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BRIEF REPORTS

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Scaling behavior of the punctuated-equilibrium model of evolution

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The existence of scaling behavior in real physical time in the punctuated-equilibrium model of evolution proposed recently from Bak and Sneppen [Phys. Rev. Lett. **71**, 4083 (1993)] is assured provided that the characteristic mutation time of a species varies exponentially with its fitness. A self-consistent condition on the characteristic fitness is also derived.

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Biological evolution takes place in bursts separated by a relatively long period of quiescence [1]. In fact, extinction may be episodic at all scales [2]. To capture the essence of this scaling behavior, a self-organized critical model of biological evolution, called the punctuated equilibrium model, is introduced recently by Bak and Sneppen [3]. An ecosystem in the model is made up N species, and a scalar between zero and one, called fitness, is assigned to each species. The higher the fitness, the more adaptable to the ecosystem and hence the less likely to mutate the species is. Thus the one with the minimum fitness in the system is most likely to mutate or extinct next. Fitness is therefore also a measure of the barrier against mutation.

The one-dimensional punctuated equilibrium model of evolution is summarized below: N species are arranged on a line with periodic boundary condition. At each time step, the species with minimum fitness together with its two nearest neighbors are going to mutate by replacing their fitness by uniform and uncorrelated random numbers between zero and one. The updating process is repeated forever. Scaling behavior is observed in the distribution of distance between successive mutations once the stationary state is reached, which is a signature of self-organized criticality. They found a threshold fitness of value 0.67±0.01, above which we have zero probability of finding a minimum fitness s_{min} and the distribution of fitness of all species is uniform. Similar results are found for both the higher dimensional [4] and the mean field models (where K randomly chosen sites other than the one with minimum fitness mutate) [5].

It is believed that the characteristic mutation time for a species with fitness s goes as

$$g(s) = Ae^{\lambda s} \tag{1}$$

for some $A > 0$, and $\lambda \gg 0$ [2,6]. In fact, this is the reason why the least fit species is always chosen to mutate next [3]. As a result, different cellular automaton time steps may correspond to different real physical times elapsed. For every fitness s, $g(s)$ defines its characteristic mutation time. So it is unclear if the mutation of different species in real physical time in the punctuated equilibrium models exhibit scaling or not. Nevertheless, it is certain that the presence or absence of scaling behavior in real time depends on the form of g.

Now I am going to show the existence of scaling behavior in real physical time in the punctuated equilibrium models. And when no confusion is possible, a real physical time will simply be called a time.

The probability that two successive mutation is separated by time T is given by

$$P(T) = \int \mu(s_{min})\delta[T - g(s_{min})]ds_{min} , \tag{2}$$

where μ is the stationary probability distribution of the minimum fitness s_{min} and δ is the usual Dirac delta function. Provided that g is strictly increasing and differentiable (thus g^{-1} exists), Eq. (2) can be rewritten as

$$P(T) = \frac{\mu[g^{-1}(T)]}{\left.\frac{dg}{ds}\right|_{g^{-1}(T)}} \tag{3}$$

as long as T is in the range of g [and $P(T) = 0$ otherwise]. Assuming the validity of Eq. (1), Eq. (3) becomes

$$P(T) = \frac{\mu(\frac{1}{\lambda}\ln\frac{T}{A})}{\lambda T} . \tag{4}$$

In the mean field model, $\mu(s_{min})$ is a constant below its upper critical value s_c [5]. Immediately, Eq. (4) tells us that $1/T$ scaling is observed in $P(T)$ with the lower and upper cutoffs being A and $Ae^{\lambda s_c}$, respectively.

The situation is slightly more complicated in the one-dimensional model because the exact form of μ is unknown. However, a numerical experiment done by Bak and Sneppen suggests that (see Fig. 2 in [3])

$$\mu(s) \approx \begin{cases} \frac{2}{s_c}\left(1 - \frac{s}{s_c}\right) & \text{if } 0 \leq s \leq s_c \\ 0 & \text{otherwise ,} \end{cases} \tag{5}$$

and hence

$$P(T) \approx \frac{2}{\lambda T s_c}\left[1 - \frac{1}{\lambda s_c}\ln\frac{T}{A}\right] \approx \frac{2}{\lambda T s_c} \tag{6}$$

for $A \leq T \leq Ae^{\lambda s_c}$. Once again, $1/T$ scaling is expected over a wide range of T provided that λ is sufficiently large. Using the same argument $1/T$ scaling can be found in $P(T)$ as long as μ can be well approximated by a polynomial function of s. Thus it is expected that various variations of the punctuated equilibrium model all fall in the same universality class.

The effective rate of mutation of a species with fitness s is $\frac{1}{g(s)}$. Suppose the first species is the least fit one, then the average combined rate of mutation in the ecosystem excluding the first species is given by

$$\begin{aligned} \sum_{i=2}^{N} \frac{1}{g(s_i)} &\approx (N-1)\left\langle \frac{1}{g(s)} \right\rangle \\ &= \frac{N-1}{\lambda(1-s_c)}\left(e^{-\lambda s_c} - e^{-\lambda}\right) , \end{aligned} \tag{7}$$

where $\langle \frac{1}{g} \rangle$ denotes the expectation value of $\frac{1}{g}$. This rate should be much less than the slowest possible mutation rate for the least fit species which is $\frac{1}{g(s_c)}$. Otherwise the assumption of always letting the least fit species to mutate is not justified. This imposes a condition on the value of λ, namely

$$\lambda \gtrsim \frac{(N-1)\left(1 - e^{\lambda(s_c - 1)}\right)}{1 - s_c} \approx \frac{N}{1 - s_c} . \tag{8}$$

In particular, Bak and Sneppen's choice of $\lambda = 100$ in Fig. 3(b) of [3] for $N = 64$ is a little bit too small.

Besides the time between successive mutations, the distribution of the total number of mutations taken place in a given time T ($A \ll T \ll Ae^{\lambda s_c}$) is another important statistics to look at. For a sufficiently stiff g, this distribution is identical to that of the burst activity: namely, the number of consecutive mutations with minimum fitness less than a given value $s \lesssim s_c$ [3]. Flyvbjerg, Sneppen, and Bak [4] have argued an $s^{-3/2}$ scaling for the distribution of burst activity for the mean field model. Moreover, numerical simulation suggests an $s^{-0.9\pm0.1}$ scaling for that of the one-dimensional model [3].

In summary, scaling behaviors are observed in real physical time in the punctuated equilibrium model (and its variations). While the scaling in burst activity is relatively independent of the mutation time scale $g(s)$, the $1/T$ scaling in the time between successive mutations occurs only when g is exponentially dependent on s. In addition, an upper bound for the characteristic fitness, $s_c \lesssim 1 - \frac{N}{\lambda}$, is found which varies linearly with the total number of species N in the ecosystem.

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