

# Extinction: Bad Genes or Weak Chaos?

Ricard V. Solé  
Jordi Bascompte  
Susanna C. Manrubia

SFI WORKING PAPER: 1996-07-049

SFI Working Papers contain accounts of scientific work of the author(s) and do not necessarily represent the views of the Santa Fe Institute. We accept papers intended for publication in peer-reviewed journals or proceedings volumes, but not papers that have already appeared in print. Except for papers by our external faculty, papers must be based on work done at SFI, inspired by an invited visit to or collaboration at SFI, or funded by an SFI grant.

©NOTICE: This working paper is included by permission of the contributing author(s) as a means to ensure timely distribution of the scholarly and technical work on a non-commercial basis. Copyright and all rights therein are maintained by the author(s). It is understood that all persons copying this information will adhere to the terms and constraints invoked by each author's copyright. These works may be reposted only with the explicit permission of the copyright holder.

[www.santafe.edu](http://www.santafe.edu)



SANTA FE INSTITUTE

# Extinction: Bad Genes or Weak Chaos?

Ricard V. Solé<sup>1,2</sup>, Jordi Bascompte<sup>3</sup>  
and Susanna C. Manrubia<sup>1</sup>

(1) Complex Systems Research Group  
Departament de Física i Enginyeria Nuclear,  
Universitat Politècnica de Catalunya  
Sor Eullia d'Anzizu s/n, Campus Nord, Mdul B4  
08034 Barcelona, Spain

(2) Santa Fe Institute,  
1399 Hyde Park Road, Santa Fe, NM87501, USA

(3) Department of Ecology and Evolutionary Biology,  
University of California  
Irvine, CA 92717, USA

Submitted to Proceedings R. Soc. London B

Keywords: Self-organized criticality, Macroevolution, Extinctions  
Running head: Extinctions and Chaos

## Summary

The dynamics of extinction and diversification of life is not a simple random process, driven by arbitrary inputs. Biotic interactions are known to play a very important role in the population response to physical factors. In spite of this fact, it is not clear how the ecological scale is related with the macroevolutionary one. In this paper we suggest that both levels are, at least to some extent, decoupled. Using a simple model of large-scale evolution, we show how an  $n$ -species ecosystem evolves towards a critical state where extinctions of all sizes are generated. This state involves a situation where high unpredictability is present. The basic properties of the overall macroevolutionary pattern are well reproduced and a new interpretation for this process is suggested.

# 1 Introduction

Populations change in time, often in rather complex ways (May, 1974; Bascompte and Sol, 1995). Sometimes, they go extinct. Extinctions can be associated with external factors as changes in sea level or the fall of an asteroid. However, biotic interactions play at least an equally important role: epidemics or the introduction or disappearance of a single species can trigger changes in population densities in other species. Eventually, the players in a community can be associated in an unlikely chain of events. Interactions can be extremely complex and involve apparently unrelated species. A very interesting example is the effect of the introduction of a mammalian virus to Southern England on the large blue butterfly (*Maculina arion*) (Ratcliffe, 1979). The chain involved rabbits, certain type of grasses, a species of ants and the caterpillars of the blue butterfly.

Population fluctuations are a classical problem in theoretical ecology. The standard mathematical approach is the Lotka-Volterra (LV)  $n$ -species model,

$$\frac{dN_i}{dt} = N_i \left( \epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j(t) \right) \quad (1)$$

where  $\{N_i\}$ ,  $i = 1, \dots, n$  are the populations of each species. These models have been explored in deep. Two main qualitative problems have been considered: (i) small- $n$  problems, involving two or three species and (ii) large- $n$  models, involving a full network of interacting species. In the last case, the problem of stability versus complexity (May, 1974; Tilman *et al.*, ) remains still open. The so called community matrix  $\Gamma = (\gamma_{ij})$  is the basic subject of all these studies.

Figure (1) near here

Many interesting theoretical results have been obtained when certain assumptions over  $\Gamma$  hold (May, 1974; Svirzhev and Logofet, 1983). The following, and already classical result was obtained by May in randomly connected food webs (May, 1972). Let  $C$  be the fraction of non-zero elements in  $\Gamma$  and let  $\sigma^2$  be the variance of the set  $\{\gamma_{ij}\}$ . It was shown that the system will be stable if  $\sigma\sqrt{nC} < 1$  and unstable otherwise. This transition is sharply defined for large  $n$ . This result, though may be not directly applicable to real ecosystems (Pimm, 1991; see however Kenny and Loehle, 1991) shows us that thresholds to complexity and stability can exist in generic ecosystem models.

Nevertheless, the stability of a given ecosystem is not a rigid property. Long term changes are always threatening stability and the community structure and species competition change over time. Extinction can occur and many examples are available (Keitt and Market, 1996; for a review, see Pimm, 1991, and references

therein). These extinctions only involve one or a few species but on a larger time scale, larger events can occur. In fact, the study of the available evidence from the fossil record (Benton, 1995a) shows events of all sizes, from small to mass extinctions (Jablonski, 1987).

As an example, in figure 1 we show the time fluctuations in the extinction rate (for genera) of marine animals. We see a wide range of fluctuations and the computation of the power spectrum  $P(f)$ , also shown, gives us a continuous, power-law decay  $P(f) \propto f^{-\beta}$  with  $\beta = 0.83 \pm 0.02$ . This result is consistent with a recent hypothesis which tries to explain the ubiquity of scale-free laws in nature: the theory of self-organized critical phenomena (Bak *et al.*, 1987; Bak and Sneppen, 1993). Self-organized criticality (SOC) is present in a wide set of systems far from equilibrium, from sandpiles and earthquakes to astrophysics and it has been suggested to be present in biological evolution (Sneppen *et al.*, 1995; Sol and Bascompte, 1996). Such systems tend to organize themselves, after a transient period, in a state with no characteristic time- or length scale other than the system size. Small, basically random changes (the fall of a sand grain or the appearance of a new species) can be enough to trigger large events. In figure 2 a different picture of the discontinuous nature of extinction events is shown. Here the total number of Trilobita families is shown from the early Ordovician to the late Permian. The number of families falls several times, but the height of this steps shows a very wide range of values.

David Raup (Raup, 1993) used this example to ask the key question: did the trilobites do something wrong? Were they genetically inferior? Or had they simply bad luck? Ideally, the answer to this question, which involves the large scale, should be the result of the rules working at the shorter scale. In such a case, we could find a generalization of the previous equations, perhaps involving noise, and the observed extinction pattern would be obtained. But can such large-scale events be included in a generalized version of Lotka-Volterra equations? An affirmative answer to this question implies that macroevolution is correctly described from the lower-scale population dynamics and a reductionist approach would be justified. In some sense, large-scale evolution (and extinction) could be reduced to the microscale (Maynard Smith, 1989). This view, however, is not shared by all evolutionary biologists (Eldredge, 1985).

Figure (2) near here

An important contribution to this problem came from theoretical ecology and is known as the Red Queen Hypothesis (van Valen, 1973; Stenseth and Maynard Smith, 1984; Benton, 1995b). This hypothesis maintains that the different species within a community keep constant ecological relationships to each other, and that these interactions are themselves evolving. This theory predicts a constant extinction rate

of species (or other taxa) in agreement with available data. This picture of evolution implies that bursts of extinction and speciation will happen only in response to changes in the physical environment.

A key ingredient of macroevolution is, in our view, absent in the LV approximation: the essentially discrete nature of extinction and diversification and the contingent nature of both processes. Once a species is gone, diversification of the surviving species will occur. This process will generate new arrangements in the community structure, which might lead to new extinctions.

In this paper we want to analyse this problem by means of a simple model of macroevolution. The basic ingredients (extinction, diversification and networks dynamics) will be included. In particular, we want to stress the existence of higher-level mechanisms explaining some of the patterns observed in the fossil record. As we will see, a new interpretation for the extinction pattern is obtained.

## 2 Evolution model

Previous models of evolution leading to critical states have been based in the so called Bak-Sneppen (BS), (Bak and Sneppen, 1993) or the Kauffman-Johnsen model (Kauffman and Johnsen, 1991). These are oversimplified pictures of evolving ecosystems leading to power laws. However, none of them involve real extinctions nor diversification, although some alternatives to these models have been explored. See for instance the niche invasion model of Kauffman (Kauffman, 1995) or the modified BS model introduced by Newman and Roberts (Roberts and Newman, 1996). Recently (Sol, 1996; Sol and Manrubia, 1996) such ingredients have been explicitly taken into account in a new model of species interaction. Here we follow this last approximation.

The Lotka-Volterra equations (1) are too difficult to manage if  $\Gamma$  is formed by time-dependent terms. We want to retain the basic qualitative approach, but our interest is shifted from population sizes to the appearance and extinction of species. Here species are assumed to be a binary variable:  $S_i = 0$  (extinct) or  $S_i = 1$  (alive). The state of such species evolves in time (now assumed discrete) according to

$$S_i(t+1) = \Phi \left( \sum_{j=1}^n \gamma_{ij}(t) S_j(t) \right) \quad (2)$$

with  $i = 1, \dots, N$ . Here  $\Phi(z) = 1$  if  $z > 0$  and zero otherwise. Equation (2) can be understood as the discrete counterpart of (1), but involving a much larger time scale. In our model (Sol, 1996; Sol and Manrubia, 1996), the  $i$ -th species is in fact represented by the set of connections  $\{\gamma_{ij}, \gamma_{ji}\}$ ,  $\forall j$ . The elements  $\gamma_{ij}$  are the *inputs*

and define the state of the species. The symmetric elements  $\gamma_{ji}$  are the *outputs* and represent the influence of this species over the remaining ones in the system.

The dynamics is defined in three steps:

(i) Changes in connectivity. Each time step we change one connection  $\gamma_{ij}$  which takes a new, random value  $\gamma_{ij}(t+1) \in [-1, 1]$ , for each  $i = 1, \dots, N$ , with  $j \in \{1, \dots, N\}$  chosen at random. This rule is linked with the internal changes involving the species interactions. They could be associated with external causes or simply be the result of small changes as a consequence of coevolution. This rule introduces random, small changes into the network.

(ii) Extinction. The local inputs  $\mathcal{F}_i = \sum_j \gamma_{ij}(t)S_j(t)$  are computed, and all species are synchronously updated following (2). If the  $k$ -th species goes extinct, then all the connections that define it are set to zero, that is  $\gamma_{kj} = \gamma_{jk} \equiv 0, \forall j$ . This updating introduces extinction and selection of species. Those sets of connections which make a species stable will remain. But in removing a given species, some positive connections, with a stabilizing effect on other species can also disappear, and the system can become more unstable.

(iii) Replacement. Some species are now extinct (i. e.  $S_k = 0$ ) and empty sites are then available for colonization. Diversification then is introduced. A living species is picked up at random and “copied” in the vacant spaces. The new species are basically identical to the one randomly chosen, except for a small random change in all their connections. Specifically, let  $S_c$  the copied species. For each extinct species  $S_j$  (vacant spaces), the old connections are set to zero, and the new connections  $\gamma_{ij}$  and  $\gamma_{ji}$  are given by  $\gamma_{kj} = \gamma_{cj} + \eta_{kj}$  and  $\gamma_{jk} = \gamma_{jc} + \eta_{jk}$ . Here  $\eta$  is a small random variation (we took  $\eta = 0.05$ ). In this way, the new species are the result of the diversification of one of the survivors.

Figure (3) near here

The previous rules can be summarized in figure 3, where a small ecosystem is shown. In our previous study, it was shown that the system evolves to a critical state with power laws in the extinction sizes (i. e.  $N(s) \approx s^{-\tau}$ , with  $\tau \approx 2$ ) and waiting times until extinction. The model shows punctuated equilibrium, as found in the real fossil record (Gould and Eldredge, 1993). But here there is no separation between “mass” and “background” extinctions. All of them are generated by the same dynamical process, and no particular extinction size is privileged.

### 3 Criticality and Unpredictability

In this section we want to analyse in which way the critical state is reached and the interpretation of the resulting dynamical pattern. The random changes in the

network connections make the trophic links between species more and more complex. We can quantify their complexity by means of an adequate statistical measure. Let us first consider the time evolution of connections. Let  $P(\gamma^+)$  and  $P(\gamma^-) = 1 - P(\gamma^+)$  be the probability of positive and negative connections, respectively. The time evolution of  $P(\gamma^+, t)$  is defined by the master equation

$$\frac{\partial P(\gamma^+, t)}{\partial t} = P(\gamma^-, t)P(\gamma^- \rightarrow \gamma^+) - P(\gamma^+, t)P(\gamma^+ \rightarrow \gamma^-) \quad (3)$$

From the definition of the model, we have a transition rate per unit time given by  $P(\gamma^+ \rightarrow \gamma^-) = P(\gamma^- \rightarrow \gamma^+) = 1/(2N)$  and so we have an exponential relaxation  $P(\gamma^+, t) = (1 + (2P_0 - 1)\exp(-t/N))/2$ , where  $P_0 = P(\gamma^+, 0)$ . This result leads immediately to an exponential decay in the local inputs,  $\mathcal{F}_i(t) \propto \exp(-t/N)$ . As a result, the system evolves towards a critical state where the inputs introduced by the coevolving partners are small and so small changes involving single connections can generate extinctions.

Figure (4) near here

We can use the entropy of connections per species, i. e. the Boltzmann entropy

$$H(P(\gamma^+, t)) = -P(\gamma^+, t)\log(P(\gamma^+, t)) - (1 - P(\gamma^+, t))\log(1 - P(\gamma^+, t)) \quad (4)$$

as a quantitative characterization of our dynamics. The Boltzmann entropy (also known as the Shannon entropy) gives us a measure of disorder but also a measure of uncertainty (Ash, 1965). It is bounded by the following limits:  $0 \leq H(P(\gamma^+, t)) \leq \log(2)$ . These limits correspond to a completely uniform distribution of connections (i. e.  $P(\gamma^+, t) = 1$  and  $P(\gamma^-, t) = 0$ ) with zero entropy and to a random distribution with  $P(\gamma^\pm, t) = 1/2$  which has the maximum entropy. Our rules make possible the evolution to the maximum network complexity, here characterized by the upper limit of the entropy.

As we can see in figure 4,  $H(P(\gamma^+, t))$  grows, after a large extinction event, towards its maximum value  $H^* = \log(2)$ , with sudden drops near large extinctions. So our system slowly evolves towards an “attractor” characterized by a randomly connected network. At such state, small changes of strength  $1/N$  can modify the sign of  $\mathcal{F}_i$  and extinction may take place. At this point, one clearly sees what is the role that external perturbations play: for them to trigger a large extinction, it is necessary that they act on a system located close to the critical state (here, the network close to the maximum entropy). A large extinction will never be found in a system with a low entropy of connections even with a reasonably large external perturbation. This is a key property of SOC systems. More specifically, a SOC system



has an *order parameter* that defines the transition displayed by the system (in our case the change from no-extinctions to extinctions) as a second order (or continuous) phase transition. This order parameter has been shown to be the extinction rate, while the control parameter is the average value of the connections  $\langle \gamma_{ij} \rangle$  (Sol and Manrubia, 1996). For  $\langle \gamma_{ij} \rangle > 0$  no extinction will be found for a large enough system, while for  $\langle \gamma_{ij} \rangle < 0$  extinctions of all sizes (up to system size) can be found.

We can see that a wide distribution of extinctions is obtained: it is a power-law distribution,  $N(s) \approx s^{-\tau}$  with  $\tau = 2.05 \pm 0.06$ , consistent with the information available from the fossil record (Raup, 1986, 1993; Sol and Bascompte, 1996). This result also agrees with the Newman-Roberts model, who also obtained the same exponent within the error (Newman and Roberts, 1995; Roberts and Newman, 1996), while other models give values clearly different:  $\tau \approx 1.1$  for the BS model and  $\tau = 1$  for Kauffman-Johnsen's.

Figure (5) near here

Other properties can be explored. In particular, we could ask which type of diversification patterns are present. A direct consequence of criticality, as defined by the previous rules, is the existence of a power law in the taxonomy. If we look at a given species, it can generate, after an extinction event, one, two or many new species, and the statistical distribution will be a power law with the same exponent than before (recall that rule (iii), replacement of extinct species, copies all extinct species in a single alive one). It is interesting to see that available evidence from the fossil record shows precisely this range of values (Burlando, 1990; 1993). In our case, every time that replacement takes place, we define the new elements to be a subtaxa of the parent species chosen to be copied.

As an example, we have considered the values of the local fields at each time step. Provided that the connections take values between  $-1$  and  $+1$ , the internal fields can theoretically range from  $-N$  to  $+N$ , though large negative values will be rarely observed. We divide this interval in  $N$  pieces and at each time step we look at all the species in the system and find all the intervals that are occupied at least by one of them. The time evolution of this is shown in figure 5 just after a mass extinction (where we chose  $t = 0$ ). Black dots mean occupied sites. As we can see the previous rules generate a very complex pattern of diversification followed by extinctions. Random and ordered domains are observed.

## 4 The Red Queen revisited

Finally, let us consider the law of constant mean extinction rate, van Valen's law (van Valen, 1973). As mentioned in the introduction, this law maintains that the probability of extinction within any group remains essentially constant through time. This is a consequence of the Red Queen theory and an observational result. This is, however, an average: on average, extinction rates are constant but a close inspection of the decay curves shows both continuous and episodic decays (Raup, 1986). The sudden, episodic drops are often associated with mass extinctions and are usually assumed to be the result of external perturbations.

Figure (6) near here

The Red Queen model gives a striking, counterintuitive explanation of the constant rate of extinction. If organisms are continuously evolving and adapting, why do they not get any better, on average, to avoid extinction?

The episodic (and apparently external) nature of the species decay is easily explained by our model. Though long periods of stasis and low extinction rates give a constant decay, *the same* intrinsic dynamics generates the episodes of extinction involving several (some times many) species. These survivorship curves are shown in figure 6 where four runs of our model are displayed. Each graphic is generated by starting at a given (arbitrary) time step in the simulation and following all the species present at this time step. The exponential decay in the number of survivors is closely related to the monotonous drift that the system experiences towards the extinction threshold, due to the constant change of connections to random values. As we can see (and this is rather typical) both constant and episodic decays are observed. We do not need to seek for a special external explanation for the episodic decay. Obviously, an external cause can trigger a large extinction event by altering the network dynamics at the critical state.

In our approach, the theoretical problems derived from the Red Queen interpretation simply do not arise. Extinctions are an unavoidable outcome of network dynamics. Though some selection of connections is present after each extinction event, unpredictability always increases. As with the example of the large blue butterfly, a given species cannot predict how the other players will modify their intrinsic properties and in particular how the network will be rearranged after a new extinction. This situation is basically shared by all the players, and so all of them are, on average, equally prone to disappear in the long run.

## 5 Discussion

In this paper we have analysed the consequences of a simple model of large-scale evolution involving extinction and diversification. The model is inspired in the standard Lotka-Volterra approach but we move from the ecological time scale (where population changes are relevant) to the paleontological one (where changes in species composition occur). In the small scale, deterministic factors are usually dominant, though some types of unpredictable behavior are present, for instance when deterministic chaos is involved. In the large scale, however, continuous, random changes in the trophic links move the system towards a critical state characterized by a high unpredictability and sensitivity to small perturbations. Here is worth emphasizing that spatial degrees of freedom can play a very important role. Actually, it is well known that space can stabilize species interactions which, otherwise should not persist (Hassell *et al.*, 1991; Sol *et al.*, 1992; Bascompte and Sol, 1995). This situation allows a given ecosystem to explore a wide range of interactions and, in the long run, eventually triggered by external causes, extinction can occur.

Because of the intricate network of couplings obtained at the critical state, the problem of which species will be gone is essentially unpredictable. Contingency has been recently aduced as one of the more relevant properties of the evolutionary process (Gould, 1989) and in this paper we give a dynamical origin to this unpredictability. But in spite of the intrinsic contingency of this process, the critical state is characterized by some well defined properties: punctuated equilibrium and power laws. The first (qualitative) property is observed both in the model and in real data. Punctuated equilibrium is in fact a characteristic feature of the fossil record but it is also a typical, perhaps generic characteristic of complex systems poised at critical points (Sol *et al.*, 1996). Power laws are the statistical counterpart of punctuated equilibrium. The fossil record shows several evidences of scale-free distributions (Raup, 1993; Sol and Bascompte, 1996; Sol *et al.*, 1996). Such data sets have not been interpreted (nor reproduced) by means of classical models of population dynamics. The global pattern is emergent, resulting from the generation of complex correlations among species. This is in total agreement with the conclusions of other authors, as Gould points out: “paleontologists should conciously explore the ways in which uncritical extrapolationism limit and channel thought. Evolution works on a hierarchy of levels, and some causes at higher levels are emergent”.

To sum up, we have shown that our model of large-scale evolution is able to recover the observed evolutionary patterns. The main consequence of our study is that the network complexity of a given ecosystem always grows in time leading to essentially random nets of connections. Trophic links become very intricate in such a way that the sensitivity of the system to further changes (both biotic and physical) becomes maximum. In this sense, the Red Queen picture, where changes are made

in order to adapt the system to the biotic environment, should be replaced by an always changing system were species are gone as a consequence of the unpredictable web of biotic relations. The observed fractal properties of the fossil record would be a direct result of this unpredictability in the critical state.

## Acknowledgments

The authors thank Mike Benton, Brian Goodwin and Per Bak for interesting discussions on criticality and evolution, and M. E. J. Newman for useful comments about the manuscript. This work has been supported by a grant DGYCIT PB94-1195. JB acknowledges a Postdoctoral grant from the Spanish Ministry of Education and Science.

## 6 References

1. Ash, R.B. 1965. *Information Theory*. Dover, New York.
2. Bak, P., Tang, C. & Wiesenfeld, K. 1987. Self-organized criticality: an explanation for  $1/f$  noise. *Phys. Rev. Lett.* **59**, 381-384.
3. Bak, P. & Sneppen, K. 1993. Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* **71** 4083-4086.
4. Bascompte, J. & Sol, R.V. 1995. Rethinking complexity: modelling spatiotemporal phenomena in ecology. *Trends Ecol. Evol.* vol. 10, no. 9, 361-366.
5. Benton, M.J. 1995a, Diversification and extinction in the history of life. *Science* **268**, 52-58.
6. Benton, M.J. 1995b. Red Queen Hypothesis. In: *Palaeobiology* (ed. D.E.G. Briggs & P. R. Crowther). Blackwells. Oxford.
7. Burlando, B. 1990. The fractal dimension of taxonomic systems. *J. theor. Biol.* **146**, 99-114.
8. Burlando, B. 1993. The fractal geometry of evolution. *J. theor. Biol.* **163**, 161-172.
9. Eldredge, N. 1985. *Unfinished synthesis: biological hierarchies and modern evolutionary thought*. Oxford U. Press. New York.
10. Gould, S.J. 1989. *Wonderful Life*. Penguin. London.
11. Gould, S.J. & Eldredge, N. 1993. Punctuated equilibrium comes of age. *Nature* **366**, 223-227.
12. Hassell, M.P. , Comins, H. & May, R. M. 1991. Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255-258.
13. Jablonski, D. 1987. Mass and background extinctions: the alternation of macroevolutionary regimes. *Science* **231**, 129-133.
14. Kauffman, S. 1995. *At home in the Universe*. Viking, Great Britain.
15. Kauffman, S. & Johnsen, J. 1991. Coevolution to the edge of chaos: coupled fitness landscapes, poised states and coevolutionary avalanches. *J. theor. Biol.* **149**, 467-505.

16. Keitt, T.M. & Marquet, P.A. 1996. The introduced Hawaiian avifauna reconsidered: evidence for self-organized criticality? *J. theor. Biol.* (in press).
17. Kenny, D. & Loehle, G. 1991. Are food webs randomly connected? *Ecology* **72**, 1794-1799.
18. May, R.M. 1972. Will a large complex system be stable? *Nature* **238**, 413-414.
19. May, R.M. 1974. *Stability and complexity in model ecosystems*. Princeton U. Press, Princeton.
20. Maynard Smith, J. 1989. The causes of extinction. *Phil. Trans. R. Soc. Lond. B* **325**, 241-252.
21. Newman, M.E.J. & Roberts, B. W. 1995a. Mass extinction: evolution and the effects of external influences on unfit species. *Proc. Roy. Soc. Lond. B* **260**, 31-17.
22. Pimm, S.A. 1991. *The Balance of Nature*. Chicago Press. Chicago.
23. Raup, D.M. 1986. Biological extinction and Earth history. *Science* **231**, 1528-1533.
24. Raup, D.M. 1993. *Extinction: bad genes or bad luck?* Oxford U. Press. Oxford.
25. Ratcliffe, D. 1979, The end of the large blue butterfly. *New Scientist* **8**, 457-458.
26. Roberts, B.W. & Newman, M.E.J. 1996. A model for evolution and extinction. *J. theor. Biol.* (in press).
27. Sneppen, K., Bak, P., Flyvbjerg, H. & Jensen, M.H. 1995. Evolution as a self-organized critical phenomenon. *Proc. Natl. Acad. Sci. USA* **92**, 5209-5213.
28. Sol, R.V., Bascompte, J. & Valls, J. 1992. Nonequilibrium dynamics in lattice ecosystems: chaotic stability and dissipative structures. *Chaos* **2**, 387-395.
29. Solé, R.V., Manrubia, S.C., Luque, B., Delgado, J. & Bascompte, J. 1996. Phase transitions and complex systems. *Complexity* vol. 1 **4**, 13-26.
30. Sol, R.V. & Bascompte, J. 1996. Are critical phenomena relevant to large-scale evolution? *Procs. R. Soc. London B* **263**, 161-168.

31. Solé, R.V. 1996. On macroevolution, extinctions and critical phenomena. *Complexity* vol. 1 **6**.
32. Sol, R.V. & Manrubia, S.C. 1996. Extinction and self-organized criticality in a model of large-scale evolution. *Phys. Rev. E* **54**, (in press).
33. Sol, R.V., Manrubia, S.C., Benton, M. & Bak, P. 1996, (submitted).
34. Stenseth, N.C. & Maynard Smith, J. 1984. Coevolution in ecosystems: Red Queen evolution or Stasis? *Evolution* **38**, 870-880.
35. Svirezhev, Yu. M. & Logofet, D. O. 1983. *Stability of biological communities*. MIR Publishers, Moscow.
36. van Valen, L. (1973) A new evolutionary law. *Evol. Theory* **1**, 1-30.

## 7 Figure captions

[1] (a) Proportional rate of extinction as a function of the geologic time (here each time unit = 2 Myr) for genera of marine animals during the Phanerozoic (adapted from Allen and Briggs, 1989); (b) Power spectrum  $P(f)$  obtained from the previous time series. It gives a scaling relation  $P(f) \propto f^{-\beta}$  with  $\beta = 0.83 \pm 0.02$ . Such a result is consistent with a scale-free phenomenon (see text)

[2] Decay of families of Trilobita from the early Ordovician to the late Permian, when they went extinct. We can see a wide set of changes from small extinctions to very large, as the one occurred at the end of the Ordovician period.

[3] An example of the rules used in the evolution model. Here an  $N = 6$  network is shown, with a given connectivity (a). In (b), two extinct species are shown as empty circles. At (c), the last rule (diversification) is applied. The empty sites are occupied by the species marked by an arrow.

[4] Extinction pattern in the model. Here  $N = 100$  species are used, and a small time series is shown, together with the entropy. We see that large extinctions take place close to high entropies (see text).

[5] Fluctuations in the distribution of inputs  $\mathcal{F}_i$  (see text). After a large extinction ( $t = 0$  in the figure) diversification occurs (A). As can be seen, the ordered pattern is replaced by a more random one. A detail of the fluctuations is shown in B.

[6] Extinction pattern of species over time. The decay of a given initial set of species (here  $N = 100$ ) in four different situations is shown (see text). Both continuous and episodic decay are observed.