

Mass Extinctions vs. Uniformitarianism in Biological Evolution

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Abstract. It is usually believed that Darwin's theory leads to a smooth gradual evolution, so that mass extinctions must be caused by external shocks. However, it has recently been argued that mass extinctions arise from the intrinsic dynamics of Darwinian evolution. Species become extinct when swept by intermittent avalanches propagating through the global ecology. These ideas are made concrete through studies of simple mathematical models of coevolving species. The models exhibit self-organized criticality and describe some general features of the extinction pattern in the fossil record.

1 Introduction

The theory of uniformitarianism, or gradualism, was formulated in the last century by the geophysicist Charles Lyell (1830) in his tome, *Principles of Geology*. According to this theory, all change is caused by processes that we currently observe which have worked at the same rate at all times. For instance, Lyell proposed that landscapes are formed by gradual processes, rather than catastrophes like Noah's Flood, and the features that we see today were made by slow persistent processes with time as the "great enabler" that eventually makes large changes. Uniformitarianism is a "linear" theory where the amount of change is proportional to the amount of time that has elapsed.

At first sight, Lyell's uniformitarian view is reasonable. The laws of physics are generally expressed in terms of smooth, continuous equations. Since these laws should describe all observable phenomena, it is natural to expect that the phenomena which we observe should also vary in a smooth and gradual manner. The opposing philosophy, catastrophism, claims that change occurs through sudden cataclysmic events. Since catastrophism smacks of creationism, with no connection to the natural sciences as we know them, it has been largely rejected by the scientific community.

Charles Darwin (1910) adapted Lyell's ideas of gradualism in an uncompromising way. According to his theory, evolution proceeds through random mutations followed by selection of the fitter variants. This slow process takes place at all times and all places at a steady rate. Darwin took it for granted that such a process would necessarily force evolution to follow a smooth, gradual path. Consequently, Darwin denied the existence of mass extinctions where a large fraction of species would abruptly disappear.

1.1 Avalanches and Punctuated Equilibrium

However, we know that many natural phenomena evolve intermittently (Bak and Paczusi 1995; Paczusi, Maslov, and Bak 1996). The dynamics may follow a step-like pattern with long, dormant plateaus where little change takes place interrupted by sudden bursts, or avalanches, of concentrated activity. The magnitudes of the bursts may extend over a wide range. Even though uniformitarianism, as opposed to catastrophism, has historically dominated both geology and paleontology, prototypical examples of intermittent behavior lie in these two domains.

Earthquakes: For instance, the crust of the earth accommodates large, devastating earthquakes in which hundreds of thousands of people are killed. Most of the time the crust of the earth appears to be stable. These periods of stasis are punctuated by earthquakes or avalanches taking place on a fault structure that stores information about the history of the system.

In fact, the size distribution of earthquakes follows a simple power law known as the Gutenberg-Richter law (1956). The power law demonstrates that earthquakes have no typical scale; otherwise the distribution would have a signature at that scale. The smooth variation from small to large events suggests that a common dynamical mechanism is responsible for all earthquakes, regardless of their size. Volcanic eruptions constitute another intermittent phenomenon in geophysics. Solar flares, pulsar glitches, and the formation of neutron stars are examples of intermittent behavior in astrophysics. All these phenomena are examples where avalanches of activity exhibit power law distributions similar to the Gutenberg Richter law. There is no way to accommodate the power law distribution for earthquake sizes within the framework of a linear theory such as uniformitarianism.

A Gutenberg-Richter Law for Extinctions: One might, therefore, suspect that Darwin's use of uniformitarianism in a theory of evolution may also need to be reexamined. In fact, about twenty years ago, Gould and Eldredge (1977) proposed that biological evolution takes place in terms of punctuations, where many species become extinct and new species emerge, interrupting periods of low activity or stasis. Figure 1 shows the record of extinction events as recorded by J. J. Sepkoski (1993). These extinction events in biology are analogous to earthquakes in geology. Note the spikes of extinction events spanning a range of magnitudes. The largest events are associated with the Cambrian explosion 500 million years ago, and the Permian extinction 200 million years ago. Raup (1986) has plotted similar data as a histogram (figure 2) where each column shows the number of 4 million periods with a given extinction intensity. The smooth variation from the smallest to the largest extinctions indicates a common mechanism. Actually, punctuated equilibrium usually refers to the intermittent dynamics of a single species, where morphological change is concentrated in short time periods interrupted by long periods of stasis.

1.2 External Shocks: "Bad Luck"

The extinctions of species appear to take place simultaneously across families; they "march to the same drummer". This could be explained if mass extinctions were caused by large, exogenous cataclysms, i. e. if extinctions were due to "bad luck" rather than "bad genes". For example, in the most prominent theory, Alvarez, Alvarez, and Michel (1980) suggest that the Cretaceous extinction event where the dinosaurs disappeared was caused by a meteor hitting the earth some 55 million years ago. Indeed, a large crater was observed near the Yucatan peninsula in Mexico. However, in order for an exogenous event such as a meteor to wipe out an entire species, it must have a global effect over the entire area that the species occupies; otherwise the impact would be insufficient to cause extinction, except for species with small local populations. In addition, extinctions of species take place all the time without an external cause. Extinctions are taking place right now! These extinction events are obviously not caused by a meteor. Some are known to be intrinsic to evolution, being caused by humans.

In his book *Bad Genes or Bad Luck*, Raup (1982) distinguishes between bad luck, extinctions from external sources, and bad genes, extinctions due to intrinsically poor fitness. Whether or not external shocks play an important role in evolution, it is important to understand the dynamics of biological evolution in the absence of these shocks.

1.3 Evolution of Isolated vs. Many Interacting Species

In early theories of evolution, by Fisher (1932) and others, evolution of a single species in isolation was considered. Individuals within each species mutate, leading to a distribution of fitnesses, and the fitter variants were selected. This leads to a fitness which always increases smoothly *ad infinitum*. Many biologists appear content with this state of affairs, and rarely is the need for a more comprehensive theory expressed. For instance, Maynard Smith (1993), in his book *The Theory of Evolution* notices with great satisfaction that nothing important has changed in the 35 years intervening between his first and second editions.

However, Fisher's picture of a species evolving in isolation does not appear to us to be able to explain any of the intricacy, diversity, and complexity of real life. This is because evolution is a cooperative phenomenon. Species form ecologies where they interact with each other in a global ecology with predator-prey relationships and food webs. For example, humans depend on the oxygen emitted by trees and other plants. It is quite likely that the interaction of many species in a global ecology plays a more important role in evolution than the specific behavior of a single or a few species in isolation.

Our approach is to consider biology as a large, dynamical system with very many degrees of freedom. Interactive systems like biology may exhibit emergent behavior which is not obvious from the study of typical local interactions and detailed behaviors of two or three species. Indeed, the population dynamics of a few interacting species has been described in terms of coupled differential equations, known as Lotka-Volterra, or replicator equations. These equations

may lead to interesting, chaotic behavior, but of course not to mass extinction or punctuated equilibrium. Traditional evolutionary theory may be able to explain the behavior of a few generations involving a few hundred rats, but it can not explain evolution on the largest scale in which trillions of organisms interact throughout billions of years.

2 Self-Organized Criticality

A few years ago, Bak, Tang, and Wiesenfeld (1987, 1988) suggested that large dynamical systems may organize themselves into a highly poised "critical" state where intermittent avalanches of all sizes occur. The theory, self-organized criticality (SOC), is a nonlinear theory for how change takes place in large systems. It has become a general paradigm for intermittency and criticality in Nature. Evolution to the critical state is unavoidable, and occurs irrespective of the interactions on the smallest scales which we can readily observe. A visual example is a pile of sand on a flat table, onto which sand is gradually added. Starting from a flat configuration, the sand evolves into a steep pile which emits sandslides, or avalanches, of all sizes. This idea has been successfully applied to a variety of geophysical and astrophysical phenomena, in particular to earthquakes where it provides a natural explanation for the Gutenberg-Richter law. It is now broadly accepted that earthquakes are a self-organized critical phenomenon (Newman, Turcotte, and Gabrielov 1995). One may think of SOC as the underlying theory for catastrophism.

Can this nonlinear picture be applied to biological evolution? Even if we accept Darwin's mechanism for evolution, it is difficult to extract its consequences for macroevolution. In contrast to the basic laws of physics which are described by equations such as Newton's equations, or Maxwell's equations, there are no "Darwin's Equations" to solve, as one of our editors, Henrik Flyvbjerg, once pointed out. It may seem rather hopeless to try to mathematically describe macroevolution without the fundamental microscopic equations. On the other hand, we know from our experience with many body collective phenomena that statistical properties of the system at large scales may be largely independent of small scale details. This is called "universality." The interactions are more important than the details of the entities which make up the system. Universality belies the usual reductionist approach in the physical sciences where features at large scales are explained in terms of models at successively smaller scales with more and more details included. Universality is a way to throw out almost all of these details.

Thus, our studies are based on abstract mathematical models. The models cannot be expected to reproduce any specific detail that may actually be observed in nature, such as humans or elephants. The confrontation between theory and reality must take place on a statistical level. This is not unusual in the natural sciences. Quantum mechanics and thermodynamics are inherently statistical phenomena. Chaotic systems are unpredictable, so comparison with experiment or observations must also be on the statistical level. Indeed, the

Gutenberg-Richter law is a statistical law which can be explained in terms of grossly over-simplified SOC models for earthquakes. One might hope to be able to do the same for biology.

We shall argue that life may be a self-organized critical phenomenon. Periods of stasis where evolutionary activity is low are interrupted by coevolutionary avalanches where species become extinct and new species emerge. Good genes during periods of stasis are no guarantee for survival. Extinctions may take place not only due to "bad luck" from external effects, like meteors, but also due to bad luck from freak evolutionary incidents endogenous to the ecology. Biological evolution operating in the critical state can explain a variety of empirical observations, including the lifetime distribution of species and the occurrence of mass extinctions.

3 Co-evolutionary Avalanches

Stuart Kauffman of the Santa Fe Institute was among the first to suggest that life might be a self-organized critical phenomena where evolution takes place in terms of co-evolutionary avalanches of all sizes. Together with Sonke Johnsen (Kauffman and Johnsen 1991) he studied complex models of very many species forming an interactive ecology, the NKC-models. In these models, each species evolves in a rough fitness landscape, with many local peaks, employing a picture invented by Sewall Wright 50 years ago Wright (1982) (figure 3) in his seminal work, *The Shifting Balance Theory*. Populations are modified by means of mutation and differential selection towards higher fitness. Random mutations allow individuals to cross barriers, formed by troughs of lower fitness and move to other maxima. Then they might initiate a population at or near the new maximum.

Each species can be thought of as a group of individuals in the vicinity of some fitness peak, and may be represented by the genetic code of one of those individuals. In Kauffman's models, the genetic code is represented by a string of N bits or genes (0011011....11101000). Each configuration has a fitness associated with it, which can be calculated from an algorithm, the NK-algorithm. The contribution to the fitness from each gene or "trait" depends on the state of K other genes. The fitness depends on the coupling between genes. The NK models are generalized spin glass models, invented by physicists to describe metastability and frozen behavior of magnetic systems with random interactions.

The elementary single step is what could be called a "mutation of a species". Despite the fact that this notation may raise a red flag among biologists, it will be used throughout this chapter. In evolution, this step is made by random mutations of individuals followed by selection of the fitter variant, and subsequent transformation of the entire population to that variant. The landscape is traced out as the bits are varied. By randomly mutating one bit at the time, and accepting the mutation only if it leads to a higher fitness, the species will eventually reach a local peak from which it can not improve further from single mutations. Of course, by making many coordinated mutations the species can

transform into something even more fit, but this is very unlikely. A species can not spontaneously develop wings and fly.

However, the fitness landscape of each species is not rigid; it is a rubber landscape modified when other species in the ecology change their properties. For instance, the prey of some predator may grow thicker skin (or become extinct), so that the fitness of the predator is reduced. Within the landscape picture, this corresponds to a deformation where the fitness peak the predator previously occupied has vanished. The predator might find itself down in a valley instead of up on a peak. Then it may start climbing the fitness landscape again, for instance by developing sharper teeth, until it reaches a new local peak. This may in turn affect the survivability of other species, and so on.

Kauffman and Johnsen represented the interdependence of species in terms of their model. Mutating one of the N genes in a species affects K genes within the species and also affects the fitnesses of C other species. This is called the NKC model. Now, starting from a random configuration, all the species start climbing their landscapes, and at the same time start modifying each other's landscapes. Their idea was that this would eventually set the system up in a poised state where evolution would happen intermittently in bursts. However, this failed to occur.

Either of two scenarios would emerge. i) If the number of interactions, C , is small, the ecology evolves to a frozen state where all species rest on a local peak of their respective landscapes, and no further evolution takes place. A random, external environment is introduced by randomly flipping genes. This initiates avalanches where a number of species evolve. However the avalanches are small, and the ecology soon comes to rest in a new frozen state. ii) If the number C is large, the ecology goes to a highly active chaotic state, where the species perpetually evolve without ever reaching a peak. In this case, the coevolutionary avalanches never stop. Only if the parameter C is carefully tuned does the ecology evolve to a critical state.

Kauffman and Johnsen argued that the ecology as a whole is most fit at the critical point. "The critical state is a nice place to be," Kauffman claims. However, it can be proven that the NKC models do not self-organize to the critical point (Flyvbjerg and Lautrup 1992; Bak, Flyvbjerg, and Lautrup 1992). Divine intervention is needed. Apart from the question as to what type of dynamics may lead to a critical state, the idea of a poised state operating between a frozen and a disordered, chaotic state makes an appealing picture for the emergence of complex phenomena. A frozen state cannot evolve. A chaotic state cannot remember the past. This leaves the critical state as the only alternative.

4 A Simple Model for Evolution

Bak and Sneppen (Bak and Sneppen 1993; Sneppen et al 1995) introduced a simple model to describe the main features of a global interactive ecology. In one version of the model, L species are situated on a one dimensional line, or circle. Each species interacts with its two neighbors, to the left and to the right.

The system can be thought of as a long food chain. Instead of specifying the fitness in terms of a specific algorithm, the fitness of the species at position i is simply given as a random number, f_i , say between 0 and 1. The fitness is not specified explicitly in terms of an underlying genetic code, but is chosen as a random function of these variable. Probably not much is lost since we do not know the actual fitness landscapes anyway.

At each time step the least fit species is selected for mutation or extinction. This is done by finding the smallest random number in the system. By inspection of the fitness landscape in figure 3, it is clear that species located on low fitness peaks have a smaller distance to find better peaks than species with higher fitness. The barriers to find better peaks can be thought of as the number of coordinated mutations needed. So the time it takes to reach a higher peak increases exponentially with the size of the barriers and can become astronomically large if the genetic mutation rate is low. This justifies the selection of the least fit species as the next in line for mutation.

The mutation of a species is represented by replacing its random number with a new random number. One might argue that the new random number should be higher than the old one, but this does not change the behavior, so for mathematical simplicity we replace the old random number with a completely new random number between 0 and 1. One might think of this elementary event either as an extinction of a species occupying a certain ecological niche followed by the replacement with another species, or as a pseudo-extinction where a species mutates. As far as our mathematical modeling is concerned, this doesn't make any difference. The mutation of the species at site i results in a change in the physical properties of that species, so that it affects the fitnesses of its two neighboring species. For simplicity, this is modelled by choosing a new, randomly selected, fitness for the neighbors also. One might argue their fitness should only be affected slightly, say less than $1/10$, or that their fitness should generally be worsened. Again, the details of the model do not affect the resulting outcome, so we choose a completely new random number.

To summarize: *At each time step in the simulation, the smallest fitness, and the fitness of the two neighbors are each replaced with new random fitnesses. This step is repeated again and again. That's all!*

What could be simpler than replacing some random numbers with some other random numbers? Despite the simplicity, the outcome of the process is nontrivial. One might suspect that the model would be so simple that it would easily yield to mathematical analysis, but the complexity of its behavior sharply contrasts with its simple definition. We shall see that modified versions of the model are more tractable.

In particular, a multi-trait evolution model (Boettcher and Paczuski 1996), which behaves similarly to the Bak-Sneppen model, can be completely solved. Instead of each site i having a single fitness f_i it has many fitnesses associated with its M different traits that evolve independently. The introduction of many internal traits is consistent with paleontological observations indicating that evolution within a species is "directed"; morphological change over time is

concentrated in a few traits, while most others traits of the species are static (Kaufmann 1993). The multi-trait model includes the Bak-Sneppen model when $M = 1$ and is solvable when $M \rightarrow \infty$.

4.1 The Self Organized Critical State

Figure 4 shows a snapshot of the fitnesses after billions of updates for a Bak-Sneppen ecology with 300 species. Most of the fitnesses are above a critical value, or gap, $f_c = 0.67002$ (Paczuski, Maslov, and Bak 1996). Note however a localized area in the species space where the fitnesses are below this gap. The next species to mutate is the one with the lowest fitness, #110. The fitness of this species and its two neighbors are updated. It is very likely that the next species to mutate is nearby. Subsequent evolution takes place within this localized burst. After a while, there will be no more species below the gap, and a new burst, or avalanche, will start somewhere else in the system.

During the avalanche, the species are mutating again and again, until eventually a self-suspended, stable network of species has been reestablished. The size, s , of the burst can be measured as the total number of mutations separating instances with no species in the gap. Figure 5 shows the distribution of burst sizes. There are avalanches of all sizes, with a power law distribution

$$P(s) \sim s^{-\tau} \text{ where } \tau \simeq 1.07 . \quad (1)$$

The power law for large sizes shows that the ecology has self-organized to a critical state. The large avalanches represent mass extinction events, like the Cambrian explosion (Gould 1989). During the large avalanches, nature tries one combination after another until a relatively stable configuration is reached, and a period of stasis in this area of the global ecology begins.

As a consequence of the interaction between species, even species that possess well-adapted abilities, with high barriers, can be undermined in their existence by weak species with which they interact. For instance, a species with fitness above the critical gap never mutates on its own. However, eventually it may be hit by "bad luck" because a mutation among its neighbors destroys its pleasant and stable life. A species can go extinct through no fault of its own and for no apparent external "reason" such as a meteor. Nature is not fair! A high fitness is only useful as long as the environment defined by the other species in the ecology remains intact.

Figure 6 shows the accumulated number of mutations of an arbitrary single species in the model. Note the relatively long periods of stasis, interrupted by bursts of activity. One might imagine that the amount of morphological change of a species is proportional to the the total number of mutations, so the curve shows punctuated equilibrium behavior. The large jumps represent periods where very many subsequent mutations take place at a rapid pace, because an ecological co-evolutionary avalanche happens to visit the species. Thus, the big jumps between "useful" or highly fit states are effectuated by cumulative small jumps through intermediate states which could exist only in the temporary environment of a burst. The curve is a Cantor set, or Devil's staircase, invented by the

mathematician Georg Cantor in the last century. The length of the period of stasis is the "first return time" of the activity for a given species. That quantity also has a power law distribution (Maslov, Paczuski, and Bak 1995). In evolution, this time can be thought of as the lifetime of a species before it undergoes a (pseudo)extinction. In fact, the distribution of lifetimes of fossil genera (Sepkoski 1993) appears to follow a power law with a characteristic exponent $\simeq 2$ (Sneppen et al. 1995).

As a consequence of the power law distribution of burst sizes, most of the evolutionary activity occurs within the few large avalanches rather than the many smaller "ordinary" events. Self-organized criticality can thus be thought of as a theoretical justification for catastrophism.

4.2 Comparison with the fossil record

The time unit in the computer simulations is a single update step. Of course, this does not correspond to time in real biology. Based on the rugged fitness landscape picture, the time-scale for traversing a barrier of size b is exponential in the barrier height, which is roughly proportional to the fitness, so $t_i \sim \exp(f_i/T)$. Here T is an effective temperature which represents an average mutation rate in the genetic code. In real biology, there is no search committee locating the least fit species, but mutation takes place everywhere at the same time. In the limit where the effective temperature T approaches zero, the minimal fitness is always selected next for mutation. Punctuated equilibrium behavior can exist only where the mutation rate is slow; otherwise there would not be long periods of stasis. A system with a high mutation rate will not have sufficient memory to develop complex behavior, since any new development will be erased in a relatively short time span.

Sneppen et al. (1995) performed a simulation where at each time step a mutation takes place everywhere with probability $p = \exp(-f_i/T)$. Figure 7 shows the resulting space-time plot of the activity, with $T = 0.01$. Note the temporal separation of the avalanches, which show up as connected black areas. The information in this diagram can be presented differently. In figure 8, the time scale has been coarse grained in a simulation over 8000 steps into 60 equal time intervals. The total amount of events in each time step is plotted as a function of time. Note the similarity with Sepkoski's plot, figure 1. During each time period, there are generally many avalanches. One can show that the resulting distribution for the total number of events in each period approaches a Pareto-Levy distribution, which has power law tails for large events. The information in Raup's histogram of Sepkoski's data is too sparse to test whether or not it represents a Pareto-Levy distribution.

In the Bak-Sneppen model, the number of species is conserved. It does not allow for speciation where one species branches into two species, but might be justified as a consequence of competition for resources. Vandewalle and Ausloos (1995) have constructed a model where phylogenetic trees are formed by speciation, starting from a single species. This model also evolves to the critical state, with extinction events of all sizes.

Of course, it would be interesting if one could perform controlled experiments on evolution. The second best is to construct artificial evolution in the computer. Ray (1992) and Adami (1995) have done just that. They created a world of replicating and mutating program segments. Adami found that evolution in this artificial world exhibits punctuated equilibria, with a lifetime distribution of organisms following a power law, indicating that the system self-organizes into a critical state.

4.3 External Effects

To what extent is evolution described by such simple models affected by external events, such as temperature variations, volcanic eruptions, neutrino bursts, or meteors? Schmultzi and Schuster (1995) studied a model where extinction takes place when the fitness of a species falls below a random number drawn from an independent distribution. The random number represents the effect from external sources. Self-organized criticality and punctuated equilibria were also found. Newman and Roberts (1995) took a similar approach. The species were assigned not only barriers for spontaneous mutation, but independent random fitnesses. At each point in time, species with fitnesses less than a randomly varying external perturbation would go extinct, in addition to species mutating spontaneously. The external perturbations initiate avalanches. They found a power law distribution of co-evolutionary avalanches, with an exponent $\tau \simeq 2$.

5 Theory

Theoretical developments to mathematically describe the behavior of these abstract computer models have taken two routes. The first is a phenomenological approach that we have undertaken in collaboration with Sergei Maslov (Paczuski, Maslov, and Bak 1994, 1996). We have made a unified theory of avalanche dynamics which treats not only evolution models but also other complex dynamical systems with intermittency such as invasion percolation, interface depinning, and flux creep. Complex behavior such as the formation of fractal structures, $1/f$ noise, diffusion with anomalous Hurst exponents, Levy flights, and punctuated equilibria can all be related to the same underlying avalanche dynamics. This dynamics can be represented as a fractal in d spatial plus one temporal dimension. In particular, the slow approach to the critical attractor, i.e. the process of self-organization, is governed by a "gap" equation for the divergence of avalanche sizes as the gap in the fitness distribution approaches the critical value, starting from the flat gapless initial distribution. Figure 9 shows the minimum value of the fitness vs. the number of update steps. The envelope function of this curve is the gap. Avalanches of activity below the gap separate the instances where the gap grows. Clearly, the avalanches become bigger and bigger as time goes on.

We have developed a scaling theory that relates many of the critical exponents describing various physical properties to two basic exponents characterizing the fractal attractor. The phenomenological theory does not provide information about the values of those exponents.

The second approach has been aimed at obtaining exact results for specific models. For the multitrait model (Boettcher and Paczuski 1996), an explicit equation of motion for the avalanche dynamics can be derived from the microscopic rules. Exact solutions of this equation, in different limits, proves the existence of simple power laws with critical exponents that verify the general scaling relations mentioned above. Punctuated equilibrium is described by a Devil's staircase with a characteristic exponent $\tau_{\text{FIRST}} = 2 - d/4$ where d is the spatial dimension. Actually, for the multi-trait evolution model, the distribution of avalanche sizes is known exactly when $M \rightarrow \infty$. It is

$$P(s) = \frac{\Gamma(s + \frac{1}{2})}{\Gamma(\frac{1}{2}) \Gamma(s + 2)} \sim s^{-3/2} \text{ for } s \gg 1 \quad (2)$$

This distribution of sizes is the same as for the random neighbor models in which each species interacts with 2 randomly chosen other species in the ecology rather than with near neighbors on a regular grid (Flyvbjerg et al. 1993; deBoer et al. 1995). The power law has a characteristic exponent $\tau = 3/2$ rather than $\tau = 1.07$ for the Bak-Sneppen chain.

In the multitrait model, avalanches propagate via a "Schrödinger" equation in imaginary time with a nonlocal potential in time. This nonlocal potential gives rise to a non-Gaussian (fat) tail for the subdiffusive spreading of activity. For the chain, the probability for the activity to spread beyond a species distance r in time s decays as $\sqrt{\frac{24}{\pi}} s^{-3/2} x \exp[-\frac{3}{4}x]$ for $x = (\frac{r^4}{s})^{1/3} \gg 1$ (Paczuski and Boettcher 1996). This anomalous relaxation comes from a hierarchy of time scales, or memory effect, that is generated by the avalanches. In addition, a number of other correlation functions characterizing the punctuated equilibrium dynamics have been determined exactly. For instance, the probability for a critical avalanche to affect a species at distance r is exactly $12/((r+3)(r+4))$ in one dimension.

6 Acknowledgments

This work is supported by the Division of Materials Science, U. S. Department of Energy under contract # DE-AC02-76CH00016. We are grateful for discussions and collaborations leading to the results summarized here with K. Sneppen, H. Flyvbjerg, and S. Maslov. We thank Mike Fuller for biologically relevant comments on our paper.

References

- Adami, C. (1995): Self-organized criticality in living systems. *Phys. Lett. A* **203**, 29-32
 Alvarez, L. W., Alvarez, F. A., Michel, H. W. (1980): Extraterrestrial cause for the Cretaceous-Tertiary extinction *Science* **208**, 1095-1108
 Bak, P., Flyvbjerg, H., Lautrup, B. (1992): Coevolution in a rugged fitness landscape. *Phys. Rev. A* **46**, 6724-6730

- Bak, P., Paczuski M. (1995): Complexity, contingency, and criticality. *Proc. Natl Acad. Sci. USA* **92** 6689-6696
- Bak, P., Sneppen, K. (1993): Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* **71**, 4083-4086
- Bak, P., Tang, C., Wiesenfeld K. (1987): Self-organized criticality. An explanation of $1/f$ noise. *Phys. Rev. Lett.* **59**, 381-384
- Bak, P., Tang, C., Wiesenfeld K. (1988): Self-organized Criticality. *Phys. Rev. A* **38**, 364-374
- Boettcher S., Paczuski M. (1996): Exact results for spatiotemporal correlations in a self-organized critical model of punctuated equilibria. *Phys. Rev. Lett.* **76**, 348-351
- Darwin, C. (1910): *The Origin of Species* (Murray, London), 6th edition.
- deBoer, J., Derrida, B., Flyvbjerg, H., Jackson, A. D., Wettig, T. (1994): Simple model of self-organized biological evolution. *Phys. Rev. Lett.* **73**, 906-909
- Fisher, R. A. (1932): *The Genetical Theory of Natural Selection*
- Flyvbjerg, H., Bak P., Jensen, M. H. Sneppen, K. (1995): A self-organized Critical Model for Evolution, in *Modelling the Dynamics of Biological Systems*. E. Mosekilde and O. G. Mouritsen (Eds.) (Springer Berlin, Heidelberg, New York) pp 269-288
- Flyvbjerg, H., Lautrup, B. (1992): Evolution in a rugged fitness landscape. *Phys. Rev. A* **46**, 6714-6723
- Flyvbjerg, H., Sneppen K., Bak P. (1993): Mean field theory for a simple model of evolution. *Phys. Rev. Lett.* **71**, 4087-4090
- Gould, S. J. (1989): *Wonderful Life* (Norton, New York)
- Gould, S. J., Eldredge N. (1977): Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology* **3**, 114-151
- Gutenberg B., Richter C. F. (1956): *Ann. Geofis.* **9**, 1
- Kauffman, S. A. (1993): *The Origins of Order: Self-Organization and Selection in Evolution* (Oxford University Press, Oxford)
- Kauffman, S. A., Johnsen, S. J. (1991): Coevolution to the edge of chaos: Coupled fitness landscapes, poised states, and coevolutionary avalanches. *J. Theo. Biology* **149**, 467-505
- Maslov, S., Paczuski, M., Bak, P. (1994): Avalanches and $1/f$ noise in evolution and growth models. *Phys. Rev. Lett.* **73**, 2162-2165
- Maynard Smith, J. (1993): *The Theory of Evolution* (Cambridge University Press, Cambridge)
- Newman, M. E. J., Roberts, B. W. (1995): Mass extinctions: Evolution and the effects of external influences on unfit species. *Proc. Roy. Soc. London B* **260**, 31
- Newman, W. L., Turcotte D. L., Gabrielov A. M. (1995): Log-periodic behavior of a hierarchical failure model. *Phys. Rev. E* **52**, 4827
- Paczuski, M., Maslov, S., Bak, P. (1994): Field theory for a model of self-organized criticality. *Europhys. Lett.* **27**, 97-100; Erratum **28**, 295-296
- Paczuski, M., Maslov, S., Bak, P. (1996): Avalanche dynamics for evolution, growth, and depinning models. *Phys. Rev. E* **53**, 414
- Paczuski, M., Boettcher, S. (1996): in preparation
- Raup, D.M. (1982): *Extinction. Bad Genes or Bad Luck?* (Oxford University Press, Oxford)
- Raup, D. M. (1986): Biological extinction in history. *Science* **231**, 1528-1533
- Ray, T. (1992): in *Artificial Life II* ed. C. G. Langton (Addison-Wesley, Reading Massachusetts)
- Schmultzi, K., Schuster, H. G. (1995): Introducing a real time scale into the Bak-Sneppen model. *Phys. Rev. E* **52**, 5273

- Sepkoski, J. J. Jr. (1993): Ten years in the library: New data confirm paleontological patterns *Paleobiology* 19, 43-51
- Sneppen, K., Bak P., Flyvbjerg H., Jensen, M. H. (1995): Evolution as a self-organized critical phenomena. *Proc. Natl. Acad. Sci. USA* 92, 5209-5213
- Vandewalle, N., Ausloos, M. (1995): Self-organized criticality in phylogenetic-like tree growth. *J. de Phys. (Paris)* 5, 1011-1025
- Wright, S. (1982): Character change, speciation, and the higher taxa. *Evolution* 36, 427-443

Fig.1. Temporal pattern of extinctions recorded over the last 600 million years, as given by J. Sepkoski (1993). The ordinate shows an estimate of the percentage of species that went extinct within intervals of 5 million years

Fig. 2. Histogram of extinction events as shown by Raup (1986). The histogram is based on the recorded time of extinction of 2316 marine animal families

Fig. 3. Fitness landscape. Note that the species with low fitnesses have smaller barriers to overcome in order to improve their fitness than species with high fitnesses

Fig. 4. Snapshot of fitnesses f for 300 species during an avalanche in the evolution model. Most of the f values are above the critical value. The cluster of active species with $f < f_c$ participate in the avalanche and undergo frequent changes (Paczuski et al. 1996)

Fig. 5. Distribution of the size of avalanches in the critical state for the one dimensional evolution model. The straight line on the log-log plot indicates a power law with an exponent $\tau \simeq 1.07$ (Paczuski et al. 1996)

Fig. 6. Accumulated number of mutations for a single species, or a single ecological niche in the stationary state. The curve exhibit punctuated equilibrium behavior, with periods of stasis interrupted by intermittent bursts. The curve is a Cantor set, or a Devil's staircase

Fig. 7. Space time plot of the activity. The horizontal axis is the species axis. The time at which a species mutates is shown as a black dot. The avalanches appear as connected black areas. Calculation was done for a value of the mutation parameter $T = 0.01$ (Sneppen et al. 1995)

Fig. 8. Temporal pattern of evolution, with $T = 0.01$. Note the similarity with Sepkoski's plot, figure 1 (Sneppen et al. 1995)

Fig. 9. The self-organization process for a small system. $f_{\min}$ vs time is shown (crosses). The full curve shows the gap, which is the envelope function of $f_{\min}$. On average, the avalanche size grows as the critical point is approached, and eventually diverges, as the gap approaches the critical value 0.6700. (Paczuski et al. 1996)