Unification of Small and Large Time Scales for Biological Evolution: Deviations from Power Law

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We develop a *unified* model that describes both "micro" and "macro" evolutions within a single theoretical framework. The ecosystem is described as a *dynamic network*; the population dynamics at each node of this network describes the "microevolution" over *ecological* time scales (i.e., birth, ageing, and natural death of individual organisms), while the appearance of new nodes, the slow changes of the links, and the disappearance of existing nodes accounts for the "macroevolution" over *geological* time scales (i.e., the origination, evolution, and extinction of species). In contrast to several earlier claims in the literature, we observe strong deviations from power law in the regime of long lifetimes.

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The recent surge in the modeling of biological evolution and extinction of species, using the concepts and techniques of statistical physics, has been stimulated partly by the claims (see [1–4] for reviews) that the statistical distributions of several quantities associated with the extinction of species follow power laws. However, almost all of these models focus only on the macroevolution (i.e., the evolution of species on geological time scales). Neither the birth, ageing, and, eventually, the death of the individual organisms nor the detailed population dynamics make explicit appearance in these theoretical descriptions. In reality, of course, it is the death of individual organisms that causes an entire population to be wiped out.

Therefore, we develop a *unified* model of an ecosystem that describes both micro- and macroevolutions. The ecosystem is described as a dynamic network. The microevolution over ecological time scales, i.e., birth, growth (ageing), and natural death of individual organisms, is described by the dynamics within each node [5]. The network itself evolves slowly with time; over sufficiently long time scales, populations of some species would drop to zero, indicating their extinction, and the corresponding nodes would be deleted from the network. On the other hand, appearance of new nodes, together with their own population of individual organisms, signals origination of new species. In addition, the links of the network also change slowly to capture the adaptive evolution of the species by random mutations over geological time scales.

The dynamic network.— At any arbitrary instant of time t, the model consists of $N(t)$ *species* each of which may be represented by one of the N nodes of a dynamic network; the total number of nodes is not allowed to exceed $N_{\max}$. Our model allows $N(t)$ to fluctuate with time over the range $1 \leq N(t) \leq N_{\max}$. The population (i.e., the total number of organisms) of a given species, for instance, i at any arbitrary instant of time t is given by $n_i(t)$. The limited availability of resources, other than food, in the ecosystem imposes an upper limit $n_{\max}$ of the allowed population of each species. Thus, the total number of organisms $n(t)$ at time t is given by $n(t) = \sum_{i=1}^{N(t)} n_i(t)$. Both $N_{\max}$ and $n_{\max}$ are time independent in the model.

The interactions.—Prey-predator interactions are captured through the matrix $\mathbf{J}$. The influence *of* species j *on* species i is given by J_{ij}; in general, $J_{ij} \neq J_{ji}$. The only restriction we impose initially on the elements of $\mathbf{J}$ is that $J_{ii} = 0$; i.e., none of the organisms preys on any other member of the same species. Since in all practical situations food webs specify only the sign of J_{ij}, we allow the off-diagonal elements of J_{ij} to take only the values $+1$ and -1. Thus, $J_{ij} = 1 = -J_{ji}$ indicates that j is the prey and i is the predator. Similarly, the situations $J_{ij} = -1 = J_{ji}$ and $J_{ij} = 1 = J_{ji}$ correspond, respectively, to *competition* and *cooperation* between the species i and j. We assign the values $+1$ or -1 to the off-diagonal elements of $\mathbf{J}$ randomly with equal probability in the initial state of the ecosystem [6]. However, our model can be easily generalized to take into account any other architecture of food webs [7,8].

We now argue that the matrix $\mathbf{J}$ accounts not only for the *interspecies* interactions but also *intraspecies* interactions. First of all, note that, if $J_{ij} > 0$, then the species j is a prey of the species i if, simultaneously, $J_{ji} < 0$, whereas the species j cooperates with i if, simultaneously, $J_{ij} > 0$ and $J_{ji} > 0$. Therefore, if $J_{ij} > 0$, the quantity $(J_{ij} - J_{ji})/2$ is unity if the species j is a prey of the species i, but it vanishes if the species i and j mutually cooperate. Similarly, if $J_{ij} < 0$, the quantity $-(J_{ij} - J_{ji})/2$ is unity if the species j is a predator of i, but it vanishes if the species i and j compete against each other. Now, consider the two sums

$$S_i^{\pm} = \pm \sum_{j=1}^{N} \frac{(J_{ij}^{\pm} - J_{ji})}{2} n_j, \tag{1}$$

where the superscript $\pm$ on J_{ij} indicates that the sum is restricted to only the positive (negative) elements J_{ij}. The sum S_i^+ is a measure of the total food *currently* available to the ith species, whereas $-S_i^-$ is a measure of the total population of the ith species that would be, at the same time, consumed as food by its predators. If the food available is less than the requirement, then some organisms of the species i will die of *starvation*, even if none of them are killed by any predator. This way the matrix **J** can account for the shortfall in the food supply and the consequent competition among the organisms of the species i.

The collective characteristics of species.—The age of an arbitrary individual organism, for example, α of the species i at time t, is denoted by the symbol $X(i, \alpha; t)$. In our model each species i is *collectively* characterized by [6,9]: (i) The *minimum reproduction age* $X_{\text{rep}}(i)$, (ii) the *birth rate* $M(i)$, (iii) the *maximum possible age* $X_{\max}(i)$, and (iv) the elements J_{ij} and J_{ji} $(j = 1, 2, \ldots, N)$. An individual of the ith species can reproduce only after attaining the age $X_{\text{rep}}(i)$. Whenever an organism of ith species gives birth to offsprings, $M(i)$ of these are born simultaneously. None of the individuals of the ith species can live longer than $X_{\max}(i)$. Thus, even if an individual manages to escape its predators, it cannot live longer than $X_{\max}(i)$ because of "natural death" caused by ageing.

The dynamics of the ecosystem.—The state of the system is updated in discrete time steps as follows.

Step I—birth: Assuming, for the sake of simplicity, the reproductions to be *asexual*, each individual organism α $[\alpha = 1, \ldots, n_i(t)]$ of the species i $[i = 1, 2, \ldots N(t)]$ is allowed to give birth to $M(i; t)$ offsprings at every time step t with probability (per unit time) $p_b(i, \alpha; t)$, which is nonzero only when the individual organism age $X(i, \alpha; t) > X_{\text{rep}}(i; t)$.

Step II—natural death: At any arbitrary time step t, the probability (per unit time) of "natural" death (due to ageing) of an individual organism α of species i is $p_d(i, \alpha; t)$.

Step III—mutation: With probability p_{mut} per unit time, all the species simultaneously readjust one of the incoming interactions J_{ij} by assigning it a new value of either $+1$ or -1 with equal probability [6].

Step IV—starvation death and killing by prey: If $n_i - S^+$ is larger than S^-, then food shortage will be the dominant cause of premature death of a fraction of the existing population of the species i. On the other hand, if $S^- > n_i - S^+$, then a fraction of the existing population will be wiped out primarily by the predators. In order to capture these phenomena, at every time step t, in addition to the natural death due to ageing, a further reduction of the population by

$$C \max(S^-, n_i - S^+) \tag{2}$$

is implemented where $n_i(t)$ is the population of the species i that survives after the natural death step above. C is a constant of proportionality that basically sets the time scale of the population dynamics. If implementation of these steps makes $n_i \leq 0$, species i becomes extinct.

Step V—speciation: At each time step, the niches (nodes) left empty by extinction of species are refilled by new species, with probability p_{sp}. All the simultaneously refilled nodes of the network originate from *one common ancestor* which is picked up randomly from among the surviving species. All the interactions J_{ij} and J_{ji} of the new species are identical to those of their common ancestor; each new species, however, either competes or cooperates with its ancestor species. The characteristic parameters $X_{\max}$, X_{rep}, M_j of each of the new species differ randomly by ± 1 from the corresponding parameters for their ancestor.

Probability of birth: We chose the *time-dependent* probability of birth per unit time as

$$p_b(i, \alpha) = \left[\frac{X_{\max}(i) - X(i, \alpha)}{X_{\max}(i) - X_{\text{rep}}(i)}\right]\left(1 - \frac{n_i}{n_{\max}}\right) \quad \text{iff } X(i, \alpha) \geq X_{\text{rep}}(i) \quad \text{and} \quad X_{\max}(i) > X_{\text{rep}}(i). \tag{3}$$

Note that in the limit of vanishingly small population, i.e., $n_i \to 0$, we have $p_b(i, \alpha) \to 1$ if $X(i, \alpha) = X_{\text{rep}}(i)$ and, then, p_b decreases linearly [10] as the organism grows older. However, since the ecosystem can support only a maximum of $n_{\max}$ individual organisms of each species, $p_b(i, \alpha; t) \to 0$ as $n_i(t) \to n_{\max}$, irrespective of the age of the individual organism α [11].

Probability of natural death: We assume the probability of natural death (due to ageing) to have the form [12]

$$p_d(i, \alpha) = \left[\frac{X(i, \alpha)M(i) - X_{\text{rep}}(i)}{X_{\max}(i)M(i) - X_{\text{rep}}(i)}\right] \quad \text{if } X(i, \alpha) \geq X_{\text{rep}}(i), \tag{4}$$

$$p_d(i, \alpha) = \left[\frac{X_{\text{rep}}(i)M(i) - X_{\text{rep}}(i)}{X_{\max}(i)M(i) - X_{\text{rep}}(i)}\right] \quad \text{if } X(i, \alpha) < X_{\text{rep}}(i), \tag{5}$$

provided $X_{\max}(i)M(i) > X_{\text{rep}}(i)$. In all other situations, $p_d(i, \alpha) = 1$. Note that, for a given $X_{\max}$ and X_{rep}, the larger is the M the higher is the p_d for any age X. Therefore, each species has a tendency to increase M for giving birth to a larger number of offsprings, whereas the higher mortality for higher M opposes this tendency.

The longest runs in our computer simulations were continued up to a maximum of 5×10^6 time steps. If each time step in our model is assumed to correspond to a real time of the order of 1 yr, then the time scale of 5×10^6 yr, over which we have monitored our model ecosystem, is comparable to real geological time scales.

Since we faced difficulty in getting high quality data, with reasonably good statistics, for $N_{\max} > 100$ and $n_{\max} > 1000$, we have carried out most of our simulations with $N_{\max} = 50$, 100, and $n_{\max} = 100$, 1000, only. The

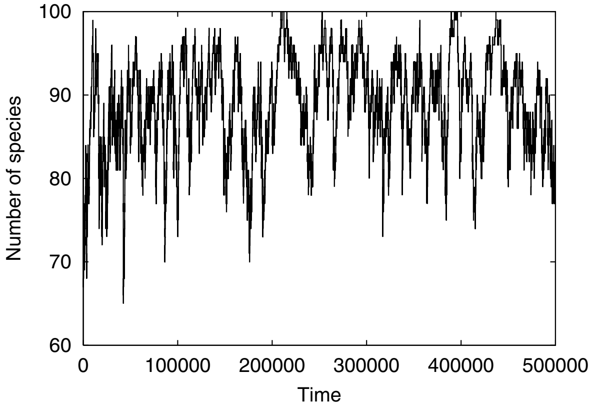

FIG. 1. The total number of species $N(t)$ is plotted against time; the corresponding parameter set is $N_{\max} = 100$, $n_{\max} = 1000$, $C = 0.1$, $p_{sp} = 0.001$, $p_{\mathrm{mut}} = 0.001$.

data obtained from the different runs, each starting from a random initial condition, were averaged. Both CRAY-T3E and SUN workstations were used for the simulations.

In Fig. 1, we plot the total number of species, $N(t)$, in a particular run, starting from a single initial condition, up to half a million time steps. In Fig. 2, we plot the corresponding variation of the total population $n(t)$ over relatively short interval of 20 000 time steps only. These clearly demonstrate that the evolution has periods of "stasis" during which organisms populations keep fluctuating; the stases are interrupted by occasional bursts of rapid extinctions followed by slower recovery.

The average distributions of the lifetimes of the species are plotted in Fig. 3 for one set of values of the parameters. Clearly, the data are consistent with a power law; the effective exponent, which is, approximately, 2, is also consistent with the corresponding estimate quoted in the literature [1,2]. However, in Fig. 3, the power law holds only over a limited range [13]. Since real ecosystems are much more complex than our model ecosystem and the available fossil data are quite sparse, it is questionable whether real extinctions follow power laws and, if so, over how many orders of magnitude.

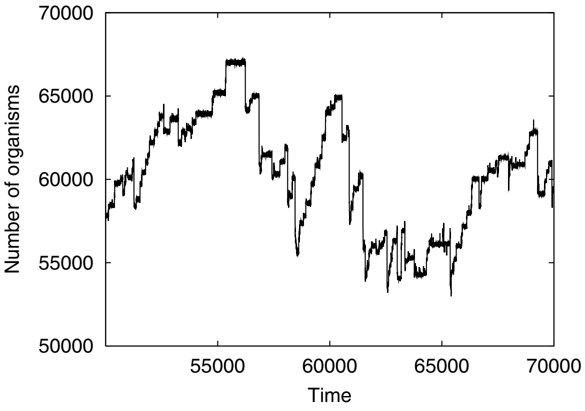

FIG. 2. The total number of organisms $n(t)$ is plotted against time over a *relatively short part* of the evolution of the ecosystem. The parameter values are identical to those in Fig. 1.

We have also observed (not shown) that the higher is the mutation probability p_{mut} the lower is the lifetime. But, p_{sp} had a weaker effect on the same data. However, if p_{sp} is too small to maintain adequate pace of recovery of the ecosystem after mass extinctions, the entire ecosystem collapses.

Figure 4 shows the time-averaged age distribution in the populations of a species as well as the distributions of $X_{\max}$, X_{rep}, and M. We see that the minimum age of reproduction X_{rep} is quite small, as usual in the employed

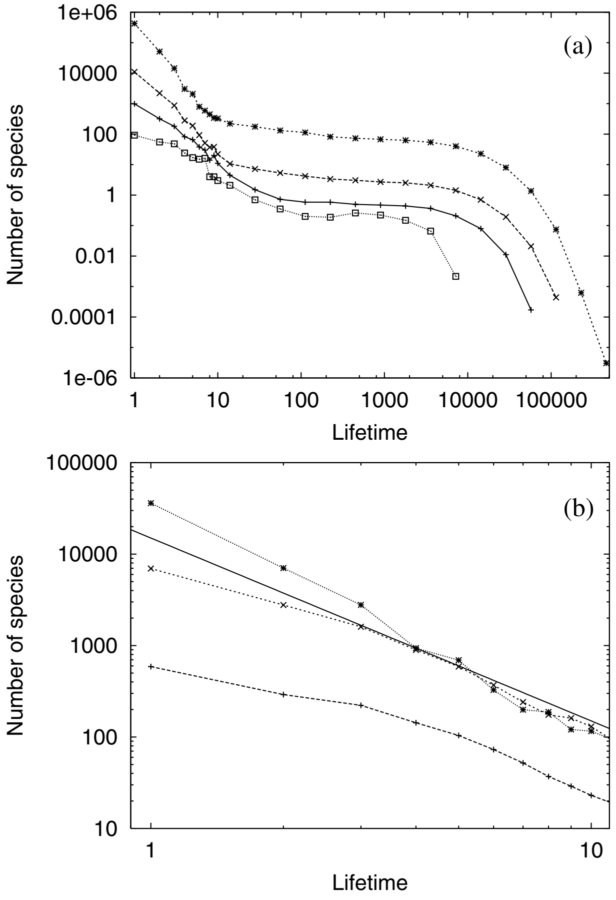

FIG. 3. Log-log plots of the distributions of the lifetimes of the species in an ecosystem with (a) $n_{\max} = 100$, (b) $n_{\max} = 1000$. In (b), the data beyond the lifetime of 10 are not shown to emphasize the initial power law regime (symbolized by the straight line with slope -2. The other common parameters for both the figures are $N_{\max} = 50$, $p_{sp} = 0.01$, $p_{\mathrm{mut}} = 0.001$. The symbols $\square$, +, $\times$, and * in (a) correspond to maximum simulation times 5×10^3, 5×10^4, 5×10^5, and 5×10^6, respectively, while the symbols +, $\times$, and * in (b) correspond to the maximum simulation times 10^4, 5×10^4, and 4×10^5, respectively. Each of the data points has been obtained by averaging over 18 to 176 runs, each starting from a new random initial state.

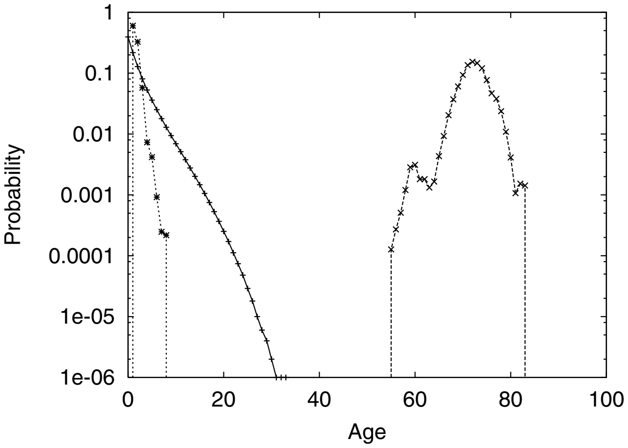

FIG. 4. Semilog plot of the distributions of X (+), $X_{\max}$ (×), and X_{rep} (*); the parameter values are the same as those in Fig. 1.

ageing model [9]. The age distribution decays stronger than a simple exponential, indicating a mortality increasing with age as it should be [12]. The genetic death ages $X_{\max} \simeq 72$ are far above the upper end $\simeq 31$ of the age distribution, as is appropriate for animals in the wild [10]. Finally, Fig. 5 shows the distribution of $M(i)$; this is relatively much broader than the distributions of $X_{\max}$ and X_{rep}.

Not only the total number of species and the interspecies interactions but also the collective characteristics, namely, X_{rep}, $X_{\max}$, and M, of each species vary following a stochastic dynamics. Thus, our model is capable of *self-organization.* The population dynamics within the framework of Lotka-Volterra equations have been considered earlier [14] for only a few species. But, these do not account for the age distributions as the entire population of each species is represented *collectively* by a single dynamical variable in contrast to the explicit birth, growth, and death of individual organisms captured in our model.

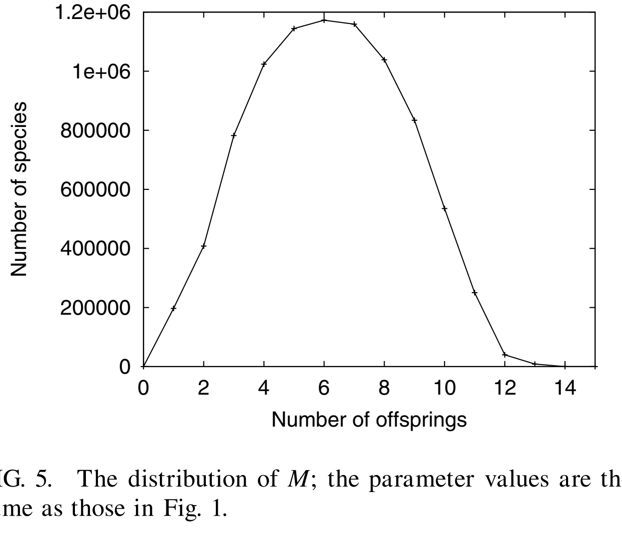

FIG. 5. The distribution of M; the parameter values are the same as those in Fig. 1.

Since we have observed strong deviations from power law in the distributions of lifetimes of species even in the Sole-Manrubia model [15], in spite of the absence of detailed "microdynamics" in the latter, we strongly believe that this is a generic feature of evolution and extinction of species. It would be interesting to investigate the *geographical effects* on our model ecosystem by reformulating it on a lattice [16].

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