

## The Bak-Sneppen model on scale-free networks

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**Abstract.** – We investigate by numerical simulations and analytical calculations the Bak-Sneppen model for biological evolution in scale-free networks. By using large-scale numerical simulations, we study the avalanche size distribution and the activity time behavior at nodes with different connectivities. We argue the absence of a critical barrier and its associated critical behavior for infinite-size systems. These findings are supported by a single-site mean-field analytic treatment of the model.

Many real systems, ranging from biological systems such as food webs [1–3] to communication systems [4,5], exhibit properties that lie in between those of regular lattices and random graphs [6]. They are usually referred to as complex networks [7]. These networks may have large clustering coefficients like regular lattices but also have a small diameter which is a typical feature of random graphs. Among the class of complex networks, a particular role is played by *scale-free* networks (SF) [8] in which there are not characteristic fluctuations in the connectivity of the nodes. This implies that the probability  $P_k$  that a node is connected with other  $k$  nodes follows a power law, *i.e.*,  $P_k \sim k^{-\gamma}$ , in contrast to *exponential* graphs in which  $P_k$  is exponentially bounded [6,7,9].

SF networks have recently been recognized to describe several real growing networks [3–5, 8,10], and at the same time have proved to show very peculiar features with respect to physical properties such as damage tolerance [11], epidemic spreading [12], and diffusion properties [13]. It is then natural to ask whether and to what extent the topology of these complex networks would affect many of the results obtained for punctuated evolution models in regular lattices.

In this letter, we study the Bak-Sneppen model (BS) [14] on SF networks. We perform large-scale numerical simulations and find that, contrary to what is observed in regular lattices and in exponential networks, the system self-organizes into a stationary state characterized by the lack of a critical threshold barrier in the thermodynamic limit. This result is confirmed analytically by constructing the genealogical tree of the avalanches and performing a mean-field approach which takes into account the strong fluctuations of the network's connectivity

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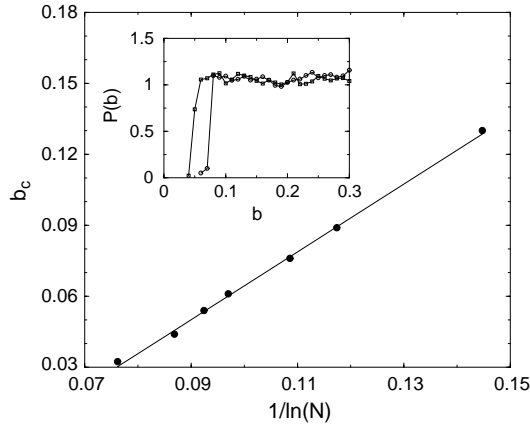


Fig. 1 – Threshold barriers for several system sizes ranging from  $N = 10^3$  to  $N = 5 \times 10^5$ . The inset shows the distribution of barriers in the stationary state for systems of size  $10^4$  (circles) and  $10^5$  (squares) for  $b < 0.3$ .

distribution. Finally, we discuss the consequences that the present results could have in the general context of punctuated evolution models.

The standard BS model [14] can be considered as an ecological system formed by many species that interact one with each other if they are in contact, *i.e.*, the interactions are local. To each node of the graph we allocate a random *fitness* barrier  $b_i \in [0, 1)$  ( $i = 1, \dots, N$ ) that represents the ability of species to survive or mutate [14]. The fitness are initially uniformly distributed between 0 and 1 and the dynamics is updated according to the following rules: i) at each time step, the species with the minimum barrier  $b_{\min}$  is located and mutated by assigning a new random value for its fitness. This somehow mimics the Darwinian principle that the least-fit species evolve by mutation or disappear; and ii) the species directly linked to the species with  $b_{\min}$  change their fitnesses to new random numbers as the result of their interactions. By applying these rules repeatedly, after a transient period and regardless of the initial distribution of fitness barriers, the fitness distribution  $P(b)$  of the system evolves toward a self-organized stationary state where several physical quantities can be measured. In previous studies on *regular geometries* and *exponential networks* [15–17], it has been found that the distribution of barriers tends, in the limit of infinite system sizes, to a step-like function characterized by the existence of a single parameter  $b_c$ . In these cases, for  $b < b_c$  the distribution  $P(b) = 0$ , otherwise,  $P(b)$  is equal to a constant value.

In order to study the BS model on a SF topology, we use the network obtained using the algorithm of ref. [8]. This is a stochastic growing network model in which at each time step a new node (or vertex) is added to the network and connected preferentially to the already existing ones with a probability that depends on their connectivities. In practice, we start with a small number  $m_0$  of disconnected nodes and at each time step the network grows by adding a new vertex. This is connected to  $m$  old ones  $i$  with a probability  $\Pi(k_i) = k_i / \sum_j k_j$ . By iterating this scheme, a network of size  $N$  with connectivity distribution  $P_k \sim k^{-3}$  develops. As a first step, we performed numerical simulations of the BS model in SF networks with sizes ranging from  $N = 10^3$  to  $N = 5 \times 10^5$ . The BS dynamics is iterated to achieve a stationary state giving rise to the step function behavior usually observed in regular lattice. On SF networks, however, it appears that the critical barrier  $b_c$  is not an intrinsic quantity and that  $b_c \rightarrow 0$  if  $N \rightarrow \infty$ . Figure 1 shows the dependency of the critical barrier on the system size.

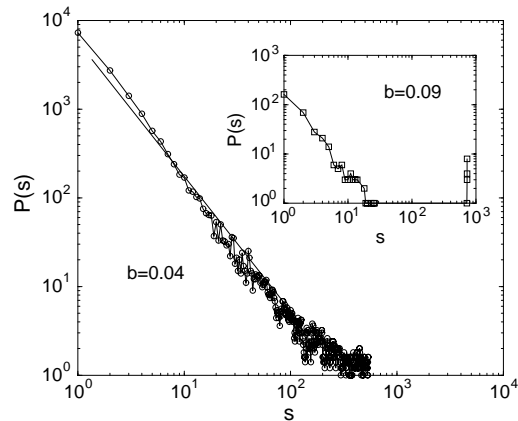


Fig. 2 – Avalanche size distributions for  $b = 0.04$  and  $b = 0.09$  (inset). The system, which consists of  $N = 10^5$  species, has the threshold value at  $b_c = 0.044$ . The data were recorded after a transient of  $10^6$  mutations. A full line corresponding to a power law with exponent  $\tau = 1.5$  has been drawn for comparison.

It turns out that as the system size is increased the critical barrier  $b_c$  shifts leftward and goes to zero logarithmically as  $b_c \sim 1/\ln N$ . Thus, in the thermodynamic limit ( $N \rightarrow \infty$ ), there is no threshold barrier; *i.e.*  $b_c = 0$ . Above the threshold, the distribution of barriers is flat with overimposed statistical fluctuations. A further check of this behavior is provided by the analysis of the burst activity (avalanche) in the system. An avalanche is defined as the number of subsequent mutations below a certain threshold. In fig. 2, we show the avalanche size distribution for two different values of avalanche threshold  $b$ . For this system, which consists of  $N = 10^5$  species, the critical barrier is  $b_c = 0.044$ . For values of  $b$  below  $b_c$ , the avalanches are distributed according to a power law  $P(s) \sim s^{-\tau}$ , with  $\tau = 1.55 \pm 0.05$ , a value close to the mean-field exponent  $\tau = 3/2$  observed in other versions of the BS model [16] and in self-organized critical models [18]. The inset illustrates that, as soon as the  $b$  barrier is placed above the threshold, the distribution splits into two parts (see the inset) and is characterized by the excess of large avalanches signaling that we are in the supercritical region. If the barrier  $b$  were further increased, then there would be only one avalanche whose size will be limited only by the observation time. Besides, for very large system sizes the absence of a critical barrier makes that even for small  $b$  the avalanche size distribution looks like the inset of fig. 2 indicating the lack of a critical point.

The numerical evidence tells us that the BS model behavior radically changes in SF networks. The lack of a threshold can be intuitively understood by recalling that for regular lattices and for networks in which the connectivity distribution is exponentially bounded, the threshold barrier decreases as the number of neighbors with which a species interacts increases. This is the case studied in [17], where an ecology consisting of  $N$  species, each one interacting with  $z_i$  neighbors, was studied. In this model, the  $z_i$  neighbors are drawn from a Poisson distribution with a mean  $\langle z \rangle$ . When increasing  $\langle z \rangle$  and thus the connectivity, it was observed that the threshold barrier  $b_c$  decreases. In SF networks like the one studied here, the fact that the fluctuations in the number of neighbors of each species diverge ( $\langle k^2 \rangle = \infty$ ) makes null the threshold barrier when  $N \rightarrow \infty$ . It is worth remarking that the absence of a critical threshold due to the strong fluctuations of the SF networks connectivity has recently been reported for epidemic spreading [12, 19] and percolation-like phase transitions [11].

In order to support with analytical considerations the absence of a critical barrier, we will analyze the burst-like activity observed in the evolution process following a MF approach. MF approaches are expected to give the right solution for growing random networks which are defined by nonlocal random topologies. Let us define a  $b$  avalanche when there is one specie  $i$  with  $b_i \leq b$  while for all the others  $b_j > b$ . The  $b$  avalanche lasts until all the barriers are above the  $b$  barrier. Thus, if there is a critical barrier  $b_c$ , the avalanches should always be finite for  $b < b_c$  since below the threshold it is expected that no species remain forever. Otherwise, there is a nonzero probability to observe an infinite avalanche that approaches one, as we move away from the critical barrier. Let us assume that  $0 < b < b_c$ . Thus, a  $b$  avalanche must be finite.

Within a  $b$  avalanche one can build a genealogical tree as was shown in ref. [16]. A node in this tree represents a species whose barrier goes below  $b$  at some step. Since we have assumed that the avalanche is finite, this species will be selected for evolution at some later step, assigning a new random barrier to it and its neighbors. In this process, the barrier of the species itself and those of its neighbors may go below the threshold again and, in such a case, they are represented by other nodes in the tree. The fact that these nodes are causally related is represented by a direct link from the ancestor (the species with the minimum barrier) to its sons (the species whose barriers go below  $b$ ). The generation  $t$  of a node in this tree is then defined as the number of nodes one needs to pass in order to arrive at that node starting from the node that triggered the avalanche. As we have assumed that the avalanche is finite, the relative density of species whose fitness values are below the critical barrier should vanish in the stationary state.

Let  $\phi_k(t)$  be the relative density of nodes at generation  $t$  with given connectivity  $k$ . This connectivity is taken as the connectivity of the real SF network, where the BS evolution rules take place, and not to that corresponding to the genealogical tree. The rate equations for  $\phi_k(t)$  are given by

$$\partial_t \phi_k(t) = -(1-b)\phi_k(t) + bk[1-\phi_k(t)]\Theta(b). \quad (1)$$

The first term on the r.h.s. takes into account that, when a species is selected for evolution, with probability  $1-b$  its new randomly assigned barrier may be above  $b$ . The second term considers the fraction of nodes  $1-\phi_k(t)$  whose barriers are above  $b$ , but change their barriers because they have a link to the species selected for evolution. The factor  $b$  takes into account that the new barrier will be below  $b$  with probability  $b$ .  $\Theta(b)$  denotes the probability that a link points to a node selected by evolution, and  $k\Theta(b)$  the probability that a species with connectivity  $k$  have a link pointing to the species which are going to evolve. By using the MF considerations of ref. [12], this probability is given by the number of links belonging to species with connectivity  $k$ ,  $kP_k N$ , divided by the total number of links  $\sum_s sP_s N$ . Hence, making the summation over  $k$  it results that

$$\Theta(b) = \sum_k \frac{kP_k \phi_k}{\sum_s sP_s}. \quad (2)$$

In the stationary state  $\partial_t \phi_k(t) = 0$  and from eqs. (1) and (2) we obtain two self-consistent equations from which one obtains  $\Theta(b)$  and  $\phi_k$ . Finally, the stationary density of nodes with barrier below  $b$  is  $\phi = \sum_k \phi_k$ . This set of equations is analogous to the one studied in [12]. The solution gives that, for SF networks with  $2 < \gamma \leq 3$  and for any value of  $b$ , the stationary density of species below  $b$  is finite and, therefore, in the thermodynamic limit there is a finite probability to obtain an infinite avalanche where strictly speaking,  $\phi$  is nonzero. However,

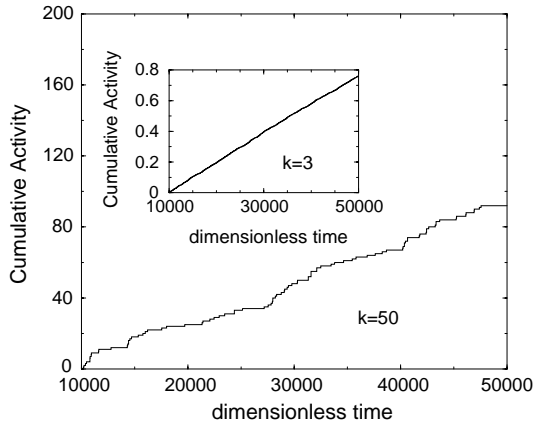


Fig. 3 – Cumulative activity for species with  $k = 50$  and  $k = 3$  (inset) neighbors. In this case,  $k = 3$  corresponds to the minimally connected species. The activity strongly depends on the species' connectivity and for highly connected species it is  $\sim 100$  times that of the minimally connected sites. The punctuated equilibrium behavior can be nevertheless observed for both sub-populations.

this result is in contradiction with our initial assumption that  $0 < b < b_c$ , for which the avalanches should be finite. Hence, we conclude that for  $2 < \gamma \leq 3$  there is not a finite threshold  $b_c$  when  $N \rightarrow \infty$ . For any finite-system size, the threshold, although very small, is not zero since there is a finite probability that all species have their fitness values above the critical barrier at the same time. It is worth noting at this point that the above arguments can be used to easily show that for exponential networks with an average connectivity  $\langle k \rangle$  the scenario at the stationary state is completely different. In this case  $\Theta(b) \approx \phi$  and it results that there is a finite threshold barrier which is given by  $b_c = \frac{1}{1+\langle k \rangle}$ , as can be seen by direct comparison with the numerical values reported in [17],  $b_c = 0.3446 \approx 1/3$  and  $b_c = 0.2575 \approx 1/4$  for  $\langle k \rangle = 2$  and  $\langle k \rangle = 3$ , respectively. Thus, for exponential networks, the threshold barrier is in general finite and it is determined by the first moment of the degree distribution  $\langle k \rangle$ . On the contrary, in SF networks, the lack of a threshold barrier takes place when the second moment  $\langle k^2 \rangle$  diverges, *i.e.* when  $\gamma \leq 3$ . The peculiar topology of these networks gives rise to the existence of a few nodes with a very high number of neighbors, and thus the fluctuations in the number of neighbors emanating from each node are unbounded (that is, the second moment diverges). This fact becomes determinant for the dynamics of the system. We would like to remark that our results are on the same line as those obtained in spreading dynamics on SF networks where the critical parameter is related to the first and the second moments through the relation  $\langle k \rangle / \langle k^2 \rangle$  [12, 19] which implies a vanishing threshold in the thermodynamic limit. However, we emphasize that real networks have always a finite size  $N$  and thus a finite effective threshold, although extremely small for very large system sizes.

The peculiar features of the BS model depend on the highly heterogeneous nature of SF networks. As a further evidence of this heterogeneity, we explore how the activity in the network is distributed according to the nodes' connectivity. We have measured the number of times  $n_k$  a node with connectivity  $k$  has been selected to mutate because it has the minimum barrier among all the species. The results obtained show that the activity is concentrated in the species with high connectivities. This indicates that the activity patterns are strongly correlated with the connectivity of each site. Species with high degrees of interaction with their neighborhoods are thus more susceptible to mutate or become extinct than their coun-

terparts. Speciation mechanisms [20] during evolution have been suggested as key natural processes to explain the evolutionary patterns found in all lineages. For speciation to be accomplished, it has been proposed both geographical isolation and environmental stress as important triggering factors. In the model studied here, the nodes in the network represent species, whereas the links between them correspond to the complex dependency relationships that can be established in an ecosystem, for example, through a food web or predator-prey relationship. Therefore, the species with high connectivities may be thought of as being more stressed than others with low connectivities. Consequently, we expect that the punctuated equilibrium pattern be manifested in a significant reduction in the cumulative activity of the lowly connected species as compared to that of the highly connected ones. Figure 3 shows the cumulative activity for species with connectivity  $k = 50$  and  $k = 3$  (inset). As can be clearly seen, the punctuated equilibrium behavior appears in both sub-populations. However, the higher the species connectivities, the shorter the periods of intensive activity. Thus, for the *same* time window, speciation and rapid episodes of major evolutionary changes are expected to take place in the more stressed, highly dependent species. This correlation has been observed in several studies [21]. Besides, the fact that speciation can occur rapidly over a large area containing millions of individuals has been documented by Williamson [22], who studied a series of mollusk fauna of the eastern Turkana basin, in Africa.

In summary, we have studied the BS model on scale-free networks. We have shown that the highly interacting species play a key role in the evolution process. Numerical results as well as analytical arguments point out the absence of a critical threshold barrier in the thermodynamic limit. For real system, which are always of finite size, the threshold, although very small, exists. We have also found that the activity patterns are strongly correlated with the topology of the network. Finally, we have outlined the possible implications our results may have for speciation events.

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