Self-Organized Criticality and Punctuated Equilibria

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Many natural phenomena evolve intermittently, with periods of tranquillity interrupted by bursts of activity, rather than following a smooth gradual path. Examples include earthquakes, volcanic eruptions, solar flares, gamma-ray bursts, and biological evolution. Stephen Jay Gould and Niles Eldredge have coined the term "punctuated equilibria" for this behavior. We argue that punctuated equilibria reflects the tendency of dynamical systems to evolve towards a critical state, and review recent work on simple models. A good metaphoric picture is one where the systems are temporarily trapped in valleys of deformable, interacting landscapes. Similarities with spin glasses are pointed out. Punctuated equilibria are essential for the emergence of complex phenomena. The periods of stasis allow the system to remember its past history; yet the intermittent events permit further change.

KEYWORDS: Self-Organized Criticality, Punctuated Equilibrium, Avalanches, Landscapes, Glassy Dynamics.

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I. INTRODUCTION

At the time of Darwin, the geophysicist Charles Lyell formulated the philosophy of uniformitarianism, according to which everything should be explainable in terms of the currently observable processes working at all times and all places with the same intensity. No new principles need to be established for the great and the lengthy. Lyell took for granted that this would lead to a smooth type of dynamics.

Darwin accepted Lyell’s uniformitarian vision, and believed that his mechanism for evolution, random mutation followed by selection and proliferation of the fitter variants, would necessarily lead to a gradual evolution. He even brought a copy of Lyell’s work with him on the beagle. He went as far as to deny the occurrences of mass extinction events. Within the uniformian view, mass extinctions must necessarily be caused by external cataclysmic events, and most investigators have assumed this without further ado, looking for meteors, volcanic eruptions and flooding events as the cause of mass extinction.

Lyell’s view may seem surprising in light of the fact that large events dominate his own science, geophysics. Large earthquakes killing thousands of people occur with merciless regularity, as do volcanic eruptions and catastrophic floodings. So what is wrong with his theory? Basically, the statement of uniformitarianism is a statement of linearity. Small impacts have small effects. The combined effect of many small impacts is a response with a Gaussian distribution, with vanishing probability of large events. Systems in equilibrium are linear, so the underlying picture is one where nature is in balance. However, in Physics we are aware that many dynamical systems show non-equilibrium, non-linear behavior. In particular, large dynamical systems are known to evolve to critical states, where the response to small impacts may be enormous, reflecting a divergent susceptibility.

Indeed, evidence has been mounting that evolution in fact proceeds in a stepwise fashion with long periods of apparent tranquillity in the development of most species, interrupted by rapid intermittent activity. The failure to find “missing links” in the paleontological data and the occurrence of fluctuations of all sizes in the extinction rates for species over time
have put the gradualistic belief into question. The fact that extinction events occur over a broad range of scales, including the smallest, indicates that a common intrinsic mechanism is at work.

Gould and Eldredge [3] have proposed punctuated equilibrium as a means to reinterpret the data, where species experience lengthy periods of stasis in between short periods of rapid adaptation that leave little trace of a missing link. While plausible, this theory does not explain the dynamical origin of this phenomenon in many different systems. In recent years, much effort has been spent on finding a process that generically leads to punctuated equilibrium behavior (for reviews, see Refs. [4], [21]).

We shall discuss a simple model of such an evolution process. A fitness value is assigned to each species in the system. The fitness reflects the species’ ability to survive in its environment, consisting of other species and external factors. The fitness values, together with the interrelation of species (e. g. in a food chain), represent a complicated fitness landscape in which species co-evolve, ruled by Darwinian principles. Local updating rules for the fitness of each species leads the system into a state of self-organized criticality (SOC) [5] with co-evolutionary avalanches of all sizes in the species ecology, and punctuated equilibrium behavior in the evolution of each species. Adjustments in the fitness of one species imply changes in the fitness landscape experienced by interacting species. We show that a hierarchical structured landscape emerges which stores the memory of past activity [23]. In this landscape we find that fitness values are “ultrametrically” related, borrowing a phrase known from the study of spin glasses. Disturbances dissipate slowly (like power laws), and avalanches exhibit aging behavior.

II. LANDSCAPES AND EVOLUTION MODELING

A powerful metaphoric picture of biological evolution was proposed by S. Wright (for a review, see Ref. [6]) who long ago introduced the idea of species evolving in a rugged fitness landscape with random mutation and differential selection towards higher fitness. This
contrasts with generally accepted ideas of Fisher \[7\] and others, whose view of evolution can be translated into one where the individual species climb an infinite hill with a constant slope at a constant rate. Even today, many models consist of single species evolving in more sophisticated but static environments. In our view, none of these scenarios contain any hint as to the origin of the intricate complexity, involving the interaction between myriads of species, which characterizes real Life. Few theories consider evolution as a process with many degrees of freedom, representing many different species.

One class of models that do include the many body aspect of evolution has been proposed by Kauffman and Johnson \[8\]. These so-called NKC-models are remarkable because they introduce the idea of a dynamically evolving fitness landscape. Here the fitness landscape is no longer merely a rigid stage for the individual species, but is itself formed by the ever-changing properties of other species, providing a model of co-evolution. Unfortunately, these models are very complicated, and interesting features (such as criticality and punctuated equilibrium) only emerge under very special circumstances, specifically when a parameter characterizing the roughness of the landscape is tuned to a critical point at a phase transition.

A much simplified model of evolution in which many species co-evolve in a dynamically formed fitness landscape has been proposed recently by Bak and Sneppen \[9\]. Species are considered to be perfectly distinguishable entities whose overall fitness with respect to their environment can be simply characterized by a single number on the unit interval. This value can be thought of as the fitness value of a local peak in a fitness landscape. Species are placed on a lattice, which could for instance be a one dimensional food chain. Each species interacts with its neighbors. At each time step the “weakest” species, that is the one with the lowest fitness, is “mutated” (following Darwinian principles \[10\]), or, equivalently, eliminated and replaced by another species. This process is effectuated by replacing the fitness value with a random number drawn from a flat distribution between 0 and 1. This event in turn forces changes in the fitnesses of interrelated species. Their fitness landscape has changed by no fault of their own! In the model we simply replace the fitness values of all nearest neighbors with new random numbers from the same distribution.
The most important consequence of this model is that no matter what the initial state, the system evolves inevitably (self-organizes) into a “critical” state in which correlations in space and time between events are distributed without any characteristic scale except for the system size itself (i.e. the number $N$ of species in the system). The robustness of this macroscopic behavior with respect to all but the most drastic modification in the local update rules is necessary for any model that is not to rely on “divine intervention”. A snapshot of a typical finite system near the critical state is shown in Fig. 1. All but a few of the fitness values are distributed evenly above a certain critical fitness value $\lambda_c$, leaving a gap below. In fact, a rigorous equation that describes the formation of the gap from an initial condition consisting of evenly distributed numbers to this critical state has been derived (“gap-equation”) [12] [11]. The fitness values above this threshold $\lambda_c$ represent species that are very unlikely to ever become the weakest species in the system. They have reached stasis, i.e. they are in an apparent equilibrium that will only be punctuated when a weak neighboring species undermines their adaptation to the environment. The species with fitness values below this threshold value are the most active, i.e., most likely to mutate or go extinct, since they are the most likely to become a global minimum at some time step. These active species undergo a rapid sequence of changes until they and their neighbors collectively reach high fitness values to regain stasis, where the network of species is in a state of temporary balance.

The active species form avalanches of all sizes which represent those fluctuations that are found in real evolutionary activity. An avalanche here consists of all such active sites between two consecutive points in time when all values are above threshold. If we count the returns of activity to any one species in the critical state, we find a “devil’s staircase”, Fig. 2, with plateaus of stasis (distributed according to a power law) punctuated by short periods of rapid activity. Thus, this model provides a dynamical explanation of punctuated equilibrium emerging from Darwinian principles.

Many interesting features have been unearthed about this and other models of SOC, most of which have been summarized in Ref. [11]. Here we want to focus on a variety of
aspects in the Bak-Sneppen model that are related to the complicated, ever-changing fitness landscape which each species faces.

III. FITNESS LANDSCAPES, AVALANCHE HIERARCHIES AND GLASSY BEHAVIOR

Each species in the system is frozen into a state of stasis, except for a vanishingly small number of time steps (see the devil’s staircase in Fig. 2) when the local changes in the fitness landscape require adaptive activity. This change in the local fitness landscape is caused by a similar adaptive move in a neighboring species at some previous time, and so on. If a smaller fitness value has been assigned to a species, the barrier against motion in this landscape has been lowered. But if a species and all its neighbors have fitness values anywhere above \( \lambda_c \), further spontaneous mutations will not take place until the activity returns to that species. The system is attracted to a state in which all fitness values are somewhere above threshold. There is a continuum of such states. Different states are separated by intermittent activity in form of avalanches that rearrange the system in a trial-and-error search.

The avalanches are hierarchically structured. Consider the time signal of such an avalanche in form of the fitness value \( \lambda_{\min}(s) \) of the weakest species as a function of update time \( s \), Fig. 3. The distribution of avalanches is given by a power law. Considering the infinite, critical avalanche, we can regard every update as a starting point of a sub-avalanche labeled by \( \lambda_{\min}(s) \) which ends at the first time when \( \lambda_{\min}(s') > \lambda_{\min}(s) \) for \( s' > s \). Clearly, a \( \lambda_{\min}(s) \) avalanche can only end when all of its sub-avalanches with \( \lambda_{\min}(s'') < \lambda_{\min}(s) \) for all \( s < s'' < s' \) have ended. And a \( \lambda_c \) avalanche can only end when all of its sub-avalanches have ended, and so on. Thus, a picture of hierarchically constrained dynamics emerges in which faster degrees of freedom block slower ones, similar to the phenomenological description of slow relaxation in glassy systems given by Palmer, Stein, Abrahams, and Anderson in Ref. [13]. This was pointed out by Ref. [15]. Actually, The similarity with spin glasses is pretty straightforward. The fitnesses can be thought of as barriers against further action, i.
e. the barriers that atoms have to traverse in order to get to a better energy minimum. Once the atom jumps, the barriers of neighbor atoms are affected. The duration of avalanches in the self-organized critical state is found to be broadly distributed, following a power law, as a mark of this constrained relaxation process.

By design, all active fitness values (in general, all values that had been active at some time) are ultrametrically related [14]. By choosing a site with a specific (parental) fitness value at each update to create new (offspring) fitness values in its neighborhood, a causal link between previous and future fitness values is established, similar to relations in a family tree. In the evolving avalanche, for instance, any two active fitness values are related in a unique way to a closest common ancestor such that the ultrametric relation between any three of them holds, see Fig. 4. It is found that the ultrametric separation between two consecutively updated fitness values is also distributed in a power law, another indication of the highly correlated, slow relaxation process in evolving avalanches.

This ultrametric structure is reminiscent of earlier models for relaxation in spin glasses due to Ogielski and Stein, and Schreckenberg [16]. There the endnodes on a fixed ultrametric tree are the states between which a random walker proceeds, by following jump probabilities that are chosen with respect to the ultrametric distances between states. The jumps of the walker correspond to the jumps in consecutive activity in the Bak-Sneppen model. But in the Bak-Sneppen model, the jump probabilities and a (random) ultrametric tree structure emerge dynamically. In fact, the jump probabilities in this model are closely linked to the extremal process of always choosing the smallest fitness value in each update, and would become short-range, if an arbitrary active sites were to be updated instead.

Since the Bak-Sneppen model can be thought of as the dynamics in a rugged landscape, it is not surprising to find phenomena in the Bak-Sneppen model that are usually associated with spin glasses [17]. For instance, it can be shown (see below) that the updating rules lead to a build-up of memory of past activity over all scales, resulting in equations similar to those for correlations in spin glasses [18]. Furthermore, detailed studies of the temporal activity reveal that avalanches age [19]: the probability $P(t, t_w)$ for the activity to return for
the first time to a site at time $t + t_w$ depends on the age $t_w$ of the avalanche at the previous pass \[21\]. The connection between hierarchically structured dynamics and aging has been made previously, again in the context of spin glasses \[22\].

**IV. THE MULTI-TRAIT MODEL**

As a realistic extension of the Bak-Sneppen model, one may consider making the survivability of each species conditional upon a number ($M$) of independent traits associated with the different tasks that it has to perform \[23\]. We find that such a model preserves the generic properties (such as punctuated equilibrium) of the Bak-Sneppen model to which it reduces for $M = 1$. In the limit $M \to \infty$, this model allows rare analytical insights into the dynamics of avalanches in the SOC state.

For $M = \infty$, an exact evolution equation for avalanches can be derived directly from the microscopic update rules. The SOC state emerges as a particular point in the equation where simple diffusive behavior is replaced by long-range memory which the avalanche develops. Its solution provides a set of exact scaling coefficients that explicitly verifies many of the proposed scaling relations for this class of extremal models \[24\]. Furthermore, it elucidates the subtle properties that evolve from the irreversible dynamics, such as the Levy-flight distribution of adaptive activity and the ultrametric structure of the avalanche. These features are intimately connected to the distribution of “backward” avalanches which is obtained in closed form. For a derivation of these results, see Refs. \[23,15\].

As in the Bak-Sneppen model, a species is represented by a single site on a lattice. But in the multi-trade model the collection of traits for each species is represented by a set of $M$ numbers in the unit interval. A larger number represents a better ability to perform that particular task, while smaller numbers pose less of a barrier against mutation. Therefore, we “mutate” as before at every time step the smallest number in the entire system. Now, each neighboring species has one of its $M$ numbers replace. Which one of the $M$ numbers is selected for such an update is determined at random, since we assume
that a mutation in the traits of one species can lead to an adaptive change in any one of the traits of a neighboring species. Thus, on a nearest-neighbor site, any number that is part of the avalanche has a $1/M$ chance to be eliminated from the avalanche. In a nutshell, the model is solvable for $M = \infty$ because fitness values below threshold in the avalanche evolve statistically independent from one another and can be eliminated only by becoming the global minimum. But for any $M \leq \infty$, the interaction between the fitnesses of species leads to a chain reaction of coevolution that inevitably evolves to a self-organized critical state as in the Bak-Sneppen model, $M = 1$. It is important to note that all the properties of the Bak-Sneppen model that indicate a rugged fitness landscape are present also for arbitrary $M$ including $M = \infty$. While this multi-trait model shares some features with earlier mean-field versions [25], it preserves nontrivial spatio-temporal correlations including the Devil’s Staircase and punctuated equilibria much like the Bak-Sneppen model.

To describe these spatio-temporal correlations, we define $F(r, s)$ to be the probability for an avalanche in the SOC state to survive precisely $s$ steps and to have affected a particular site of distance $r$ from its origin. Due to the statistical independence of active fitness values, one can find an exact evolution equation for $F(r, s)$ at $M = \infty$.

In Ref. [23] that equation was used to show that the system becomes “critical” with power laws for the avalanche duration and for the spatial extent of avalanches. Thus, at least two scaling coefficients can be found:

$$F(r = 0, s) \sim \frac{s^{-\frac{3}{2}}}{\sqrt{\pi}} (s \gg 1), \quad \text{and} \quad -\partial_r \sum_{s=0}^{\infty} F(r, s) \sim 24r^{-3} (r \gg 1), \quad (1)$$

i.e. $\tau = 3/2$ and $\tau_R = 3$. All other critical coefficients of the model can be determined from these two via scaling relations [24]. For instance, the spatial extent of the activity in the SOC state spreads in a subdiffusive manner, $r \sim s^{1/D}$, where $D = 4$ is the avalanche dimension given by $\tau_R - 1 = D(\tau - 1)$. Below we verify the scaling relation for $D$ explicitly by calculating the diffusion behavior directly [15]. Other critical exponents that can be determined explicitly are $\gamma = 1$, $\nu = \sigma = 1/2$, $\tau_{f}^{dll} = 2$, and $\tau_{b}^{dll} = 3/2$ (For a definition of these exponents see Ref. [24].
In a long-lived avalanche, each site is visited many times, leading to punctuated equilibrium behavior, characterized by the distribution of first returns of the activity to a given site, $P_{\text{FIRST}}(s)$. It has been found that $P_{\text{FIRST}}(s) \sim s^{-\tau_{\text{FIRST}}}$ for large $s$ with $\tau_{\text{FIRST}} = 2 - d/D$.

For $M \to \infty$ we find that $\tau$ and $\tau_R$, and hence $D$, do not change with dimension $d$, and it is

$$\tau_{\text{FIRST}} = 2 - d/4 \quad (d \leq 4).$$

Thus, for $d = 1$ we predict $\tau_{\text{FIRST}} = 7/4$, and we find numerically $\tau_{\text{FIRST}} = 1.73 \pm 0.05$.

In Ref. [13] it is shown for sufficiently large $r$ and $s$ that

$$\frac{\partial F(r, s)}{\partial s} \sim \frac{1}{2} \nabla_r^2 F(r, s) + \frac{1}{2} \int_0^s V(s - s') F(r, s') ds',$$

which is a “Schrödinger” equation in imaginary time for $F(r, s)$ with a nonlocal kernel $V(s) = F(r = 0, s) - 2\delta(s)$. This nonlocal potential with the integral kernel $V(s)$ contains all of the history dependence of the process. In its absence the system would be purely diffusive with a Gaussian tail $F \sim e^{-r^2/s}$. In its presence the probability to have reached a site at distance $r$ at time $s$ gets contributions from avalanches that reached $r$ at earlier times $s' < s$. These contributions are weighted according to $V(s - s')$ which has a power-law tail, representing the memory of the avalanche of previous activity over all time scales. The ultrametric tree structure of avalanches shows that they can be divided into sub-avalanches. Avalanches contributing to $F(r, s)$ consist of sub-avalanches, one of which reaches $r$ in time $s'$ while the other’s combined duration is $s - s'$. The sub-avalanche structure gives a hierarchy of time scales. This changes the relaxation dynamics to be non-Gaussian. The form of Eq. (3) is reminiscent of equations that describe slow dynamics and aging in spin glasses [18].

Using a Laplace transform and steepest-decent analysis of the inverse transform integral, one finds a form for the propagator that might be rather general for systems with SOC [20]:

$$F_\chi(r, s) \sim \exp \left[ -C \left( \frac{r^D}{s} \right)^{1/4} \right] \quad \left( r^D \gg s \gg 1 \right).$$

Assuming that for any system with SOC the history dependence is given by $V(s) \sim s^{-\alpha}$, it is $D = 2/(1 - \alpha)$. For $M \to \infty$, it is $\alpha = 3/2$, i.e. $D = 4$, and the constant $C = 3/4$. Since
$1 < \alpha < 2$, diffusion is slowed down ($D > 2$) because the activity has a tendency to revisit sites, and the system remembers these previously visited sites.

Thus, an intricate structure emerges in the self-organized critical state of this intriguingly simple model. At many places we eluded to similar phenomena observed in spin glasses. In fact, although their connection is not at all clear, the Bak-Sneppen model might provide a more accessible setting to study some of the phenomena shared with much more complicated spin glass systems.
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FIGURES

FIG. 1. Snapshot of the stationary state in the one dimensional Bak-Sneppen model. Except for the avalanche which consists of small fitness values in a localized region, almost all the fitness values in the system are above a self-organized threshold $\lambda_c$. 

![Graphical representation of the Bak-Sneppen model](image-url)
FIG. 2. Punctuated equilibrium behavior for the evolution of a single species in the one-dimensional $M = \infty$ model. The vertical axis is the total number of returns of the activity to some site as a function of time $s$. Note the presence of plateaus (periods of stasis) of all sizes. The distribution of plateau sizes scales as $s^{-7/4}$. 

![Graph showing punctuated equilibrium behavior](image-url)
FIG. 3. Sequence of minimal random numbers $\lambda_{\text{min}}(s)$ chosen for an update at time $s$ in a $\lambda_c$ avalanche for $M = \infty$. The durations avalanches within the hierarchy of $\lambda$ avalanches is indicated by forward arrows, where $\lambda = \lambda_{\text{min}}(s)$. Longer avalanches with larger values of $\lambda$ contain many shorter avalanches which have to finish before the longer avalanche can terminate. Note that an update punctuates any $\lambda$ avalanche with $\lambda \leq \lambda_{\text{min}}(s)$. 
FIG. 4. Ultrametric tree structure. At any given time, indicated by the vertical axis, all of the active sites below threshold have an ancestry which forms a tree. The ultrametric distance between any pair is the distance back in time to the first common ancestor.