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# Food-web based unified model of macro- and microevolution

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We incorporate the generic hierarchical architecture of foodwebs into a ‘‘*unified*’’ model that describes both micro- and macroevolutions within a single theoretical framework. This model describes the microevolution in detail by accounting for the birth, ageing, and natural death of individual organisms as well as prey-predator interactions on a hierarchical dynamic food web. It also provides a natural description of random mutations and speciation (origination) of species as well as their extinctions. The distribution of lifetimes of species follows an approximate power law only over a limited regime.

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## I. INTRODUCTION

The questions of ‘‘origin’’ and ‘‘evolution’’ have always fascinated scientists in all disciplines. Physicists have focused attention mostly on cosmological evolution and origin of universe. On the other hand, chemists and biologists have studied chemical evolution (i.e., formation of elements and compounds) as well as prebiotic evolution and origin of life. Similarly, paleontologists try to understand the origin of species and evolution of ecosystems by reading ‘‘history of life written on stone’’ in the form of fossil records. In a recent paper [1] we developed a dynamic network model for studying some generic features of the biological evolution of ecosystems. In this paper we extend that model by incorporating the generic trophic-level architecture of food webs and show how it can account for evolution at both ecological as well as geological time scales.

## II. EARLIER MODELS AND THEIR LIMITATIONS

Because of the close similarity between the evolution of interacting species and that of conventional systems of interacting agents studied in statistical physics, several models of macro evolution of ecosystems have been reported over the last decade in the physics literature (see Refs. [2–4] for recent reviews). Some of these describe macroevolution as random walks on fitness landscape [5,6] (see also Refs. [7,8] for reviews), while some others have been formulated in terms of a matrix of interspecies interactions [4,9]. However, most of these models of macro evolution do not account for the dynamics of populations of species even in a collective manner. In other words, such models ignore biological details that are certainly important on *ecological* time scales and, therefore, cannot provide a natural description of origin, evolution, and extinctions in terms of population dynamics.

On the other hand, the Lotka-Volterra equation [10] has been used extensively in the mathematical modeling of population dynamics of prey-predator systems. However, for the study of population dynamics of entire ecological communities one needs a model of the food web [11]. A food web [12–14] corresponding to an ecosystem is a graphic description of prey-predator relations. More precisely, a food web is a directed graph where each node is labeled by a species' name and each directed link indicates the direction of flow of nutrient (i.e., *from* a prey *to* one of its predators). However, most often, these models assume static food webs, where interspecies interactions are assumed to be independent of time. But, in real ecosystems, species are known to change their food habits with time [15]. These changes in diets may be caused by scarcity of the normal food and abundance of alternative food resources. This may also arise from the adaptations of the prey species that tend to avoid being eaten by predators through camouflage or other mechanisms. Therefore, Lotka-Volterra-type models with time-independent food webs cannot be expected to account for macro evolution of the ecosystem over *geological* time scales.

Limitations of both these approaches are well known [16], and attempts have been made to merge population dynamics and macroevolution within a single mathematical framework [17]. Population dynamics is monitored in Abramson's macroevolutionary model [18] in a simplified manner. However, Abramson postulated an oversimplified model of dynamically evolving food web that, essentially, consists of a single food chain. Amaral and Meyer [19] developed a macroevolutionary model with a dynamically evolving food web where niches are arranged in a hierarchical trophic-level architecture. However, population dynamics of the species does not enter explicitly in this model. The strength of this model is its simplicity as some of its properties, e.g., its self-organized criticality, can be studied analytically [20,21]. However, we feel, more details need to be included to address a wider range of biologically relevant questions.

## III. THE “UNIFIED” ECOSYSTEM MODEL

To our knowledge, our recent unified model [1] is one of the first few [22,23] that describes not only macroevolution of origin (speciation) and extinction of species on geological time scales but also micro evolutionary processes, for example, the birth, growth (ageing), and natural death of individual organisms as well as the effects of prey-predator in-

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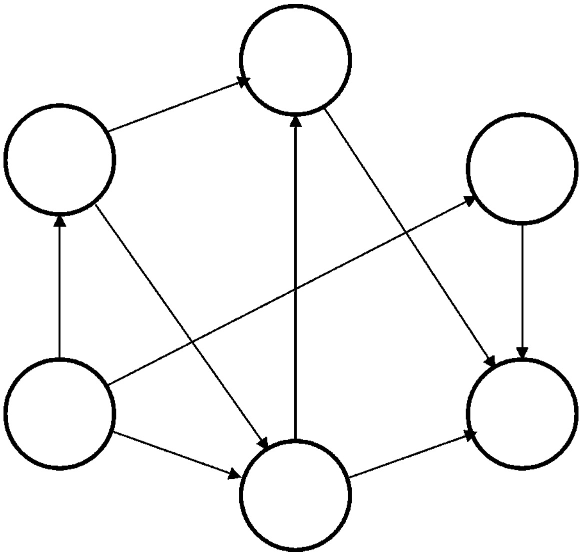

FIG. 1. A schematic representation of the network model, with *random* food-web architecture, considered in Ref. [1]. The circles represent the niches in the ecosystem. The arrows indicate the directions of nutrient flows *to* the species at an arbitrary stage during the evolution of the ecosystem.

teractions on their populations. Our "unified" model, reported in Ref. [1], can be schematically represented by the random network shown in Fig. 1. Each node of this network, denoted by the circles, represents a niche that can be occupied by at most one species at a time. In that paper [1] we postulated a simple random, but dynamic, food web ignoring the hierarchical organization of species in food webs. In this paper we postulate a generic hierarchical food web, where niches are arranged in different trophic levels, with biologically realistic interspecies interactions.

### A. Architecture of the network

As in our earlier work [1], we model the ecosystem as a dynamic *network* each node of which represents a niche that can be occupied by at most one species at a time. We assume a generic *hierarchical architecture* of this network (see Fig. 2) in order to capture the organization of species in different trophic levels of food webs [12]. If the $i$th species occupies the $\nu$th node at the $\ell$th trophic level of the food web, we denote its position by the ordered pair $\ell,\nu$. We assume only one single species at the highest level $\ell=1$. Each node at level $\ell$ leads to $m$ branches at the level $\ell+1$; therefore, the maximum allowed number of nodes in level $\ell$ is $m^{\ell-1}$ and the allowed range of $\ell$ is $1 \leqslant \ell \leqslant \ell_{max}$. The hierarchical architecture helps us in capturing a well-known fact that in the normal ecosystems the higher is the trophic level the fewer are the number of species.

### B. The network is dynamic

The faster dynamics within each node captures microevolution, i.e., the birth, growth (ageing), and natural death of the individual organisms. Moreover, the network itself evolves slowly over sufficiently long-time scales. For example, the adaptive evolution of the species takes place through alterations in some of their crucial characteristics by random mutations. Furthermore, as the ecosystem evolves with time, the populations of some species would drop to zero, indicating their extinction, and the corresponding nodes would be slowly reoccupied by new species through the process of speciation.

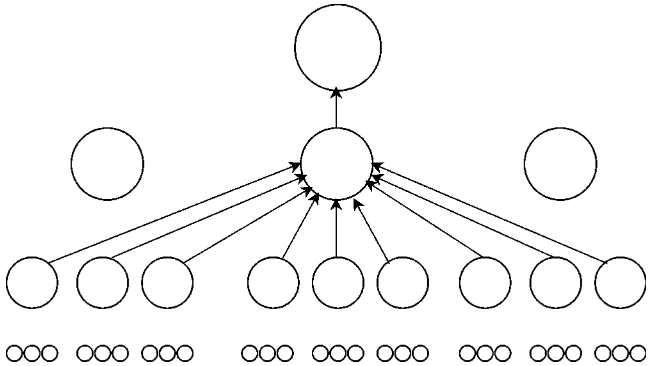

FIG. 2. A schematic representation of the network model, with *hierarchical* food-web architecture. The circles represent the niches in the ecosystem. Each arrow represents the direction of nutrient flow. All possible nutrient flows *to* the species occupying the second node at the second level and that occupying the highest level are shown explicitly.

At any arbitrary instant of time $t$ the model consists of $N(t)$ *species* each of which occupies one of the nodes of the dynamic network. The total number of species cannot exceed $N_{max}=(m^{\ell_{max}}-1)/(m-1)$, the total number of nodes. Our model allows $N(t)$ to fluctuate with time over the range $\ell \leqslant N(t) \leqslant N_{max}$. The population (i.e., the total number of organisms) of a given species, say, $i$, at any arbitrary instant of time $t$ is given by $n_i(t)$. The intra species interactions among the organisms of the same species for limited availability of resources, other than food, 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 $n(t)=\Sigma_{i=1}^{N(t)} n_i(t)$. Both $N_{max}$ and $n_{max}$ are time-independent parameters in the model.

### C. Interactions in the food web

Between any two species $i,k$ that occupy two adjacent trophic levels there is either a link ($J_{ik}=\pm 1$) or no link ($J_{ik}=0$). The sign of $J_{ik}$ gives the direction of trophic flow, i.e. it is $+1$ if $i$ eats $k$ and it is $-1$ if $k$ eats $i$. Thus, $J_{ik}=0$ means that there is no prey-predator relation between the two species $i$ and $k$.

If we neglect parasites and herbivorous insects on trees, then, in general, predators are rarer and bigger than their prey [24]. This is very naturally incorporated in the hierarchical food-web structure of our model by assuming that each predator needs $m$ prey animals to survive (see factor $m$ below). The maximum number of individuals on each level $\ell$ is $m$ times bigger than on its predator level $\ell-1$ in the model, and when we imagine the predator mass to be $m$ times the prey mass, then the maximum (and initial) amount of biomass on each level is the same. In this way, the body size and abundance of a species are strongly correlated with the food web and its interactions with other species [25,24].

The $J$ account not only for the interspecies interactions but also intraspecies interactions. Let $S_i^+$ be the number of all prey individuals for species $i$ on the lower trophic level, and $S_i^-$ be $m$ times the number of all predator individuals on the higher trophic level. Since a predator eats $m$ prey per time interval, $S_i^+$ gives the available food for species $i$, and $S_i^-$ is the contribution of species $i$ to all predators on the higher level. If the available food $S_i^+$ is less than the requirement, then some organisms of the species $i$ will die of *starvation*, even if none of them is killed by any predator. This way the model can account not only for the interspecies prey-predator interactions but also for the intraspecies interactions arising from the competition of individual organisms during shortage of food supply.

Note that the food resources of a given species are not restricted to only the lower branches emanating from that node but it can also exploit the species at the lower-level nodes emanating from other nodes at its own trophic level. Moreover, note that although there is no direct interaction between species at the same trophic level in our model, they can compete, albeit indirectly, with each other for the same food resources available in the form of prey at the next lower trophic level.

### D. The collective characteristics of species

An arbitrary species $i$, occupying the $\nu$th node at the $\ell$th level is *collectively* characterized by [1] (i) the *minimum reproduction age* $X_{rep}(i)$, (ii) the *birth rate* $M(i)$, and (iii) the *maximum possible age* $X_{max}(i)$. An individual of the species $i$ can reproduce only after attaining the age $X_{rep}(i)$. Whenever an organism of this species gives birth to offsprings, $M(i)$ of these are born simultaneously. None of the individuals of this species can live longer than $X_{max}(i)$, even if an individual manages to escape its predators.

Note that, in several earlier works the reproductive success was modeled mathematically by assigning a ‘‘fitness’’ to a species or to an individual organism. The use of the term fitness has an interesting history [26]. In contrast to these earlier works, in our models, we assign a minimum reproductive age, a maximum possible age, and the birth rate to model the reproductive success (or failure). It has been felt [26] that fitness merely summarizes, instead of explaining, the ability to survive and reproduce. On the other hand, the interplay of the $M, X_{rep}$, and $X_{max}$, we hope, will be able to explain why some species survive while others become extinct.

### E. 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 reproduction to be *asexual*, each individual organism $\alpha$ [$\alpha = 1, \ldots, n_i(t)$] 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's age $X(i,\alpha;t) \geqslant X_{rep}(i;t)$.

*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 $\alpha$ of species $i$ is $p_d(i,\alpha;t)$.

*Step III: mutation*. With probability $p_{mut}$ per unit time, each of the species simultaneously increases or decreases, with equal probability, their $X_{rep}$, $X_{max}$, and $M$ by unity. (The ages are restricted to the interval from 1 to 100, and $M > 0$.) Moreover, with the same probability $p_{mut}$ per unit time, they also readjust one of the links $J$ from prey and one of the links $J$ to predators [9]; if the link $J$ was zero, it is assigned a new value of $\pm 1$ whereas if the link was nonzero it is assigned a new value of zero. These readjustments of the incoming and outgoing (in the sense of nutrient flow) interactions are intended to capture the facts that each species tries to minimize predators but look for new food resources.

*Step IV: starvation death and killing by prey*. If $n_i - S_i^+$ is larger than $S_i^-$ 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 $S_i^- > n_i - S_i^+$, 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

$$C \max(S_i^-, n_i - S_i^+) \tag{1}$$

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. If implementation of these steps makes $n_i \leqslant 0$, species $i$ becomes extinct.

*Step V: speciation*. After the extinction of, typically, half of the species in a trophic level, the niches (nodes) left empty are refilled by new species, with probability $p_{sp}$. All the simultaneously refilled nodes in a trophic level of the network originate from *one common ancestor* which is picked up randomly from among the surviving species at the same trophic level. All the interactions $J$ of the new species are identical to those of their common ancestor. The characteristic parameters $X_{max}$, $X_{rep}$, $M$ of each of the new species differ randomly by $\pm 1$ from the corresponding parameters for their ancestor.

### F. Probability of birth

We assume the *time-dependent* probability $p_b(i,\alpha)$ (of individual $\alpha$ in species $i$) of giving birth per unit time to decrease linearly with age, from its maximum value, attainable at the minimum reproduction age, down to zero at the maximum lifespan. It is multiplied with a Verhulst factor $1 - n_i/n_{max}$ and equals this factor at $X = X_{rep}$. Thus, in the limit of vanishingly small population, i.e., $n_i \to 0$, we have $p_b(i,\alpha) \to 1$ if $X(i,\alpha) = X_{rep}(i)$ and, thereafter, $p_b$ decreases linearly [27] 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 $\alpha$ [28].

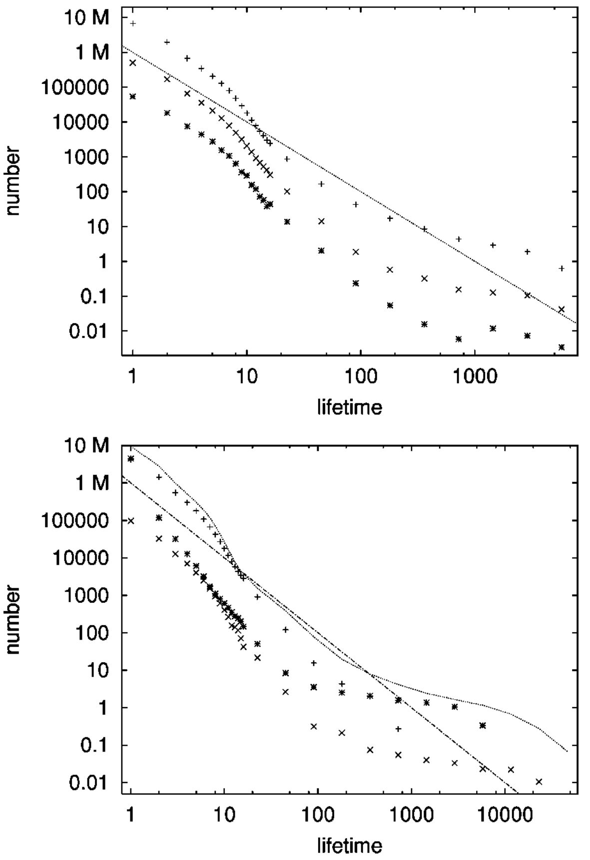

FIG. 3. Log-log plots of the distributions of the lifetimes of the species in an ecosystem with $n_{max}=10^2$–$10^4$ and 600–60 000 iterations. The line with slope $-2$ corresponds to a power law distribution that has been predicted by many theories. The common parameters for both plots are $m=2$, $\ell=5$ (i.e., $N_{max}=31$), $p_{sp}=0.1$, $p_{mut}=0.0001$, $C=0.05$. In the upper plot, the symbols $+$, $\times$, and * correspond to $n_{max}=10^2$, $10^3$, and $10^4$ averaged over 6400, 640, and 64 systems, respectively. In the lower plot, $n_{max}=1000$ (except for the line where $n_{max}=100$) and the maximum simulation time is 600 ($+$) and 60 000 ($\times$ and line) iterations; * corresponds to $m=12$, $\ell=3$ after 6000 iterations; 640 systems were averaged over for short and intermediate times, and 64 for the longest time. Each system started from a new random initial state.

### G. Probability of natural death

Similarly, we assume the probability $p_d$ of "natural" death (due to ageing) to increase linearly with age [29] and to reach unity at the maximum lifespan $X_{max}$ of the species: $p_d=(XM-X_{rep})/(X_{max}M-X_{rep})$. (For $X<X_{rep}$ the death probability, instead, has the constant value that $p_d$ attains at $X=X_{rep}$; if the above denominator is negative, $p_d=1$.) 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 larger number of offsprings whereas the higher mortality for higher $M$ opposes this tendency [30].

## IV. RESULTS

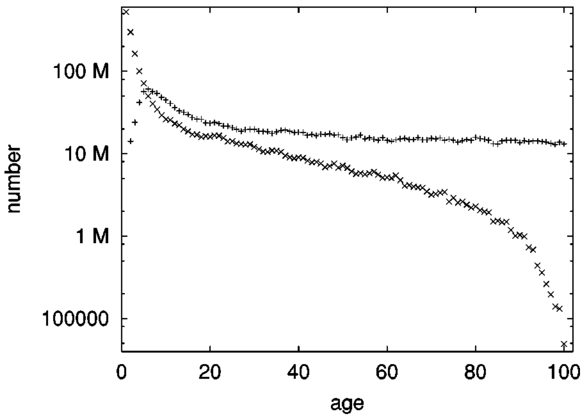

FIG. 4. Semilog plot of the distributions of $X_{rep}$ ($\times$) and $X_{max}$, taken from the simulations symbolized by the curved line in the lower part of Fig. 2: $m=2$, $\ell=5$,$n_{max}=100$, $t=60\,000$, 640 systems.

In our simulations initially, $M=10$,$X_{max}$ is distributed randomly between 2 and 99 independently for each species, $X_{rep}$ randomly between 1 and $X_{max}$, and the population randomly between 1 and $n_{max}/2$. The ages of the individuals vary randomly between 1 and $X_{max}$ of their species.

Going through all the five steps mentioned above for all the individuals of each species constitutes one *time step* ("iteration") in our model; all times in this model are measured in the units of these "iterations." The longest runs in our computer simulations were continued up to a million 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 a million years, over which we have monitored our model ecosystem, is comparable to real speciation time scales.

### A. Lifetime distributions

The average distributions of the lifetimes of the species are plotted in Fig. 3 for various sets of values of the parameters. Only very approximately, the data are consistent with a

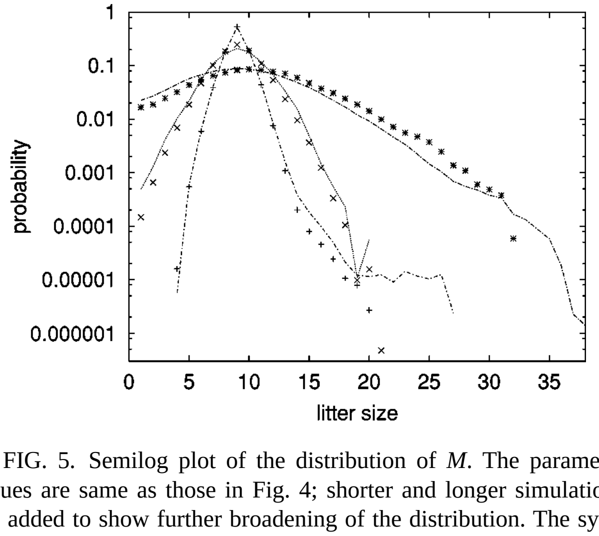

FIG. 5. Semilog plot of the distribution of $M$. The parameter values are same as those in Fig. 4; shorter and longer simulations are added to show further broadening of the distribution. The symbols $+$, $\times$, and * correspond to 600, 60 000, and 600 000 iterations, respectively, using 6400, 640, and 1 systems. The lower lines, using 64 lattices with $n_{max}=100$, $t=6000$, show the broadening with increasing mutation rate $p_{mut}=0.00001$, 0.001, and 0.01.

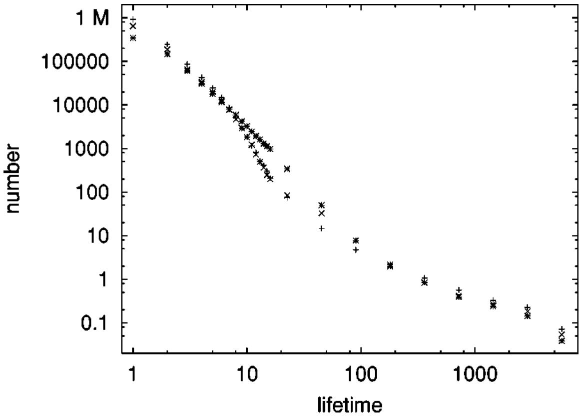

FIG. 6. Log-log plot of the distribution of lifetimes for speciation probabilities $p_{sp}=0.02(+)$ and 0.5 $(\times)$, and (squares, with $p_{sp}=0.1$) for Gompertz mortality assumption: $p_d = \exp[(\max(X,X_{rep})-X_{max})/M]$, using 640 systems for $n_{max}=100$ and $t=6000$.

power law; the effective exponent, which is $\approx 2$, is also consistent with the corresponding estimate quoted in the literature [2,3]. However, in Fig. 3 the power law holds only over a limited range [31] of times; for longer times a plateau seems to develop. 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.

### B. Distributions of Species Characteristics

Figures 4 and 5 show the time-averaged distributions of $X_{max}$, $X_{rep}$, and $M$. We see that the minimum age of reproduction $X_{rep}$ is quite small, as usual in a similar ageing model [32]. The age distribution (not shown) decays stronger than a simple exponential, indicating a mortality increasing with age as it should be [29]. The genetic death ages $5 < X_{max} < 100$ reach ages far above the upper end $\simeq 50$ of the age distribution (for the species on top of the food web), as is appropriate for animals in the wild [27]. Finally, Fig. 5 shows the distribution of $M(i)$ which is still broadening even after 60 000 iterations.

We have also observed (not shown) that the higher is the mutation probability $p_{mut}$ the lower is the lifetime of the ecosystem; this is consistent with the intuitive expectation that a higher rate of mutation leads to higher levels of biological activity in the ecosystem thereby leading to the extinction of larger number of species. Figure 5 from these data shows that the broadening of the histogram for $M$, i.e., the equilibration process, is determined by the product $p_{mut}t$ giving the average number of mutations per species. But, $p_{sp}$ had weaker effect on the same data as shown in Fig. 6. The same figure also shows a somewhat better power law at short times if the above linear increase of the mortality with age is replaced by an exponential increase (Gompertz law [27]).

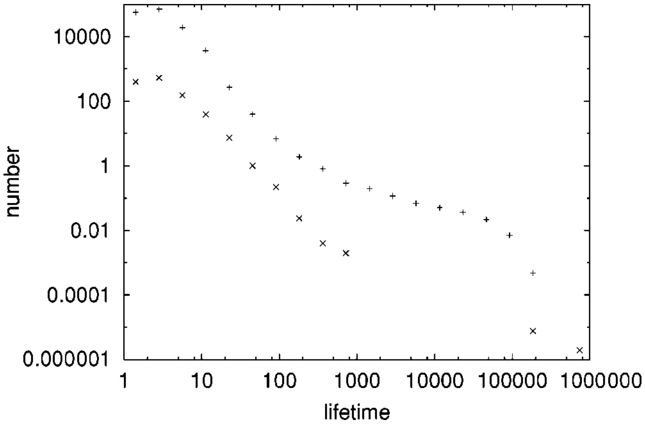

FIG. 7. Log-log plot of the distribution of lifetimes for the whole ecosystem of $\ell$ trophic layers, with $\ell=5$, $m=2$ and $\ell=3$, $m=6$, from 1 and 10 systems only; $n_{max}=100$.

### C. Collapse of fragile ecosystems

We model an ecosystem with a *fixed* number $\ell$ of trophic levels; thus as soon as we find one level to be extinct completely, we regard the ecosystem as destroyed and try to build a new one for the same parameters, changing only the random numbers. Hundreds of such attempts are needed for a successful system lasting the prescribed number (like as 6000) of iterations, see Fig. 7. This method simulates the billions of years which natural evolution needed to build the present life on the earth.

## V. SUMMARY AND CONCLUSION

In summary, we have presented a unified model which describes not only the birth, ageing, and death of individuals as well as population dynamics on short time scales but also the long-time evolution of species, their origination (speciation), and extinction. The total number of species, the interspecies interactions, and the collective characteristics, namely, $X_{rep}$, $X_{max}$, and $M$, of each species vary following a stochastic dynamics with Darwinian selection. Thus, our model is capable of *self-organization*.

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