Environmental Changes, Coextinction, and Patterns in the Fossil Record

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We introduce a new model for large scale evolution and extinction in which species are organized into food webs. The system evolves by two processes: origination/speciation and extinction. In the model, extinction of a given species can be due to an externally induced change in the environment or due to the extinction of all preys of that species (coextinction). The model is able to reproduce the empirical observations without defining a fitness function or invoking competition between species.
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The identification of the mechanisms responsible for large-scale evolution and extinction is a topic of heated debate [1–8]. The basic problem can be summarized by two questions. The first one centers on the cause of mass extinction: Is it external to the system—e.g., because of extraterrestrial impacts [9–12]—or is it internal and because of the nonlinear dynamics of the ecosystem [13–16]? The second question centers on the mechanisms for selecting the species that become extinct: In standard extrapolation of Darwinian evolution theory, it is assumed that competition leads to the extinction of less fit species [13–18], but some authors argue that competition might not be a determinantal factor for macroevolution [1,2,5]. The fossil record has yet to answer these questions unequivocally [3,19–22]. Quantitative modeling approaches [13–16] have consistently included competition among species as a fundamental mechanism. Here, we show that a quantitative model that does not include competition among species may reproduce the empirical observations, particularly the apparent statistical fractality of the fossil record [7,23], and the scale-free distribution of extinction sizes [3,5,6].

The literature on large-scale species extinction reports on two key empirical results. First, the probability density that a number s of species becomes extinct during a given time interval decays as a power law, $P(s) \sim s^{-\tau}$, with an exponent $\tau \approx 2$ [15,16,21]. Second, the power spectrum $S(f)$ of the time series of extinction sizes also appears to decay as a power law, $S(f) \sim f^{-\beta}$, with $\beta \approx 1$ [7], which would imply that the sequence of extinction is long-range correlated. These results impose severe constraints on the models attempting to describe the extinction/evolution process. A power law decay of the probability of extinction sizes implies that there is no characteristic size for extinction events; i.e., the dynamics are scale-free and incidents of mass extinction are likely due to the same mechanisms as smaller extinction events. The hypothesis that the mass extinctions are generated by the same dynamics as smaller extinction events is consistent with the apparent self-similarity of the fossil record [7].

Quantitative models have been proposed to explain the patterns in the fossil record. Many are based on the assumption that extinction events are a consequence of the competition between species; i.e., the least fit species become extinct and are replaced by new species [13–18]. These changes affect the fitness of other species leading to bursts of extinction of all sizes. Several of the models [14,15] self-organize into a critical state in which many quantities are known to scale as a power law [16]. However, recently it has been shown that mechanisms other than self-organized criticality, such as coherent noise [17,18], can lead to power law scaling without requiring the system to be in a critical state.

In this Letter, we test the hypothesis that competition between species—understood as being mediated through a fitness function—is *not* a fundamental ingredient for the explanation of the fossil record. This hypothesis is in agreement with statements that Darwinian competition, while important at the level of individuals within a population (microevolution), might not be relevant at the level of stable species (macroevolution) [1,2]. Thus, we propose a quantitative model for large-scale extinction and evolution that does not attempt to define the fitness of the interacting species, but assumes instead that the relevant mechanisms for macroevolution are random changes in the environment [10,11], and coextinctions [24] due to the interactions between species along food chains [8,15,25]. The model is able to reproduce both the power law distribution of extinction sizes and the fractality of the fossil record. These results suggest that the concept of "the survival of the fittest" might *not* be a fundamental ingredient for the description of the fossil record.

The model is defined as follows. Species can occupy niches in a model ecosystem with L trophic levels in the food chain, and N niches in each level. Species from the first level, $\ell = 0$, are assumed to be autotrophic (i.e., they produce their food through, e.g., photosynthesis), while species from levels $\ell > 0$ are assumed to be heterotrophic. That is, a species occupying a niche in level $\ell > 0$ feeds from at most k species occupying niches in level $\ell - 1$
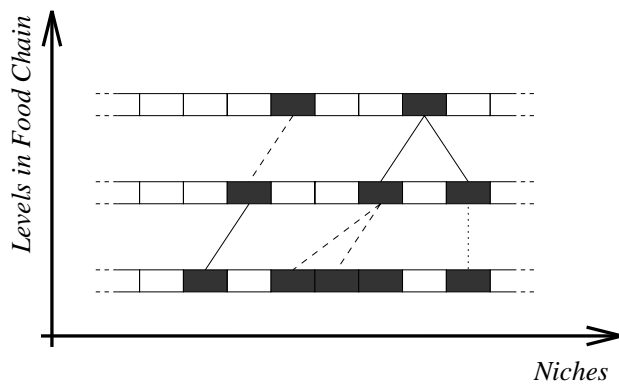

FIG. 1. Schematic definition of the model. The evolution of the system takes place in a lattice in which each site represents a niche in the "ecosystem." The system is organized into "trophic levels"; a species in level ℓ feeds from at most k species in level $\ell - 1$, except for species at the first level which are autotrophic. In most of the simulations there are six levels with 1000 niches per level. The state of the system is fully described by stating the niches which are occupied by a species with the list of its preys. We start the simulations with $N_o \approx 50$ species occupying niches in the first trophic level of the food chain. In the figure, the dark cells are occupied by a species; the lines emerging from a cell link the species to its preys. The system evolves through two processes, origination and extinction. Origination: A niche in level ℓ is randomly selected, and if a species exists there, a speciation is attempted. A new niche is then randomly selected in one of the levels $\ell - 1$, ℓ, or $\ell + 1$, and if no species occupies that niche, a new species is created. Extinction: A fraction p of species in the first level are randomly selected for extinction. Then we remove for all species in the second level links to preys in the first level that have become extinct. Whenever all links have been removed for a species in the second level, it becomes extinct as well. This procedure is repeated up the food chain until the top level is reached. If, for the configuration in the figure, the leftmost species in the lowest level would become extinct, then the leftmost species in the other levels would also become extinct.

(Fig. 1). We do not consider in the model any kind of structure of the niches within a given trophic level; that is, niches i and $i + 1$ in level ℓ do not need to be occupied by similar species or to be geographically close. Finally, we assume that the preys of a new species are chosen at *random* from existing species in the trophic level below. The model starts with N_0 species in level $\ell = 0$ and evolves according to the following rules:

(i) *Origination.*—Every existing species gives rise, at a rate μ, to the creation of a new "potential" species that tries to occupy a randomly selected niche in the same trophic level or in one of the two neighboring levels. This speciation event occurs if the selected niche is not yet occupied by an existing species. Preys for the new species are selected at random from existing species in the trophic level below.

(ii) *Extinction.*—At rate 1 (in some arbitrary time unit), a fraction p of species in the first level are randomly selected for extinction. Then, any species in the second level for which all preys became extinct also becomes extinct. This procedure is repeated up to level L.

These rules imply that the number of species in the system is not kept constant. In particular, if the origination rate is smaller than a threshold value, then all species become extinct; i.e., the model has absorbing states [26]. The rules for speciation imply that the origination rate of new successful species is proportional to the number N_s
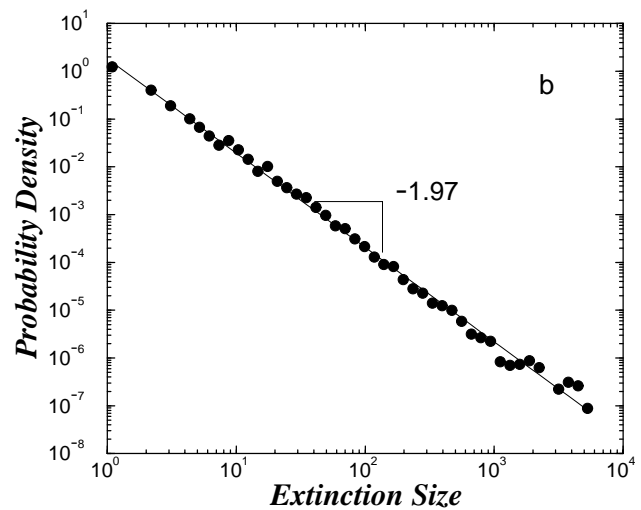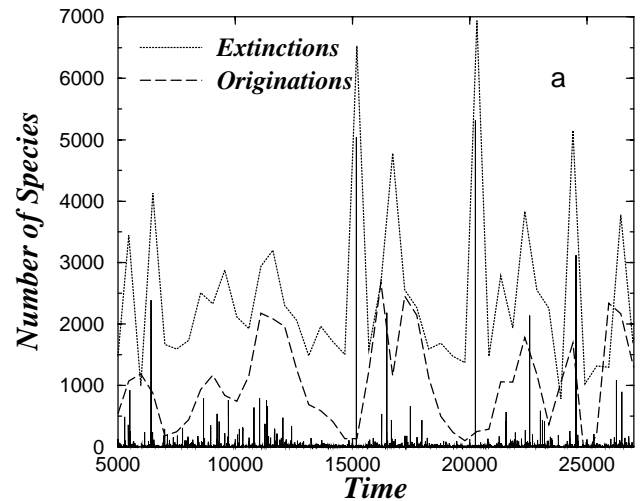

FIG. 2. Extinction events are scale-free. (a) Time sequence of extinction events for the model. The lower line (spikes) shows the individual events, while the upper curves show the total number of extinctions and the total number of originations during consecutive nonoverlapping intervals of 512 time steps. The origination curve is shifted downward by 1000 for clarity. Note that events of all sizes (up to nearly the system size of 6000 species) are present. The results shown are for a system with $k = 3$, six levels, and 1000 niches per level, a speciation rate of $\mu = 0.02$, and an extinction probability (due to environmental changes) of $p = 0.01$. The results are only very weakly dependent on the values of the parameters. Note the strong correlation between the two curves, in agreement with empirical observations [6,27]. (b) Probability density function of events size. The results shown are for the stationary state of runs consisting of 80 000 time steps. The stationary state is reached after approximately 2000 time steps. The distribution is well described by a power law with an exponent $\tau = 1.97 \pm 0.05$, which is consistent with empirical measurements [21].
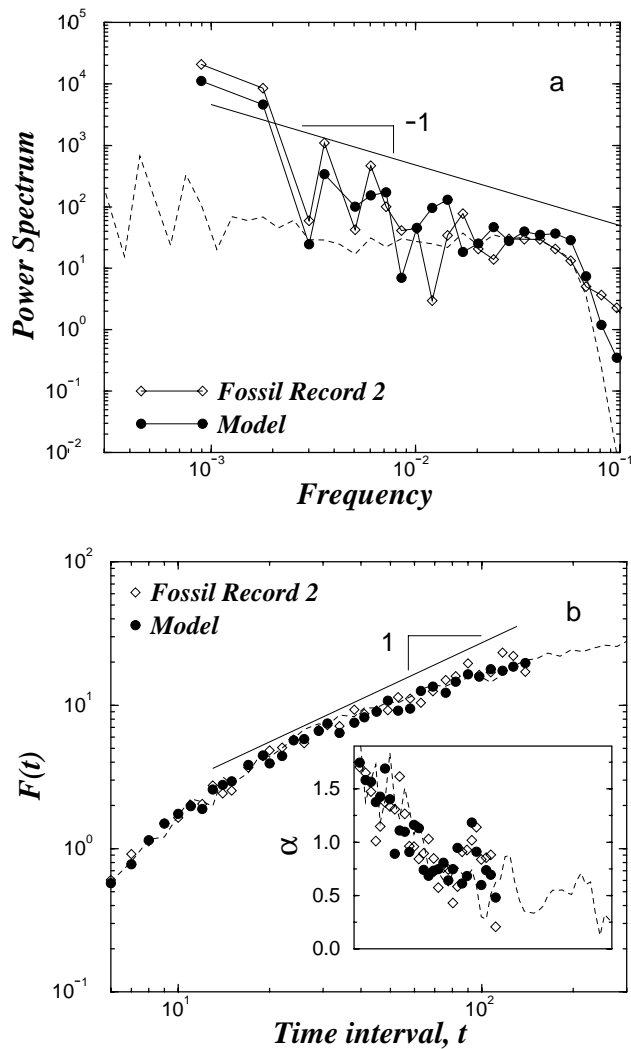
FIG. 3.   Correlations in time series of extinction events for the fossil record [6] and for the model. For the model, we consider two sequences, one with 512 points (dark circles) and another with 4096 points (dashed line). (a) Power spectrum: We find that for about 1 order of magnitude the data for the shorter sequences appears to scale as a power law with an exponent of −1. However, it seems that such scaling does *not* hold for longer sequences, for which the power spectrum becomes flat, suggesting that the sequence crosses over to uncorrelated behavior. (b) Detrended fluctuation analysis [28]: We find that $F(t)$, which measures fluctuations at different time scales, scales as a power law with an exponent close to 1 for about 1 order of magnitude. In the inset, we show the values of the exponent for a local fit to a power law. Again all curves seem to behave in a similar fashion. However, the results suggest that no true scaling regime exists for time scales shorter than 300. For larger time scales the exponent becomes 1/2 which suggests an uncorrelated process—i.e., white noise.

of species in the system (leading to exponential growth, in agreement with the results of [6]), and to the number of empty niches $NL - N_s$ (which takes into consideration the limited resources of the system [18]). Although the finite size of the system introduces constraints on the creation of new species, the model does not involve any competition between existing species.
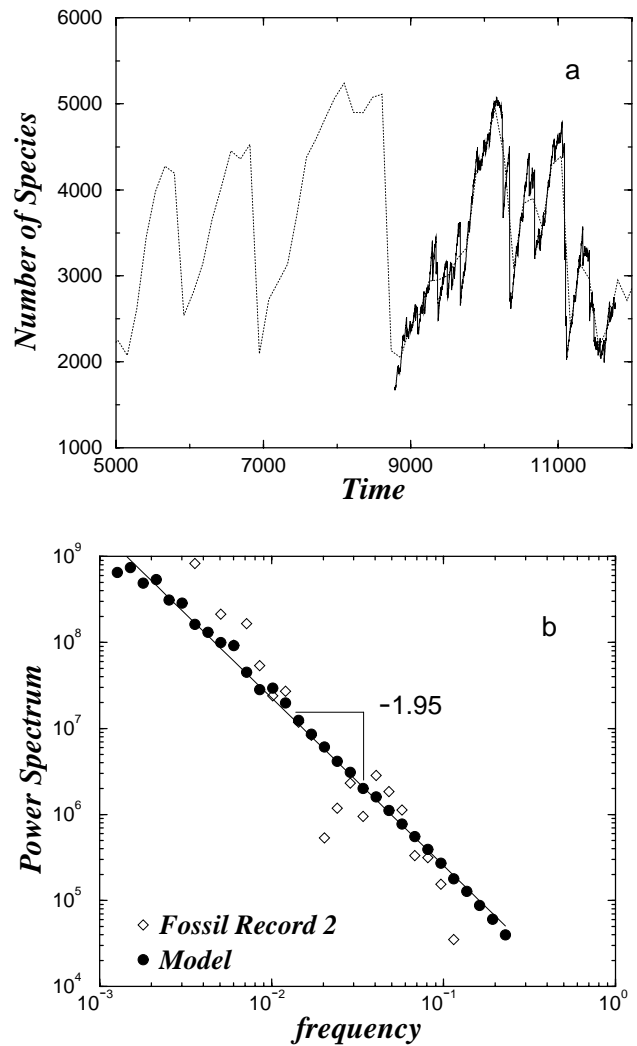
FIG. 4.   Fractality of species diversity. (a) Number of species in the model as a function of time. The thicker dotted line shows the number of species measured at intervals of 128 time steps. The continuous line, shown for a shorter period of time, is sampled for every time step. Note the complex structure of the curve at very small time scales, which suggest that the fluctuations have a self-affine [28] structure [7]. (b) We investigate the power spectrum of the signal in (a) and also of the empirical data [6]. We find that the power spectrum scales as a power law with an exponent $\beta = 1.95 \pm 0.05$, which is consistent with Brownian motion and with the results of Fig. 3.

Figure 2 shows our results for the time sequence of extinction and origination events. The first interesting observation is that both signals are intermittent with very large events appearing at a high rate. Furthermore, there is a strong correlation between the extinction and origination curves, which is in qualitative agreement with empirical observations [6,27]. Finally, we find that the size of the extinction events has a distribution which decays with a power law tail with an exponent $\tau = 1.97 \pm 0.05$, in agreement with empirical observations [15,16,21].

In order to further demonstrate the ability of our model to reproduce quantitatively the empirical data on extinction and origination, we compare in detail our results with

the recent results of Ref. [7]. We therefore study the temporal correlations of extinction events for the model and compare our results with the analysis of the fossil record [6]. Figure 3 shows that the model results agree well with the empirical data, when we consider model sequences of the same lengths as available in the fossil record. This agreement is found for the power spectrum as well as for the method of detrended fluctuation analysis, which allows accurate estimates of correlation exponents *independent* of local trends [28]. Note, however, that once we consider longer records generated by the model, we find that the results cross over to uncorrelated behavior (white noise). In fact, the analysis of local slopes (see the inset of Fig. 3b) indicates a similar trend for the empirical data as well, suggesting that extinction events might become uncorrelated at long time scales.

To clarify this result, we study the fluctuations in the number of species in the model (Fig. 4a). The analysis of the power spectrum (Fig. 4b)—which quantifies the correlations in the fluctuations—shows self-affine scaling [28] for the model with an exponent $\beta = 1.95 \pm 0.10$, which is consistent with Brownian motion. This result confirms the behavior suggested by Fig. 3, i.e., the crossover to uncorrelated behavior at large enough time scales. We analyze the data in [6] and find a similar behavior (Fig. 4b). These results are in agreement with the findings of a recently published paper [29].

The model proposed here is able to reproduce key statistical properties of the fossil record, for both the extinction and the origination of species. In contrast with many models in the literature, these results are obtained *without* having to assume that species have an intrinsic fitness, and that less fit species become extinct due to competition between species. In the model, mass extinctions are due to the amplification effect of predator-prey interactions that propagate along the food chain [8].

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