Unified “micro”- and “macro”- evolution of eco-systems: Self-organization of a dynamic network

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Very recently we have developed a dynamic network model for eco-systems that achieved “unification” of “micro” and “macro”-evolution. We now propose an extension of our model so as to stabilize the eco-system and describe speciation in a more realistic manner.

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I. INTRODUCTION

It is now widely believed that functional networks abound in biological systems, from molecular level (e.g., genetic and metabolic networks) to the levels of cells, organisms and species. An eco-system may be viewed as a functional network of species where the (directed) links of the network represent the inter-species interactions. These interactions include not only prey-predator interactions but also competitions between species, for the same resources, as well as possible cooperations. Each species is also a network of individual organisms; the intra-species interactions can be cooperative or competitive. The problems of evolutionary ecology have been investigated extensively from the perspective of statistical physics.

In recent papers we have developed a model from the perspective of dynamic networks, by incorporating both inter-species and intra-species interactions, for studying some generic features of the biological evolution of eco-systems. In this paper, following a brief review of this model and its main results, we propose an extension of the model so as to capture speciation in a more realistic manner.

II. EARLIER MODELS AND THEIR LIMITATIONS

For convenience, most of the earlier theories focussed attention either on “micro”- evolution on ecological time scales (e.g., annual variations in the populations of species, mortality rates, etc.) or on “macro”-evolution that is most prominent on geological times scales (e.g., the phenomena of speciation or extinction). The ecological models that describe population dynamics using, for example, Lotka-Volterra type equations, usually ignore macro-evolutionary changes in the eco-system. On the other hand, most of the macro-evolutionary models do not explicitly explore the ageing and age-distributions of the populations of various species in the system. The models of ageing and dynamics of age-distributed populations, usually, focus on only one single species and do not incorporate the inter-species interactions that are, however, crucially important for their extinctions.

But, in reality, evolution is a continuous process. When monitored at short intervals and over a not-too-long period of time, the ecological processes dominate the visible changes in the eco-system. However, if the same system is watched over sufficiently long period of time, the macro-evolutionary changes cannot be missed. Therefore, it is desirable to have a “unified” theoretical model that would unfold the natural continuous process while simulated on a computer. Very recently, attempts have been made by several groups to merge population dynamics and “macro”-evolution within a single mathematical framework. These efforts may have been made feasible, at least in part, because of the availability of fast computers. In our models we have achieved not only the merger of population dynamics and “macro”-evolutionary processes but also detailed description of birth, ageing and death of individual organism so that the age-distributions in the populations of different species can also be monitored.

Moreover, for the study of population dynamics of the species in the eco-system one needs a model of the food web, 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). In contrast to most of the contemporary models published in the physics literature

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(ref.22 is one of the few exceptions), we incorporate the trophic level structures of real food webs through a generic hierarchical model 8. Besides, in order to capture ecological and evolutionary processes within the same theoretical framework, we allow the food web to evolve slowly with time 22.

III. THE NETWORK MODEL: COMPONENT AND MOTIVATIONS

A. Architecture of the network

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. The network considered in our earliest formulation of the "unified" model 7 can be schematically represented by a random network. In a subsequent paper 8 we replaced the random architecture by a generic hierarchical one, where niches are arranged in different trophic levels, with biologically realistic inter-species interactions. 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.

We assume only one single species at the highest level $\ell = 1$. There are $m^{\ell-1}$ levels at the $\ell$-th level where $m$ is a positive integer. The allowed range of $\ell$ is $1 \leq \ell \leq \ell_{\text{max}}$. 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 $N_{\text{max}} = (m^{\ell_{\text{max}}-1})/(m-1)$, the total number of nodes. Our model allows $N(t)$ to fluctuate with time over the range $1 \leq N(t) \leq N_{\text{max}}$. 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 $n_i(t) \leq n_{\text{max}}$. Thus, the total number of organisms $n(t)$ at time $t$ is given by $n(t) = \sum_{i=1}^{N(t)} n_i(t)$. Note that $\ell_{\text{max}}$, $m$ (and, therefore, $N_{\text{max}}$) and $n_{\text{max}}$ are time-independent parameters in the model.

The network itself evolves slowly over sufficiently long time scales. For example, random genetic mutations are captured by implementing random tinkering of some of the intra-node characteristics which will be introduced in the next subsection. The inter-node interactions change slowly to capture adaptive co-evolution of species thereby altering the graph that represents the network. Even the occupants of the nodes can change with time because, as the eco-system evolves, 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.

B. Intra-node characteristics, mutations and dynamics

The faster dynamics within each node captures “micro”-evolution, i.e., the birth, growth (ageing) and natural death of the individual organisms. For simplicity, we assume the reproductions to be asexual. An arbitrary species $i$ is collectively characterized by 7:

(i) the minimum reproduction age $X_{\text{rep}}(i)$,
(ii) the birth rate $M(i)$,
(iii) the maximum possible age $X_{\text{max}}(i) = 100 \times 2^{(1-\ell)/2}$ that depends only on the trajectory level occupied by the species.

An individual of the species $i$ can reproduce only after attaining the age $X_{\text{rep}}(i)$. 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 $X_{\text{max}}(i)$, even if an individual manages to escape its predators. The explicit form of $X_{\text{max}}$ assumed above is intended to mimic the fact that the species at the higher trophic level usually have higher lifespan.

During each time step, because of random genetic mutations, $X_{\text{rep}}$ and $M$ independently increase or decrease by unity, with equal probability, $p_{\text{mut}}$. $X_{\text{rep}}$ is not allowed to exceed a predetermined (large) positive integer while $M$ is restricted to remain positive.

The intra-species competitions among the organisms of the same species for limited availability of resources, other than food, imposes an upper limit $n_{\text{max}}$ of the allowed population of each species. In order to capture this requirement, we assume the time-dependent probability $p_b(i, \alpha)$ (of individual $\alpha$ in species $i$) of giving birth per unit time to be a product of two factors; one of the factors is a standard Verhulst factor $1 - n_i/n_{\text{max}}$ whereas the other factor takes into account the age-dependence of $p_b(i, \alpha)$. For an organisms, this second factor becomes non-zero only when it attains the corresponding minimum reproductive age $X_{\text{rep}}$; this non-zero factor is assumed to be of the form $(X_{\text{max}} - X)/(X_{\text{max}} - X_{\text{rep}})$. Note that the latter factor is unity at $X = X_{\text{rep}}$, and thereafter decreases linearly with age, to zero at $X_{\text{max}}$. Thus in the limit of vanishingly small population, i.e., $n_i \to 0$, we have $p_b(i, \alpha) \to 1$ if $X(i, \alpha) = X_{\text{rep}}(i)$ and, thereafter, $p_b$ decreases linearly as the organism grows older. However, $p_b(i, \alpha; t) \to 0$ as $n_i(t) \to n_{\text{max}}$, irrespective of the age of the individual organism $\alpha$. Occasionally, random mutations mentioned
above can lead to anomalous situations where some organisms may have $X_{rep} > X_{max}$; for such organisms $p_b(i, \alpha; t) = 0$ for all $t$ and these fail to reproduce during their entire life time.

Similarly, we have the probability $p_d$ of “natural” death (due to ageing) to be a constant $p_d = \exp(-r(X_{max} - X_{rep})/M)$, where $r$ is a small fraction, so long as $X < X_{rep}$. However, for $X > X_{rep}$, the probability of natural death increases exponentially (following Gompertz law) as $p_d = \exp[-r(X_{max} - X)/M]$. Note that, for a given $X_{max}$ and $X_{rep}$, the larger the $M$ the higher is the $p_d$ for any age $X$. Therefore, in order maximize reproductive success, 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 \[24\].

Because of the natural death mentioned above and, more importantly, prey-predator interactions (to be described in the next subsection), the populations of some species may fall to zero. The nodes left empty by such extinct species are then re-filled by new species. In order to capture this process of speciation, all the empty nodes in a trophic level of the network are re-filled by random mutants of one common ancestor which is picked up randomly from among the non-extinct species at the same trophic level. The subsequent accumulation of random mutations over sufficiently long time leads to the divergence of the genomes of the parent and daughter species that is an essential feature of speciation.

However, occasionally, all the niches at a level may lie vacant. Under such circumstances, all these vacant nodes are to be filled by a mutant of the non-extinct species occupying the closest lower level. In our computer simulations, the search for this non-extinct species is carried out in steps, if even the lower level is also completely empty, the search for survivor shifts to the next lower level and the process continues till the lowest level is reached. If all the nodes, starting from the lowest, up to a certain level ever fall vacant, then, no new speciation takes place and the starvation deaths of the species propagate up the layers ending, finally, with the collapse of the entire eco-system.

C. Inter-node interactions and dynamics

The interaction between any two species $i, k$ that occupy two adjacent trophic levels is given by $J_{ik}$. 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 $i$. In the absence of any prey-predator interaction between the species $i$ and $k$, $J_{ik} = 0$. For simplicity, we assume the absolute value (magnitudes) of all the non-vanishing interactions to be unity. 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.

The $J$ account not only for the inter-species interactions but also intra-species competitions for food. 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. Because of the larger body size of the predators, we assume that a predator eats $m$ prey per time interval. Then, $S_i^+$ gives the available food for species $i$, and $S_i^-$ is the contribution of species $i$ to the available food for all predators on the next 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.

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.

It is well known that each species tries to minimize predators but, at the same time, looks for new food resources. In order to capture this, at each time step, each of the species in our model, with the probability $p_{mut}$, re-adjusts a link $J$ from one of its predators and another to one of its potential preys \[28\]. If the link $J_{ij}$ to the species $i$ from a higher level species is non-zero, it is reassigned a new value $J_{ij} = J_{ji} = 0$. On the other hand, if the link $J_{ik}$ to a species $i$ from a lower level species $k$ was zero, the new values assigned are $J_{ik} = 1, J_{ki} = -1$.

D. Initial conditions and update rules

The requirements of computational resources increase exponentially with increasing $\ell_{max}$. Therefore, in almost all our simulations we chose $\ell_{max} = 5$, although we verified that the qualitative features of the data were similar in case of smaller $\ell_{max}$. In our simulations, we always began with a random initial condition where $M = 1$ for all species. Since larger species occupy the higher trophic levels and are expected to live longer than those at lower levels, we assigned $X_{max} = 100, 71, 50, 35, 25$ to the species at level $\ell = 1, 2, 3, 4, 5$, respectively. Initially, $X_{rep}$ was assigned randomly between 1 and $X_{max}$, the population randomly between 1 and $n_{max}/2$. The ages of the individuals in the initial state varied randomly between 1 and the $X_{max}$ of the corresponding species.

The state of the system is updated in discrete time steps as follows:
Step I- Birth: Each individual organism $\alpha$ ($\alpha = 1, ..., n_i(t)$) of the species $i$ ($i = 1, 2, ..., N(t)$) is allowed to give birth to $M_i(t)$ offspring at every time step $t$ with probability (per unit time) $p_b(i, \alpha; t)$ the explicit form of which has been mentioned above.

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, mutations of intra-node characteristics and the interactions $J$ are implemented.

Step IV- Starvation death and killing by prey:
At every time step $t$, in addition to the natural death due to ageing, a further reduction of the population by

$$C \max(S_i^-, n_i - S_i^+)$$

(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: The nodes left empty by extinction are re-filled by new species, with probability $p_{sp}$ following the algorithm for speciation mentioned above.

The longest runs in our computer simulations were continued up to $10^8$ 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 total time for which we have monitored our model eco-system, is comparable to real geological times scales.
IV. RESULTS

A. Lifetime distributions

The average distributions of the lifetimes of the species are plotted in Fig.1. It is not possible to fit a straight line through the data over the entire range of lifetimes although only a limited regime is consistent with a power-law with the effective exponent 2, which has been predicted by several models of “macro”-evolution [4, 5]. The overlap of the curves for different simulation times establishes that our simulations have reached the asymptotic regime where effects of initial conditions have been completely washed out. Because of the various known limitations of the available fossil data, it is questionable whether real extinctions follow power laws and, if so, over how many orders of magnitude.

B. Distributions of Species Characteristics

We define the mortality rate by the relation $-d \frac{\ln(survivors)}{d(age)}$. The mortality rate extracted from the raw data is plotted against age in Fig.2. The shape of this curve is consistent with the usual census data that show a minimum in childhood and exponential increase in adults.

During the early stages of the macro-evolution, the distributions of $M$ broadens. But, with further passage of time it shrinks and reaches a stationary form where the largest $M$ is around 30 (for the parameter set used in our simulations). This is consistent with the view that organisms have a choice of either faster reproduction and shorter life or slower reproduction and longer life span.

FIG. 2: Semi-log plot of the mortality function against age of the individual organisms at the highest trophic level. The same symbols in Fig.1 and Fig.2 correspond to the same set of parameter values.
C. Collapse of fragile ecosystems

One crucial effect of the generalization of the rule for speciation proposed in this paper is that the eco-systems are now much more stabilized than in our earlier papers \[7, 8\]. In our earlier work, reported in ref.\[8\] we allowed an empty node to be re-occupied by one of the non-extinct species from only the same level where the extinct node was located. If, by chance, all the nodes of one level fell vacant at some stage, no speciation could take place; this would trigger an avalanche of extinctions that would propagate upward in the food chain because of starvation of the organisms and eventually lead to a collapse of the entire eco-system. In contrast, in the current version of our model, speciation is allowed to take place from lower levels if all the nodes in an entire level become vacant. This reduces the possibility of collapse of the eco-system but does not rule it out completely. Work on further stabilization of the eco-system with variable $\ell_{max}$ is in progress and will be reported elsewhere in a future publication \[29\].

V. SUMMARY AND CONCLUSION

In summary, we have extended our dynamic network model for unified description of micro- and macro-evolution. A majority of the main characteristics of the model are emergent properties of the self-organizing dynamics of the system. The main effect of the extension of the speciation dynamics proposed in this paper is that even after large avalanches of extinctions the eco-system can recover by speciation and bio-diversification starting from the surviving species at the low trophic levels. Consequently, the complete collapse of the eco-system becomes extremely rare and the distribution of the litter size $M$ became stationary much faster.

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