicates that the ecology of interacting species has evolved to a self-organized critical state [3, 4]. Nevertheless, there has so far been no theoretical support. Here, we present for the first time a model of an evolving biology, which self-organizes to a critical steady state. Although the model is very abstract, and necessarily immensely oversimplified, we believe that it contains elements representing the mechanism of real evolution.

"Self-organized criticality" [5, 6] refers to the tendency of large dynamical systems to organize themselves into a "poised" state far out of equilibrium with propagating avalanches of activity of all sizes. The concept has been successfully applied to a number of geophysical and astrophysical phenomena. The self-organized critical state is sometimes, quite misleadingly, called "the edge of chaos" since it separates a frozen inactive state from a "hot" disordered state with high activity everywhere.

In 1990, Bak, Chen, and Creutz [3] demonstrated that the Game of Life, a cellular automaton simulating a society of living organisms operates at, or very near, the critical state when driven by random mutations. The speculation was boldly ventured that real life is a self-organized critical phenomenon. However, the criticality may well be accidental in the sense that small modifications of the model tend to drive the system away from criticality.

The idea was taken up by Kauffman and Johnsen [4] who studied the evolution of species in interactive models, denoted as NKC models. The models exhibit a transition from order to disorder when the amount of interaction between the species increases. The existence of this transition has been proven rigorously by Bak, Flyvbjerg, and Lautrup [7] in a mean field version of the model. Despite a significant effort in studying various versions of the models [8] it appears that some external tuning of parameters is always needed in order to bring the system to the globally correlated critical state; i.e., the criticality is not self-organized.

Our philosophy is similar to Kauffman's, but differs in a decisive manner. Despite the fact that selection happens on the scale of single individuals, we consider evolution in a coarse-grained sense, where an entire species is represented by a single fitness. The species are adapting to a rugged multipeaked fitness landscape [9]. The fitness of each species is affected by other species to which it is coupled in the ecosystem. Adaptive moves by one coevolutionary partner, therefore, may change the fitness and the fitness landscapes of other coevolutionary partners.

The "fitness landscape" represents the ability of species to survive as a function of their genetic code. In theoretical models the landscape might be defined in terms of a spin-glass model, where the fitness (negative energy) depends on the configuration of spins. Single spin flips represent adaptive moves or "mutations." Accepting only a new configuration if it increases the fitness, the species evolves to a local fitness maximum. This adaptive motion is fast. Further evolution takes place only if nonbeneficial moves are accepted with some low probability, so the species are almost always at local fitness maxima. (This is in agreement with the observation that the fossil record tends to lack intermediate stages between recorded species.)

The stability of each species is characterized by a barrier height separating its local fitness maximum from other better maxima. The barrier height is a measure of the number of bits, or the amount of genetic code, which has to be changed. Single bit mutation occurs often, but complicated modifications, such as developing wings to allow a creature to fly, are prohibitively unlikely to occur since they involve large coordinated evolutionary moves. The time scale for mutation is exponential in the barrier height. When the fitness is high, it is difficult to find bet-

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ter maxima nearby, so those states are relatively stable. When the fitness is low it is more likely to find nearby better states, so the barriers are low.

For each species, i, we therefore consider only the smallest barrier, B_i. The barriers are our measure of stability. The jump across the barrier can be thought of as either a mutation of the species or the substitution of one species by a better one in an ecological niche. Since the smallest barriers generally are related to the lowest fitness and the highest barriers correspond to the highest fitness, the barriers are also a measure of fitness. Since the small barriers are unstable, a collection of noninteracting species would converge towards a deeply frozen "dead" state with the highest barriers, or fitness. Nothing is more fit than stable, inert material.

However, the fundamental driving mechanism for biology is that species interact with each other, for geographical or other reasons. For instance, the interaction could represent the fact that the two species are consecutive links of a food chain. When a species makes an adaptive move, it changes the fitness landscapes of its neighbors. A species with a high barrier and unable to mutate on its own might then eventually be affected by a mutating neighbor, causing a reduction of the barrier which facilitates the mutation.

Our model, intended to represent the main features of all of this, is defined and simulated as follows: (i) N species are arranged on a one-dimensional line with periodic boundary conditions. (ii) A random barrier, B_i, equally distributed between 0 and 1, is assigned to each species. At each time step, the ecology is updated by (iii) locating the site with the lowest barrier and mutating it by assigning a new random number to that site, and (iv) changing the landscapes of the two neighbors to the right and left, respectively, by assigning new random numbers to those sites, too.

Note that instead of representing the species explicitly in terms of their genetic code, for instance by a spin-glass type model, we are working directly with the resulting fitness, assuming that any adaptive move simply leads to a new random fitness. The selection of the smallest barrier is justified by the exponential separation of time scales. In the beginning, subsequent events are quite uncorrelated in space, but as the barrier heights increase, it becomes more and more likely that near neighbors of spontaneously mutating species are next to mutate. The events become correlated. After an extensive transient period, the distribution becomes stationary. Following Sneppen and Jensen [10] we then measure the distribution, $C(x)$, of the distance x between subsequent mutations (Fig. 1). The straight line on the log-log plot indicates a power law distribution, $C(x) = x^{-3.15\pm0.05}$; hence the system is critical. This does not depend on the initial conditions, so the critical state is a global attractor for the dynamics; hence it is self-organized. The exponent appears to be the same as the one studied in a string model by Sneppen and Jensen [11], and we are convinced they belong to the same universality class.

Figure 2 shows the distribution of barriers in the critical state. All mutations turn out to take place through barriers which are less than a self-organized critical value, $B_C = 0.67 \pm 0.01$. The threshold defines the maximal waiting time between successive mutations. Evolution takes place at a fast pace through small barriers and there is no time (and no need) to make large individual mutations. In contrast, the need for large coordinated mutations makes the traditional noncooperative Darwinian evolution prohibitively slow. In a noninteractive biology, the species would reach the state with all fitnesses equal to 1, but extremely slowly. Even if at each step the least fit species are extinct in our model, the resulting fitness in our ecology is far out of equilibrium; that is, far from the optimal one with unit barriers only. This can be thought of as a collective "Red Queen" effect [12], where

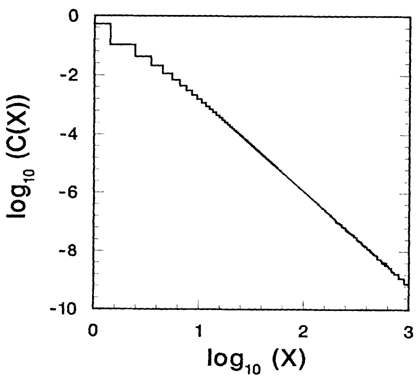

FIG. 1. Distribution of distances $C(x)$ between successive mutations. The power law indicates that the ecology has self-organized into a critical state.

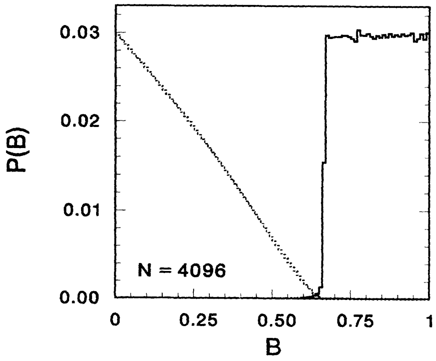

FIG. 2. Distribution of barriers in the critical state (right curve). There is a self-organized upper threshold $B_C = 0.67 \pm 0.01$ for spontaneous mutation. The distribution is flat above the threshold, with statistical fluctuations. The distribution of the minimum barriers is also shown (left curve); it vanishe (by definition) above the self-organized threshold.

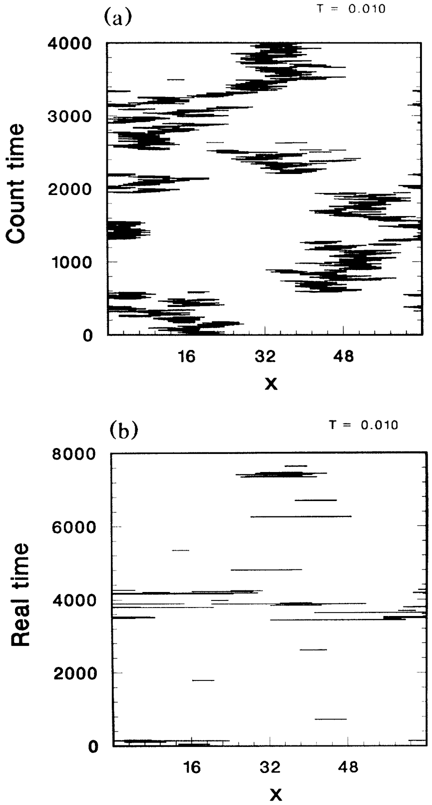

FIG. 3. Punctuated equilibrium behavior for an ecology consisting of 64 species. (a) Mutation activity vs time measured as the total number of mutations. (b) Mutation activity vs "real time" calculated in terms of subsequent accumulation of $\propto \exp(-B_a/T_{\rm car})$ with B_a denoting the active barrier; $T_{\rm car}$ (here 0.01) sets a characteristic time scale for the mutations.

adaptive moves do not bring you any further benefits. Life is synonymous with volatility and evolution rather than stability and fitness.

The intermittency of the evolution is illustrated in Fig. 3 where we monitor mutation activity in an ecology consisting of 64 species. In Fig. 3(a) we count time in terms of the number of mutations, whereas Fig. 3(b) shows the activity versus the accumulated real time, assuming that the duration of a mutation is exponential in the barrier traversed in that mutation.

Figure 4 shows the activity versus time in a local segment of ten consecutive sites. We again observe long periods of passivity interrupted by sudden bursts of activity: the model exhibits punctuated equilibria. One way of characterizing this intermittency is to consider subsequent sequences, or avalanches, of mutations through barriers below a certain threshold. When there has been no activity for a time period defined by this threshold, the avalanche is considered over. The size, s, of an avalanche is defined as the number of subsequent mutations below the threshold.

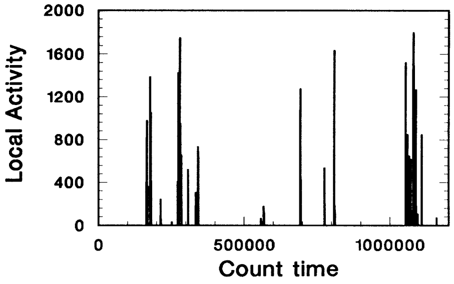

FIG. 4. Punctuated equilibrium behavior. Activity vs time in a local segment of ten consecutive sites is shown for a system of size $N = 512$. Time is measured in units of the number of mutations. In real time, the intermittency is further enhanced by the exponential enlargement of the periods of stasis.

With this definition there is a hierarchy of avalanches, each defined by their respective thresholds. This could also be seen by the self-similarity of Fig. 3(b) under magnification of the time scale. During the avalanche, some sites may mutate more than once. For a threshold close below the global self-organized threshold shown in Fig. 2, the distribution of avalanches displays a power law, $N(s) = s^{-0.9\pm0.1}$ (Fig. 5), indicating coevolutionary avalanches of all scales, including catastrophic ones.

Extrapolating to real biology, large events in the evolutionary history may be thought of as large coevolutionary avalanches caused by the intrinsic dynamics of biology. Thus, although of course not excluded, there may be no need for large cataclysmic events such as volcanic eruptions or a meteorite. Equating stability with fitness, the fitness is low within the large avalanches, whereas the fitness is high during the periods of stasis with low activity. The observed pattern of intermittency can be directly associated with Raup's data, although the exponent for the avalanches appears to be too low. In higher dimensions the exponent turns out to be higher;

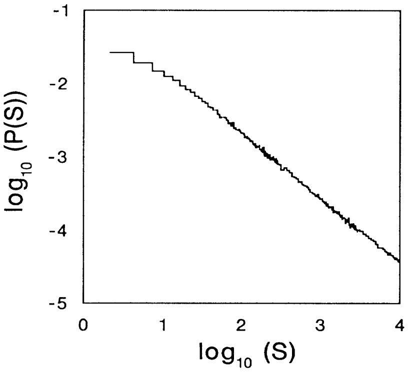

FIG. 5. Distribution of avalanche sizes in the critical state. Here an avalanche is defined by subsequent sequential activity below punctuation of the barrier $B = 0.65$.

e.g., in 2D the exponent is about 1.1, in seemingly better agreement.

The mechanism of evolution in the critical state can be thought of as an exploratory search for local better fitness, which is rarely successful, but sometimes has enormous effect on the ecosystem.

We have studied many different versions of the model, in different dimensions, with random connections (mean field) [13], with other types of interactions, with different ways of modifying landscapes of interacting species, etc. In all cases we found self-organized criticality; i.e., the behavior is robust, as it must be in order to represent real evolution. One interesting observation is that for systems with many connections, i.e., large complexity, the barriers are lowered further, thus speeding up exponentially the time scale for coevolutionary dynamics. As a high mutation rate is associated with low fitness, it is clear that the time scale for the survival of complex species is relatively small.

We believe that the dynamics of the present model could be easily implemented in models where the individual fitness landscapes are defined explicitly in terms of, for instance, Kauffman's NKC models [4], spin glasses [8], or random energy models [7]: One should always choose the species with the lowest fitness for mutation, and one should define composite avalanches rather than single avalanches which may be limited. The nominal "frozen" phases with a low interaction rate, where the single avalanches are small, will then self-organize into the volatile critical state, with exponents likely to be identical with the ones found here. It would be worthwhile to perform such simulations. The error in previous thinking was probably a faulty belief that the "global fitness" or some other global quantity like the ability to perform universal computations is optimized at the critical state.

In the critical state the species are connected at all scales, as illustrated by the power law distribution of avalanches. Since all species belonging to a single avalanche become extinct together, they might well be viewed as a single organism. We thus have a hierarchical organization of organisms, up to and including the total ecology: thus one may speculate that the whole system in the self-organized critical state acts as one interconnected organism, as suggested by Lovelock's Gaia hypothesis [14].

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