A food-web based unified model of "macro"- and "micro-" evolution

Debashish Chowdhury[*1] and Dietrich Stauffer[†2]

[1]*Department of Physics, Indian Institute of Technology, Kanpur 208016, India.*
[2]*Institute for Theoretical Physics, Cologne University, D-50923 Köln, Euroland.*

We incorporate the generic hierarchical architecture of foodwebs into a "*unified*" model that describes both "micro" and "macro" evolutions within a single theoretical framework. This model describes the "micro"-evolution 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/orgination 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 focussed 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 pre-biotic evolution and "origin" of life. Similarly, paleontologists try to understand the origin of species and evolution of eco-systems by reading "history of life written on stone" in the form of fossil records. In a recent Letter [1] we developed a dynamic network model for studying some generic features of the biological evolution of eco-systems. In this paper we extend that model 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 eco-systems have been reported over the last decade in the physics literature (see [2, 3, 4] for recent reviews). Some of these describe macro-evolution as random walks on fitness landscape [5, 6] (see also [7, 8] for reviews), while some others have been formulated in terms of a matrix of inter-species 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 modelling 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, 13, 14] corresponding to an eco-system is a graphic description of prey-predator relations. More precisely, a food web is a directed graph where each node is labelled 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 inter-species interactions are assumed to be independent of time. But, in real eco-systems, 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 eco-system over *geological* time scales.

Limitations of both these approches are well known [16], and attempts have been made to merge population dynamics and "macro"-evolution within a single mathematical framework [17]. Population dynamics is monitored in Abramson's "macro"-evolutionary 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 "macro"-evolutionary 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.

[*]E-mail: debch@iitk.ac.in
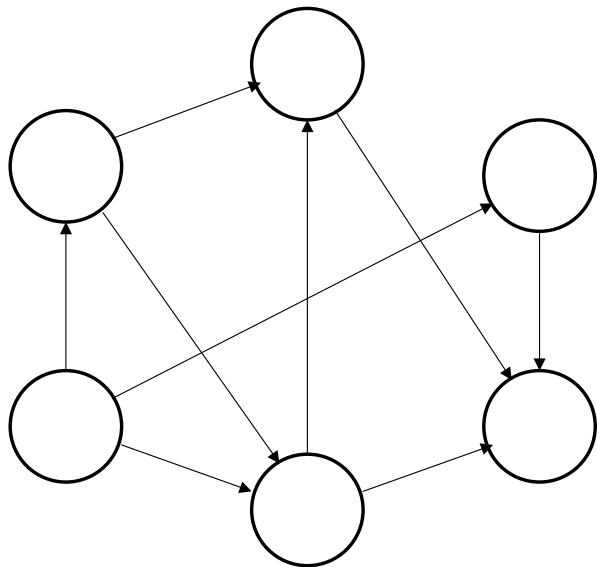[†]E-mail: stauffer@thp.uni-koeln.de

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

III. THE "UNIFIED" ECO-SYSTEM MODEL

To our knowledge, our recent "unified" model [1] is one of the first few [22, 23] that describes not only "macro"-evolution of origin/speciation and extinction of species on geological time scales but also "micro"- evolutionary processes like, for example, the birth, growth (ageing) and natural death of individual organisms as well as the effects of prey-predator interactions on their populations. Our "unified" model, reported in [1], can be schematically represented by the random network shown in figure 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 Letter [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 inter-species interactions.

A.   Architecture of the network

As in our earlier work [1], we model the eco-system 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 foodwebs [12]. If the i-th species occupies the ν-th node at the ℓ-th trophic level of the food web, we denote its position by the ordered pair
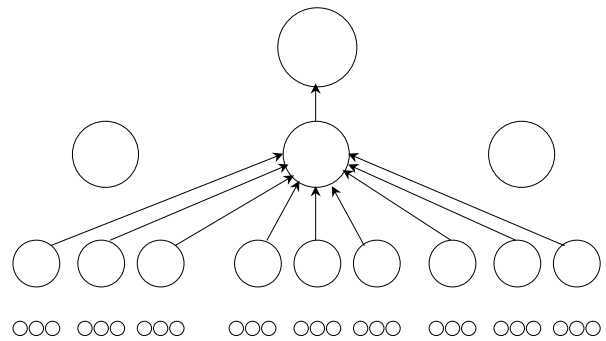

FIG. 2: A schematic representation of the network model, with *hierarchical* foodweb architecture. The circles represent the niches in the eco-system. Each arrow represents direction of nutrient flow. All possible nutrient flows *to* the species occupying the second node at the second level and that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

ℓ, ν. We assume only one single species at the highest level $\ell = 1$. Each node at level ℓ leads to m branches at the level $\ell + 1$; therefore, the maximum allowed number of nodes in level ℓ is $m^{\ell-1}$ and the allowed range of ℓ is $1 \leq \ell \leq \ell_{max}$. 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 "micro"-evolution, 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 eco-system evolves with time, the populations of some species would drop to zero, indicating their extinction, and the corresponding nodes would be slowly re-occupied by new species through the process of speciation.

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 $\ell \leq N(t) \leq N_{max}$. 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 $n(t) = \sum_{i=1}^{N(t)} n_i(t)$. 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 ℓ 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 to the food web and its interactions with other species [24, 25].

The J account not only for the *inter*-species interactions but also *intra*-species 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 inter-species prey-predator interactions but also for the intra-species 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 ν-th node at the ℓ-th level is *collectively* characterized by [1]:
(i) the *minimum reproduction age* $X_{rep}(i)$,
(ii) the *birth rate* $M(i)$,
(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 modelled 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 explainig, 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 eco-system

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 α ($\alpha = 1, ..., n_i(t)$) of the species i ($i = 1, 2, ...N(t)$) 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 non-zero only when the individual organism's age $X(i, \alpha; t) \geq X_{rep}(i; t)$.
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 α 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 and 100, and $M > 0$.) Moreover, with the same probability p_{mut} per unit time, they also re-adjust 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 ± 1 whereas if the link was non-zero it is assigned a new value of zero. These re-adjustments 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

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

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 $n_i \leq 0$, 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 re-filled by new species, with probability p_{sp}. All the simultaneously re-filled 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 ± 1 from the corresponding parameters for their ancestor.

F. Probability of birth

We assume the *time-dependent* probability $p_b(i, \alpha)$ (of individual α 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 eco-system 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 [28].

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

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}, the population randomly between 1 and $n_{max}/2$. The ages of the individuals vary randomly between 1 and the X_{max} of their species.
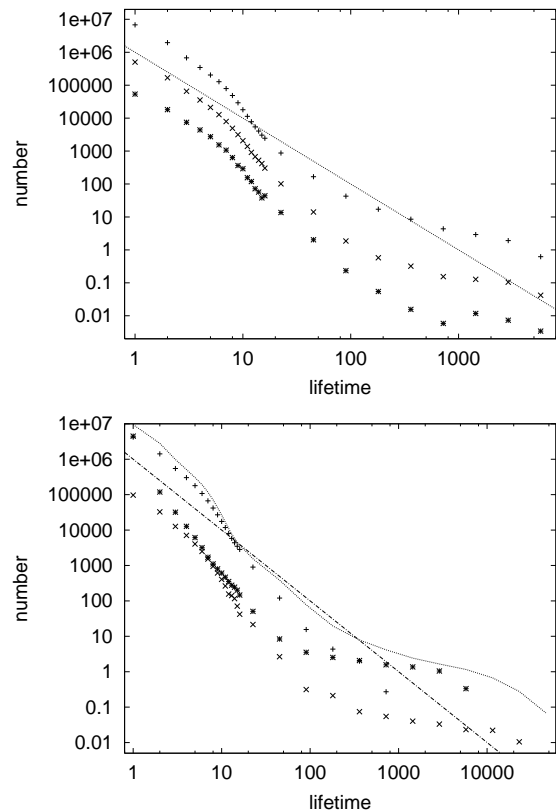

FIG. 3: Log-log plots of the distributions of the lifetimes of the species in an eco-system with $n_{max} = 10^2$ to 10^4 and 600 to 60000 iterations. The line with slope -2 corresponds to a power law distribution that has been predicted by many theories. The common parameters for both plots are $m = 2, \ell = 5$ (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 $n_{max} = 10^2, 10^3, 10^4$ 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 60000 ($\times$ 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.

The longest runs in our computer simulations were continued upto a a million time steps. If each time step in our model is assumed to correspond to a real time of the order of one year, then the time scale of a million years, over which we have monitored our model eco-system, 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 power-law; the effective exponent, which is, ap-
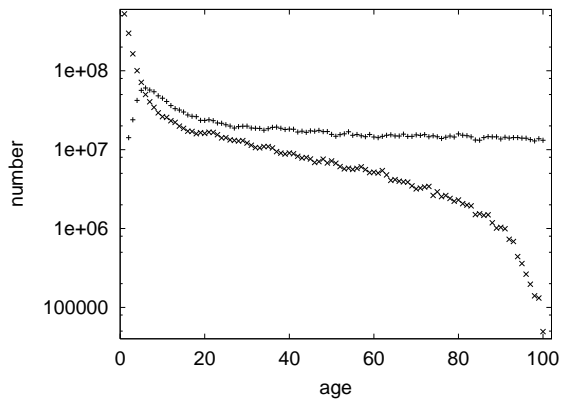
FIG. 4: Semi-log plot of the distributions of X_{rep} ($\times$) and X_{max}, taken from the simulations symbolized by the curved line in the lower part of fig.2: $m = 2, \ell = 5, n_{max} = 100, t = 60000$, 640 systems.
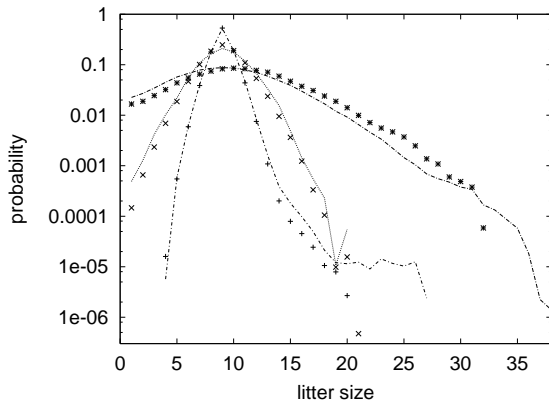

FIG. 6: Log-log plot of the distribution of lifetimes for speciation probabilities $p_{sp} = 0.02$ (+) and 0.5 ($\times$), and (squares, with $p_{sp} = 0.1$) for Gompertz mortality assumption: $p_d = \exp[(\max(X, X_{rep}) - X_{max})/M]$, using 640 systems for $n_{max} = 100$ and $t = 6000$.

FIG. 5: Semi-log 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, 60000 and 600000 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. 7: Log-log plot of the distribution of lifetimes for the whole ecosystem of ℓ trophic layers, with $\ell = 5, m = 2$ and $\ell = 3, m = 6$, from 1 and 10 systems only; $n_{max} = 100$.

proximately, 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 eco-systems are much more complex than our model eco-system 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

Figs.4,5 show the time-averaged distributions of X_{max}, X_{rep} and M. We see that the minimum age of reproduc-
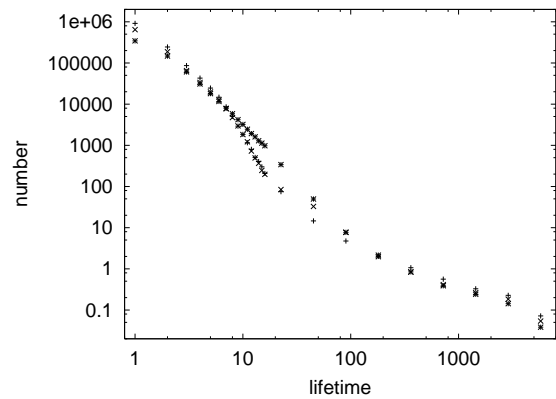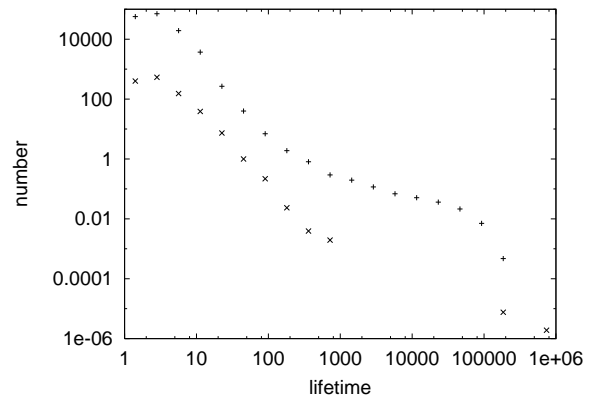
tion X_{rep} is quite small, as usual in a similar ageing model [32]. The age distribution (not shown) decays stronger than a simple exponential, indicating a mortality increasing with age as it should be [29]. The genetic death ages $5 < X_{max} < 100$ reach ages far above the upper end $\simeq 50$ 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 60000 iterations.

We have also observed (not shown) that the higher is the mutation probability p_{mut} the lower is the lifetime of the eco-system; this is consistent with the intuitive expectation that a higher rate of mutation leads to higher levels of biological activity in the eco-system thereby leading to the extinction of larger number of species. Fig.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 muta-

tions 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]).

C. Collapse of fragile ecosystems

We model an eco-system with a *fixed* number ℓ of trophic levels; thus as soon as we find one level to be extinct completely, we regard the eco-system 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 6000) of iterations, see fig.7. This method simulates the billions of years which natural evolution needed to build the present life on earth.

V. SUMMARY AND CONCLUSION

In summary, we have presented a unified model which describes not only the birth, ageing and death of indi-viduals 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 inter-species 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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