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Extremal dynamics in random replicator ecosystems

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ABSTRACT

The seminal numerical experiment by Bak and Sneppen (BS) is repeated, along with computations with replicator models, including a greater amount of features. Both types of models do self-organize, and do obey power-law scaling for the size distribution of activity cycles. However species extinction within the replicator models interferes with the BS self-organized critical (SOC) activity. Speciation–extinction dynamics ruins any stationary state which might contain a steady size distribution of activity cycles. The BS-type activity appears as a dissimilar phenomenon in comparison to speciation–extinction dynamics in the replicator system. No criticality is found from the speciation–extinction dynamics. Neither are speciations and extinctions in real biological macroevolution known to contain any diverging distributions, or self-organization towards any critical state. Consequently, biological macroevolution probably is not a self-organized critical phenomenon.

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1. Introduction

At the beginning of the 1900s, people realized the development of new species probably does not occur through any gradual evolution process [1,2]. The appearance of species apparently lacks continuity [3–6]. Evolution can possibly be described in terms of a *punctuated equilibrium*: the system of life becomes settled into a stasis, which then becomes disturbed by species appearances and avalanches of extinctions. A dramatic avalanche of extinction is often followed by rapid recovery [5,7]. In the light of fossil records, the evolution of species may appear to be a self-organized critical phenomenon, the size distribution of extinction events possibly following a power law [4,8,5,7,9].

A variety of computational approaches have been used in order to investigate the evolution of life [10–12]. The model by Bak and Sneppen [13,14,9], was claimed to self-arrange into a critical state. System states where observables are scale-free are often interpreted as critical [15–20]. In other words, critical systems show fractal properties, observables being distributed according to power-laws [15,16,18,21,17,20]. However, power-law distributed observables may appear simply as a result of a random process, and do not necessarily imply divergence [22,20,23–25].

Not all critical systems self-organize to their critical point. Scale-free behaviour may be found simply by tuning system parameters towards a critical phase transition. It obviously is disputable whether or not self-organized criticality is a phenomenon characteristic to wide variety of complex systems in Nature [26,15–17,19,15,9,20].

One of the most functional ways of modeling ecological systems is the use of replicator equations. Replicators refer to systems where a configuration of "strategies" or "species" contributes to the "fitness" or "payoff" of any particular strategy. The "fitness" or "payoff" in turn contributes to the abundance of each "strategy" or "species". An important contrast to the catalytic network model [27–33] is that the fitness regulates abundance in relation to the existing abundance. In other words, within the replicator model, parents of the same species are needed.

Early attempts to directly apply random replicator models in investigations into the evolution of life have either not produced large, complex ecosystems, or have not resulted in large, recovering avalanches of extinctions, depending on the parameters used [30,34–37]. Recently, a variety of parameters have been introduced in random replicator models, resulting as more features in the corresponding systems [38]. However, systems with fluctuations of a wide variety of sizes can only be produced by tuning the parameters [38]. The replicator ecosystems with speciation and inheritance do not self-arrange to any critical state.

There is a discrepancy between the Bak–Sneppen evolution model and the replicator models, as the latter do not show any sign of self-organized criticality. The discrepancy may be related to a question of wider applicability. It has been argued that not only evolution of a system of species in nature is a self-organized critical process [4,8,5,7,9], but that many phenomena in the complex Nature, living as well as non-living, are dominated by contingency and show self-organized critical behavior with power-law

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distributed observables [5]. We hope the present study with evolution models will give some hint whether Nature, in large, essentially consists of systems showing self-organized critical features [39,7,40].

2. Bak–Sneppen model

Key features of the Bak–Sneppen model are extremal dynamics on the one hand, and spatial correlations on the other [13,21]. The former arises from Boltzmann statistics: species with the lowest fitness barrier are assumed to mutate first. The latter constitutes a simplified description of species interaction.

Within the BS-model, any species has one property: randomly assigned fitness. Species are arranged on a one-dimensional array with periodic boundary conditions. Extremal dynamics activates the species with the lowest fitness. That species is assigned another random fitness value. Spatial correlations are introduced by simultaneously assigning new fitness values for the two nearest neighbors of the triggering species. Consequently, any mutation event changes the fitness of three species.

Along with increasing number of mutation cycles, such a system arranges to a stationary state where, in the case of a system with many species, the lowest fitness never appears to exceed a particular threshold value. In other words, the fitness space becomes divided in two phases, an active phase and an inert phase. Species with fitness in the active phase may trigger mutations, whereas species with fitness in the inert phase do not. The latter however may mutate in events triggered by one of their nearest neighbors.

Within the BS-model, an activity cycle starts when the lowest fitness falls below another threshold value, a cycle threshold taken somewhat below the phase boundary. The cycle terminates when there no longer is any species with fitness below the cycle threshold, the size of the cycle being the number of newly assigned fitness values within the cycle.

The above indicates that in the stationary state, results are likely to depend on the selection of the cycle threshold. This appears problematical. However, it has been shown that once model self-organizes to the phase boundary, it is critical at the phase boundary (“self-organizing threshold”) [41,42]. Criticality can readily be understood in terms of the probability of the smallest fitness to gain a particular value vanishing at the phase boundary. Consequently, the average activity cycle size diverges.

It also appears that there is a hierarchy of activity cycle sizes (“avalanches”) as a function of cycle threshold f_0 distance from the self-organizing threshold f_c, and average activity cycle size obeys a scaling relation [41,42]

$$\langle S\rangle \propto (f_c - f_0)^{-\gamma}. \tag{1}$$

In one dimension, the scaling exponent γ appears to be in the order of 2.7, and in two dimensions in the order of 1.7 [41,43,42]. The d-dimensional BS-system may belong to the same universality class with $d+1$ directed percolation, which would imply scaling exponents approaching unity with increasing dimensionality [43–45].

We first repeated the one-dimensional BS-experiment with a system of 300 species. Extremal dynamics did organize the fitness space in two phases, and the probability of the smallest fitness getting a particular value vanished at the phase boundary. Below the phase boundary, the average cycle size did obey the scaling law (1), with exponent γ in the order of 2.61 instead of 2.70 [cf. [43,42]], possibly due to the finite size of the present experiment.

3. One-dimensional replicator model

The one-dimensional replicator model is here designed to resemble the Bak–Sneppen model. Instead of designing any speciation procedure, a constant number of species is introduced, the initial abundance of any species corresponding to the inverse of the number of species. Random interaction coefficients are drawn from a Gaussian distribution of zero mean and unit variance, the interaction coefficients constituting a square matrix of linear dimension corresponding to the number of species. The diagonal of the matrix is then replaced by self-interaction coefficients, drawn from a Gaussian with predetermined mean value and 20% standard deviation [cf. [38]].

The interaction matrix produced according to the procedure above is fully occupied, and any species interacts with all other species. In order to compose a one-dimensional system, any species shall interact only with its neighbors within a one-dimensional array. This is implemented by applying vacancies in the interaction matrix. A nearest-neighbor interaction is produced by leaving $3n$ interaction coefficients nonvacant, with periodic boundary conditions, n corresponding to the linear size of the system. Thus there are n self-interaction coefficients and $2n$ nearest-neighbor interaction coefficients

The sparse interaction matrix produced this way corresponds to the asymmetric case. In other words, nondiagonal interaction coefficients Z_{ij} and Z_{ji} have zero covariance. In order to introduce either symmetry or antisymmetry, some amount of covariance must be induced. This was implemented by replacing Z_{ij} and Z_{ji}, for $i<j$, with

$$\begin{aligned} K_{ij} &= Z_{ij} \\ K_{ji} &= \Gamma Z_{ij} + \sqrt{1-\Gamma^2}\, Z_{ji}, \end{aligned} \tag{2}$$

where Γ refers to a symmetry parameter with values between unity and negative unity, the value zero corresponding to the asymmetric interactions. Correspondingly, K_{ij} and K_{ji} refer to nondiagonal interaction coefficients with possibly some covariance.

A fitness vector is then produced as the product of the interaction matrix and the configuration vector $\mathbf{x}$, or equivalently

$$F_i = \frac{K_{ij} x_j}{\sum x}. \tag{3}$$

Any species abundance is then assumed to change according to the replicator equation

$$\left(\frac{\Delta x}{x}\right)_i = F_i - \langle F\rangle = F_i - \frac{\mathbf{x}\cdot\mathbf{F}}{\sum x}. \tag{4}$$

Equations (3) and (4) are applied repeatedly until an equilibrium species configuration is found.

Extremal dynamics is then applied to the one-dimensional replicator system by mutating the species with lowest fitness. Mutation of the species corresponds to reassigning the interaction coefficients where the mutating species is involved. This immediately changes the fitnesses of the mutating species and its nearest neighbors according to Eq. (3). Further, the abundances of all the species are changed according to Eq. (4). Again, Eqs. (3) and (4) are applied repeatedly until equilibrium species abundances are found.

Species with abundance vanishing below a small threshold value in the vicinity of zero are considered extinct and removed from the system. This must be done in order to avoid a fitness barrier to be formed by clusters of at least three species with zero abundances at zero fitness, according to Eq. (3). Such a barrier would ruin any extremal dynamics.

Extremal dynamics will possibly make the system to self-organize. The eventual self-organizing threshold f_c, in terms of

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