A coarse-grained model of evolution with variable system size

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The fact that extinction events seem to be episodic on all scales, as noted by Raup [1], has aroused much interest in the last few years. It has been conjectured that the power-law decrease of the number of extinction events $p(s)$ with increasing size s is the result of the competitive dynamic between species. Ecosystems might drive themselves into a critical state where little change (e.g. the mutation of a single species) can trigger an "avalanche" that may span the whole system. For this kind of dynamic Bak et al. [2] have coined the name Self-Organized Criticality (SOC). Several simple models of evolution exhibiting SOC have been proposed, among them models by Kauffman and Johnsen [3], Bak and Sneppen [4], Manrubia and Paczuski [5]. These models act on species rather than on individuals. We will call models acting on species "coarse-grained".

Recently, Newman and Sneppen [6] introduced a new class of models. These so called "coherent noise" models are clearly not SOC but nevertheless show a power law distribution of avalanche sizes. Newman [7] compared such a model with the analysis of the fossil record performed by Raup. For his model he found an exponent of the power-law close to 2, which is in good agreement with the fossil record. Thus Newman came to the conclusion that there is no evidence for SOC as the major driving force for extinction.

However, the above mentioned models have one major drawback. In all these models the system size is kept constant and species that go extinct are replaced by new ones instantaneously. This is in clear contrast to the biological reality. After a major extinction event, the number of species in the ecosystem is significantly reduced, and the process of regrowth of new species can take a long time.

We here propose a generalization to the coherent noise model used by Newman, where the refilling of the system is done in finite time. Newman's model is defined as follows: The system consists of N species, each possessing a threshold x_i of tolerance against stress, chosen from a probablity distribution $p_{\text{thresh}}(x)$. At each time-step, a stress η is generated at random with a distribution $p_{\text{stress}}(\eta)$ and all species with $x_i < \eta$ are removed from the system and immediately replaced with new ones. Furthermore, a small fraction f of the species is chosen at random and given new thresholds. In our model, on the other hand, the fraction of species with $x_i < \eta$ is removed permanently from the system, but in every time-step there is some growth of new species.

The natural way to define the regrowth of the species is logistic growth,

$$\frac{\mathrm{d}N}{\mathrm{d}t} = gN\Big(1 - \frac{N}{N_{\max}}\Big)\,, \tag{1}$$

where g is the growth rate and $N_{\max}$ the maximal system size, imposed by external constraints. Since our model is discrete, we calculate the amount of new species in every time step from a discretized solution of Equation 1.

Our model reduces to the original one in the limit $g \to \infty$. For that reason our model should behave like Newman's for high growth rates, i.e. exhibiting a power-law decrease of event sizes with the same exponent. Numerical simulations show that this is indeed true. Moreover, we find that even for very small growth rates the event sizes are power-law distributed with an exponent that is virtually independent of the growth rate.

An extension to the analysis of Sneppen and Newman [6] shows that the shape of the time-averaged distribution $\bar{\rho}(x)$ of threshold variables x_i does not depend on g. Consequently the exponent of the power-law should be independent of the respective growth rate. Additionaly, we find a simple formula for the time-average of the system size $\bar{N}$, viz.

$$\bar{N} = \Big(1 - \frac{A - f}{g}\Big) N_{\max}\,, \tag{2}$$

where A is a constant that depends on f and on the distributions $p_{\mathrm{thresh}}(x)$ and $p_{\mathrm{stress}}(\eta)$.

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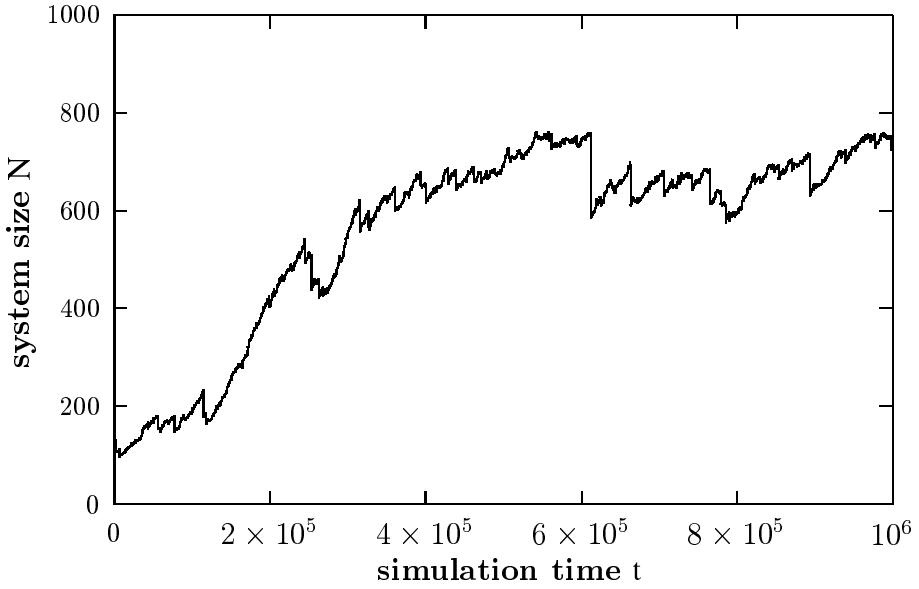

Figure 1: The evolution of the system size N in time. The parameters are $g = 4 \times 10^{-5}$, $\sigma = 0.05$, and $f = 10^{-5}$ with exponentially distributed stress.

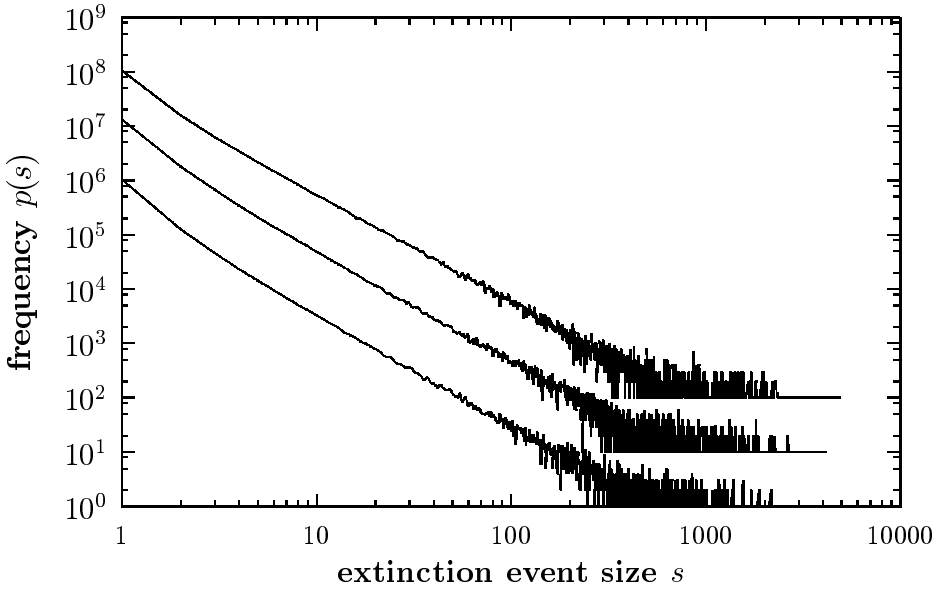

Figure 2: The distribution of extinction events for a system with exponentially distributed stress, $\sigma = 0.05$. The growth rate is, from bottom to top, $g = 4 \times 10^{-5}$, $g = 0.002$, $g = 10$. It can be seen that the power-law behavior does depend only marginally on the growth rate. The curves have been rescaled so as not to overlap.

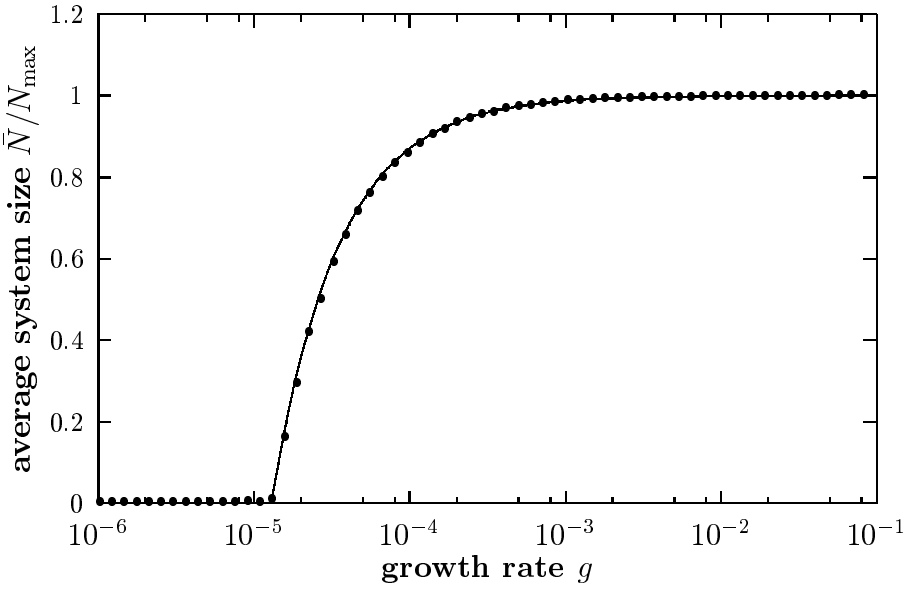

Figure 3: The average system size $\bar{N}$ versus the growth rate g. We used exponentially distributed stress with $\sigma = 0.05$ and $f = 10^{-5}$. The solid line is the analytic expression, the points are the simulation results.

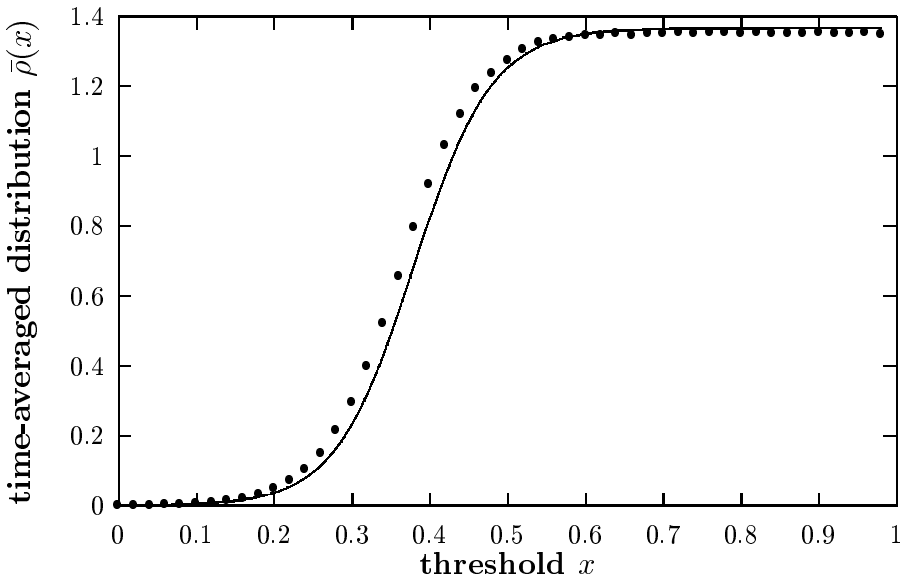

Figure 4: The time averaged distribution $\bar{\rho}(x)$. The parameters used are $g = 4 \times 10^{-5}$, $\sigma = 0.05$, and $f = 5 \times 10^{-4}$ with exponentially distributed stress. The solid line is the analytic expression, the points are the simulation results.