

Received:

5 April 2016

Revised:

25 July 2016

Accepted:

16 August 2016

Heliyon 2 (2016) e00144



Evolution models with extremal dynamics

Petri P. Kärenlampi *

University of Eastern Finland, PO Box 111, Joensuu 80101, Finland

* Corresponding author.

E-mail address: petri.karenlampi@uef.fi (P.P. Kärenlampi).

Abstract

The random-neighbor version of the Bak-Sneppen biological evolution model is reproduced, along with an analogous model of random replicators, the latter eventually experiencing topology changes. In the absence of topology changes, both types of models self-organize to a critical state. Species extinctions in the replicator system degenerates the self-organization to a random walk, as does vanishing of species interaction for the BS-model. A replicator model with speciation is introduced, experiencing dramatic topology changes. It produces a variety of features, but self-organizes to a possibly critical state only in a few special cases. Speciation-extinction dynamics interfering with self-organization, biological macroevolution probably is not a self-organized critical system.

Keywords: Statistical physics, Mathematical biosciences

1. Introduction

The evolution of life apparently proceeds as a stepwise process, instead of a smooth development [1, 2]. The emergence of species apparently lacks continuity [3, 4, 5, 6]. Evolution can possibly be described in terms of a *punctuated equilibrium*: the system of life settles into a stasis, which then becomes disturbed by species appearances and avalanches of extinctions. An avalanche of extinctions is often followed by rapid recovery [5, 7]. 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, 5, 7, 8, 9].

A few computational approaches have been used in order to investigate the evolution of life [10, 11, 12]. The model by Bak and Sneppen [9, 13, 14], was claimed to self-arrange into a critical state. System states where observables are scale-free are often interpreted as critical [15, 16, 17, 18, 19, 20]. In other words, critical systems show fractal properties, observables being distributed according to power-laws [15, 16, 17, 18, 20, 21]. However, power-law distributed observables may appear simply as a result of a random process, and do not necessarily imply criticality, in the sense that the distribution of some observable would diverge [20, 22, 23, 24, 25].

Not all critical systems are self-organized. Scale-free behavior 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 [9, 15, 16, 17, 19, 20, 26].

One functional way of modelling ecological systems is the use of replicator equations. Replicators refer to systems where a configuration of “strategies” or “species” contributes to the “payoff” or “fitness” of any particular strategy. The “payoff” or “fitness” in turn contributes to the abundance of each “strategy” or “species”. A difference to a catalytic network model [27, 28, 29, 30, 31, 32, 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. It has been shown that the generalized Lotka-Volterra – system is a tedious way of implementing a replicator system [34].

Early attempts to apply random replicator models 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, 35, 36, 37, 38]. Recently, a variety of parameters have been, resulting as more features in the corresponding systems [34]. However, systems with fluctuations of a wide variety of sizes can only be produced by tuning the parameters; the replicator ecosystems with speciation do not self-arrange to any critical state [34].

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. A recent investigation with one-dimensional models indicates extinction dynamics may interfere with self-organization [39]. The discrepancy possibly is 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, 5, 7, 8, 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 distributed observables [9]. 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 [7, 40, 41].

We will introduce a sequence of evolution models, focusing in multidimensional systems. First, we implement a finite random-neighbor Bak-Sneppen (BS) model [14, 42, 43, 44, 45], where the number of species and average among-species connectivity appear as relevant system parameters. Then, we establish an analogous finite random replicator model where however topology may change due to species extinctions, as well as due to re-allocation of connections. In this model, inheritance is introduced. Relative strength of self-interaction, as well as symmetry of interactions, appear as additional free parameters. Finally, we introduce a replicator model with speciation. Instead of preferential attachment [46] or fitness network [47] we stick to BS-type extremal dynamics. Such a model, originating from a single species, experiences drastic topology changes, and possibly mimics biological macroevolution in Nature.

2. Model

2.1. Model 1

2.1.1. *Bak-sneppen random neighbor model*

Key features of the Bak-Sneppen (BS) model are extremal dynamics on the one hand, and spatial correlations on the other [13, 21]. The former is based on the assumption that species with the lowest fitness barrier mutate first. The latter constitutes a simplified description of species interaction. In the one-dimensional model, any species interacts with two nearest neighbors [13, 21]. Later on, the treatment has been extended to higher-dimensional lattices [48], small-world networks [49, 50], scale-free networks [42, 43, 44], as well as random graphs as a special case of the latter [14, 45, 51].

Within the BS-model, any species has one independent property: randomly assigned fitness. Extremal dynamics activates the species with the lowest fitness. That species is assigned another random fitness value. Spatial correlations are applied by simultaneously assigning new fitness values for the immediate neighbors of the triggering species. In multidimensional cases, the randomly assigned neighbors may arise either from a quenched or an annealed randomness [14, 43, 51].

Along with increasing number of mutation cycles, a BS-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 [13, 14, 21, 52]. 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”) [52, 53]. Criticality can readily be understood in terms of the probability of a particular fitness to be the smallest fitness vanishes 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 [52, 53]

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

In one dimensional regular lattice system, the scaling exponent γ appears to be in the order of 2.7, and in two dimensions in the order of 1.7 [52, 53, 54]. The d -dimensional BS-system has been believed to belong to the same universality class with $d + 1$ directed percolation, which would imply the scaling exponent approaching unity with increasing dimensionality [53, 54, 55, 56]. In random neighbor systems, the exponent thus should approach unity [14, 22, 52, 57]. A self-organization threshold of $1/(1 + k)$, where k is the average degree of minimum-fitness nodes, has been reported for random-neighbor systems in the annealed case [14, 43, 45, 58].

We first implemented random-neighbor BS-experiments, with both annealed and quenched randomness, with 300 and 3000 species (or nodes). The annealed case corresponds to a new drawing of among-species connections of the triggering species at the instant of any mutation event. 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. Fig. 1 shows the probability density of smallest fitness in the annealed case. There obviously is a size effect, the phase boundary gaining a lower value with the larger system (dotted lines in Fig. 1), in comparison to smaller systems with similar average degree of the nodes. Disappearing species interactions (connectivity getting to zero) degenerates the self-organization to a random process within the entire fitness space. Interestingly,

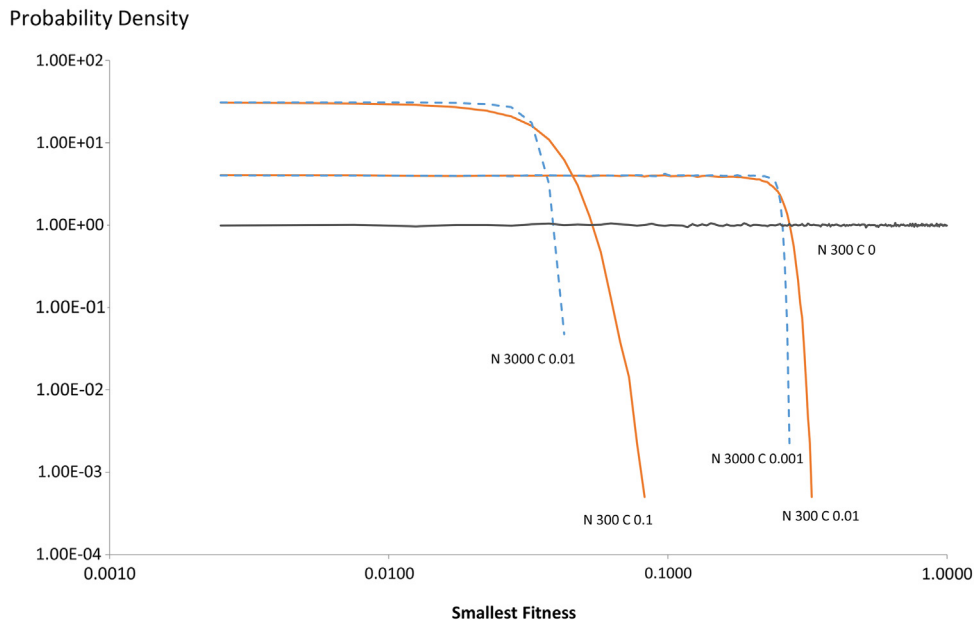


Fig. 1. Probability density of smallest fitness with random-neighbor BS-systems with annealed disorder. Results for quenched disorder were similar. Labels refer to the number of species (nodes) in any experiment, as well as the connection probability between nodes.

results for the systems with quenched disorder were virtually indistinguishable from the annealed results shown in Fig. 1 [cf. 43, 44].

Fig. 2 shows the average activity cycle size as a function of the cycle threshold f_0 distance from the self-organizing threshold f_c , apparently following the power law (1) with exponent γ which very significantly differs from unity, in direct contradiction with previously presented arguments [14]. The scaling exponent approaches unity only in the case of vanishing species interaction, where

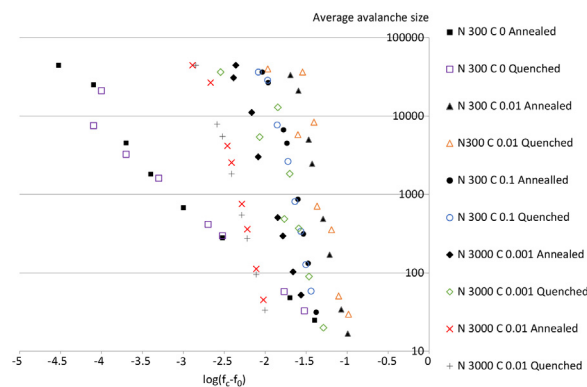


Fig. 2. Average activity cycle size in the random-neighbor BS-model, as a function of separation between the self-organizing threshold and cycle threshold. Legend refers to the number of species (nodes) in any experiment, as well as the connection probability between nodes.

self-organization has degenerated to a random process (Fig. 2). In other cases the exponent is in the order of 4, regardless whether the randomness in species connections is quenched or annealed, the quenched case apparently showing somewhat more scattering. Such an exponent indicates that the system is not in the universality class of directed percolation [53, 54, 55, 56].

2.2. Model 2

2.2.1. Multidimensional replicator model with inheritance

The multidimensional replicator model is here designed to resemble the Bak-Sneppen – model in the sense that evolutionary steps mutate the properties of existing species, instead of creating a previously non-existing species. The initial abundance of any species corresponds 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. 34]. Elements appearing in the model are summarized in Table 1.

The interaction matrix produced according to the procedure above would be fully occupied. Vacancies are introduced by replacing some of the interaction matrix elements by zero values. This happens by assigning any nondiagonal interaction matrix element a connectivity parameter, drawn from Gaussian distribution of zero mean and unit variance. Vacancy appears in the interaction matrix in case the individual connectivity parameter is smaller than a predetermined threshold value. The average among-species connectivity corresponds to the Gaussian probability mass of parameter values exceeding the threshold for among-species connectivity. Vacancies are symmetric with respect to the interaction matrix diagonal.

Table 1. Summary of elements appearing in the replicator model.

x	Abundance Vector (Configuration Vector)
z	Asymmetric Interaction Matrix
u	Self-Interaction Vector
u	Mean Value of Self-Interaction
C	Matrix of Connectivity Parameters
Γ	Symmetry Parameter
K	Interaction Matrix
F	Fitness Vector
I	Inheritance Parameter

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 is implemented by replacing Z_{ij} and Z_{ji} , for $i \leq j$, 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, with the value zero corresponding to the asymmetric interactions. Correspondingly, K_{ij} and K_{ji} refer to non-diagonal interaction coefficients with possibly some covariance.

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

$$F_i = \frac{K_{ij}x_j}{\sum_k x_k} \tag{3}$$

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

$$\frac{\Delta x_i}{x_i} = F_i - \langle F \rangle = F_i - \frac{\mathbf{x} \cdot \mathbf{F}}{\sum_k x_k} \tag{4}$$

Eqs. (3) and (4) are applied repeatedly until an equilibrium species configuration is found. Extremal dynamics is then applied to the 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. It also corresponds to resampling the species that interact with the mutating species through the sparse interaction matrix. In the latter sense the model resembles the annealed case of the BS-model.

Technically, inheritance contributes to the mutation process as follows. First, independent interaction coefficients for the mutated (daughter) species are drawn from Gaussian with zero mean and unit variance. Then, eventual symmetry is introduced using Eq. (2). Third, interaction coefficients are partially inherited as

$$\begin{aligned} K_{iC} &= IK_{iP} + \sqrt{1 - I^2} K_{iD} \\ K_{Cj} &= IK_{Pj} + \sqrt{1 - I^2} K_{Dj} \end{aligned} \tag{5}$$

where K_{iP} , K_{Pj} are interaction coefficients for the parent species, K_{iD} , K_{Dj} are independently created interaction coefficients for the daughter species, K_{iC} , K_{Cj} are partially inherited (combined) interaction coefficients for the daughter species, and I is inheritance.

Links between species (nodes) are also inherited. In other words, the connectivity parameters determining the vacancies in the interaction matrix are partially inherited. Any daughter species is drawn a set of independent connectivity parameters from a Gaussian with zero mean and unit variance. Then, partially inherited (combined) connectivity parameters are produced as

$$C_{iC} = IC_{iP} + \sqrt{1 - I^2}C_{iD} \quad (6)$$

where C_{iP} are connectivity parameters for the parent species, and C_{iD} are independently created connectivity parameters for the daughter species. The connectivity parameters, as well as vacancies, are symmetric with respect to the matrix diagonal. Vacancy appears in the interaction matrix in case the combined connectivity parameter is smaller than a predetermined threshold value.

Mutation of interaction coefficients and among-species connections immediately changes the fitnesses of the mutating species and the connected species 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. Then, species with abundance vanishing below a small threshold value in the vicinity of zero are considered extinct and removed from the system.

Extremal dynamics will possibly make the system to self-organize. The eventual self-organizing threshold f_c , in terms of fitness, will depend on system parameters. However the scaling ansatz of Eq. (1) may well be attempted. It appears from Fig. 3 that average activity cycle size within the replicator model apparently follows power-law scaling, with exponent γ similar to the one in the BS-system in Fig. 2. We also find from Fig. 3 that there are two groups of data. The left group corresponds to system parameters which do not induce many species extinctions. The right group corresponds to systems where 299 of initial 300 species went extinct.

Species extinctions obviously interfere the scaling behavior (Fig. 3). In the absence of extinctions, extremal dynamics organizes the fitness space into an active phase and an inert phase. The number of species reducing to one, the self-organization degenerates to a random walk in the fitness space. Scaling behavior of such a system obviously depends on the kind of distribution where the single self-interaction coefficient is drawn from.

A more detailed investigation of Fig. 3 reveals that strongly antisymmetric systems retain a significant number of species, whereas asymmetric systems do not. Partially antisymmetric systems with strong self-interaction retain many species, whereas partially antisymmetric systems with weak self-interaction do not [cf. 34, 59, 60].

Average avalanche size

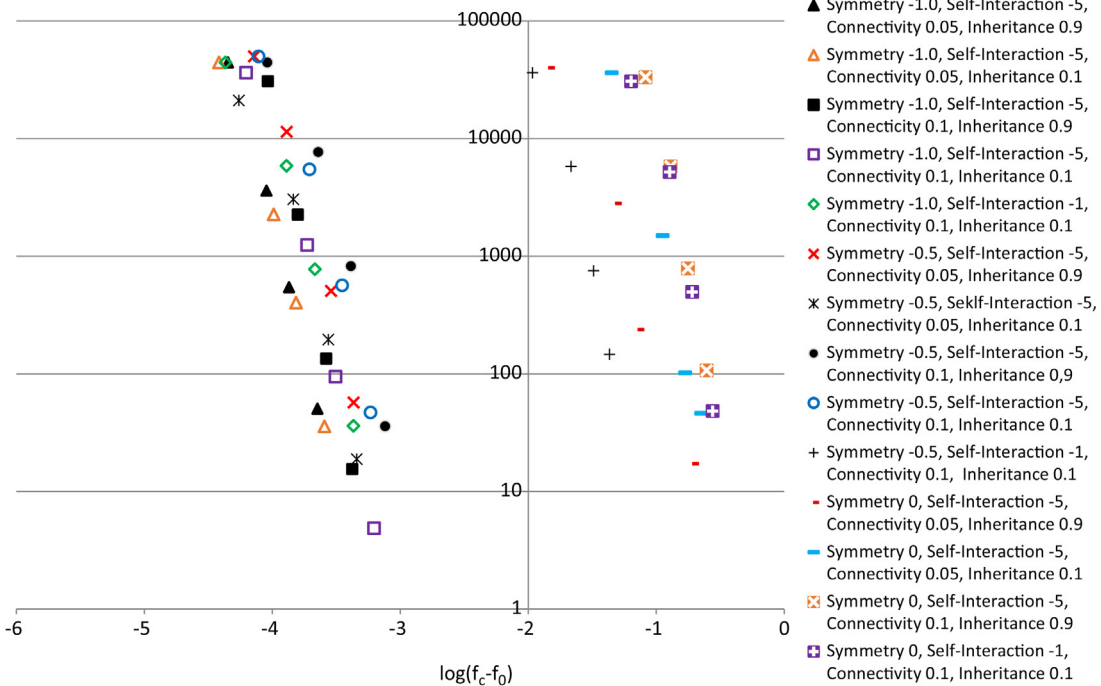


Fig. 3. Average activity cycle size in the multidimensional replicator model, as a function of separation between the self-organizing threshold and the cycle threshold. Legend refers to the symmetry parameter (Eq. (2)), mean value of self-interaction coefficient, probability of among-species connection, and inheritance parameter (Eqs. (5) and (6)).

It is worth noting that particular values of the mutation parameters, *i.e.* symmetry, self-interaction and connectivity do not necessarily correspond to similar observable properties of the evolved system. Extremal dynamics involves the species with the lowest fitness, which does not necessarily correspond to average values of such properties. In the case of the right grouping of systems in Fig. 3 with devastating extinctions, the observable properties rather significantly differ from the corresponding mutation parameters.

2.3. Model 3

2.3.1. Replicator model with speciation

The replicator models above were designed to mimic the BS-model with a constant number of species. This kind of an approach does not tell how life has evolved in the first place. A replicator model for the evolution of life (“macroevolution”) probably should be initiated with a single species, followed by further speciations, within- and among-species interactions, and eventual species extinctions. Any resulting system trajectory will possibly depend on system parameters.

A replicator model with speciations and extinctions is here implemented in terms of extremal dynamics. The first species is introduced with unit abundance. It is assigned an interaction matrix of dimension one. The single matrix element Z_{11} is drawn from a Gaussian with predetermined mean value and 20% standard deviation [cf. 34]. Another species is then introduced with abundance at the species extinction limit, and added to the bottom of the species configuration column vector. The interaction matrix is extended by a column on the right, and by a row at the bottom. Independent among-species interaction coefficients for the new species are drawn from a Gaussian with zero mean and unit variance, and eventual symmetry is introduced using Eq. (2). Then, inheritance is considered by applying Eq. (5). It is worth noting that the self-interaction coefficient K_{PP} becomes partially inherited into the among-species interaction coefficients K_{PC} and K_{CP} (Eq. (5)). Then, the self-interaction coefficient for the new species is drawn from the Gaussian distribution with the predetermined mean value and 20% standard deviation.

Links between species (nodes) are also inherited. A set of independent connectivity parameters from a Gaussian with zero mean and unit variance are drawn for the daughter species. Then, partially inherited (combined) connectivity parameters are produced according to Eq. (6). Vacancies are again symmetric with respect to the interaction matrix diagonal. According to Eq. (6), there must be a self-connectivity parameter C_{PP} of the parent species which becomes partially inherited to C_{PC} and C_{CP} . For inheritance purposes, the diagonal of the matrix of connectivity parameters contains a finite value, even if self-interaction always takes place. Again, vacancy appears in the interaction matrix in case a non-diagonal combined connectivity parameter is smaller than a predetermined threshold value.

After any speciation and related manipulation of the configuration vector and interaction matrix, a fitness vector is created according to Eq. (3), and any species abundance is changed according to the replicator Eq. (4). Again, Eqs. (3) and (4) are applied repeatedly unless an equilibrium species configuration is found. Then, species with abundance below the extinction limit are identified and removed from the system. Extremal dynamics again means that in any further speciation cycle the species with the lowest fitness in the equilibrium configuration is taken as the parent species.

The sum of species abundances, as defined above, generally exceeds unity. The absolute ecosystem size naturally depends on model parameters. The average species abundance in relation to the speciation abundance is

$$\frac{\langle x \rangle}{\varepsilon} = \frac{n}{N} + \frac{1}{N\varepsilon} \quad (7)$$

Eq. (7) simply results from the first species appearing at unit abundance, and the

following species at abundance ϵ ; n refers to the number of speciations, and N to the number of living species. It can readily be shown that application of the replicator Eq. (4) does not change the sum of species abundances.

Fig. 4 and Fig. 5 show some system trajectories, in terms of number of living species, for the replicator systems with speciation and extinction, for weak and strong inheritance, respectively. System parameters significantly contribute to system behavior. Strong self-interaction and antisymmetry in speciation (Eq. (2)) results in large, stable systems. Asymmetry in speciation, along with weak self-interaction results in smaller systems with significant fluctuations (Fig. 4 and Fig. 5).

In order to investigate eventual self-organization of the replicator systems shown in Fig. 4 and Fig. 5, we will plot a few trajectories of smallest fitness. Fig. 6 shows the antisymmetric case from Fig. 4. Extremal dynamics apparently organizes the fitness space in two phases. However data does not indicate whether there is a critical transformation into the inert phase, in which case average activity cycle size would diverge as the cycle threshold f_0 approaches the self-organization threshold f_c (Eq. (1)). Fig. 7 shows the partially antisymmetric case from Fig. 4. An apparent self-organization threshold is visible, but there is no inert phase in the fitness space. Mass extinctions in Fig. 4 are related to the smallest fitness in Fig. 7

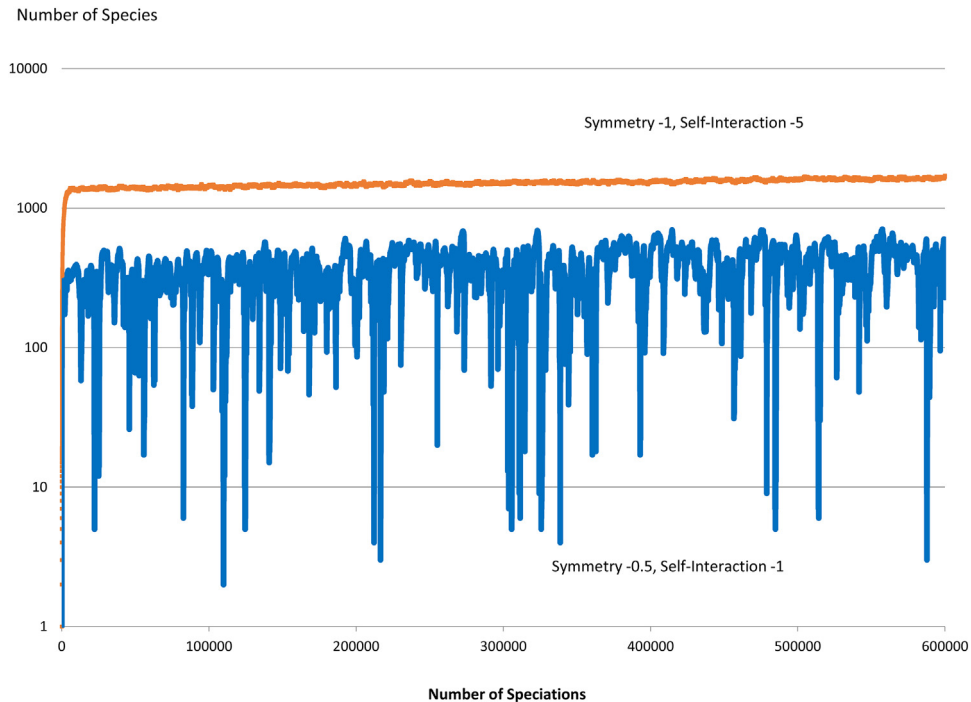


Fig. 4. Number of living species as a function of the number of speciations in replicator systems with weak inheritance ($I = 0.1$ in Eqs. (5) and (6)). Probability of randomly drawn among-species connection is 0.05, and inherited self-connectivity parameter corresponds to connectivity 0.95.

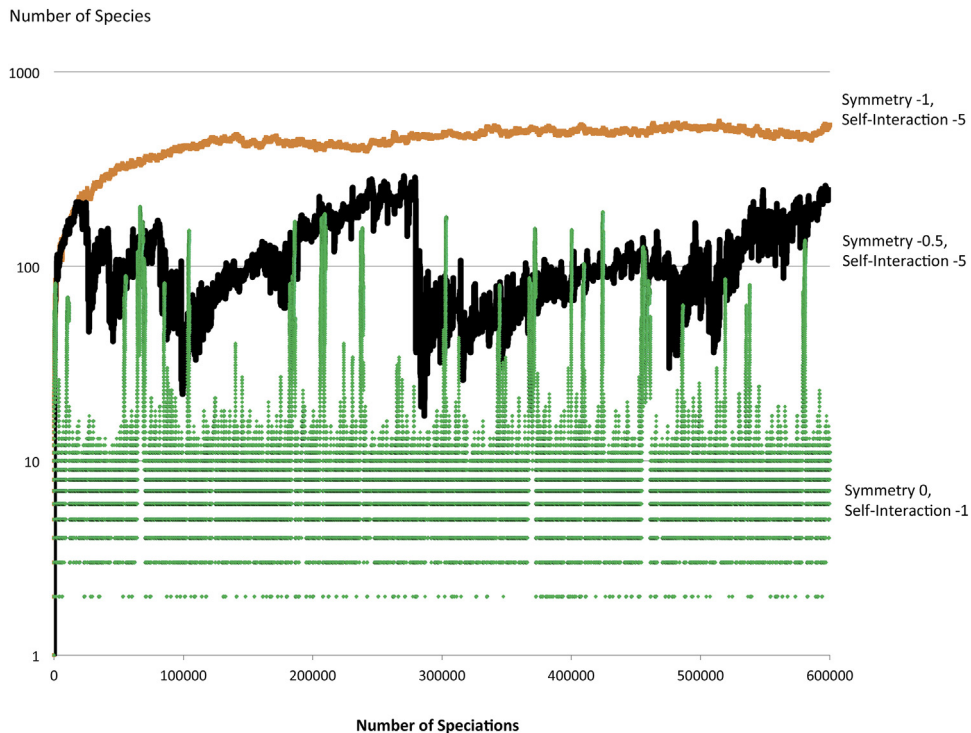


Fig. 5. Number of living species as a function of the number of speciations in replicator systems with strong inheritance ($I = 0.9$ in Eqs. (5) and (6)). Probability of randomly drawn among-species connection is 0.05, and inherited self-connectivity parameter corresponds to connectivity 0.95.

exceeding the prospective self-organization threshold. The inverse relationship of the number of living species and the value of smallest fitness is particularly clear in the partially antisymmetric case of Fig. 5 (smallest fitness trajectory not shown in the Figures). Topology changes obviously interfere with the self-organization, deteriorating any stationary self-organized critical state.

The symmetry parameter shown in Fig. 3, Fig. 4, Fig. 5, Fig. 6 and Fig. 7 regulates the amount of covariance in the generation of nondiagonal interaction coefficients according to Eq. (2). It does not necessarily correspond to the symmetry of an established interaction matrix since the interaction coefficients are partially inherited according to Eq. (5). Fig. 8 shows two trajectories of interaction matrix symmetry for the case of high inheritance and strong self-interaction. We find that young systems are symmetric. This is due to the interaction coefficients inheriting the parent species according to Eq. (5). In the very beginning, with just one initiating species, $K_{1P} = K_{P1}$ and thus $K_{1C} \approx K_{C1}$ for large I . Later on, the symmetry parameter of Eq. (2) comes more strongly into play, but some effect of the initial symmetry remains. With fully antisymmetric speciation according to Eq. (2), for the dataset shown in Fig. 5, the interaction matrix symmetry fluctuates

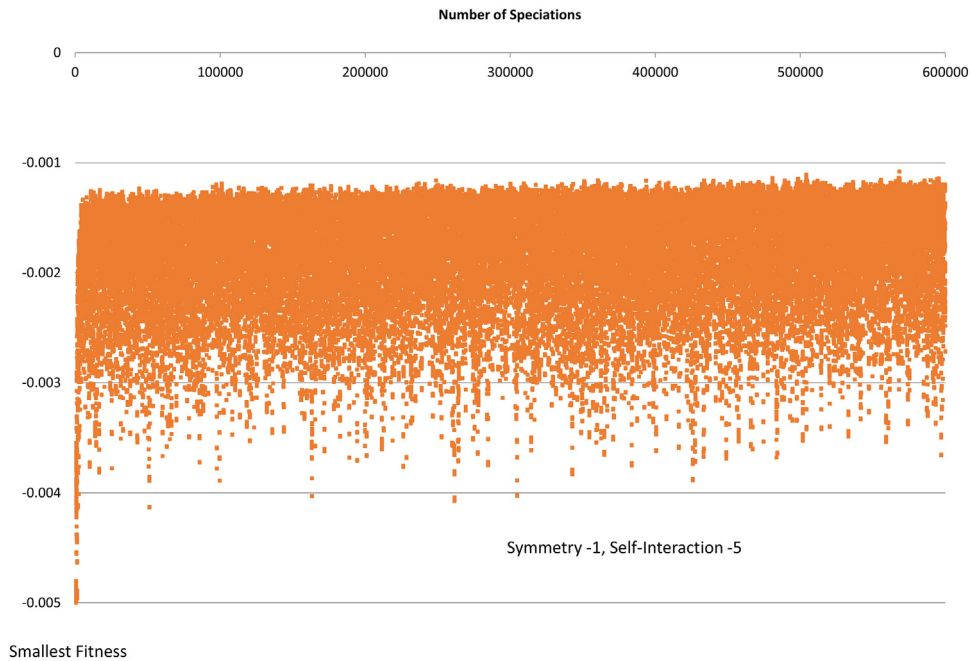


Fig. 6. Smallest fitness as a function of the number of speciations in a replicator system with antisymmetry in speciation and weak inheritance ($I = 0.1$ in Eqs. (5) and (6)). Probability of randomly drawn among-species connection is 0.05, and inherited self-connectivity parameter corresponds to connectivity 0.95.

around zero (Fig. 8). In the case of partially antisymmetric speciation (Fig. 5), the interaction matrix symmetry fluctuates between -0.3 and unity (Fig. 8).

A phenomenon similar to that demonstrated in Fig. 8 for interaction matrix symmetry also takes place in the case of connectivity. The latter depends on the magnitude of the self-connectivity parameter to be inherited. Both of the phenomena appear in the case of strong inheritance. In the case of weak inheritance the second term of the right-hand-side Eq. (5) dominates. Consequently, even if $K_{1P} = K_{P1}$, K_{1C} is not in general closely related to K_{C1} . In all fluctuating systems, regardless of inheritance, connectivity appears to increase as the number of species collapses.

Scaling of the average activity cycle size according to Eq. (1) for the replicator systems with speciations and extinctions is shown in Fig. 9. We find that the data again appears in two groupings. Inspection of the corresponding trajectories of smallest fitnesses revealed that the left group corresponds to systems where the fitness space is, at least apparently, divided into an active phase and an inert phase as in Fig. 6. The right group corresponds to systems where fluctuations in the number of living species interferes with the self-organization as in Fig. 7. In the latter case a well-defined self-organization threshold does not exist. Technically the threshold is represented by the greatest observed value of minimum fitness

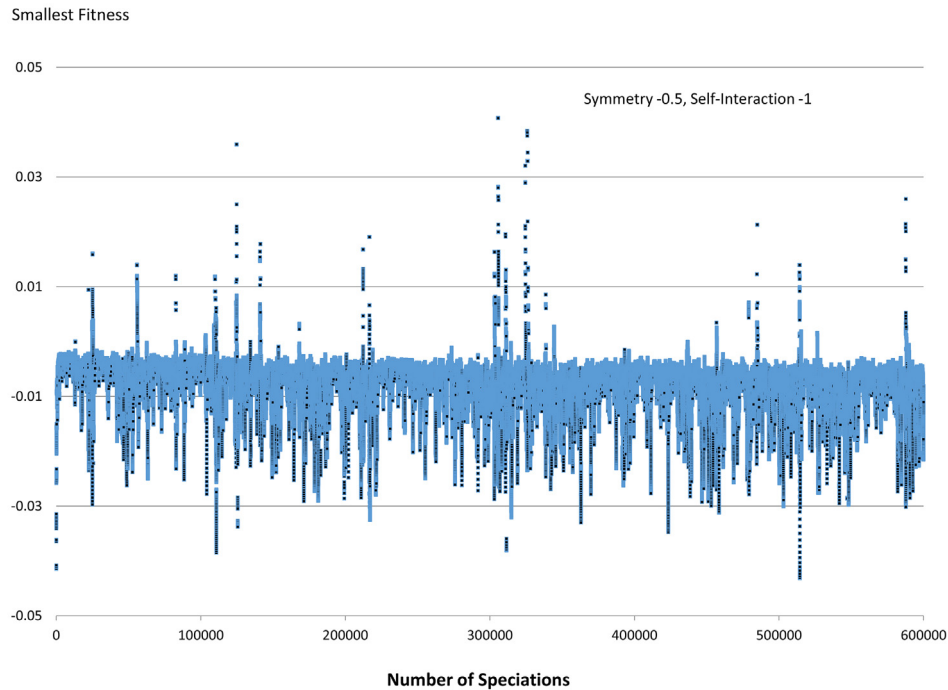


Fig. 7. Smallest fitness as a function of the number of speciations in a replicator system with partial antisymmetry in speciation and weak inheritance ($I = 0.1$ in Eqs. (5) and (6)). Probability of randomly drawn among-species connection is 0.05, and inherited self-connectivity parameter corresponds to connectivity 0.95.

(Fig. 7), which results in observations shifting to the right in Fig. 9. In the left group, the scaling exponent γ (Eq. (1)) appears to be in the same order as those appearing in Fig. 2 and Fig. 3, whereas observations in the right group do not follow power-law scaling.

3. Discussion

The random-neighbor Bak-Sneppen model self-organizes into two phases in the fitness space, and the distribution of activity cycle sizes diverges at the phase boundary. However the scaling exponent for average activity cycle size significantly differs from that of directed percolation [53, 54, 55, 56].

In the absence of among-species interactions, the self-organized criticality of the BS – evolution model degenerates into a random walk in the fitness space. In the case of a replicator system, a somewhat less oversimplified representation of the Nature, species extinctions degenerate self-organization to a random walk. The magnitude of topology changes in terms of extinctions depends on system parameters.

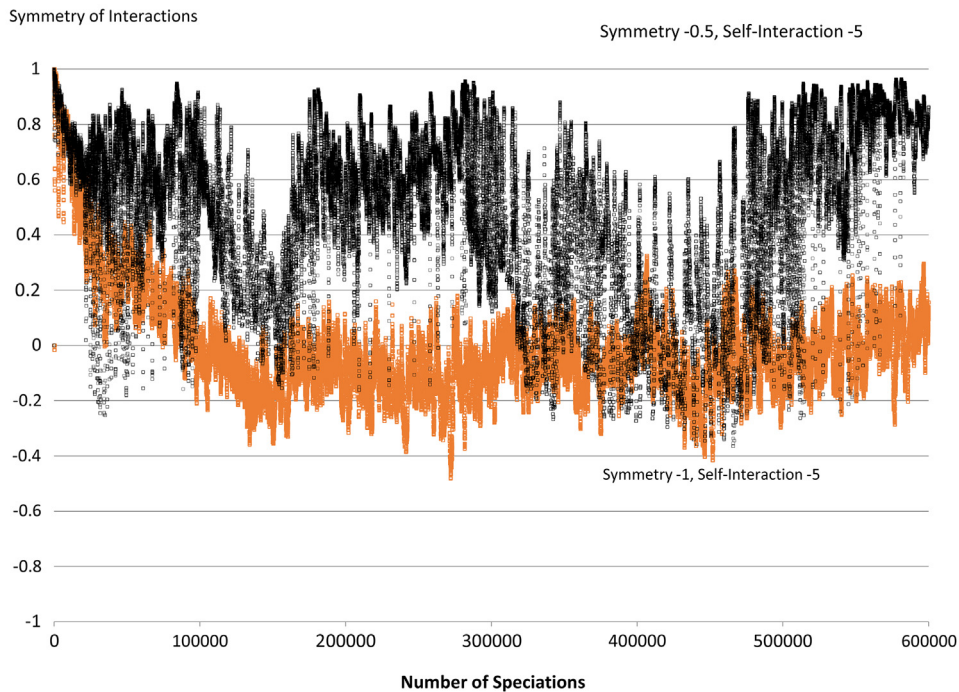


Fig. 8. Symmetry of interactions as a function of the number of speciations in replicator systems with strong inheritance ($I = 0.9$ in Eqs. (5) and (6)). Probability of randomly drawn among-species connection is 0.05, and inherited self-connectivity parameter corresponds to connectivity 0.95.

A more realistic macroevolution model possibly should initiate with a single species, followed by further speciations with inheritance, within- and among-species interactions, and eventual species extinctions. Such a model contains quite a few parameters, of which any system trajectory will depend on. However it appears that symmetry of interactions, together with the magnitude of self-interaction, dominates behavior [cf. 34, 59, 60]. Stationary, antisymmetric systems with strong self-interaction appear to self-organize into two phases in the fitness space (Fig. 6). However, paleontological records indicate that the number of species (or genera) in real living systems fluctuates [4, 5, 7, 8]. In systems with fluctuating number of species, the Bak-Sneppen – type self-organized criticality becomes interfered by topology changes induced by speciation-extinction – dynamics [cf. 39] (Fig. 7). Thus the BS-type self-organized criticality must be concluded not to apply to biological macroevolution.

In the case of systems with extinctions, it is not only the BS – mutation activity where self-organized criticality in principle could be detected. The extinction dynamics might display a variety of extinction avalanche sizes. However the system does not self-organize: achievement of such a state requires tuning of parameters [cf. 34]. In addition, no critical phase transition, or any diverging distribution, is known to appear in real biological extinction dynamics.

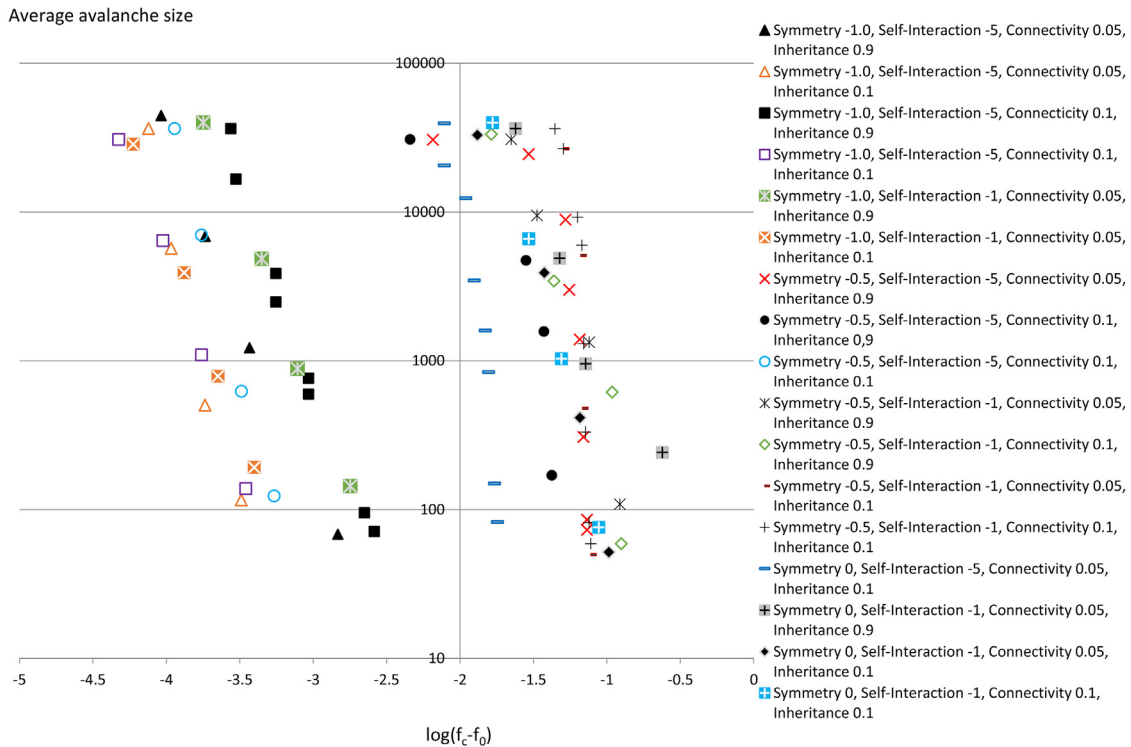


Fig. 9. Average activity cycle size in the multidimensional replicator model with speciations and extinctions, as a function of separation between the self-organizing threshold and the cycle threshold. Legend refers to the symmetry parameter (Eq. (2)), mean value of self-interaction coefficient, probability of among-species connection, and inheritance parameter (Eqs. (5) and (6)).

Consequently, biological macroevolution probably is not a self-organized critical process.

It is worth noting that while the parameters describing the existence of among-species interaction on the one hand and the magnitude of species interaction on the other are partially inherited, there is no explicit description of spatial segregation in the present model. In general, segregation is considered a significant speciation mechanism [1, 2]. In the case of high inheritance, many daughter species tend to interact rather strongly with its parent species.

Spatial segregation of course could be introduced. That would, however, complicate the model, and have significance mostly in the case of high inheritance. The present results appear to be robust regardless the degree of inheritance: stationary systems are established in the case of high antisymmetry and strong self-interaction, and they appear to self-organize to two phases in the fitness space (Fig. 6 and Fig. 9). Regardless of the inheritance, systems with fluctuating number of species do not self-organize and thus do not obey the BS-type self-organized criticality (Fig. 7 and Fig. 9).

Quite a few phenomena in Nature obey non-trivial scaling. Some of them show self-similarity [61, 62]. Some investigators have proposed self-organized criticality to frequently appear in the complex Nature [9]. Speciation-extinction dynamics interfering with self-organization, and consequently biological macroevolution not being a self-organized critical system, indicates that self-organized criticality possibly is not a phenomenon characteristic to a wide variety of complex systems in Nature [cf. 7, 40, 41].

Declarations

Author contribution statement

Petri P. Kärenlampi: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Competing interest statement

The author declares no conflict of interest.

Additional information

No additional information is available for this paper.

Acknowledgement

The author is grateful to Drs. Tobias Galla, Jan Åström and Kimmo Mattila for their advice regarding computations, as well as the Finnish Grid Initiative for computation resources.

References

- [1] O.F. Cook, Factors of species-formation, *Science* 23 (587) (1906) 506–507.
- [2] O.F. Cook, Evolution without isolation, *Am. Nat.* 42 (503) (1908) 727–731.
- [3] N. Eldredge, S.J. Gould, Punctuated equilibria: an alternative to phyletic gradualism, In: J.M. Schopf Thomas (Ed.), *Models in Paleobiology*, Freeman, Cooper and Co., San Francisco, 1972, pp. 82–115.
- [4] D.M. Raup, J.J. Sepkoski Jr., Mass extinctions in the marine fossil record, *Science* 215 (1982) 1501–1503.

- [5] J.J. Sepkoski Jr., Ten years in the library: new data confirm paleontological patterns, *Paleobiology* 19 (1993) 43–51.
- [6] N. Eldredge, J.N. Thompson, P.M. Brakefield, S. Gavrilets, D. Jablonski, J.B. C. Jackson, R.E. Lenski, B.S. Lieberman, M.A. McPeck, W. Miller III, The dynamics of evolutionary stasis, *Paleobiology* 31 (2005) 133–145.
- [7] J. Alroy, Dynamics of origination and extinction in the marine fossil record, *PNAS* 105 (2008) 11536–11542.
- [8] D.M. Raup, J.J. Sepkoski Jr., Periodicity of extinctions in the geologic past, *PNAS* 81 (1984) 801–805.
- [9] P. Bak, *How Nature Works, The Science of Self-Organized Criticality*, Oxford University Press, 1997.
- [10] P. Bak, K. Chen, M. Creutz, Self-organized criticality in the 'Game of Life', *Nature* 342 (1989) 780–782.
- [11] S.A. Kauffman, S. Johnsen, Coevolution to the edge of chaos: coupled fitness landscapes, poised states, and coevolutionary avalanches, *J. Theor. Biol.* 149 (1991) 467–505.
- [12] P. Bak, H. Flyvbjerg, B. Lautrup, Coevolution in a rugged fitness landscape, *Phys. Rev. A* 46 (1992) 6724–6730.
- [13] P. Bak, K. Sneppen, Punctuated equilibrium and criticality in a simple model of evolution, *Phys. Rev. Lett.* 71 (1993) 4083–4086.
- [14] H. Flyvbjerg, K. Sneppen, P. Bak, Mean field theory for a simple model of evolution, *Phys. Rev. Lett.* 71 (1993) 4087–4090.
- [15] P. Bak, C. Tang, K. Weisenfeld, Self-organized criticality: an explanation of $1/f$ noise, *Phys. Rev. Lett* 59 (1987) 381.
- [16] P. Bak, C. Tang, K. Weisenfeld, Self-organized criticality, *Phys. Rev. A* 38 (1988) 364.
- [17] M. Paczuski, P. Bak, S. Maslov, Laws for stationary states in systems with extremal dynamics, *Phys. Rev. Lett.* 74 (1995) 4253.
- [18] Z. Olami, H.J. Feder, K. Christensen, Scaling, phase transitions, and nonuniversality in a self-organized critical cellular-automaton model, *Phys. Rev. Lett.* 68 (1992) 1244.
- [19] P. Bak, M. Paczuski, Complexity, contingency and criticality, *PNAS* 92 (1995) 6689.

- [20] R.V. Solé, J. Bascompte, Are critical phenomena relevant to large-scale evolution? *Proc. R. Soc. B* 263 (1996) 161–168.
- [21] K. Sneppen, P. Bak, H. Flyvbjerg, M.H. Jensen, Evolution as a self-organized critical phenomenon, *PNAS* 92 (1995) 5209.
- [22] J. de Boer, A.D. Jackson, T. Wettig, Criticality in Simple Models of Evolution, *Phys. Rev. E* 51 (1995) 1059–1074.
- [23] M.E.J. Newman, S.M. Fraser, K. Sneppen, W.A. Tozier, Comment on "Self-organized criticality in living systems", *Phys. Lett. A* 228 (20) (1997) 202–204.
- [24] M.E.J. Newman, Evidence for self-organized criticality in evolution, *Physica D* 107 (1997) 293–296.
- [25] B.W. Roberts, M.E.J. Newman, A model for evolution and extinction, *J. Theor. Biol.* 180 (1996) 39–54.
- [26] P. Bak, K. Chen, M. Creutz, Self-organized criticality in the 'Game of Life', *Nature* 342 (1989) 780–782.
- [27] S. Jain, S. Krishna, Autocatalytic sets and the growth of complexity in an evolutionary model, *Phys. Rev. Lett.* 81 (1998) 5684–5687.
- [28] S. Jain, S. Krishna, Emergence and growth of complex networks in adaptive systems, *Comput. Phys. Commun.* 121-122 (1999) 116–121.
- [29] S. Jain, S. Krishna, A model for the emergence of cooperation, interdependence and structure in evolving networks, *PNAS* 98 (2002) 543–547.
- [30] S. Jain, S. Krishna, Large extinctions in an evolutionary model: the role of innovation and keystone species, *PNAS* 99 (2002) 2055–2060.
- [31] S. Jain, S. Krishna, Crashes, recoveries, and "core shifts" in a model of evolving networks, *Phys. Rev. E* 65 (2002) 1–4 026103.
- [32] S. Jain, S. Krishna, Graph theory and the evolution of autocatalytic networks, In: S. Bornholdt, H.G. Schuster (Eds.), *Handbook of Graphs and Networks: From the Genome to the Internet*, Wiley-VCH Verlag GmbH & Co., KGaA Weinheim, FRG, 2005, pp. 355–394.
- [33] A. Samal, H. Meyer-Ortmanns, Preferential attachment renders an evolving network of populations robust against crashes, *Physica A* 388 (2009) 1535–1545.
- [34] P.P. Kärenlampi, Symmetry of interactions rules in incompletely connected random replicator ecosystems, *Eur. Phys. J. E* 37 (6) (2014) 56.

- [35] B. Drossel, P.G. Higgs, A.J. McKane, The influence of predator-pray population dynamics on the long-term evolution of food web structure, *J. Theor. Biol.* 208 (2001) 91–107.
- [36] K. Tokita, A. Yasutomi, Emergence of a complex and stable network in a model ecosystem with extinction and mutation, *Theor. Popul. Biol.* 63 (2003) 131–146.
- [37] K. Tokita, A. Yasutomi, Mass Extinction in a Simple Mathematical Biological Model, (1997) arXiv:adap-org/9702004.
- [38] R. Happel, P.F. Stadler, The Evolution of Diversity in Replicator Networks, *J. Theor. Biol.* 195 (1998) 329–338.
- [39] P.P. Kärenlampi, Extremal Dynamics in Random Replicator Ecosystems, *Phys. Lett. A* 379 (37) (2015) 2209–2214.
- [40] R.V. Solé, J. Bascompte, Are critical phenomena relevant to large-scale evolution? *Proc. R. Soc. B* 263 (1996) 161–168.
- [41] M.E.J. Newman, A model of mass extinction, *J. Theor. Biol.* 189 (1997) 235–252.
- [42] Y. Moreno, A. Vazquez, The Bak-Sneppen model on scale-free networks, *Europhys. Lett.* 57 (2002) 5.
- [43] N. Masuda, K.I. Goh, B. Kahng, Extremal dynamics on complex networks: Analytic solutions, *Phys Rev. E* 72 (6) (2005) 066106.
- [44] S. Lee, Y. Kim, Coevolutionary dynamics on scale-free networks, *Phys. Rev. E* 71 (2005) 057102.
- [45] D. Garlaschelli, A. Capocci, G. Caldarelli, Self-organized network evolution coupled to extremal dynamics, *Nature Physics* 3 (2007) 813–817.
- [46] R. Albert, A. Barabási, Statistical mechanics of complex networks, *Rev. Mod. Phys.* 74 (47) (2002).
- [47] G. Caldarelli, A. Capocci, P. De Los Rios, M.A. Muñoz, Scale-Free Networks from Varying Vertex Intrinsic Fitness, *Phys. Rev. Lett.* 89 (2002) 258702.
- [48] P. De Los Rios, M. Marsili, M. Vendruscolo, High-Dimensional Bak-Sneppen Model, *Phys. Rev. Lett.* 80 (1998) 5746.
- [49] M.F. Elettrey, Multiobjective Bak-Sneppen model on a small-world network, *Chaos Soliton. Frac.* 26 (3) (2005) 1009–1017.
- [50] R.V. Kulkarni, E. Almaas, D. Stroud, Evolutionary dynamics in the Bak-Sneppen model on small-world networks, (2016) arXiv:cond-mat /9905066.

- [51] K. Christensen, R. Donangelo, B. Koiller, K. Sneppen, Evolution of Random Networks, *Phys. Rev. Lett.* 81 (1998) 2380.
- [52] M. Paczuski, S. Maslov, P. Bak, Avalanche Dynamics in Evolution, Growth and Depinning models, *Phys. Rev. E* 53 (1995) 414.
- [53] P. Grassberger, The Bak-Sneppen model for punctuated evolution, *Phys. Lett. A* 200 (1995) 277–282.
- [54] M. Paczuski, S. Maslov, P. Bak, Field Theory for a Model of Self-Organized Criticality, *Europhys. Lett.* 28 (1994) 295–296.
- [55] T.S. Ray, N. Jan, Anomalous approach to the self-organized critical state in a model for "life at the edge of chaos", *Phys. Rev. Lett.* 72 (25) (1994) 4045–4048.
- [56] K.A. Takeuchi, M. Kuroda, H. Chaté, M. Sano, Experimental realization of directed percolation criticality in turbulent liquid crystals, *Phys. Rev. E* 80 (2009) 051116.
- [57] J. de Boer, B. Derrida, H. Flyvbjerg, A.D. Jackson, T. Wettig, Simple model of self-organized biological evolution, *Phys. Rev. Lett.* 73 (6) (1994) 906–909.
- [58] G. Caldarelli, A. Capocci, D. Garlaschelli, A self-organized model for network evolution. Coupling network evolution and extremal dynamics, *Eur. Phys. J. B* 64 (3) (2008) 585–591.
- [59] H. Rieger, Solvable model of a complex ecosystem with randomly interacting species, *J. Phys. A: Math. Gen.* 22 (1989) 3447–3460.
- [60] T. Galla, Random replicators with asymmetric couplings, *J. Phys. A: Math. Gen.* 39 (2006) 3853–3869.
- [61] B.B. Mandelbrot, *The Fractal Geometry of Nature*, Freeman, 1983.
- [62] *Fractals and disordered systems*, In: A. Bunde, S. Havlin (Eds.), Springer, 1993.