Sole-Manrubia model of biological evolution: some new insights

Debashish Chowdhury\textsuperscript{1} and Dietrich Stauffer\textsuperscript{2}

\textsuperscript{1}Department of Physics, Indian Institute of Technology, Kanpur 208 016, India.
\textsuperscript{2}Institute for Theoretical Physics, University of Cologne, 50923 Köln, Germany.

The Sole-Manrubia model of “macro”-evolution describes the origination, evolution and extinction of species on geological time scales. We report some properties of this model which provide deep insight into this simple model which captures several realistic features.

I. INTRODUCTION

Several fundamental questions on the origination, evolution and extinction of species have been addressed in the recent years by theoretical treatments of dynamic network models using the concepts and techniques of non-equilibrium statistical mechanics\textsuperscript{1,2}. Kauffman\textsuperscript{3} pioneered a model which describes biological evolution as a “walk” in a “fitness landscape” and argued that the eco-system adaptively evolves so as to be delicately poised “at the edge of chaos”. On the other hand, Bak and Sneppen\textsuperscript{4}, suggested an alternative way of implementing the Darwinian principle of selection (the “survival of the fittest”): this dynamics naturally leads the eco-system to a “self-organized” critical state\textsuperscript{5}. These models implicitly assume a primarily biotic cause of extinctions. However, models based on purely abiotic causes, which arise from “environmental stresses” also lead to similar pattern of extinctions of species\textsuperscript{2,6}.

A few years ago Sole and Manrubia (SM)\textsuperscript{7} introduced one such model of “macro”-evolution that takes into account the inter-species interactions explicitly. They reported several statistical properties of the model as well as their biological implications. In this paper we report some other statistical properties of this model; some of these features are qualitatively similar to the corresponding results obtained in a more recent model\textsuperscript{8}. Moreover, we re-interpret some of the quantities in their approach to extract some relevant biological implications of the model. Furthermore, we introduce a new correlation function throwing light on the “volatility” of the fitness and the level of “coherence” in the changes of fitness of the species in this model.

II. THE MODEL

For the sake of completeness, we briefly present the SM model and its main published results.

The system consists of $N$ species, each labelled by an index $i$ $(i = 1, 2, \ldots, N)$. The states of the $i$-th species is represented by a two-state variable $S_i$: $S_i = 0$ or 1 depending on whether it is extinct or alive, respectively. The inter-species interactions are captured by the interaction matrix $J$; the element $J_{ij}$ denotes the influence of the species $j$ on the species $i$. If $J_{ij} > 0$ while, simultaneously, $J_{ji} < 0$ then $i$ is the predator and $j$ is the prey. On the other hand, if both $J_{ij}$ and $J_{ji}$ are positive (negative) they are the two species cooperate (compete).

The dynamics of the system consists in updating the states of the system (i.e., to determine the state at the time step $t + 1$ from a complete knowledge of the state at the time $t$) in the following three steps:

\begin{enumerate}
  \item \textit{Step (i)}: One of the input connections $J_{ij}$ for each species $i$ is picked up randomly and assigned a new value drawn from the uniform distribution in the interval $[-1, 1]$, irrespective of its previous magnitude and sign.
  \item \textit{Step (ii)}: The new state of each of the species is decided by the equation

  \begin{equation}
  S_i(t + 1) = \Theta\left(\sum_{j=1}^{N} J_{ij} S_j(t) - \theta_i\right)
  \end{equation}

  where $\theta_i$ is a threshold parameter for the species $i$ and $\Theta(x)$ is the standard step function, i.e., $\Theta(x) = 1$ if $x > 0$ but zero otherwise. If $S(t + 1)$ becomes zero for $m$ species, then an extinction of size $m$ is said to have taken place.
  \item \textit{Step (iii)}: All the niches left vacant by the extinct species are refilled by copies of one of the randomly selected non-extinct species.
\end{enumerate}

Sole and Manrubia recorded extinctions of sizes as large as 500 and the distributions of the sizes of these extinctions could be fitted to a power law of the form $N(m) \sim m^{-\alpha}$ with an exponent $\alpha \approx 2.3$. Moreover the periods of stasis $t_s$ were also found to obey a power law $N(t_s) \sim t_s^{-\gamma}$ with the exponent $\gamma \approx 3.0$. However, surprisingly, in none of their papers\textsuperscript{3,9}, Sole and his collaborators reported the distributions of the lifetimes of species which, according to some claims (see, for example, refs.\textsuperscript{1,2} for references to the experimental literature and data analysis), also follows a power law.
FIG. 1: Log-log plots of the distributions of the lifetimes of the species in the SM model with $N = 100$, $t_w = 10^6$, $t_m = 8 \times 10^6$ (+), $N = 300$, $t_w = 10^4$, $t_m = 8 \times 10^4$ (x), $N = 1000$, $t_w = 10^4$, $t_m = 8 \times 10^4$ (*). The solid line (with slope $-1$) and the dashed line (with slope $-1.5$) are drawn just for the comparison of the simulation data with power law of the form $N_t \sim t^{-x}$.

FIG. 2: Distribution of the fitnesses of the species in the SM model with $N = 100$, $t_w = 10^5$, $t_m = 10^6$.

III. RESULTS AND DISCUSSIONS

In most of the food webs recorded so far only the sign (but not the magnitude) of the inter-species interactions are noted. Moreover, all the qualitative features of the SM model remain unchanged if, instead of allowing the elements $J_{ij}$ to take any real value in the domain $[-1, 1]$ with equal probability, we allow $J_{ij}$ to be only $+1$ or $-1$ with equal probability. Therefore, we work with the simpler version of the SM model where each of the elements of $J$ are discrete.
FIG. 3: Distributions of the incremental changes (per unit time step) in the fitness of the species in the SM model with $N = 100$, $t_w = 10^5$, $t_m = 10^6$.

binary variables that can be either $+1$ or $-1$.

In our simulations we let the system “warm up” for $t_w$ time steps, starting from a random initial condition, and then run it for further $t_m$ time steps during which collect the data.

A. Distribution of lifetimes

It has been claimed in the literature [1, 2] that the distributions of the lifetimes of the extinct species, estimated from the fossil data, can be fitted to a power law of the form

$$P_t(\tau) \sim \tau^{-x}$$

(2)

where several possible values of $x$, ranging from 1 to 2 have been suggested. However, the log-log plot of our data in fig. 1, obtained from the simulation of the SM model, demonstrates that an approximate power-law-like behaviour is seen only over nearly one decade of short lifetimes while strong deviations from power-law are seen for longer lifetimes. While the sharp drop of the curves in the tail region can be attributed to finite time effects, the deviations from the early power-law-like region at around $\tau \simeq 10$ is neither an artefact of finite time of simulation nor that of finite size of the system [9].

B. Fitness

It was originally pointed out by SM [7] that $f_i = \sum_{i,j} J_{ij} S_j - \theta_i$ may be taken as a measure of the “fitness” of the species $i$; the larger the $f_i$ the higher is the fitness of the corresponding species $i$. This definition of “fitness” is, of course, consistent with the expectation in the Darwinian scenario that, at any arbitrary stage of evolution, the species with positive fitness would not become extinct. Instead of studying the statistics of $P(f_i)$, or its time-average, SM investigated the relation between the species-averaged value of $f_i$, i.e., $f_T = \sum_i f_i/N$, and the size of the extinctions.

We have now computed the time-averaged probability distribution $< P(f_i) >$, following SM, we also take $\theta_i = 0$ for all $i$. From this distribution (see fig. 2) it is clear that, on the average, there are very few species which do not possess adequate fitness required for survival and, therefore, become extinct. However, the distribution $P(f_i)$ fluctuates with time and exhibits significant negative fitnesses when extinction occurs. In these stochastic network models of ecosystems, the species become extinct because of “bad luck” rather than “bad genes” [10].
FIG. 4: The sizes of the extinctions and the volatility are plotted against time in (a) and (b), respectively. Data are shown only over approximately two and half orders of magnitude, from the top, to highlight the strong correlation between the two quantities plotted in (a) and (b).

We define the incremental change of fitness of a species, say, $i$, per unit time step as

$$\Delta f_i(t) = f_i(t) - f_i(t - 1) \quad (3)$$

The distribution of $\Delta f_i$ is shown in fig.3; it falls roughly exponentially in the tail region.

C. Volatility and Coherence

Borrowing the concept of “volatility” in financial markets [11, 12], we now define the “volatility” in the eco-system by

$$V(t) = C_1 \sum_i (\Delta f_i)^2 \quad (4)$$
FIG. 5: The correlation function $C$ is plotted against time. The data for $C < 10^7$ are not shown to make the plot less crowded and making the comparison with fig. more convenient.

and the time-dependent correlation function by

$$C(t) = C_2 \sum_{i<j} (\Delta f_i)(\Delta f_j)$$  \hspace{1cm} (5)

where the normalization factors $C_1$ and $C_2$ can be chosen appropriately. For simplicity, we worked with $C_1 = 1 = C_2$. We have also measured the sizes of the extinctions by the fractions $m/N$ where $m$ is the numbers of species that become extinct simultaneously at the same time step and $N$ is the total number of species in the system.

Large extinctions occur when volatility is also large (see fig.4). $C$ is a measure of "coherence" in the changes in the fitness of the species during the same period of time. Interestingly, this correlation function is very rarely negative. Even when it takes negative value, the corresponding magnitude is not large. So, most of the species do not profit from the extinction of others.

D. Single common ancestor

Each node $i$ ($i = 1, 2, ..., N$) carries a label $L(i)$ that indicates the identity of its ancestor. In the initial state we assign $L(i) = i$. During the evolution of the system, whenever a node $\beta$ becomes extinct and is, therefore, re-populated by the species occupying the node $\alpha$ we re-label the node $\beta$ with $L(\alpha)$, i.e., the node $\beta$ also carries the label $L(\alpha)$. From our simulation we have always found that, after sufficiently long time, all the nodes carry the same label thereby indicating that all the living organisms at that stage share a single common ancestor from which all the wide variety of species have appeared as a result of massive diversification. This is perfectly consistent with theory \cite{13} and the fossil record \cite{14}. The distributions of the sizes of phylogenic trees had already been studied by Sole and Manrubia \cite{7}.

IV. SUMMARY

We have computed the distribution of the lifetimes of the species in SM model; the deviations from the pure power-law behavior observed for the SM model is similar to that in a recent model that describes both "macro"-evolution as well as "micro"-evolution \cite{8}. We have also interpreted $f_i = \sum_j J_{ij}S_j$ as the fitness of the species $i$ and investigated the distributions of fitness as well as the incremental changes of fitness per unit time. Finally, we have introduced the concepts of volatility and coherence; computing these for the SM model as functions of time, we have demonstrated their close relation with the sizes of extinctions.
V. ACKNOWLEDGEMENT

This work is supported in part by the Alexander von Humboldt Foundation and by the Deutche Forschungs-gemeinschaft (DFG) through a joint Indo-German research project. We also thank the Supercomputer center, Jülich, for computer time on their CRAY-T3E.

[1] B. Drossel, Adv. Phys. 50, 209 (2001)
[2] M.E.J. Newman and R.G. Palmer, [dap-org/9908002](https://doi.org/10.1023/A:1021882508365)
[3] S. Kauffman The Origins of Order: Self-organization and selection in Evolution (Oxford University Press, New York, 1993)
[4] P. Bak How Nature Works (Copernicus books, New York, 1999)
[5] H.J. Jensen, Self-organized Criticality: Emergent Complex Behavior in Physical and Biological Systems (Cambridge University Press, Cambridge, 2000)
[6] M.E.J. Newman, J. Theor. Biol. 189, 235 (1997)
[7] R.V. Sole and S.C. Manrubia, Phys. Rev. E 54, R42 (1996); 55, 4500 (1997)
[8] D. Chowdhury, D. Stauffer and A. Kunwar, [cond-mat/0207352](https://arxiv.org/abs/cond-mat/0207352)
[9] D. Chowdhury and D. Stauffer, unpublished.
[10] D. Raup, Extinctions: Bad Genes or Bad Luck? (Oxford University Press, 1993)
[11] R.N. Mantegna and H.E. Stanley, An Introduction to Econophysics: Correlations and Complexity in Finance (Cambridge University Press, 1999)
[12] J.P. Bouchaud and M. Potters, Theory of Financial Risks: From Statistical Physics to Risk Management (Cambridge University Press, 2000)
[13] T.E. Harris, The Theory of Branching Processes (Dover Publications, New York, 1989)
[14] M.J. Benton, Science 268, 52 (1995)