

Ecological model of extinctions

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We present numerical results based on a simplified ecological system in evolution, showing features of extinction similar to that claimed for the biosystem on Earth. In the model each species consists of a population in interaction with the others, that reproduces and evolves in time. Each species is simultaneously a predator and a prey in a food chain. Mutations that change the interactions are supposed to occur randomly at a low rate. Extinctions of populations result naturally from the predator-prey dynamics. The model is not pinned in a fitness variable, and natural selection arises from the dynamics. [S1063-651X(96)01612-1]

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I. INTRODUCTION

The evolution of living organisms is a fascinating phenomenon that has intrigued the imagination of the scientific and nonscientific community. However, the formulation of mathematical models falls necessarily to drastic simplifications. For example, evolution has often been considered as a “walk” in a rugged landscape. Following this line, Bak and Sneppen (BS) have proposed a model of biological evolution [1] that has become quite interesting to the physics community due to its simplicity and the insight it provides to the problem. It has been shown that this model evolves to a self-organized critical (SOC) state, and is kept there by the means of avalanches of evolutionary activity. This is appealing for a model of biological evolution, since it has been observed that life on Earth could be in a SOC state [2,3]. Nevertheless, models based in fitness landscapes, or in a concept of fitness different from the biological one, have been criticized from a biological point of view [3,4].

Since one of the characterizing aspects of life, and perhaps the most fundamental one, is that of self-replication, it is our belief that more realistic models should involve a dynamic population for each species. The starting point of combining population dynamics with evolution is the association of the rates of birth and death and the carrying capacity with phenotypes (observable features that arise from the genotype and are, then, subject to mutation) [5]. The fitness, namely, the expected number of offspring produced by an individual, arises from them. In this way, the process of natural selection is directed by the ecological interactions instead of by a nonbiological notion of relative fitness.

Extinction is an essential component of evolution. The great majority of species that have ever lived on Earth are now extinct [6]. There exist competing hypotheses that account extinction as originating from within the biosystem, or from external causes—what has been called “bad genes or bad luck.” In any case, the pattern of extinctions and of surviving species or groups of species is certainly an interesting problem to model, to understand, and eventually to check with the fossil record.

We show in this contribution a simple model of a large ecological system in evolution. This produces features of extinction similar to those claimed for the biosystem on Earth. We have chosen to study an ecological model in which each

species consists of a population interacting with the others, that reproduces and evolves in time. The system is supposed to be a food chain, and the interactions to be between predator and prey. Mutations that change the interactions are supposed to occur randomly at a low rate. Extinctions of populations result from the predator-prey dynamics. This approach can be thought of as midway between the microscopic simulation of “artificial life” by Ray and Adami [7], and the coarse-grain description of models like BS’s.

II. THE MODEL

Our model ecosystem consists of a number of species that interact and evolve in time. In the course of its time evolution the populations grow and shrink following a set of equations. Eventually, some of the species become extinct as a result of their interaction with the others. Every now and then we change one of the phenotypic features of one of the species, mimicking a random mutation of its genome. This modification produces a perturbation in the dynamics of the ecosystem, and eventually leads to the extinctions.

To be more precise, let us consider a simple example of a food web, namely, a one-dimensional food chain. N species interact in such a way that the species i feeds on the species $i-1$, and is eaten by the species $i+1$. The species 1 is an autotroph: it feeds at a constant rate on an “environment.” The species N , the top of the chain, is not eaten by any species, but dies giving its mass to the environment. Each species has a population that evolves in time and interacts with its neighbors in the chain. Furthermore, we consider this evolution in discrete time, which is often more realistic than a continuous one [5] and simpler to simulate in a computer.

As has been said above, each species acts as a predator with respect to the one preceding it in the chain, and as a prey with respect to the one following it. As a further simplification, we suppose that there are no intrinsic birth and death rates, apart from those arising from the predation and prey contributions. Let us propose the equations governing this behavior [8]. As a predator, the “population” (a continuous density) of the species i , n^i , changes from time t to time $t+1$ according to

$$\Delta n_t^i = k_i n_t^{i-1} n_t^i (1 - n_t^i / c_i), \quad (1)$$

where k_i is a rate of growth of the predator population and c_i is a carrying capacity that accounts for a limitation imposed by the environment. Note that (1) includes this carrying capacity in a logistic factor to avoid an unbounded growth of the population. Also observe that the growth is proportional to the population of prey, without a ‘‘satiation’’ factor. Similarly, as a prey, the population of the species i will diminish according to

$$\Delta n_i^i = -g_i n_i^i n_i^{i+1}. \quad (2)$$

The parameters k_i , g_i , and c_i are the phenotypic features of our species. In the course of the evolution we allow them to change, mimicking random mutations. Moreover, they are the same for all the individuals of each single population. We do not model races, traits, polymorphisms, or any phenotypic variation within a species, and when a mutation occurs it is assumed that the whole population ‘‘moves’’ instantly to the new state. In this sense, we are modeling the coevolution of the species and disregarding the evolution of a single one as well as other important phenomena such as the formation of new species [9].

Combining the two roles of predator and prey that each species performs, and the special status of the ends of the chain, we can write the following set of equations for the evolution of the system:

$$\begin{aligned} \Delta n_i^i &= k_i n_i^{i-1} n_i^i (1 - n_i^i / c_i) - g_i n_i^{i+1} n_i^i \quad \text{for } i=1, \dots, N, \\ n^0 &= n^{N+1} = 1, \end{aligned} \quad (3)$$

where we have introduced two fictitious species, 0 and $N+1$, to take account of the border condition.

We make two simplifications to the system (3): (1) we assume that all the carrying capacities are equal, and equal to 1; (2) we assume that $g_i = k_{i+1}$. In this way we reduce the number of parameters that define the phenotypic features of the ecosystem.

The dynamics of the system is as follows. At time $t=0$, all the populations and interactions are chosen at random with uniform distribution in the interval $(0,1)$. Then the populations begin to evolve according to the system (3). In the course of the evolution driven by Eq. (3) a population can go to zero. As this can happen asymptotically, we consider a species extinct if its population drops below a given threshold. This is reasonable since actual biological populations are discrete. In order to keep constant the number of species we replace an extinct one with a new one, which can be thought of as a species coming to occupy the niche left by the extinct one [10]. The new population, and the (two) new interactions with its neighbors in the chain, are also drawn at random from a uniform distribution in the interval $(0,1)$. On top of this dynamics of predation and extinctions, we introduce random mutations. In each time step a mutation is produced with probability p ; the species to mutate is chosen at random and the mutation itself consists of the replacement of the species with a new one, with a new population and new interactions with its predators and prey [all random in $(0,1)$].

Observe that we do not introduce the fitness of a species as a dynamical variable. We do not even need to compute it

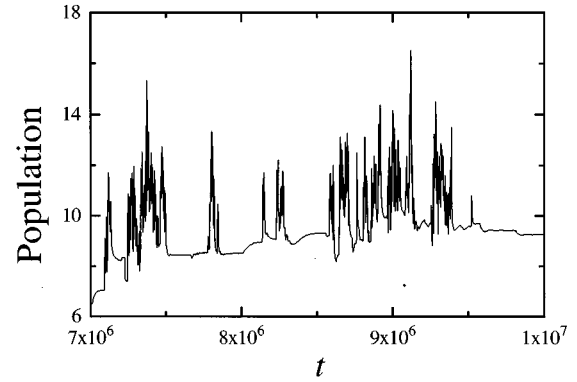


FIG. 1. Evolution of the whole population of a chain of 100 species. Probability of mutation $P_{\text{mut}} = 10^{-5}$. Observe the superposition of small oscillations and the much larger spikes signaling the mutations and extinctions.

from the ‘‘phenotypes’’ k_i . The fitness, the degree of adaptation of a species to the ecosystem, arises from the phenotypes, the populations, and the dynamics, and it determines whether a species will thrive or become extinct. Chance is introduced by the random mutations (and the random replacement of extinct species). It provides the material the natural selection works on. This, in turn, determines the survival of the fittest by simply eliminating from the system those species that cannot cope with the competing environment. We believe in this way we avoid a fundamental problem in the models of evolution as a walk in a fitness landscape, namely, that the concept of fitness is not the biological one [4].

III. RESULTS OF THE NUMERICAL SIMULATION

We have run our model for several chain sizes, ranging from 50 to 1000 sites, and for times of about 10^7 steps. In the results reported below we let the system evolve, during a transient period, from the initial random state to an organized one.

In Fig. 1 we show a typical evolution of the whole population, $\sum_{i=1}^N n^i$. Although each population greatly changes in the course of time (which is not shown in the picture), we observe that the whole population remains relatively stable. This is due to the saturation factor in the predation term of the evolution equations. This whole population shows a short time oscillatory dynamics governed by the competition between species through the set of equations (3), and a long time evolution characterized by periods of relative stasis and periods of fast change. This feature is the effect of mutations and extinction of some species. Without the extinctions and mutations, the dynamics of the system should probably be chaotic. But it is not this feature that we want to analyze here. Instead, we shall focus on the pattern of extinctions.

As the set of k_i represents the phenotypes of the whole ecosystem, its distribution, $P(k)$, can be used to characterize its state. Let us observe what happens in the course of time, including the transient mentioned above. Initially the k_i are chosen at random, and thus its distribution is flat in $(0,1)$,

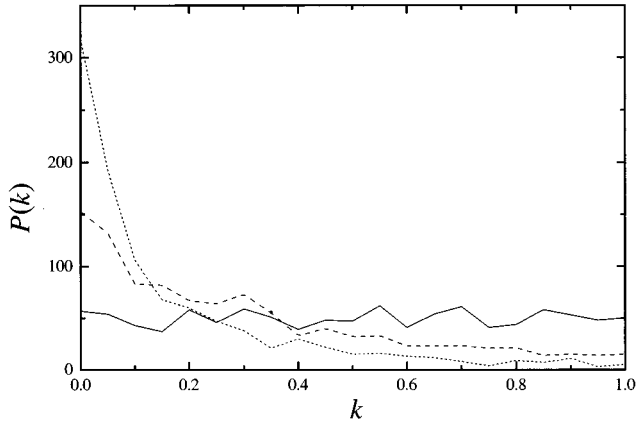


FIG. 2. Distribution $P(k)$ of the interactions in a chain of 1000 species. Solid line: initial distribution; dashed line: $t=5000$; dotted line: $t=5 \times 10^6$. $P_{\text{mut}}=10^{-5}$.

with mean 0.5. This is shown in Fig. 2 as a full line. As time passes, and as a result of the dynamics, this distribution shifts to a nonuniform one, as shown in Fig. 2 with dashed lines. The whole distribution shifts towards lower values of the interaction, showing a tendency of the system to reduce the coupling between the species. In the course of the evolution this distribution fluctuates following the pattern of mutations and extinctions, but preserves its form.

Figure 3 shows the above mentioned fluctuations in $P(k)$ as the evolution of the mean value of k_i in the system, after the transient. It corresponds to the same run as Fig. 1, and the same time window is shown. Similarly to that, it displays a pattern of periods of stasis interrupted by periods of fast change, but without the short time oscillations displayed by the population. There are periods of stasis of all lengths, to a degree that the unique scale of the figure cannot display. This feature of a lack of a typical length will be analyzed immediately. Observe in this figure that the mean value oscillates around 0.24, corresponding to a distribution like that shown in Fig. 2 with a dotted line.

The extinction events also display this characteristic pattern of periods of stasis and periods of change, without a

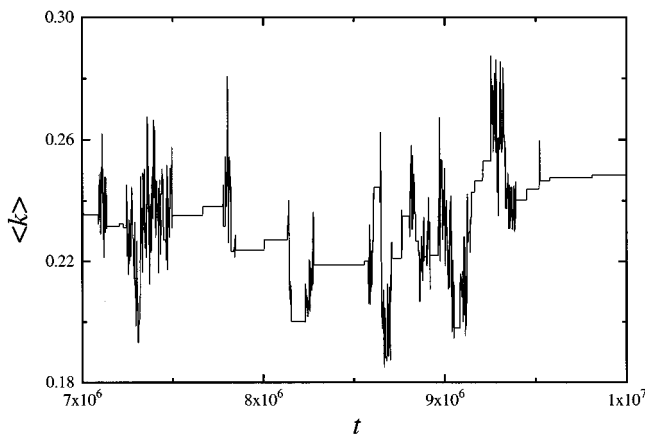


FIG. 3. Evolution of the mean value of the interactions, $\langle k \rangle$, of a chain of 100 species. $P_{\text{mut}}=10^{-5}$. The plot corresponds to the same run as that of Fig. 1.

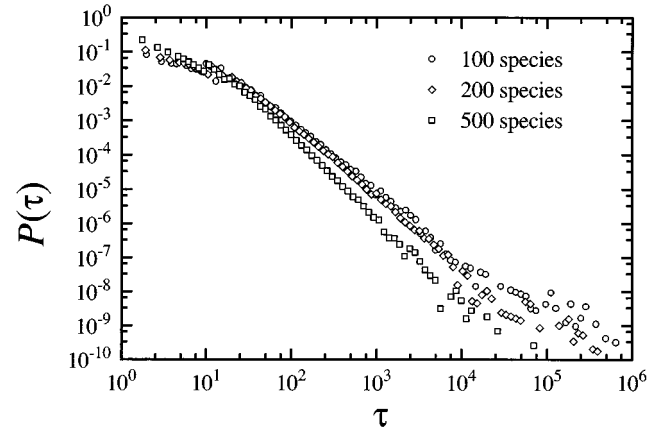


FIG. 4. The distribution $P(\tau)$ of time τ between two consecutive extinctions. $P_{\text{mut}}=10^{-5}$.

typical size. In order to characterize this, we have chosen the time between two consecutive extinction events, τ , the distribution of which is shown in Fig. 4 for several system sizes and probabilities of mutation. Observe that they follow a power law for several decades of large values of τ , before a region where the effects of the finite size of the system start to appear. This is a sign that the system has self-organized into a critical state. In other words, the extinction events are distributed in the time axis in such a way that the time between extinctions does not have a characteristic duration—as it should have if the distribution were exponential. Extinctions appear to come in bursts, or avalanches, of any size.

In Fig. 5 the pattern of extinction events of the system is seen in the course of time. The graphic displays time in the abscissa and the index in the food chain in the ordinate. Each dot marks the moment in which a species has become extinct, each cross, a species that suffers a chance mutation. It can be seen that some mutations trigger avalanches of extinction, and that these propagate in the “prey” direction. (Bear in mind that an extinct species is replaced by a random new one, most probably with a larger population than its predecessor, and observe that this has a negative impact in the corresponding prey.) It is also apparent that these avalanches have a complex shape in space time. It is not easy to measure their size since, as can be seen in Fig. 5, they overlap. See, for example, a mutation that is *not* followed by any avalanche (lower left), another that triggers a very small one (lower right), and several that start events of varying size. In any case, let us define a time step Δt , divide the time axis with it, and count the number of extinctions in each interval. Now, let us call the fraction of species that have become extinct in each interval the *size* S of the extinction. S will obviously depend on the time step and on the size of the system: $S=S(\Delta t, N)$. If the system is in a critical state this function will obey some scaling law on the variable N . In Fig. 6 we have scaled the distribution of the system size $S(N)$, $P(S, N)$, obtained for different system sizes according to the ansatz

$$P(S, N) = N^\beta f(SN^\nu). \quad (4)$$

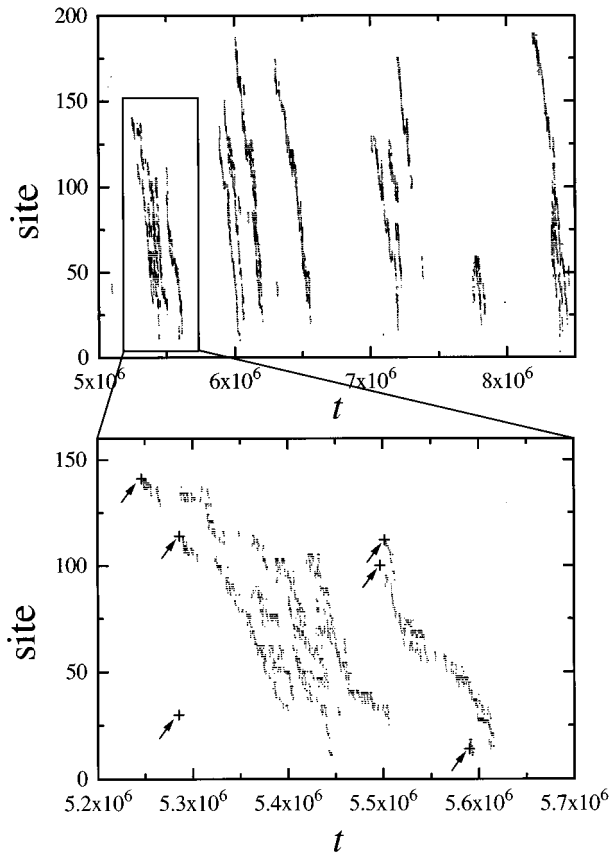


FIG. 5. Space-time pattern of extinctions as they occur in a chain of 200 species. The lower plot shows a detail of the upper one. Each dot is an extinction event. Crosses, shown by arrows, indicate mutations. $P_{\text{mut}} = 10^{-5}$.

We can observe that the four curves collapse to a single one, showing the scaling behavior that is typical of a critical state.

IV. CONCLUSIONS

We have introduced a simple model of coevolution and extinction in a food chain. This consists of a finite chain of species of predators and prey. Their populations evolve in

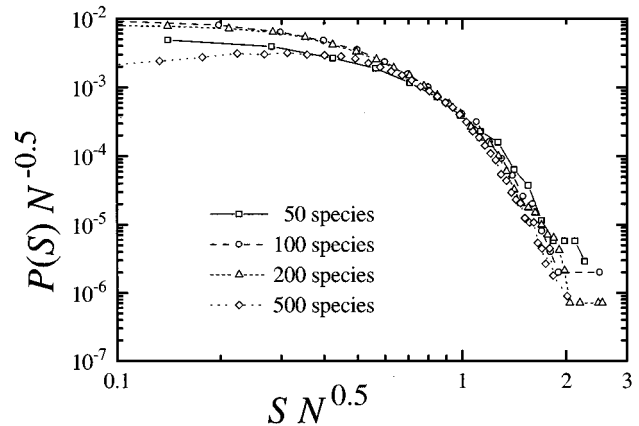


FIG. 6. Scaled distribution of the size of the extinctions, $P(S)$, as a function of the scaled size, S . The four curves correspond to systems of $N=50, 100, 200$, and 500 species.

time following Lotka-Volterra-like equations. Evolution is mimicked by randomly changing a phenotype. Natural selection is provided by the deterministic behavior of the dynamical system, which produces the extinction of any species that cannot cope with its interactions. No relative fitness or fitness landscape had to be invoked. Nevertheless, the pattern of extinctions displayed by this model ecosystem appears to be similar to that proposed for the biosystem on Earth. Namely, the system seems to be in a critical state, in which extinctions occur in avalanches. The time between extinctions, and the lifetime of any species follow distributions that behave like power laws of time, implying that there is no typical size for the time that a species remains in the system. It should be of interest, in a future work, to study the precise instability that produces the shift of the distribution of the interactions towards low values. The analytical treatment of this problem is currently under study.

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