Random networks created by biological evolution

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We investigate a model of evolving random network, introduced by us previously [Phys. Rev. Lett. 83, 5587 (1999)]. The model is a generalization of the Bak-Sneppen model of biological evolution, with the modification that the underlying network can evolve by adding and removing sites. The behavior and the averaged properties of the network depend on the parameter $p$, the probability to establish link to the newly introduced site. For $p = 1$ the system is self-organized critical, with two distinct power-law regimes with forward-avalanche exponents $\tau = 1.98 \pm 0.04$ and $\tau' = 1.65 \pm 0.05$. The average size of the network diverge as power-law when $p \to 1$. We study various geometrical properties of the network: probability distribution of sizes and connectivities, size and number of disconnected clusters and the dependence of mean distance between two sites on the cluster size. The connection with models of growing networks with preferential attachment is discussed.

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I. INTRODUCTION

Irregular networks or random graphs composed of units of various kind are very frequent both in nature and society (which is, however, nothing but a special segment of nature). Examples range from vulcanized polymers, silica glasses, force chains in granular materials, mesoscopic quantum wires, to food webs, herding effects in economics, world-wide-web links, “small-world” networks of personal contacts between humans and scientific collaboration networks.

Modeling of such networks is not quite easy and analytical results are relatively rare (examples, without any pretence of completeness, can be found in [1,3,4,22,26–31]). Numerical simulations are still one of the principal tools. However, even in the case when the properties of a given class of random networks are relatively well established, either analytically or numerically, as is the case of small-world networks, the serious question remains, why do these networks occur in nature. In other words, what are the dynamical processes, which generate these networks. Indeed, one can study, for example, various networks of species in co-evolution, but it is difficult to infer from these studies only, which networks are closer to the reality that the others. In the context of biological evolution models, there was recently a few attempts to let the networks evolve freely, i.e. in order to check, which types of topologies might correspond to “attractors” of the process of natural evolution.

The model introduced in a preceding Letter [18] is based on extremal dynamics and basically follows the Bak-Sneppen model of biological evolution [14]. Extremal dynamics (ED) models are used in wide area of problems, ranging from growth in disordered medium, dislocation movement, friction, to biological evolution. Among them, the Bak-Sneppen (BS) model plays the role of a testing ground for various analytical as well as numerical approaches (see for example [22,26,31]). The idea of ED is the following. The dynamical system in question is composed of a large number of simple units, connected in a network. Each site of the network hosts one unit. The state of each unit is described by a single dynamical variable $b$, called barrier. In each step, the unit with minimum $b$ is mutated by updating the barrier. The effect of the mutation on the environment is taken into account by changing $b$ also at all sites connected to the minimum site by a network link. Because a perturbation can propagate through the links, we should expect that the topology of the network can affect substantially the ED evolution.

General feature of ED models is the avalanche dynamics. The forward $\lambda$-avalanches are defined as follows [22]. For fixed $\lambda$ we define active sites as those having barriers $b < \lambda$. Appearance of one active site can lead to avalanche-like proliferation of active sites in successive time steps. The avalanche stops, when all active sites disappear again. Generally, there is a value of $\lambda$, for which the probability distribution of avalanche sizes obeys a power law without any parameter tuning, so that the ED models are classified as a subgroup of self-organized critical models [32]. (This, of course, can hold only for networks of unlimited size.) The set of exponents describing the critical behavior determines the dynamical universality class the model belongs to.

It was found that the universality class depends on the topology of the network. Usually, regular hypercubic networks or Cayley trees are investigated. For random neighbor networks, mean-field solution was found to be exact [18,27]. Also the tree models were found to belong to the mean-field universality class. A one-dimensional model in which the links were wired randomly with probability decaying as a power $\mu$ of the distance was introduced [44,45]. It was found that the values of critical exponents depend continuously on $\mu$. The BS model on a small-world network was also studied [46].

Recently, BS model on random networks, produced by
bond percolation on fully connected lattice, was studied [16]. Two universality classes were found. Above the percolation threshold, the system belongs to the mean-field universality class, while exactly at the percolation threshold, the avalanche exponent is different. A dynamics changing the topology in order to drive the network to critical connectivity was suggested.

There are also several recent results for random networks produced by different kind of dynamics than ED, especially for the threshold networks [13] and Boolean networks [20,21].

The geometry of the world-wide web was intensively studied very recently. It was found experimentally that the network exhibits scale-free characteristics, measured by the power-law distribution of connectivities of the sites [38,39]. Similar power-law behavior was observed also in the actor collaboration graph and in the power grids [22]. A model was suggested [6] to explain this behavior, whose two main ingredients are continual growth and preferential attachment of new links, where sites with higher connectivity having higher probability to receive additional links. The latter feature resembles the behavior of additive-multiplicative random processes, which are well known to produce power-law distributions [36,37].

The model introduced in [6] is exactly soluble [40]. Variants including aging of sites [41,42], decaying and rewiring links [43-44] were also studied. The preferential attachment rule, which apparently requires unrealistic knowledge of connectivities of the whole network before a single new link is established, was justified in a very recent work [45], where higher probability of attachment at highly connected sites results from local search by walking on the network.

In the preceding Letter [18] we concentrated on the self-organized critical behavior and extinction dynamics of a model in which the network changes dynamically by adding and removing sites. It was shown that the extinction exponent is larger than the upper bound for the BS model (given by the mean-field value) and is closer to the experimentally found value than any previous version of the BS model. In the present work we introduce in Sec. II a generalized version of the model defined in [18] and further investigate the self-organized critical behavior in Sec. III. However, our main concern will be about the geometric properties of the network, produced during the dynamics. These results are presented in Sec. IV. Section V makes conclusions from the results obtained.

II. EVOLUTION MODEL ON EVOLVING NETWORK

We consider a system composed of varying number $n_u$ of units connected in a network, subject to extremal dynamics. Each unit bears a dynamical variable $b$. In the context of biological evolution these units are species and $b$ represent the barrier against mutations. For the main novelty of our model consists in adding (speciation) and removing (extinction) units, let us first define the rules for extinction and speciation. The rules determining which of the existing units will undergo speciation or extinction will be specified afterwards.

(i) If a unit is chosen for extinction, it is completely removed from the network without any substitution and all links it has, are broken.

(ii) If a unit is chosen for speciation, it acts as a “mother” giving birth to a new, “daughter” unit. A new unit is added into the system and the links are established between the new unit and the neighbors of the “mother” unit: each link of the “mother” unit is inherited with the probability $p$ by the “daughter” unit. This rule reflects the fact that the new unit is to a certain extent a copy of the original, so the relations to the environment will be initially similar to the ones the old unit has. Moreover, if a unit which speciates has only one neighbor, a link between “mother” and “daughter” is also established.

The extremal dynamics rule for our model is the following.

(iii) In each step, the unit with minimum $b$ is found and mutated. The barrier of the mutated unit is replaced by a new random value $b'$ taken from uniform distribution on the interval $(0,1)$. Also the barriers of all its neighbors are replaced by random numbers from the same distribution.

The rules determining whether a unit is chosen for extinction or speciation are the following.

(iv) If the newly assigned barrier of the mutated unit $b'$ is larger than new barriers of all its neighbors, the unit is chosen for speciation. If $b'$ is lower than barriers of all neighbors, the unit is chosen for extinction. In other cases neither extinction nor speciation occurs. As a boundary condition, we use the following exception: if the network consists of a single isolated unit only, it is always chosen for speciation.

(v) If a unit is chosen for extinction, all its neighbors which are not connected to any other unit also chosen for extinction. We call this kind of extinctions singular extinctions.

The rule (iv) is motivated by the following considerations. We assume, that well-adapted units proliferate more rapidly and chance for speciation is bigger. However, if the local biodiversity, measured by connectivity of the unit, is bigger, there are fewer empty ecological niches and the probability of speciation is lower. On the other hand, poorly adapted units are more vulnerable to extinction, but at the same time larger biodiversity (larger connectivity) may favor the survival. Our rule corresponds well to these assumptions: speciation occurs preferably at units with high barrier and surrounded by fewer neighbors, extinction is more frequent at units with lower barriers and lower connectivity. Moreover, we suppose that a unit completely isolated from the rest of the ecosystem has very low chance to survive. This leads to the rule (v).

From the rule (iv) alone follows equal probability of
adding and removing a unit, because the new random barriers are taken from uniform distribution. At the same time the rule \((v)\) enhances the probability of the removal. Thus, the probability of speciation is slightly lower than the probability of extinction.

![Graphs](a) before after

![Graphs](b) before after

![Graphs](c) before after

FIG. 1. Schematic illustration of the dynamical rules of the model. Speciation is shown in (a), where full square represents the extremal unit, which speciates, full circle the new, daughter unit, and open circles other units, not affected by the speciation event. The dotted link intends to illustrate that for \(p < 1\) some of the mother’s links may not be inherited by the daughter. Extinction is shown in (b), where the extremal unit, which is removed, is indicated by full square. The unit denoted by full circle is the neighbor removed by the singular extinction. In (c) an example of an extinction event is shown, which leads to the splitting of the network into disconnected clusters.

The degree of disequilibrium between the two depends on the topology of the network at the moment and can be quantified by the frequency of singular extinctions. The number of units \(n_u\) perform a biased random walk with reflecting boundary at \(n_u = 1\). The bias towards small values is not constant, though, but fluctuates as well.

The above rules are illustrated by the examples shown in Fig. 1. The networks in (a) show the effect of the speciation: a new site is created and some to the links to the mother’s neighbors are established. In (b) the extinction is shown. One of the units is removed also due to a singular extinction (rule \((v)\)). In (c) we illustrate the possibility that in the extinction event the network can be split into several disconnected clusters.

III. SELF-ORGANIZED CRITICAL BEHAVIOR

A. Crossover scaling

The model investigated in the preceding Letter \cite{18} corresponds to the value \(p = 1\). We found that in this case the model is self-organized critical. We defined newly the mass extinctions, as number of units removed during an avalanche. The distribution of mass extinctions obeys a power law with the exponent \(\tau_{\text{ext}} = 2.32 \pm 0.05\). In this section we present improved analysis of the data for the self-organized critical behavior.

![Graphs](FIG. 2. Rescaled distribution of forward avalanches in the case \(p = 1\), for the values \(\lambda = 0.03 (\triangle), \lambda = 0.05 (\bigcirc), \lambda = 0.1 (+), \lambda = 0.2 (\diamond), \lambda = 0.4 (\times), \lambda = 0.6 (\square).\) The superscript > in \(P_{\text{fwd}}^>(s)\) is to indicate that we count all avalanches larger than \(s\). In the inset we plot the dependence of the scaling parameters \(s_{\text{cross}}(+)\) and \(f_{\text{cross}}(\times)\) on \(\lambda\). The full line is the power-law \(\lambda^{-\sigma'}\) with the exponent \(\sigma' = 3.5\). The number of time steps was \(3 \cdot 10^8\) and the data are averaged over 12 independent runs.

We measured the distribution of forward \(\lambda\)-avalanches \cite{22} and we observed, contrary to the BS model that two power-law regimes with two different exponents occur. The crossover value \(s_{\text{cross}}\) which separates the two
regimes depends on $\lambda$. We observed that the distributions for different $\lambda$ collapse onto single curve, if plotted against the rescaled avalanche size $s/s_{\text{cross}}$, i.e.

$$P_{\text{fwd}}(s) \cdot f_{\text{cross}} = g(s/s_{\text{cross}})$$

(1)

where $g(x) \sim x^{-\tau+1}$ for $x \ll 1$ and $g(x) \sim x^{-\tau'+1}$ for $x \gg 1$. The data are plotted in Fig. 2. For the values of the exponents, we found $\tau = 1.98 \pm 0.04$ and $\tau' = 1.65 \pm 0.05$

We investigated the dependence of the scaling parameters $s_{\text{cross}}$ and $f_{\text{cross}}$ on $\lambda$ and we found that both of them behave as a power law with approximately equal exponent, $s_{\text{cross}} \sim f_{\text{cross}} \sim \lambda^{-\sigma'}$ with $\sigma' \approx 3.5$ (see inset in the Fig. 3). The role of critical $\lambda$ at which the distribution of forward avalanches follows a power law is assumed by the value $\lambda = 0$. This result is easy to understand. In fact, in models with fixed (or at least bounded) connectivity $c$, the critical $\lambda$ is roughly $1/c$. As will be shown in the next section, in our case the size of the system and average connectivity grows without limits, and thus the critical $\lambda$ tends to zero. Note that it is difficult to see this result without resort to the data collapse (1). Indeed, for any finite time of the simulation, the connectivity and the system size reaches only a limited value and the critical $\lambda$ seen in the distribution of forward avalanches has apparently non-zero value.

B. Comparison with the Bak-Sneppen model

If we compare the above findings with the BS model, we can deduce that in our model, with $p = 1$, the exponent $\tau$ corresponds to the usual forward-avalanche exponent, while the exponent $\tau'$ is new. The above described scaling (1) breaks down for $p < 1$ because the connectivity and the system size are limited (cf. next section).

The main difference from the usual BS model is the existence of the second power-law regime, for $s \gg s_{\text{cross}}$. It can be particularly well observed for values of $\lambda$ close to 1, where the crossover avalanche size $s_{\text{cross}}$ is small. We have seen that such avalanches start and end mostly when number of units is close to its minimum value equal to 1. Between these events the evolution of the number of units is essentially a random walk, because singular extinctions are rare [18]. This fact can explain, why the exponent $\tau'$ is not too far from the value $3/2$ corresponding to the distribution of first returns to the origin for the random walk. The difference is probably due to the presence of singular extinctions.

We measured also the distribution of barriers $P(b)$ and the distribution of barriers on the extremal site $P_{\text{min}}(b_{\text{min}})$. In Fig. 3 we can compare the results for $p = 1$ and $p = 0.95$. The sharp step observed in BS model is absent here, because the connectivity is not uniform. (For comparison, we measured also the barrier distribution in the model of Ref. [14], where the network is static, but the connectivity is not uniform. Also in that case the step was absent and the distribution was qualitatively very similar to the one shown in Fig. 3.) The large noise level for $b$ close to 1 is due to the fact that units with larger $b$ undergo mutations rarely.

IV. NETWORK GEOMETRY

In this section we analyze the geometrical properties of the network and their dependence on the parameter $p$.

A. Size of the network

The first important feature of the networks created by the dynamics of the model is their size, or the number of units within the network. This is a strongly fluctuating quantity, but on average it grows initially and after some time it saturates and keeps fluctuating around some average value, which depend on $p$. Fig. 4 shows the probability distribution of number of units $n_u$ for different values of $p$. The average number of units $\langle n_u \rangle$ was computed from these distributions and its dependence on $p$ is shown in the inset of Fig. 4. We can see that the average network size diverges for $p \to 1$ as a power law, $\langle n_u \rangle \propto (1-p)^{-\alpha_n}$ with the exponent $\alpha_n \approx 0.8$.

We can see from Fig. 4 that the distribution of number of units has an exponential tail. This corresponds to the fact that the time evolution of the network size is a
random walk with reflecting boundary at \( n_u = 1 \), with a bias to lower values, caused by the singular extinctions (for the analysis of biased random walks repelled from zero see e.g. [38]). From the decrease of average size with decreasing \( p \) we deduce that the bias due to the singular extinctions has larger effect for smaller \( p \), i.e. if the new unit created in a speciation event has fewer links to the neighbors.

FIG. 4. Distribution of number of units for different values of \( p \left( \triangle 0.85, \square 0.9, \times 0.95, + 0.97, \Diamond 0.98 \right) \). Data are averaged over \( 10^8 \) time steps. Inset: Dependence of averaged number of units on \( p \). The solid line corresponds to the power law \( \langle n_u \rangle \propto (1 - p)^{-0.8} \).

B. Connectivity

In Fig. 5 we show the probability distribution of the connectivity of network sites \( P_{\text{all}}(c) \) and distribution of connectivity of the extremal unit \( P_{\text{extremal}}(c) \). We can observe the tendency that the extremal unit has larger connectivity than average. This is in accord with the findings of Ref. [16] obtained on static networks. It can be also easily understood intuitively. Indeed, in a mutation event the barriers of neighbors of the mutated unit are changed. So, the neighbors have enhanced probability to be extremal in the next time step. Therefore, the sites with higher number of neighbors have larger probability that a mutation occurs in their neighborhood and that they are then mutated in the subsequent step.

FIG. 6. Distribution of the connectivity for all sites (full line) and for extremal sites only (dashed line), in the stationary regime for \( p = 0.98 \), averaged over \( 10^8 \) time steps. Inset: Dependence of averaged connectivity on \( p \). The solid line corresponds to the power law \( \langle c \rangle \propto (1 - p)^{-0.75} \).

The average connectivity \( \langle c \rangle \) computed from the distributions \( P_{\text{all}}(c) \) is shown in the inset of Fig. 5. We can observe that analogically to the system size also the average connectivity diverges for \( p \to 1 \) as a power law, but the value of the exponent is slightly different. We find \( \langle c \rangle \propto (1 - p)^{-\alpha_c} \) with the exponent \( \alpha_c \approx 0.75 \). From the data available we were not able do decide, whether the exponents \( \alpha_n \) and \( \alpha_c \) are equal within the statistical noise.

In Fig. 5 we can see that also the distribution of connectivity has an exponential tail, similarly to the distribution of network size. We measured also the joint probability density \( P(n_u, c) \) for the number of units and the connectivity. The result is shown as a contour plot in Fig. 7. We can see that also for large networks (large \( n_U \)) the most probable connectivity is small and nearly independent on \( n_u \). This means that the overall look of
the network created by the dynamics of our model is that there are a few sites with large connectivity, surrounded by many sites with low connectivity.

**FIG. 7.** Contour plot of the joint probability density $P(n_u, c)$ for number of units and connectivity, for $p = 0.8$, averaged over $3 \cdot 10^9$ time steps. The contours correspond to the following values of the probability density (from inside to outside): $5 \cdot 10^{-R}$, $2 \cdot 10^{-R}, 10^{-R}$, with orders $R = 3, 4, 5, 6, 7, 8$.

An interesting observation can be drawn from the results shown in Fig. 8. It depicts the joint probability density as a function of connectivity at fixed system sizes. We can see that for smaller system sizes, closer to the average number of units, the distribution is exponential, while if we increase the system size a power-law dependence develops. For example for the system size fixed at $n_u = 170$ we observe a power-law behavior $P(n_u, c) \sim c^{-\eta}$ nearly up to the geometric cutoff, $c < n_u$. The value of the exponent was about $\eta \simeq 2.3$.

This finding may be in accord with the power-law distribution in growing networks [6,40]. Indeed, in our model the power-law behavior applies only for networks significantly larger than the average size. Such networks are created during time-to-time fluctuations leading to temporary expansion of the network. So, the power-law is the trace of expansion periods in the network evolution, corresponding to continuous growth in the model of [6]. The preferential attachment, which is the second key ingredient in [6] has also an analog in our model; highly connected units are more likely to be mutated, as was already mentioned in the discussion of Fig. 6. However, here the preference of highly connected sites is a dynamical phenomenon, resulting from the extremal dynamics rules of our model.

**C. Clusters**

As noted already in the Sec. II the network can be split into several disconnected clusters. The clusters cannot merge, but they may vanish due to extinctions. We observed qualitatively that after initial growth the number of clusters exhibits stationary fluctuations around an average value, which increases when $p$ approaches 1. We measured both the distribution of the number of clusters and the distribution of their sizes. In Fig. 9 we show the distribution of the number of clusters. The most probable situation is that there is only a single cluster. However, there is a broad tail, which means that even large number of clusters can be sometimes created. The tail has a power-law part with an exponential cutoff. The value of the exponent in the power-law regime $P(n_c) \sim n_c^{-\rho}$ was about $\rho \simeq 1.2$. We have observed that the width of the power-law regime is larger for larger $p$. This leads us to the conjecture that in the limit $p \to 1$ the number of clusters is power-law distributed.

On the other hand, the distribution of cluster sizes shown in Fig. 10 has maximum at very small values. This is due to two effects. First, already the distribution of network size has maximum at small sizes, and second, if the network is split into many clusters, they have small size and remain unchanged for long time. The reason why small clusters change very rarely (and therefore can neither grow nor disappear) can be also seen from Fig. 10, where the distribution of sizes of the clusters containing the extremal site is shown. The latter distribution is significantly different from the size distribution for all clusters and shows that the extremal site belongs mostly to large clusters. In fact, we measured also the fraction indicating how often the extremal unit is in the largest cluster, if there are more than one cluster. For the same
run from which the data shown in Fig. 10 were collected, we found that this fraction is 0.97, i.e., very close to 1. A similar “screening effect” was reported also in the Cayley tree models \[31\]: the small isolated portions of the network are very stable and nearly untouched by the evolution.

$$\frac{\langle n_c \rangle}{n_c}$$

![FIG. 9. Distribution of the number of clusters, for $p = 0.98$. The straight line is a power law with exponent $-1.2$. The data were averaged over 3 independent runs, $5 \cdot 10^8$, $5 \cdot 10^8$, and $10^8$ time steps long.](image)

![FIG. 11. Dependence of the average distance of two sites within the same cluster on the cluster size, for $p = 0.95$ (full line) and $p = 0.97$ (dashed line), averaged over for $10^7$ time steps. In the inset we show the same data in the log-linear scale.](image)

**D. Mean distance**

An important feature of a random network is also the mean distance $\bar{d}$ between two sites, measured as minimum number of links, which should be passed in order to get from one site to the other. In $D$-dimensional lattices, the mean distance depends on the number of sites $N$ as $\bar{d} \sim N^{1/D}$, while in completely random networks the dependence is $\bar{d} \sim \log N$. In the small-world networks, the crossover from the former to the latter behavior is observed \[31\].

$P(s_c)$

$$\frac{P(\text{all}(s_c))}{10} \quad 10P(\text{extremal}(s_c))$$

![FIG. 10. Distribution of the cluster sizes $s_c$ for $p = 0.98$, averaged over $10^8$ time steps. Full line - all clusters, dashed line - clusters containing the extremal site. Inset: Detail of the same distribution.](image)

**V. CONCLUSIONS**

We studied an extremal dynamics model motivated by biological evolution on dynamically evolving random network. The properties of the model can be tuned by the parameter $p$, the probability that a link is inherited in
...the process of speciation. For $p = 1$ the model is self-organized critical and the average system size and connectivity grows without limits. Contrary to the usual BS model, we find two power-law regimes with different exponents in the statistics of forward $\lambda$-avalanches. The crossover avalanche size depends on $\lambda$ and diverges for $\lambda \to 0$ as a power law. The reason why the critical $\lambda$ is zero in this model is connected with the fact that time-averaged connectivity diverges for $p = 1$.

We investigated the geometrical properties of the random networks for different values of $p$. The average network size and average connectivity diverge as a power of $1 - p$. The probability distribution of system sizes has an exponential tail, which suggests that the dynamics of the system size is essentially a biased random walk with a reflecting boundary. The value of the bias grows with decreasing $p$. The joint distribution of size and connectivity shows that even for large network sizes the most probable connectivity is low. Hence, there are few highly-connected sites linked to the majority of sites with small connectivity. Moreover, the situations where the system size is far above its mean value are characterized by power-law distribution of connectivity, like in the models of growing networks with preferential attachment.

The network can consist of several mutually disconnected clusters. Even though the most probable situation contains only a single cluster, the distribution of cluster numbers has a broad tail, which shows a power-law regime with exponential cutoff. We observed the "screening effect", characterized by very small probability that the extremal site is found in any other cluster than the largest one. So, there is a central large cluster, where nearly everything happens, surrounded by some small peripheral clusters, frozen for the major part of the evolution time.

We measured also the mean distance measured along the links within one cluster. The distance grows very slowly with the cluster size; however, the increase seems to be faster than logarithmic.

Summarizing, we demonstrated that the extremal dynamics, widely used in previous studies on macroevolution in fixed-size systems is useful in creating random networks of variable size. It would be of interest to compare the properties of the networks created in our model with food webs and other networks found in the nature. For example the studies of food webs in isolated ecologies give for network sizes about 30 average connectivities in the range from 2.2 to 9, which is not in contradiction with the findings of our model. However, more precise comparisons are necessary for any reliable conclusions about real ecosystems.

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