

## EXTINCTION STATISTICS IN $N$ RANDOM INTERACTING SPECIES\*

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A randomly interacting  $N$ -species Lotka–Volterra system in the presence of a Gaussian multiplicative noise is analyzed. The investigation is focused on the role of this external noise into the statistical properties of the extinction times of the populations. The distributions show a Gaussian shape for each noise intensity value investigated. A monotonic behavior of the mean extinction time as a function of the noise intensity is found, while a nonmonotonic behavior of the width of the extinction time probability distribution characterizes the dynamical evolution.

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### 1. Introduction

Generalized Lotka–Volterra equations have been used in recent years to describe the dynamics of various kind of population species, which are main components in complex ecosystems [1–6]. To understand the complex behavior of such ecosystems is crucial to analyze the role played by the external noise on the dynamics. It has become increasingly evident that nonlinearity and noise play an important role in such complex dynamics. Recently, in fact, noise-induced effects in population dynamics, such as pattern formation, stochastic resonance, noise delayed extinction, quasi periodic oscillations, *etc.*, have been investigated with increasing interest [8–14]. Complex ecological systems evolve towards the equilibrium states through the slow process of nonlinear relaxation, which is strongly dependent on the random

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interaction between the species, the initial conditions and the random interaction with environment. One of the open problems of such ecosystems is the investigation of the time scales of extinction and survival of the species and their related statistics. Various factors affecting extinction such as migration, chaos, interaction between species, spatial synchronization, *etc.*, have been discussed in the literature [15–18]. However, there is lack of investigation on the role of external noise on the extinction process, which is the main focus of this paper. The mathematical model used to analyze the dynamics of  $N$  biological species, with spatially homogeneous densities, is the generalized Lotka–Volterra system. We consider a Malthus–Verhulst model for the self regulation mechanism and an external multiplicative noise source, taking the environment interaction into account [19, 20]. Within this model we analyzed the role of the noise in the statistical properties of the extinction times of the populations. Specifically a monotonic behavior of the mean extinction time as a function of the noise intensity is observed. The width of the distribution of the extinction times, however, has a nonmonotonic behavior as a function of the noise intensity.

## 2. The model

The dynamical evolution of our ecosystem composed by  $N$  interacting species in a noisy environment (climate, disease, *etc.*) is described by the following generalized Lotka–Volterra equations with a multiplicative noise, in the framework of Ito stochastic calculus [21]

$$dn_i(t) = \left[ \left( \left( \alpha + \frac{\varepsilon}{2} \right) - n_i(t) + \sum_{j \neq i} J_{ij} n_j(t) \right) dt + \sqrt{\varepsilon} dw_i \right] n_i(t), \quad (1)$$

where  $n_i(t) \geq 0$  is the population density of the  $i^{\text{th}}$  species at time  $t$  and  $i = 1, \dots, N$ . In Eq. (1), the first two terms describe the development of the  $i^{\text{th}}$  species without interacting with other species,  $\alpha$  is the growth parameter, and  $J_{ij}$  is the interaction matrix, which models the interaction between different species ( $i \neq j$ ). Here  $w_i$  is the Wiener process whose increment  $dw_i$  satisfy the usual statistical properties  $\langle dw_i(t) \rangle = 0$ , and  $\langle dw_i(t) dw_j(t') \rangle = \delta_{ij} \delta(t - t') dt$ . The interaction matrix  $J_{ij}$  has elements randomly distributed according to a Gaussian distribution with  $\langle J_{ij} \rangle = 0$ ,  $\langle J_{ij} J_{ji} \rangle = 0$ , and  $\sigma_j^2 = J^2/N$ . Our ecosystem contains, therefore, 50% of prey–predator interactions ( $J_{ij} < 0$  and  $J_{ji} > 0$ ), 25% competitive interactions ( $J_{ij} > 0$  and  $J_{ji} > 0$ ), and 25% symbiotic interactions ( $J_{ij} < 0$  and  $J_{ji} < 0$ ). We consider all species equivalent so that the characteristic parameters of the ecosystem are independent of the species. The formal solution of Eq. (1) is

$$n_i(t) = \frac{n_i(0) \exp \left[ \alpha t + \sqrt{\varepsilon} w_i(t) + \int_0^t dt' \sum_{j \neq i} J_{ij} n_j(t') \right]}{1 + n_i(0) \int_0^t dt' \exp \left[ \alpha t' + \sqrt{\varepsilon} w_i(t') + \int_0^{t'} dt'' \sum_{j \neq i} J_{ij} n_j(t'') \right]}, \quad (2)$$

where the term  $h_i(t) = \sum_{j \neq i} J_{ij} n_j(t)$  represents the influence of other species on the differential growth rate of the  $i^{\text{th}}$  population. The dynamical behavior of the  $i^{\text{th}}$  population depends on the time integral of the term  $h_i(t)$  and the time integral in the denominator of Eq. (2). By considering the deterministic dynamics (in the absence of external noise ( $\varepsilon = 0$ )), with a large number of interacting species (that is large interaction random matrix), we can assume that the term  $h_i(t)$  is Gaussian with zero mean and variance  $\sigma_{h_i}^2 = \sum_{j,k} \langle J_{ij} J_{ik} \rangle \langle n_j n_k \rangle = J^2 \langle n_i^2 \rangle$ , with  $\langle J_{ij} J_{ik} \rangle = \delta_{jk} \frac{J^2}{N}$ . In the absence of external noise, from the fixed-point equation  $n_i(\alpha - n_i + h_i) = 0$ , the stationary probability distribution of the populations is the sum of a truncated Gaussian distribution at  $n_i = 0$  (for  $n_i > 0$ ) and a delta function for the extinct species (for  $n_i = 0$ ). The initial values of the populations  $n_i(0)$  have also Gaussian distribution with mean value  $\langle n_i(0) \rangle = 1$ , and variance  $\sigma_{n(0)}^2 = 0.03$ . The interaction strength  $J$  determines two different dynamical behaviors of the ecosystem. Above a critical value  $J_c = 1.1$ , the system is unstable and at least one of the populations diverges. Below  $J_c$  the system is stable and asymptotically reaches an equilibrium state. The equilibrium values of the populations depend both on their initial values and on the interaction matrix. If we consider a quenched random interaction matrix, the ecosystem has a great number of equilibrium configurations, each one with its attraction basin. For an interaction strength  $J=1$  and an intrinsic growth parameter  $\alpha=1$  we obtain:  $\langle n_i \rangle = 1.4387$ ,  $\langle n_i^2 \rangle = 4.514$ , and  $\sigma_{n_i}^2 = 2.44$ . These values agree with that obtained from numerical simulation of Eq. (1).

The statistics of the species extinction has been analyzed using the mean extinction time  $\langle t_m \rangle$ , defined as

$$\langle t_m \rangle = \frac{1}{N_{\text{exp}}} \sum_{i=1}^{N_{\text{exp}}} t_m, \quad (3)$$

and its variance

$$\sigma^2 = \langle t_m^2 \rangle - \langle t_m \rangle^2. \quad (4)$$

Here  $\langle t_m \rangle$  is an ensemble average ( $N_{\text{exp}}$  is the number of simulative experiments),  $t_m$  is the average extinction time over the number of populations  $N$

$$t_m = \frac{1}{N} \sum_{i=1}^N t_{i,m}, \quad (5)$$

and  $t_{i,m}$  is the extinction of the  $i$ -th population in the  $m$ -th experiment.

### 3. Results and comments

The parameters used in our simulation are:  $\alpha = 1.2$ ,  $J = 1$ ,  $\sigma_J^2 = 0.005$ ,  $N = 400$ . The number of simulative experiments is  $N_{\text{exp}} = 1000$ , and the initial values of the average population and its standard deviation are:  $\langle n_i(0) \rangle = 1$ ,  $\sigma_{n_i(0)}^2 = 0.03$ . The dynamics of the various species are different even if they are equivalent according to the parameters in the dynamical Eq. (1). However, to change the species index by fixing the random matrix or to change the random matrix by fixing the species index should be equivalent as regards the asymptotic dynamical regime.

In the presence of the external noise ( $\varepsilon \neq 0$ ) we calculate the long time probability distribution of the species density for different values of the noise intensity. These are shown in Fig. 1.

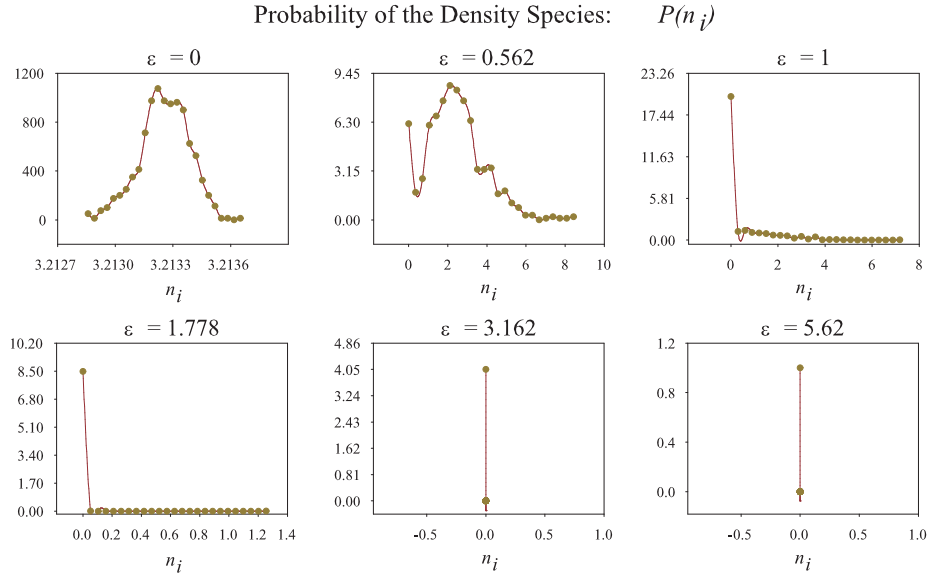


Fig. 1. Long time probability distribution of the species densities for different external noise intensities  $\varepsilon$ . Namely  $\varepsilon = 0, 0.562, 1, 1.778, 3.162, 5.62$ . Around the value  $\varepsilon = 0.562$  the distribution becomes asymmetric, and for  $\varepsilon > 1.778$ , all the species are extinct.

For increasing external noise intensity we obtain a larger probability distribution with a lower maximum (see the different scales in Fig. 1 for different noise intensity values). The distribution is asymmetric for  $\varepsilon = 0.562$  and tends to become a truncated delta function around the zero value ( $P(n_i) \rightarrow \delta(n_i)$  for  $n_i \geq 0$ , and  $P(n_i) = 0$  for  $n_i < 0$ ), for further increasing noise intensity. Specifically for high values of noise intensity (namely

for  $\varepsilon > 1.778$ ) we strongly perturb the population dynamics, and because of the presence of an absorbing barrier at  $n_i = 0$  [19], we obtain quickly the extinction of all the species. To confirm this picture we calculate the time evolution of the average number of extinct species for different noise intensities. This time behavior is shown in Fig. 2. We see that this number increases with noise intensity, obtaining a rapid transient dynamics of the system towards the extinction final state for  $\varepsilon \geq 1.778$ . This means that the species rapidly die and the probability distribution of the species density confines accordingly.

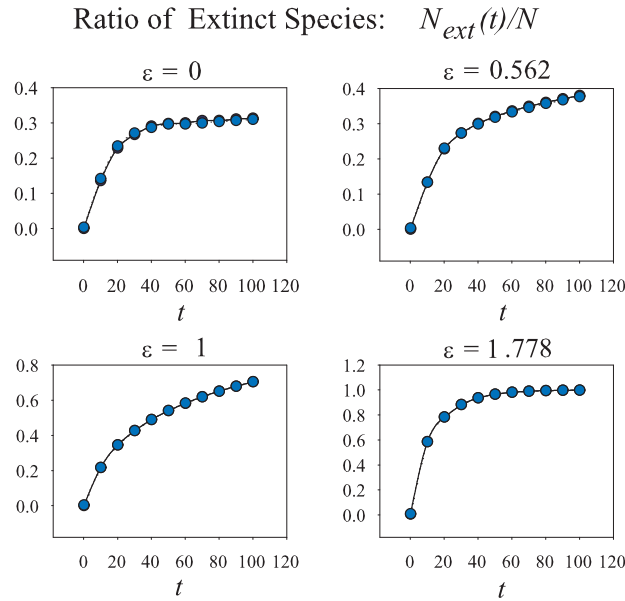


Fig. 2. Time evolution of the normalized number of the extinct species for different noise intensities  $\varepsilon$ . Namely:  $\varepsilon = 0, 0.562, 1, 1.778$ .

In the following Fig. 3 we show the probability distribution function (PDF) of the extinction times of the species. The shape of the distribution is Gaussian in the deterministic regime ( $\varepsilon = 0$ ) and in the presence of the external noise ( $\varepsilon \neq 0$ ). For low noise intensities the probability distribution becomes larger and lower until reaches the value of  $\varepsilon = 1$ . After this value of noise intensity the distribution becomes narrow and higher. The mean extinction time, which is easily visible from the figure because of the Gaussian shape distribution, decreases monotonically with increasing noise intensity. In this figure it is shown a well defined extinction time windows of the species, moving towards the absorbing barrier at  $n_i = 0$ , with increasing noise intensity.

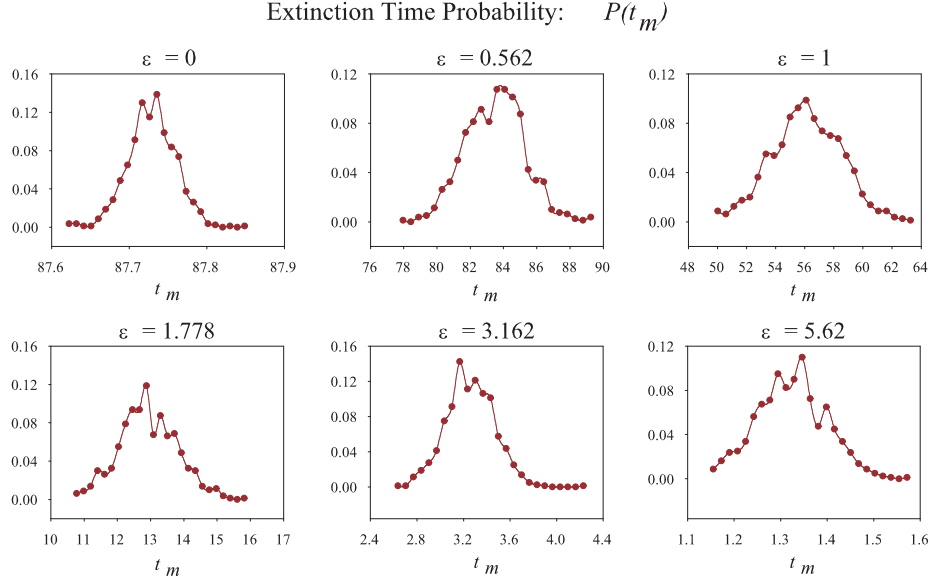


Fig. 3. Probability distribution function of the extinction times of the species, for different values of the noise intensity. Namely:  $\varepsilon = 0, 0.562, 1, 1.778, 3.162, 5.62$ . All the PDFs show a Gaussian shape distribution.

This behavior is due to the presence of the external noise and the absorbing barrier. In fact, in the deterministic case ( $\varepsilon = 0$ ), the Gaussian distribution of the extinction times is due only to the random interaction matrix. The characteristic values of the distribution, that is the mean and the variance, depend on the choice of the parameters of the model, that is the growth parameter  $\alpha$ , the interaction strength  $J$  and the initial conditions. A small amount of noise forces the system to sample more of the available range in the parameter space and therefore moves lightly the system towards the extinction. The average extinction time at  $\varepsilon = 0.562$  is less than that in the absence of external noise. This enlargement and lowering of the PDF continues until the noise intensity reaches the value of the interaction strength  $J = 1$ . After that the external noise prevails on the interaction matrix term and the extinction process proceeds quickly because of the presence of the absorbing barrier at  $n_i = 0$  (see Eq. (1)). Almost all the species extinguish in short times around a very low mean extinction time. At  $\varepsilon = 3.162$ , for example,  $\langle t_m \rangle \sim 3.3$ . Increasing the noise intensity ( $\varepsilon > 1$ ) the PDF becomes narrower and, therefore, higher.

As can be seen in Fig. 3 for  $\varepsilon = 3.162$  and  $\varepsilon = 5.62$  the species extinction happens in few time units, so that the probability of density species vanishes for the same values (see Fig. 1).

This peculiar behavior of the PDF of extinction times gives rise to the nonmonotonic behavior of the variance of the same quantity as a function of the noise intensity. This is shown in the following Fig. 4.

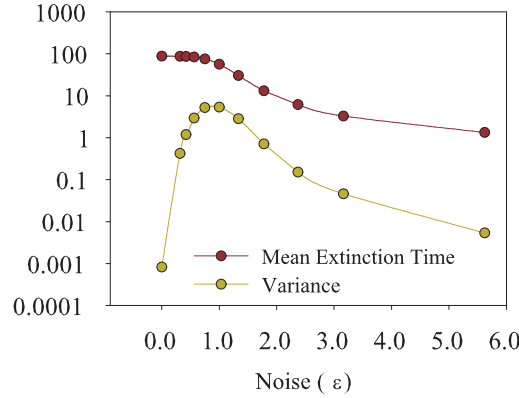


Fig. 4. Mean extinction time and variance as a function of the noise intensity  $\varepsilon$ . The variance shows a nonmonotonic behavior with a maximum at  $\varepsilon \simeq 1$  and very low values at higher noise intensities.

From this figure, the maximum of the variance at the noise intensity  $\varepsilon \simeq 1$  and the very small values of the variance at high noise intensities, are clearly visible. In the same figure the monotonic behavior of the mean extinction time  $\langle t_m \rangle$  is shown. Calculation have been repeated for different number of populations, namely:  $N = 100, 200, 300, 400$ . In all the calculations the qualitative behaviors of the mean extinction time and its variance are the same than those reported in Fig. 4.

We did not reveal any power law decay for the probability distribution of extinction times as found in previous investigations [16].

#### 4. Conclusions

The analysis of the dynamics of ecosystem composed by  $N$  random interacting species has been performed in the presence of multiplicative noise. The probability density of the extinction time of the species ( $P(t)$ ) has been evaluated for various noise intensities. The extinction times  $t_m$ s are Gaussian distributed with a mean value monotonically decreasing as a function of the noise intensity. The variance of the extinction times shows a nonmonotonic behavior, which characterizes the transient dynamics of the  $N$  random interacting species model.

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