Evolutionary dynamics in the Bak-Sneppen model on small-world networks

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We study the dynamics of the Bak-Sneppen model on small-world networks. For each site in the network, we define a “connectance,” which measures the distance to all other sites. We find radically different patterns of activity for different sites, depending on their connectance and also on the topology of the network. For a given network, the site with the minimal connectance shows long periods of stasis interrupted by much smaller periods of activity. In contrast, the activity pattern for the maximally connected site appears uniform on the same time scale. We discuss the significance of these results for speciation events.

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The theory of punctuated equilibrium (PE) states that (i) most evolutionary change associated with life on Earth occurs during speciation events, and (ii) the time scale for these speciation events is very brief compared to the lifetimes of the individual species. Thus the evolutionary history of most species is characterized by long periods of stasis punctuated by relatively brief intervals of rapid evolutionary activity. Mayr’s theory of allopatric speciation, which forms the basis of PE, suggests that the rapid evolutionary activity leading to speciation generally occurs in small isolated populations, whereas more widespread populations exhibit little evolutionary change over the same time scale. Understanding why the rates of evolutionary change differ so drastically in these two types of populations is one of the important problems of evolutionary biology. A related problem is the study of patterns of extinctions in biological history, which seem to show scale-free behavior as discussed by Raup. Stanley has argued that these problems, and most large-scale trends in evolutionary history, can be understood by using the species as a fundamental unit of evolution.

Bak and Sneppen have introduced a simple model aimed at understanding these evolutionary patterns using the species as the fundamental unit. The model is based on coevolution of species and exhibits “intermittent dynamics” - that is, species undergo long periods of little change, called stasis, which are punctuated by sudden bursts of activity called avalanches. It provides a natural explanation for the apparent scale-free behavior of the extinctions - the system evolves into a self-organized critical (SOC) state with avalanches (which are correlated with extinction events) occurring at all scales. The same model can also be used to understand the scale-free behavior of seemingly unrelated phenomena such as earthquakes, as noted by Ito. Aside from its applications to various problems, the Bak-Sneppen model is of intrinsic interest, since it is one of the simplest models giving rise to SOC behavior.

The Bak-Sneppen model, as elaborated below, has been extensively studied for regular networks. However, as argued by Watts and Strogatz, most real-life networks are neither perfectly ordered nor completely disordered but fall under the category of “small-world” networks which interpolate smoothly between the two extremes. Such networks are characterized by a high degree of local order, yet appear disordered on a large-scale because of the presence of shortcuts in the networks. Because of their wide applicability, there have recently been numerous papers characterizing the properties of such networks. In the context of species interacting in an ecosystem, examples of food webs indicate that the interactions are better represented by small-world networks rather than by a simple ordered topology.

The aim of this Letter is to examine the dynamics of the Bak-Sneppen model on small-world networks. In our analysis, we find it useful to define a site-dependent property which we call “connectance.” We find that the patterns of activity at each site are correlated with the connectance. In particular, the minimally connected site in a given network shows activity characteristic of intermittent dynamics, whereas the maximally connected site shows uniform activity on the same time scale. Furthermore, for the maximally connected site we see a drastic reduction in the stasis times in going from the ordered topology to the small-world networks. We discuss the implications of these results for speciation events.

We begin by recalling the definition of the Bak-Sneppen model. Each species is represented by a site on a 1-d lattice with periodic boundary conditions. Each lattice site is connected to its 2k nearest neighbors by a bond (so that for n interacting sites, or species, we have nk bonds). With each site we associate a random number, called the barrier value, between 0 and 1; this number plays the role of a barrier against evolutionary change for the species. The dynamics of the Bak-Sneppen model is carried out by the following rule. At each time step, we select the site with the minimal barrier value (denoted the minimal site), and assign new barrier values to this site and its 2k neighboring sites. We refer to a reassign-
ment of the barrier value at a site as activity at that site. This set of rules, called extremal dynamics, leads the system into a SOC state where the distribution of barrier values is uniform above a critical barrier value $f_c$.

The small-world networks are generated using the procedure outlined by Watts and Strogatz. We start with the 1-d lattice described above and “rewire” each bond with a probability $p$ ($0 \leq p \leq 1$). The rewiring consists of taking a given bond and moving it so that, instead of connecting two neighbors, one end of the bond is moved so as to connect with another site chosen at random, with the constraint that double bonds are forbidden. The network so formed can then be characterized by the functions $L(p)$, which is defined as the number of bonds in the shortest path between two sites, averaged over all pairs of sites, and $C(p)$ which is a measure of clustering in the graph. The network is said to fall in the small-world regime if it satisfies the conditions $C(p)/C(0) \sim 1$ and $L(p)/L(0) \sim 0$. Table I shows the values of these two ratios for the networks we studied, all of which were characterized by $n = 2000$ and $k = 2$. A recent study on food webs suggests that our choice of $k$ is often realized in practice. Finally, for each site, we define the connectance $g_i$ by

$$g_i = 1 - \frac{D_i - \min_{j \neq i} D_j}{\max_{j \neq i} D_i - \min_{j \neq i} D_j}; \quad p > 0$$

where $d(i, j)$ is the minimal distance between sites $i$ and $j$, that is, the minimal number of bonds which must be traversed in going from $i$ to $j$.

We carried out our simulations for $n = 2000$ and for $p = 0.0, 0.01, 0.04, 1.0$. For each disordered network ($p \neq 0$) we studied the dynamics for 10 different realizations. Remarkably, even though the topologies for a given $p$ value were distinct, our calculated quantities all collapsed onto the same set of curves. The results we present were obtained by sampling for $5 \times 10^9$ time steps after the stationary state characteristic of SOC had been reached. In the following, we discuss results for $p = 0.0$ and $p = 0.01$ since these capture the essential features in going from ordered to small-world networks.

In the Bak-Sneppen model, an avalanche is defined as the sequence of time steps for which the minimal site has a barrier value smaller than a threshold value $f_0$. The avalanche thus ends when the minimal site has a barrier value greater than $f_0$. For each $p$-value, we choose $f_0$ such that $\Delta f = f_c - f_0 = 0.01$. Fig. 1 shows the distribution of avalanche durations and the average number of sites covered ($N_{cov}$) by an avalanche of a given duration for $p = 0.0$ and $p = 0.01$. For $p = 0.0$ (inset) we see the expected power-law behavior with a cut-off for large avalanche sizes. For $p = 0.01$, on the other hand, we see novel features arising from the small-world properties of the network. In particular, we now see two power-law regimes, denoted by regions A and B. As the avalanche size grows, it increasingly “senses” the short-cuts in the system, and becomes more delocalized; this delocalization produces an increased slope in $N_{cov}$ in going from regime A to regime B. A more detailed analysis of this behavior will be presented elsewhere.

In Fig. 2, we show the so-called first-return plots, i.e., the distribution of waiting times between subsequent returns of activity, at the maximally connected sites for $p = 0.0$ and $0.01$. All the plots show power-law behavior followed by a cut-off which corresponds to the maximal stasis time. We note that the maximal stasis time decreases by roughly two orders of magnitude in going from $p = 0.0$ to $p = 0.01$. Thus the transition from ordered to small-world networks is marked by a drastic reduction of the maximal stasis times. The inset shows the first-return plots for the maximally and the minimally connected sites in a $p = 0.01$ network. From these plots we see that the cut-off is correlated with the connectance: higher connectance leads to a smaller cut-off time for a given network.

A dramatic consequence of the reduction in stasis times

| $p$ | $\frac{L(p)}{L(0)}$ | $\frac{C(p)}{C(0)}$ |
|-----|---------------------|---------------------|
| 0.01 | 0.14                | 0.97                |
| 0.04 | 0.06                | 0.89                |
| 1.00 | 0.02                | 0.04                |

**FIG. 1.** Number of avalanches (+) and number of sites covered (full line without symbols; $N_{cov}$) by an avalanche vs. duration $s$ of the avalanche, for $p = 0.01$. The influence of short-cuts, or small-world behavior, is reflected in the slope changes between regions A and B. In region C, finite-size effects dominate. The inset shows the same plots for $p = 0.0$. The cut-off is marked by a drastic reduction in stasis times. We note that the maximal stasis time decreases by roughly two orders of magnitude in going from $p = 0.0$ to $p = 0.01$. Thus the transition from ordered to small-world networks is marked by a drastic reduction of the maximal stasis times. The inset shows the first-return plots for the maximally and the minimally connected sites in a $p = 0.01$ network. From these plots we see that the cut-off is correlated with the connectance: higher connectance leads to a smaller cut-off time for a given network.
can be seen in Fig. 2, where we show the activity plots for the maximally connected sites for $p = 0.0$ (•) and $p = 0.01$ (∗). Note that the cut-off, which corresponds to the maximal stasis time, is reduced by 2 orders of magnitude for increasing $p$. The inset shows the distribution of stasis times for the maximally (∗) and the minimally (+) connected site in a $p = 0.01$ network.

FIG. 2. Distribution of first-return (stasis) times for the maximally connected sites for $p = 0.0$ (•) and $p = 0.01$ (∗). Note that the cut-off, which corresponds to the maximal stasis time, is reduced by 2 orders of magnitude for going from $p = 0.0$ to $p = 0.01$. The inset shows the distribution of stasis times for the maximally (∗) and the minimally (+) connected site in a $p = 0.01$ network.

For $p = 0.0$, the cumulative activity at a particular site shows a pattern of “punctuated equilibrium” behavior. In contrast, the maximally connected site at $p > 0$ shows a uniform pattern of activity on the same time scale. This behavior results from the decrease in maximal stasis time (cf. Fig. 2) with increasing $p$. This relationship is clearly indicated in the inset, which shows that the same pattern now exhibits “punctuated equilibrium” behavior on a much smaller time scale. The correlation between maximal stasis time and connectance for a given network can be seen in Fig. 1, where the activity is plotted for the sites with maximal and minimal connectance at $p = 0.01$. The minimally connected site shows a pattern of “punctuated equilibrium,” whereas the site with maximal connectance exhibits uniform behavior. In short, the periods of stasis are significantly reduced when either $p$ or $g$ is increased.

The uniform activity pattern seen for $p > 0$ may appear to be at variance with the theory of punctuated equilibrium. But in fact, we argue that this behavior actually supports that theory in the form postulated by Gould and Eldredge. We first clarify the correspondence between our idealized model and an ecosystem. As already noted, the sites correspond to species, while the network of connections between them can be viewed as representing the food web of the ecosystem. Activity at a site represents a significant change for the corresponding species population in the ecosystem; an accumulation of activity can lead to either speciation or extinction. Our model does not distinguish between the two, and we expect instances of both speciation and extinction to be proportional to the amount of activity. Finally we note that a bond between two species represents a dependency link between them, which is typically, but not exclusively, a predator-prey relationship.

We now discuss the correspondence between the activity patterns described above and the theory of punctuated equilibrium. We note that the staircase pattern seen in Fig. 3(a) corresponds to an evolutionary process called anagenesis, in which the entire ancestral species evolves into a new species. But, as noted by Stanley, most speciation processes in nature are actually branching processes (called cladogenesis), in which a new species is created from a geographically isolated subpopulation of the ancestral species. During cladogenesis, the ancestral species shows little change (stasis), whereas the isolated sub-population undergoes rapid evolutionary change. This is the basic process involved in the theory of punctuated equilibrium. Thus, what is required is that the periods of stasis be greatly reduced for the isolated population, in comparison to the ancestral species. This is precisely what is seen in Fig. 3(a); in these plots, increasing $p$ results in much shorter periods of stasis and hence, an activity plot which has the appearance of uniformity in time.

Thus, our scenario for the time sequence of allopatric speciation events, as motivated by our simulations, is the following. (1) A sub-population migrates to a peripherally isolated region, such as an island. We expect the island ecology to have a higher value of $p$ for the interaction network; hence, the periods of stasis for the isolated sub-population should be much smaller than those of the
ancestral population. (2) The migration event itself initiates a period of activity on the island [12], while stasis continues to prevail for the ancestral population. The combination of these two effects gives rise to rapid evolutionary change leading to speciation for the island population, and simultaneously stasis in the ancestral population.

Note that this model does not exclude other proposed mechanisms, such as the “founder effect” proposed by Mayr [3], but instead is complementary to them. Our scenario focuses on the coevolutionary activity in different ecosystems and thus on effects external to the species populations, whereas the other mechanisms focus on the internal characteristics of the species populations. For example, the founder effect requires that the peripherally isolated population be small, and therefore more amenable to rapid change. Speciation can, however, occur rapidly over a large area containing many millions of individuals. In particular, Williamson [13] has shown that, in a group of African lakes in the Turkana basin, the species underwent significant phylegetic change over only 5 x 10^4 years, whereas the ancestral populations remained virtually unchanged in their parental waters. In this case, the observed speciation events cannot be explained by the founder effect, as argued by Williamson, but they do seem consistent with our proposed scenario.

Our calculations show that, for a given network, the patterns of activity are strongly correlated with the connectance. How is this observation reflected in studies of real ecosystems? One possibility is the following: since the bonds in the network corresponds to dependency links, the species with high connectance have a high degree of dependency - i.e., they are specialists (stenotypic) - whereas species with low connectance are generalists (eurotypic). As already noted in Fig. 4, the cumulative activity is an order of magnitude larger for the maximally connected site than for the one with minimal connectance. Based on our model, we therefore expect stenotypic species to speciate or go extinct more often than their eurotypic counterparts. This correlation between ecological specialization and speciation and extinction rates has been observed in numerous studies [14].

In summary, we have extended the 1-d Bak-Sneppen model to small-world networks. This extension allows us to distinguish different sites in the network, and thereby the species in an ecosystem, based on a site-dependent property which we call connectance. We find that the activity patterns are strongly correlated with the topology of the network and with the connectance. Finally, we discuss the possible implications of these results for speciation events.

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FIG. 4. Cumulative activity for sites with (a) maximal and (b) minimal connectance for p = 0.01. The maximally connected site has a cumulative activity which is ~40 times that of the minimally connected site.