# Self-organized criticality in Evolution

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In this essay, I present a very simple numerical model for species evolution developed by Sneppen *et. al.*[1]. The model assumes random interactions between neighboring species. It is observed that the model quickly self-organizes into a critical state characterized by extinction events at all scales (that follow power law distributions). The model successfully predicts the "punctuated equilibrium" observed in the history of the major mass extinctions. An interesting conclusion to the model is that catastrophic events are *intrinsic* to it and major external sources of mayhem (such as a meteor) are not needed to explain major extinctions.

## 1 Criticality in Evolution

Many studies of the fossil record by Raup[2] have demonstrated that extinction events occur in concentrated bursts. During such events, many genetically unrelated species often disappear simultaneously. These coordinated extinctions occur at many different scales of magnitude and some events even reach catastrophic levels (e.g.: the disappearance of the dinosaurs). What is most surprising is that the distribution of extinction events display scaling behavior [3]. For example, the power spectrum of the extinction history (as a function of frequency) scales just like $1/f$ noise over about two decades, as displayed in figure 1; other scaling laws are observed for the extinction distribution as a function of magnitude, for the lifetime of a genus, etc. This is very suggestive of a class of critical behavior called self-organized criticality (SOC), such as that observed in the distribution of earthquakes, of avalanches in a growing sand pile, or of noise in an electrical wire, etc.

SOC[4] is often a characteristic of systems far from equilibrium that are driven by a weak but random force (such as dropping grains of sand at a random location on a sand pile). Sometimes the system will get stuck into meta-stable states (such as a "bump" of sand that doesn't fall because of friction) and the driving force will cause avalanches (such as sand falling) whose magnitudes are not proportional to the original driving force and occur at all size scale. The behavior of avalanches is tied to the states of the system, which is effectively connected at many different length-scales, so that an extra grain of sand could roll down the pile just as easily as it could make it collapse. This kind of phenomena is more typical for systems that interact through thresholds (e.g.: a sand "bump" will hold a certain amount of weight before falling) rather than through continuous potentials. The critical state itself is "stable" in the sense that once it is reached, it is maintained (in terms of its statistical properties), and it is "self-organizing" in the sense that no external tuning is needed to reach it: it is the natural end behavior of such a system.

## 2 The Model

An abstract, but very simple, model is used to describe an ecology. Species are characterized by their "fitness" (which is a quantity that describes their aptitude to survive in their current environment) and by their neighbors (in one case, species are assumed to lie on a line, like birds on a wire, so that each species has two neighbors). As time passes, the genetic mutations occur and species travel along trajectories in a "fitness landscape", which is a concept expressing the multi-dimensional mapping of the genetic makeup of a species onto a value for its fitness. The fitness landscape is assumed to be bumpy, and species are located at local maxima of the fitness (and if they aren't, then small mutations will quickly bring them there). In order to become more "fit", a species needs to overcome an evolutionary barrier (which requires a large mutation) to be able to fall within the scope of another, different, "bump" in the landscape. Of course, the landscape is also a function of the species' environment (which includes its neighbors), and a change in fitness (a.k.a.: a significant mutation) of one species will have serious repercussions on the fitness of other species. The Sneppen model streamlines the features of the fitness landscape in order to make the problem tractable. One key assumption is that, in a rugged landscape, species with a low fitness will be subjected to smaller mutation barriers than species with maximal fitness. Thus, we expect that the species with the lowest fitness/barrier will be the first to experience a major mutation (assuming a mutation probability of $p = e^{fitness/timestep}$), given a sufficiently low mutation rate.

The simulation procedure is as follows. Species are initially assigned random fitnesses (barriers) between 0 and 1. At each simulation time step, the species with the lowest fitness evolves to another "bump" in the landscape and acquires a new random fitness (between 0 and 1). Similarly, its two nearest neighbors are affected by the mutation and they see their own fitness reassigned to new random values. This entire process is repeated many times. This re-shuffling of fitnesses can also be interpreted in different ways. We can say that the weak species has become extinct and that its niche has been filled by a *new* species (with a random fitness), or that it has evolved. The extinct species' neighbors environment is changed (the old species might have been a predator or prey, etc.) and as a consequence, they are assigned a new random fitness.

## 3 Results

Initially, the species' fitnesses are distributed at random (with a uniform distribution between 0 and 1). After the simulation is started, the weakest species mutate and the overall distribution evolves until it reaches a stable point in which the species' fitnesses are uniformly distributed in the interval between 2/3 and 1 (for the "line" spatial configuration of species); these results are displayed in figure 2. Only the species whose fitness fall below the lower critical fitness 2/3 ever become extinct (or evolve), and can bring down healthy species with them in cascade events (called "avalanches" in SOC speak).

This exceedingly simple system exhibits rather complex behavior. The power spectrum of the extinctions distribution displays a power law behavior, meaning that there is no intrinsic scale (in either time or magnitude) at which extinctions occur, and so does the distribution of the species' lifetimes. The various exponents calculated do not match perfectly with the measured ones, but that is to be anticipated, because the simulations are run in low spatial dimensions (1D in the case described here). Exponents have been shown to vary with the dimension of the species connectivity lattice (though they are robust under most other changes of parameters or method), and it is obvious that real species interactions cannot be accurately modeled on 1D or 2D lattices. The simulation predicts the "punctuated equilibrium" behavior of extinction events as well (see figure 3).

## 4 Discussion

It must first be noted that the model described above is not specifically a model of the evolution of species. It is simply a model for elements that interact in complex ways (simulated by abstract random potentials) with their neighbors. The only input from evolution theory is the fact that species mutations occur in discrete steps (S.J. Gould's "punctuated equilibrium" theory). This provides the discrete random driving force.

Since this model is obviously very rudimentary, it would be silly to claim that is explains species extinction. However, fundamental lessons can be still learned from it. The most interesting aspect of the simulation is that it explains the scaling behavior of evolution as arising solely from the network of interaction between species. This is in stark contrast with generally accepted ideas that extinctions are caused by external events, such as meteorites, volcanos, temperature changes, etc. Of course, such events do have evolutionary consequences, but they *are not needed* in order to account for the rich behavior and patterns of extinctions, not even to explain the catastrophic mass extinctions that have occurred on this planet!

Another surprising result of the simulation is that the system self-organizes into a "stable" critical state *as opposed to* a state of maximum fitness. A naive application of Darwin's theory would lead us to assume that species (or ecosystems) become more fit as a whole at time progresses. SOC tells us that that is probably not the case. As individual species struggle to compete more effectively, their progress will inevitably have a negative impact on some of their competitors. When the system reaches a point where all the species a relatively fit (e.g.: at the critical point in 1D, fitness $> 2/3$), mutations of one species will most likely be detrimental to its neighbors (since they were already very satisfied with the ecology as is was before). SOC in this context might be understood as the ensemble of states of a system for which the individual benefits of a mutation become compensated by the (overall negative) effects of that mutation on the ecology as a whole. This competition between individual and society might be the force that drives to system towards the "self-organized" state.

A last point of interest is that, while this model exhibits complex temporal behavior, its spatial behavior is rather unexciting. On one hand, this is a problem. If this simulation is to correctly model species interaction, one would like to see an interplay between the temporal and spatial behavior, giving rise to a rich complex behavior. On the other hand, this indicates that spatial effects might not be completely relevant for modeling the interspecies interactions. The complexity observed in extinction patterns might already be fully accounted for by the species' interaction networks (which of course might contain a lot of hidden information, such as spatial organization, which would be taken into account by the "random" potentials).

## References

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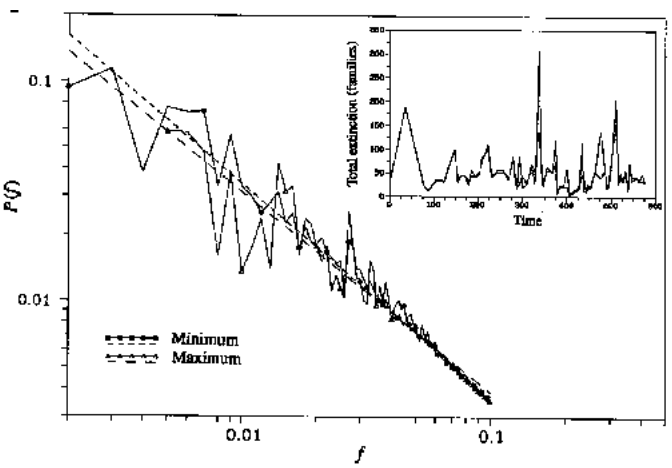

Figure 1: Power spectrum of the history of extinctions from the Cambrian (600 millions years) to the present (log-log plot).

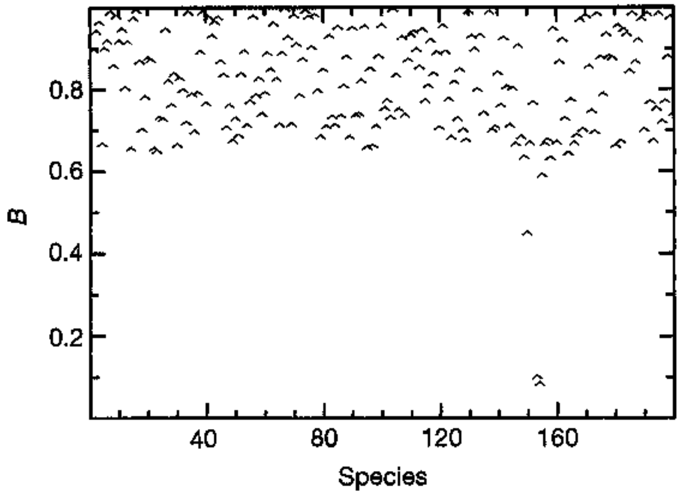

Figure 2: Species fitness (as a function of each individual species) after self-organized criticality has been reached.

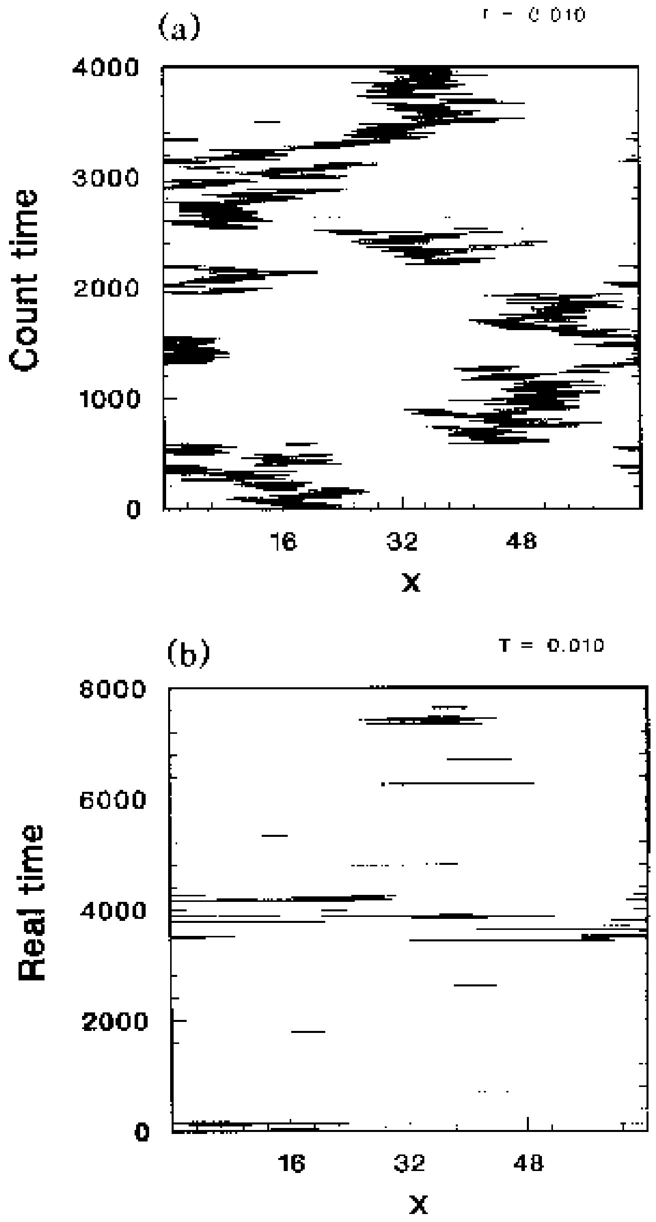

Figure 3: Species affected by an extinction event as a function of (a) simulation time (i.e.: number of mutations), and (b) real time (includes actual time for mutations to occur mutations, where $t_{mutation} \propto 1/p = e^{barrier/timestep}$). The lower axis are 64 species aligned in a row.