Mean Field Theory for a Simple Model of Evolution

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A simple dynamical model for Darwinian evolution on its slowest time scale is analyzed. Its mean field theory is formulated and solved. A random neighbor version of the model is simulated, as is a one-dimensional version. In one dimension, the dynamics can be described in terms of a "repetitious random walker" and anomalous diffusion with exponent 0.4. In all cases the model self-organizes to a robust critical attractor.

Introduction.—Life on Earth is presumably the most complex dynamical system known; too complex for quantitative modeling, it seems. The usual strategy in that situation is to focus either on a manageable subsystem or special case *or* on just a few aspects deemed most important for the entire system. The first approach was taken in the outstanding work by Eigen and co-workers on prebiotic evolution [1]. We choose the latter approach here, analyzing a quantitative model for Darwinian evolution in general, with an eye on qualitative features of actual evolution. The model describes an ecosystem of interacting species which evolve by mutation and natural selection [2]. Species spend most of the time at punctuated equilibria [3,4]. Casually connected escapes of species from these equilibria form avalanches of evolutionary activity with a power-law distribution of sizes. A mean field theory yields an exponent $\tau = \frac{3}{2}$ for this size distribution. The mean field description of the self-organized state is compared with a random neighbor version of the model and with a one-dimensional version. In one dimension, the dynamics can be described in terms of anomalous diffusion with exponent 0.4.

Simple as it is, the model has an ancestry: we have drawn on our earlier work on models of evolution inspired by Kauffman's work [5–7], on self-organized criticality [8], and on nonequilibrium growth of surfaces [9]. Also, we are not the first to play with toy models of evolution; see, for example, the last section of [10,11], and for a review [12].

The model.—We consider a dynamical ecosystem of interacting species which evolve by mutation and natural selection. For simplicity, we assume that no species divide into several species and no species become extinct. Thus the only effect of evolution is adaptation to the environment. The environment of each species may be thought of as a *fitness landscape* with many local maxima, supplemented with some dependence on the states of some other species. We assume that evolution to local fitness maxima takes place much faster than escapes from such maxima. This is a reasonble assumption, since

the first process is guided by a gradient, while the latter is exponentially suppressed and only occurs because of variance between individuals in a species. Viewed on its slowest time scale, then, evolution is *discrete:* species sit at local fitness maxima, and occationally a species *jumps* to another maximum. In the latter process, a species may change the fitness landscapes of other species which depend on it, to the extent that some of them no longer find themselves at local maxima. Consequently, *they* immediately jump to new maxima. This may affect yet other species in a chain reaction, a *burst* of evolutionary activity. We assume this chain reaction is subcritical and on the average involves a total of K species (see [6] for a realization of this situation), all in a time that is negligible on the slowest time scale.

We characterize the state of an ecosystem of N species by N values (x_i), $i = 1, 2, \ldots, N$. These values characterize the effective barriers towards further evolution experienced by the species at their local maxima of fitness. Since the waiting time for further evolution increases exponentially with the barrier height, the dynamics consists in selecting the species with the lowest barrier value, and replacing that value, and that of $K-1$ other species, with new values. For simplicity, we assume that the new barrier values are random, all drawn from the same uniform distribution in the interval $[0, 1]$. Results do not depend on this choice of distribution, as simple reparametrizations relate all choices. Results do depend on the way the K species are chosen. One choice consists in placing the species on the sites of a d-dimensional hypercubical lattice with nearest neighbor interactions. Thus $K = 2d+1$. We shall return to the case of $d = 1$ below.

Random neighbor and mean field model.—Here, for mathematical convenience, we select the $K-1$ interacting species at random among the N species in the ecology. This *random neighbor model* is a first step towards a solvable mean field theory. We also assume this randomness to be "annealed;" i.e., the next time the same species triggers $K - 1$ other species to evolve, they are chosen at random anew. A mean field theory can be constructed by

neglecting correlations between barrier values. Then the ith smallest barrier value, denoted by x_i, is distributed as the ith smallest number out of N drawn from the distribution $p(x, t)$ of *all* barrier values in the ecology. If we let p_i denote the distribution for x_i then our *mean field approximation* is the assumption that

$$p_i(x) = \frac{N!}{(i-1)!(N-i)!} P^{i-1}(x)p(x)Q^{N-i}(x), \quad (1)$$

where we have introduced

$$P(x) = \int_0^x dx' p(x'), \quad (2)$$

$$Q(x) = \int_x^1 dx' p(x'). \quad (3)$$

Normalization of p gives

$$\int_0^1 dx' p(x') = P(x) + Q(x) = 1, \quad \forall x. \quad (4)$$

We can easily write down the evolution equation for $p(x, t)$,

$$\begin{aligned}
p(x, t+1) = \ & p(x, t) - \frac{1}{N} p_1(x, t) \\
& - \frac{K-1}{N-1}\left(p(x, t) - \frac{1}{N}p_1(x, t)\right) + \frac{K}{N}, \quad (5)
\end{aligned}$$

where Eq. (1) gives the distribution for the smallest barrier,

$$p_1(x) = Np(x)Q^{N-1}(x), \quad (6)$$

whose removal from the set of N barrier values is represented by the second term on the right-hand side of Eq. (5). The third term on the right-hand side of Eq. (5) represents the removal of $K-1$ of the $N-1$ barrier values remaining after the smallest has been removed from the set of N values. These $K-1$ values can be any of the $N-1$ values remaining, hence are distributed as these, i.e., as $[Np(x, t) - p_1(x, t)]/(N-1)$. The last term on the right-hand side of Eq. (5) represents the addition of K new equidistributed barrier values, replacing the K values that were removed with the preceding terms. Notice that probability is conserved by Eq. (5).

Our mean field dynamics is an approximation to the master equation for the Markov process of the random neighbor model, both having one unique attractive fixed point. At this fixed point Eq. (5) is an integral equation fo $p(x)$, or, equivalently, an ordinary differential equation for $Q(x)$. It is solved by the positive root $Q(x)$ of the polynomial equation

$$\begin{aligned}
(N-K)Q^N(x) &+ N(K-1)Q(x) \\
&+ (N-1)K(x-1) = 0. \quad (7)
\end{aligned}$$

In the limit where $N \gg K > 1$, the first term in this equation is small relatively to the second term for such values of x where $Q(x)$ is less than 1 by more than $\mathcal{O}(1/N)$. Consequently we have

$$\begin{aligned}
Q(x) &= \frac{(N-1)K}{N(K-1)}(1-x) - \frac{N-K}{N(K-1)}Q^N(x) \\
&\simeq \frac{K}{K-1}(1-x) \quad \text{for } x - 1/K \gg \mathcal{O}(1/N). \quad (8)
\end{aligned}$$

Conversely, where $Q(x) \simeq 1$ we have

$$\begin{aligned}
Q(x) &= \left(\frac{(N-1)K}{N-K}(1-x) - \frac{N(K-1)}{N-K}Q(x)\right)^{1/N} \\
&\simeq (1 - Kx)^{1/N} \quad \text{for } 1/K - x \gg \mathcal{O}(1/N). \quad (9)
\end{aligned}$$

Using $p(x) = -\frac{d}{dx}Q(x)$, we have

$$p(x) \simeq \frac{K}{N} \quad \text{for } 1/K - x \gg \mathcal{O}(1/N), \quad (10)$$

$$p(x) \simeq \frac{K}{K-1} \quad \text{for } x - 1/K \gg \mathcal{O}(1/N). \quad (11)$$

The exact solution of Eq. (7) is easily obtained numerically by iteration of Eqs. (8) and (9) for $x > 1/K$ and $x < 1/K$, respectively. It is shown in Fig. 1(a) together with the resulting distribution of the smallest barrier, $p_1(x)$, both as dashed lines. The random neighbor model is easily simulated and its equilibrium distributions $p(x)$ and $p_1(x)$ are shown in Fig. 1(a) as full lines.

In the limit $N \to \infty$ we see that $p(x)$ has a discontinuity at $x = 1/K$; it vanishes below this threshold and is constant above it. It is easy to understand this result in approximate terms: Suppose $p(x) \simeq K/N$ for $0 \le x \le 1/K$ and $p(x) \simeq K/(K-1)$ for $0 \le 1/K \le x$. Then the smallest of N barrier values distributed according to p will be equidistributed below the threshold value $1/K$, and the other $N-1$ will be larger than $1/K$, typically. Thus, when the smallest barrier value is removed, none is left below threshold. Consequently, the $K-1$ additional barrier values which are randomly selected and removed must be taken from above the threshold; hence they are equidistributed by assumption about p. When we replace these K barrier values with K equidistributed values, one of these typically falls below the threshold and the other $K-1$ above. Since all of them are equi-
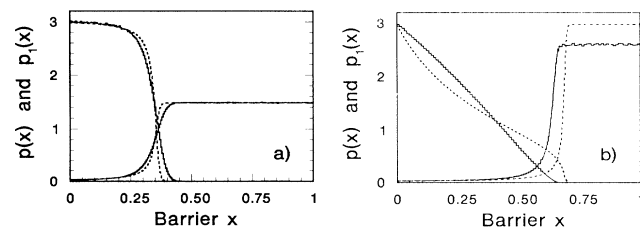

FIG. 1. (a) Equilibrium distribution of barrier values $p(x)$ and distribution of smallest barrier value $p_1(x)$ for simulated random neighbor model (full curves) and corresponding mean field theory (dashed curves). (b) Same distribution for 1D model (full curves) and mean field theory removing *two* lowest barrier values (dashed curves). All cases have $K = 3$ and $N = 100$.

distributed, p is left unchanged, as it should be.

This explanation points to another aspect of the asymptotic dynamics: If we trace in time which species trigger the bursts of evolutionary activity, then it is usually one of the species participating in recent activity. So at any given *late* time, the very species which acquired their current properties most recently are also the ones most apt to change them again. Thus, according to our model, the cockroach, which is much older than the human race, will resemble itself long after humans, as we know them, have disappeared.

Avalanches.—In order to express the causal connections between bursts of evolutionary activity, we define an *avalanche* as a causally connected sequence of activity associated with barrier values below the self-organized threshold $1/K$. Suppose that at some time all barrier values are above the threshold value. Then the next burst will, on the average, result in one barrier value below threshold, which for its part will result in another barrier value below threshold, etc. Thus the number of barriers below threshold remains constant equal to one, on the average. The actual number of barriers below threshold fluctuates and may become zero again, terminating the avalanche.

A more realistic value for the average number of barrier values below threshold can be obtained from our mean field approximation. It gives

$$NP(1/K) = \ln N - \ln \ln N - \ln(K-1)$$
$$+ \mathcal{O}(\ln \ln N / \ln N)$$
$$+ \mathcal{O}(1/\ln N) + \mathcal{O}(\ln N/N) , \qquad (12)$$

where $P(1/K) = 1 - Q(1/K)$, and $Q(1/K)$ is the solution to Eq. (7) with $x = 1/K$. With an average of $NP(1/K)$ barrier values below threshold, the fluctuation in this number needed to terminate an avalanche becomes increasingly rare with increasing N. Thus the *sizes* of avalanches, defined as the number of bursts they contain, grow with N, to diverge as $N \to \infty$.

In the limit $N \to \infty$, an avalanche defined as above can be identified with critical branching processes with branching ratio K [13]. This is done by identifying each burst with a node, and each of K new barrier values resulting from a burst with either a branch rooted in that node (if the barrier value is less than the threshold value), or with a leaf rooted in the same node (if the barrier value is above threshold). The limit $N \to \infty$ is necessary to obtain the tree structure. This identification tells us that avalanches come in all sizes s, and the larger ones are distributed according to a power law with mean field exponent

$$D(s) \propto s^{-3/2}, \qquad (13)$$

showing that there is no average size to avalanches. The avalanches are critical, because the branching process is. Since the *medium* through which these avalanches propagate—the set of N barrier values—is transformed by the avalanches and driven by them to the unique asymptotic fixed point distribution that makes the

avalanches critical, our model for biological evolution is a self-organized critical dynamical system.

One-dimensional model.—So far, we have seen criticality only in the mean field approximation. Now let us study a finite dimensional case. We have simulated the dynamics of the one-dimensional ecology and measured a number of its properties in the equilibrium state. Figure 1(b) shows the distribution of barriers, $p(x)$, and the distribution for the lowest barrier value, $p_1(x)$, as full curves. Both are for $K = 3$, $N = 100$. They do not resemble the random neighbor and mean field results for $K = 3$, $N = 100$, shown in Fig. 1(a). The dashed lines in Fig. 1(b) show results from a different mean field model, obtained also with $K = 3$ and $N = 100$, but by replacing the *two* smallest barrier values plus *one* randomly selected value with random numbers in each time step. It is easy to understand why this latter algorithm gives results much closer to the 1D results: Low barrier values are clustered in one dimension, so the replacement of the smallest barrier value together with the values on its nearest neighbor sites amounts to replacing the lowest value plus 0–2 other low values. Actually, some of the difference between the mean field and 1D results shown in Fig. 1(b) is due to finite-N effects being more pronounced in the 1D results, for example, the value of $p(x)$ for $x > 0.7$. It will approach 3 as $N \to \infty$, while the mean field value for $p(x)$ is already very close to 3 for $x > 0.7$.

Figure 2 shows a space-time map of those sites on which species change barrier values in the time interval covered. Whenever the lowest barrier value is found
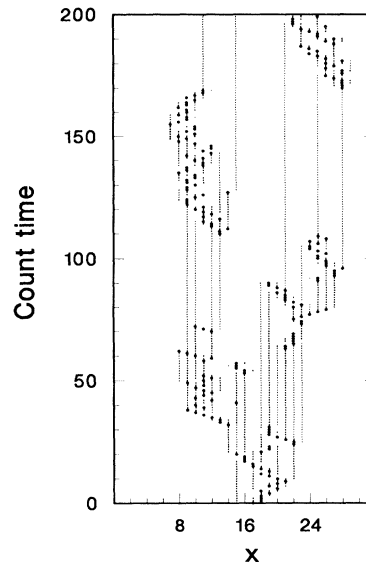
FIG. 2.   Space-time map of an avalanche in the self-organized critical state. At any time the site with minimum barrier value is shown as a large dot. Sites with barrier values below the threshold value 0.67 are shown with a small dot. The activity is seen to always return to sites below threshold.

among those $K = 3$ last renewed, the site of lowest barrier value performs a random walk, because those three sites have equal probability for being the one with smallest barrier value. The figure shows that this is what happens most frequently. When the site of lowest barrier value moves by more than one lattice spacing (jumps), it most frequently backtracks by two lattice spacings to a site that was updated in the next-to-last time step. But longer jumps occur, too; actually jumps of any length occur, as indeed they must in order to be consistent with results below. These jumps always take the walker back to a site that was updated recently, the longer jumps typically to a less recently updated site. In popular terms, the site of lowest barrier value is a "jumpy random walker with a repetitious compulsion."

Figure 3 shows three aspects of this repetitious random walk which differ from a truly random walk: The root mean square of the distance traveled vs time and the number of different lattice sites visited as a function of time both grow with exponent 0.40, in contrast to the exponent $\frac{1}{2}$ obtained for the random walker. The maximum number of updates of any state as a function of time appears to grow as $t^{0.6}$. This exponent may have a simple explanation in terms of the others: the total number of updates is proportional to time, and the number of different sites visited to $t^{0.4}$. So the number of visits to a given site (in particular to the one most often visited) should grow with exponent $1 - 0.4 = 0.6$. For the random walker this relationship reads $1 - \frac{1}{2} = \frac{1}{2}$ for the number of visits to any site, for instance, the origin of the walk.

The biological implication of this correlated spreading of evolutionary activity is that species that evolved recently are also most likely to change again; compare humans vs cockroaches above. The actual values of the exponents, here 0.4 and 0.6, depend on the dimension, here chosen to be equal to one. If our model has an upper critical dimension above which mean field theory is exact, and this dimension is a small integer, the mean field version of our model is probably the most relevant one to use in an analysis of historical biological data.

One might of course attempt a less "coarse-grained" description of evolution than the one we have introduced and studied here—one involving fitness landscapes, and interactions between species evolving in those landscapes. For example, each species can be described simply by a genetic configuration, as in [5,6], with a noise term added to the dynamics in order to allow escapes from local fitness maxima. Or each species can be represented by a population of individuals that reproduce sexually to explore the fitness landscape, and have their variability maintained by mutations, for example as described in [14]. This suggests an obvious way to include extinction and bifurcation of species. Apart from those very interesting phenomena, we believe that our extreme simplification and coarse-graining grasps the essence of what matters even for finer-grained models.
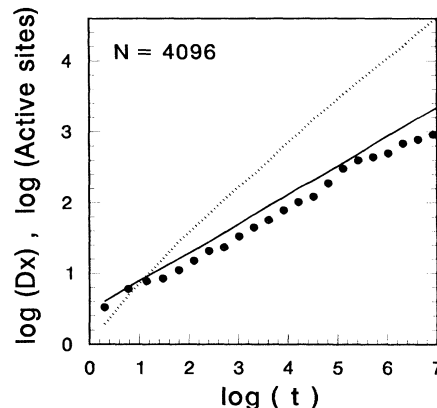
FIG. 3. Large dots: Root mean square displacement of the activity as a function of time, starting at an arbitrary time in the critical state. This quantity grows as $t^{0.4}$. Solid line: Number of different lattice sites visited as a function of time, starting at an arbitrary time in the critical state. It also grows as $t^{0.40}$. Dotted line: Maximum number of updates of any site as a function of time, starting at an arbitrary time in the critical state. It seems to grow as $t^{0.6}$.

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