

Mirroring of environmental colored noise in species extinction statistics

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We investigate a simple model for the evolution of mutating model populations that leads to a power law of extinction statistics when subject to the influence of an external colored noise. The model focuses on environmental noise as the main cause of the correlated character of the extinction statistics in the fossil record. [S1063-651X(98)06711-7]

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Since the early studies of stratigraphical geology it is known that the extinction of species from the biosphere is a common event at the geological time scale. On the other hand, due to the uncertainties in palaeoecological reconstructions at the population level there is not yet agreement on which is the main agent responsible for the species extinctions. Interspecies competition or environmental fluctuations (and ecological stresses resulting from the action of both) have been documented in the fossil record but the statistical weight of each of these processes is not yet well established [1]. Extinctions due to interspecies competition are well known not only from paleobiological studies but also from ecology and population biology. Recently, it has been proposed that interspecies competition can lead to strong nonlinear effects in species extinction or survival. This causes sudden extinctions that can at least partially explain the nature of background extinctions as found in the fossil record [3]. A more recent set of data has also provided support to $1/f$ noise in the extinction statistics tending to favor intrinsic nonlinear dynamics as underlying cause of extinctions [4]. The evidence looks very robust and possibly even some mass extinctions might be explained in terms of nonlinear effects in the biosphere [4].

On the other hand, episodes of extinction have been correlated with environmental changes; see, for example, [2]. There is growing evidence that bursts of extinction can be related with speciations in different lineages, a pattern that might be correlated with environmental variations. In the present paper we present a simple model where extinctions are a consequence of environmental changes that may lead to correlated noise in the extinction rates. The statistics of extinctions in the model is a direct consequence of the correlated noise present in the fluctuating environmental variables. It is well known that the tolerance of organisms with respect to changes in the environmental quantities (temperature, salinity, moisture, and so on) is limited: usually the optimal performance is restricted to a range depending on the organism's tolerance [5]. Let us consider a population of some kind of organism subject to the variation of the environment. In general it can be assumed the environmental parameters affecting the biosphere vary with time, either periodically or quasiperiodically or according to a more complex time series whose spectrum may be represented by a power law. A change in one of the limiting factors of the organism such as the temperature, if sufficiently slow, may permit the population to: (1) evolve under the pressure selection, shifting the *optimum* peak according to the new condi-

tions: this occurs through the strengthening of some phenotypic characters that favor the survival at that temperature, (2) migrate to regions where the conditions are better, if allowed by geographical constraints.

If the environmental change is too fast with respect to the time scales of mutation and migration, the population will not be able to follow the new conditions and the phenotypic characters of the individuals in the population will shift progressively out of the optimal range, leading the species to a risk of extinction.

Let the model population be subject to an external (colored or white) noise E_t representing an environmental variable to which the organisms in the population are sensitive (let us stay on the example of the temperature). Assuming that the optimal condition can be described by one single phenotypic variable I_t , the quantity $\Delta_t = |E_t - I_t|$ will represent the deviation of the population's average character from the best conditions [6]. As a response to a change in the environmental variable E_t the population tries to keep Δ_t at a minimum through mutations and natural selection or migration. In the first case the population shifts the average value of the variable I_t from one generation to the next, according to the laws of population genetics [7]. We assume that to reduce the difference Δ_t the phenotypic variable can jump to a new value $I_t = I_{t-\delta t} \pm \sigma_t$ with a probability π where σ_t is a maximum allowed change of the phenotype (the existence of a maximum jump of the phenotype is due to genetic constraints (see, for example, [7]) and to the finite velocity of propagation of a favorable mutation through a population) and the sign is chosen in such a way as to reduce the difference Δ_t . Such a process is not instantaneous in nature, but in any case shorter than the average time of species replacement. If the difference Δ_t is smaller than σ_t , no changes are made, $I_t = I_{t-\delta t}$. The change in the value of Δ_t may also take into account the migration of the population as a response to the environmental variation. For example, populations can migrate to lower latitudes as a response to a decrease in the temperature as well known from recent events connected with the quaternary glaciations. In the case of migration, it should be more appropriate in the model to change E_t rather than I_t ; but since only the difference between these two quantities Δ_t enters into the calculations as the parameter characterizing the deviation of the population *optimum* from the external value, it is formally the same to change the internal character I_t instead. Therefore, both migration and phenotypic variation can be accommodated in the same model varying only I_t . It could be technically easy and con-

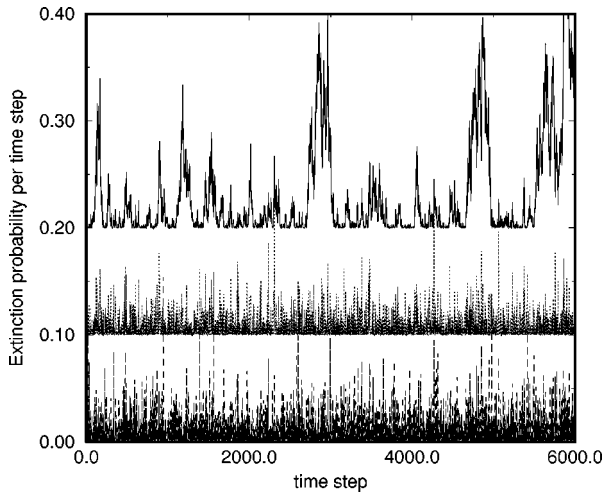


FIG. 1. The extinction probability p_{ext} from the model subject to stochastic time series with brown noise $\beta=2$ (continuous line, upper curve), pink noise, $\beta=1$ (medium line, dotted), and white noise, $\beta=0$ (lower line, dashed). To plot the graphs in the same figure the upper curve has been shifted up by 0.2, the medium by 0.1 and the two lower curves are magnified by a factor of ten. The parameters used in the calculations are the following: $\sigma_I/\sigma_E = 0.11$ (σ_E is the variance of the time series); $\pi=0.5$; $\epsilon=0.5$; $s=300$.

ceptually more satisfactory to consider migration and mutation as two separate possibilities, with different parameters and time scales. But since their relative importance in real populations is not well known and due to the expected large scattering among the different species, this would be hardly an improvement of the model. The important feature is rather that the responses of the population, natural selection or migration, need a finite time to take place, hence the existence of a finite value σ_I for the change of I_t at each time step.

We then assume that the probability of species extinction increases in a simple way as a function of Δ_t . Since the physiological response of an organism is often bell shaped as a function of the limiting factor [8] we shall consider the survival probability as a Gaussian centered at zero as a function of Δ_t . The extinction probability is then calculated as $p_{\text{ext}} = \epsilon[1 - \exp(-\Delta_t^2/s)]$ where ϵ is a constant and s is a sensitivity parameter. In general, tolerant species (eurytopic) will be characterized by relatively large values of s , while intolerant ones (stenotopic) by small values. For simplicity, we shall not be interested in the distinction between different organisms and shall keep this parameter fixed.

We now choose the time evolution for E_t in the form of a correlated time series [9], a form that can be a good model for many processes occurring on Earth. Colored time series have been considered in detail only more recently with respect to simple white noise in ecological problems [10] and in the analysis of the fossil record [11]. Figure 1 shows the extinction probability as a function of time for three simulations. Each curve corresponds to a different value of the parameter β of the time series E_t having power law $P(f) \approx f^{-\beta}$. There is a quite strict relationship between β and the correlation of the extinction probability as evident from the fact that starting with white noise ($\beta=0$) the extinction probabilities show also a statistics close to white noise. This is due to the fact that for uncorrelated noise the population

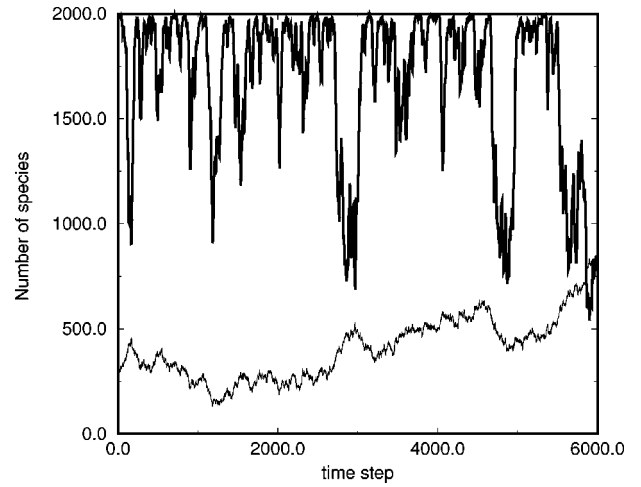


FIG. 2. The total number of species resulting from the model described by Eq. (1) subject to a brown time series, $\beta=2$ (thick line). The time series is reported in the lower curve with a thin line (it has been multiplied by an appropriate constant for potting purposes). $N_{\text{max}}=2000$, $\lambda=0.1$.

cannot suffer a continuous trend towards a given direction (increasing or decreasing E_t) and will always be close to equilibrium. The case $\beta=1$ begins to reveal a more organized pattern of the extinction probabilities that becomes very evident for brown noise, $\beta=2$. In the latter case some periods of time characterized by high extinction probability are due to a continuous trend of the variable E_t that makes the system unable to keep the internal variable I_t close to E_t . It is essential for the time series of the extinction probability to be colored, that the variance of E_t is larger than the product of the maximum jump size and the mutation probability, $\sigma\pi$, otherwise we observe a response for p_{ext} closer to white noise.

To complete the model we calculate the total number of species N resulting from such a distribution of the extinction probability. We use at each step the equation $N_{t+\delta t} = N_t + \delta t(dN/dt)$ with

$$\frac{dN}{dt} = -p_{\text{ext}}N_t + \lambda(N_{\text{max}} - N_t), \quad (1)$$

where p_{ext} is extracted from the previous calculation, λ^{-1} is the time scale of recovery of species after an extinction and N_{max} is the maximum number of species allowed. Figure 2 reports the number of species as a function of time as calculated from Eq. (1). The episodes of strong extinction are related to marked variations in the time series E_t (also plotted in the same figure) and in particular to a constantly increasing (or decreasing) value of E_t . Due to the finite value of σ_I representing the limited capability of mutating and migrating the species are not able to follow the new conditions. The continuous trend towards increase or decrease of E_t , characteristic of colored noise, may thus drive the population progressively out of the optimum.

In Fig. 3 we report the value of the exponent found for the extinction probabilities α as a function of the exponent of the environmental variable E_t , β . The plot shows a marked relation between the two quantities. In the same figure we have also reported the statistics of extinction calculated from Eq. (1) as $(N_{t+\delta t} - N_t)/N_t$. This is a quantity more similar to the one effectively measured in the fossil record, when one deals

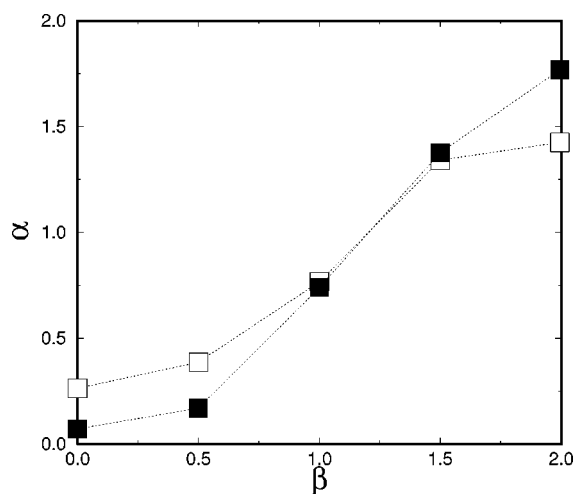


FIG. 3. The relation between the power law of the external noise E_t , β with the one characterizing the response of the model, α . With full symbols we report the statistics from the extinction probability and with empty symbols the one from the extinction fraction as calculated from Eq. (1).

with species present in a given stratigraphic sequence and not directly with probabilities; not surprisingly the two exponents are found to be close to each other. Figure 3 shows that the exponent related of the extinction statistics can in the model be related directly to the one of the time series. Present data from the fossil record seem to favor an exponent α close to one [4]. In the model's view this implies that the environmental noise should have an exponent at least larger than one. On the other hand, the presence in nature of several varying environmental quantities with possibly different exponents and also periodical behavior will in general affect the statistics of extinctions.

Finally, we would like to further comment on mass extinctions [12] also proposed as resulting from an extreme response of species communities to nonlinear effects ruling species interactions [4]. If interspecies competition can in principle explain local extinction events and their $1/f$ char-

acter, its capability to account also for global extinctions is more problematic without considering also environmental changes or at least a sort of increase in the ecological stresses. Since most species occupy limited regions due to the boundaries imposed by geographical and ecological constraints, the extinction avalanches triggered by species competition could at most propagate only through an area S of that order, at odds with the world-wide character of mass extinctions. Also the number of species involved would be limited by S with a number fraction of the order $f \sim (S/C)^\alpha$, where C is an area of continental size or larger and α an exponent between 0.2 and 0.4 [13]. We estimate in this way that interspecies competition can lead to a disappearance of a fraction less than 10% of the species of a biogeographical region. A second barrier to global avalanches is ecological rather than geographical. Mass extinctions have involved organisms with distant ecologies (marine and terrestrial for example) while presumably interspecies interactions would trigger contemporary extinctions of organisms with close ecologies. This is the main reason why external causes are usually invoked to explain mass extinctions [12]. Regarding statistical approaches, we mention that an interesting mathematical model for mass extinctions has appeared in the literature [14].

Concluding, we have considered a model of a mutating and migrating "population" subject to external disturbance in the form of colored noise. The basic ingredient is the finite time that the population needs to adapt to the new changing conditions imposed by the external environment. In brief, the correlated statistics of extinctions in the model mirrors the one of the external disturbance. We have seen that in the model, correlated noise is essential to produce bursts of extinction. It will be interesting to follow the future research on the correlations between the environmental fluctuations and the extinction episodes in the fossil record.

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