NONLINEAR RELAXATION
IN
POPULATION DYNAMICS

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Abstract
We analyze the nonlinear relaxation of a complex ecosystem composed of many interacting species. The ecological system is described by generalized Lotka-Volterra equations with a multiplicative noise. The transient dynamics is studied in the framework of the mean field theory and with random interaction between the species. We focus on the statistical properties of the asymptotic behaviour of the time integral of the i-th population and on the distribution of the population and of the local field.

1. INTRODUCTION
Systems of interacting biological species evolve through a dynamical complex process that can be conveniently described, within relatively short time scales, by generalized Lotka-Volterra equations. The multiplicity of these equations complicates their analytical in-
vestigation, especially in the case of a great number of interacting species. Nevertheless some analytical approximation for the mean field interaction between the species as well as numerical simulations give some insight into the behaviour of complex ecosystems. Basic elements of a Lotka-Volterra model are the growth parameter and the interaction parameter. For a large number of interacting species, it is reasonable, as a phenomenological approach, to choose these parameters at random from given probability distributions. Within this type of representation, the dynamics of coevolving species can be characterized by statistical properties over different realizations of parameter sets. Though the generalized Lotka-Volterra model has been explored in detail, it seems that a full characterization, either deterministic or statistical, of the conditions under which a population extinguishes or survives in the competition process has not been achieved.

In this paper we analyze the role of the noise on the transient dynamics of the ecosystem of many interacting species in the presence of an absorbing barrier, i.e. extinction of the species. Two type of interaction between the species are considered: (a) mean field interaction, and (b) random interaction. We focus on the asymptotic behaviour of the time integral of the \(i\)-th population and on the distributions of the population and of the local field, which is the total interaction of all species on the \(i\)-th population.

By introducing an approximation for the time integral of the average species concentration \(M(t)\) we obtain analytical results for the transient behaviour and the asymptotic statistical properties of the time average of the \(i\)-th population. We find that for a very large number of interacting species the statistical properties of the time average of the \(i\)-th population process are determined asymptotically from the statistical properties of the Wiener process. At the critical point and around the stability-instability transition, for mean field interaction, the system goes from a purely long time tail behaviour (namely \(M(t) \sim \sqrt{t}\)) to a new long time modified regime \(M(t) \sim \sqrt{t} e^{\sqrt{t}}\). Specifically for random interaction we find that the local field and the cavity field, which is the total interaction of all species on the \(i\)-th population when this population is absent, are different in absence of external noise while overlap quite well in the presence of the noise. This behaviour, which is very different from the analogue spin glasses problem in statistical mechanics, is reminiscent of a phase transition phenomenon. It suggest that, because all population are positive and can grow during the dynamical process of the ecosystem, each population play an important role on the total interaction between the species.

The paper is organized as follows. In the next section we describe the model. The mean field and the random interactions are considered in section 3 and 4. Our results are discussed in section 5.

2. THE MODEL

We consider an N-species generalization of the usual Lotka-Volterra system with a Malthus-Verhulst modelization of the self regulation processes for a fully connected ecological network. Therefore the Ito stochastic differential equation describing the dynamical evolution of the ecosystem is

\[
\begin{align*}
  dn_i(t) & = \left[ \left( \gamma + \frac{\varepsilon}{2} \right) - n_i(t) + \sum J_{ij} n_j(t) \right] n_i(t) dt + \sqrt{\varepsilon} n_i(t) dw_i, & i = 1, ..., N
\end{align*}
\]
where \( n_i(t) \geq 0 \) is the number of elements of the \( i \)-th species. In Eq. (1) \( \gamma \) is the growth parameter, the interaction matrix \( J_{ij} \) modelizes the interaction between different species \( (i \neq j) \) and \( w_i \) is the Wiener process whose increment \( dw_i \) satisfies the usual statistical properties

\[
< dw_i(t) > = 0; \quad < dw_i(t) dw_j(t') > = \delta_{ij} \delta(t - t') dt.
\]

(2)

Our ecosystem is composed of \( N = 1000 \) species. We consider all species equivalent so that the characteristic parameters of the ecosystem are independent of the species. The random interaction with the environment (climate, disease, etc...) is taken into account by introducing a multiplicative noise in the Eq. (1). The solution of the dynamical equation Eq. (1) is given by

\[
n_i(t) = n_i(0) \exp \left[ \delta t + \sqrt{\epsilon} w_i(t) + \int_0^t dt' \sum_{j \neq i} J_{ij} n_j(t') \right]
\]

\[
1 + \gamma n_i(0) \int_0^t dt' \exp \left[ \delta t' + \sqrt{\epsilon} w_i(t') + \int_0^{t'} dt'' \sum_{j \neq i} J_{ij} n_j(t'') \right].
\]

(3)

We consider two different types of interaction between the species: (a) a mean field approximation with a symbiotic interaction between the species; (b) a random interaction between the species with different types of mutual interactions: competitive, symbiotic and prey-predator relationship.

### 3. MEAN FIELD APPROXIMATION

We consider a mean field symbiotic interaction between the species. As a consequence the growth parameter is proportional to the average species concentration

\[
\sum_{j \neq i} J_{ij} n_j(t) = J \frac{1}{N} \sum_j n_j(t) = J m(t),
\]

(4)

and the stochastic differential equation Eq. (1) becomes

\[
dn_i = \left[ \left( J m + \gamma + \frac{\epsilon}{2} \right) n_i - n_i^2 \right] dt + \sqrt{\epsilon} n_i dw_i.
\]

(5)

In the limit of a large number of interacting species the stochastic evolution of the system is given by the following integral equation

\[
M(t) = \frac{1}{N} \sum_i \ln \left( 1 + n_i(0) \int_0^t dt' e^{J m(t') + \gamma t' + \sqrt{\epsilon} w_i(t')} \right),
\]

(6)

where

\[
M(t) = \frac{1}{N} \sum_i \int_0^t dt' n_i(t') = \int_0^t dt' m(t').
\]

(7)

is the time integral of the site population concentration average. We introduce an approximation of Eq. (6) which greatly simplifies the noise affected evolution of the system and allows us to obtain analytical results for the population dynamics. We note that in this approximation the noise influence is taken into account in a nonperturbative way, and that the statistical properties of the time average process \( M(t) \) are determined asymptotically from
the statistical properties of the process $w_{\text{max}}(t) = \sup_{0 < t' < t} w(t')$, where $w$ is the Wiener process. Starting from the following approximated integral equation for $M(t)$

$$M(t) \simeq \frac{1}{N} \sum_i \ln \left( 1 + n_i(0) e^{\sqrt{\epsilon} w_{\text{max}}} \int_0^t dt' e^{JM(t') + \gamma t'} \right)$$

(8)

it is possible to analyze the role of the noise on the stability-instability transition in three different regimes of the nonlinear relaxation of the system: (i) towards the equilibrium population ($\gamma > 0$), (ii) towards the absorbing barrier ($\gamma < 0$), (iii) at the critical point ($\gamma = 0$). Specifically at the critical point we obtain for the time average process $M(t)/t$ as a dominant asymptotic behaviour in the stability region (namely when $J < 1$)

$$\frac{M(t)}{t} \simeq \left( \frac{1}{1 - J} \right) \sqrt{\frac{2\epsilon}{\pi}} \frac{1}{\sqrt{t}}$$

(9)

and in the instability region (namely when $J > 1$)

$$\frac{M(t)}{t} \simeq e^{\langle \ln(n_i(0)) \rangle} \sqrt{\frac{2\epsilon}{\pi}} \exp \left[ \frac{\sqrt{2\epsilon}}{\pi} \right]$$

(10)

We obtain for the case (i) an explicit expression of the transition time $t_c$ as a function of the noise intensity ($\epsilon$), the initial population distribution ($n_i(0)$) and the parameters of the system ($\gamma, J$)

$$t_c \simeq \frac{1}{\gamma} \left\{ \frac{\epsilon}{2\pi \gamma} + \ln \left( 1 + \left( \frac{\gamma}{(J - 1)} \right) e^{-\langle \ln(n_i(0)) \rangle} \right) \right\}^{1/2} - \sqrt{\frac{\epsilon}{2\pi \gamma}}$$

(11)

For the cases (ii) and (iii) we obtain two implicit expressions in terms of exponential and error functions of the same quantities: $t_c, \epsilon$ and the system parameters. The transition time increases from $\gamma > 0$ to $\gamma < 0$ according to the following inequality

$$(t_c)_{\gamma < 0} > (t_c)_{\gamma = 0} > (t_c)_{\gamma > 0}.$$ (12)

This means that when the interaction between the species prevails over the resources, the presence of a hostile environment ($\gamma < 0$) causes a late start of the divergence of some population (i.e. the instability). The noise forces the system to sample more of the available range in the parameter space and therefore moves the system towards the instability. The effect of the noise is to make unstable the system earlier than in the deterministic case ($\epsilon = 0$). If we raise the intensity of the noise and keep fixed the initial distribution, we obtain the same effect of the enhancement of the variance of the Gaussian initial distribution of the population for moderate values of noise intensity (namely $\epsilon = 0.1$). For high values of noise intensity (namely $\epsilon = 1$) we strongly perturb the population dynamics and because of the presence of an absorbing barrier we obtain quickly the extinction of the populations.

4. RANDOM INTERACTION

The interaction between the species is assumed to be random and it is described by a random interaction matrix $J_{ij}$, whose elements are independently distributed according to a Gaussian distribution.
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\[ P(J_{ij}) = \frac{1}{\sqrt{2\pi\sigma_J^2}} \exp \left[ -\frac{J_{ij}^2}{2\sigma_J^2} \right], \quad \sigma_J^2 = \frac{J^2}{N}, \]  

(13)

where \( J \) is the interaction strength and

\[ < J_{ij} > = 0, \quad < J_{ij}J_{ji} > = 0. \]  

(14)

With this asymmetric interaction matrix our ecosystem contains 50% of prey-predator interactions (namely \( J_{ij} < 0 \) and \( J_{ji} > 0 \)), 25% competitive interactions (\( J_{ij} < 0 \) and \( J_{ji} < 0 \)) and 25% symbiotic interactions (\( J_{ij} > 0 \) and \( J_{ji} > 0 \)). The initial values of the populations \( n_i(0) \) have also Gaussian distribution

\[ P(n) = \frac{1}{\sqrt{2\pi\sigma_n^2}} \exp \left[ -\frac{(n - < n >)^2}{2\sigma_n^2} \right], \quad \sigma_n^2 = 0.01, \text{ and } < n >= 1. \]  

(15)

The strength of interaction between the species \( J \) determines two different dynamical behaviours of the ecosystem. Above a critical value \( J_c \) the system is unstable, this means that at least one of the populations diverges. Below the critical interaction strength, the system is stable and reaches asymptotically an equilibrium state. For our ecosystem this critical value is approximately \( J = 1.1 \). 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 vanishing noise (\( \epsilon = 0 \)), the steady state solutions of Eq.(16) are obtained by the fixed-point equation

\[ \gamma - n_i + h_i n_i = 0 \]  

(16)

where

\[ h_i = \sum_j J_{ij} n_j(t) \]  

(17)

is the local field. For a great number of interacting species we can assume that the local field \( h_i \) is Gaussian with zero mean and variance \( \sigma_{h_i}^2 = < h_i^2 > = J^2 < n_i^2 > \)

\[ P(h_i) = \frac{1}{\sqrt{2\pi\sigma_{h_i}^2}} \exp \left[ -\frac{h_i^2}{2\sigma_{h_i}^2} \right] \]  

(18)

The solutions of Eq.(16) are

\[ n_i = 0, \text{ i.e. extinction} \]  

(19)

and

\[ n_i = (\gamma + h_i)\Theta(\gamma + h_i), \quad n_i > 0, \]  

(20)

where \( \Theta \) is the Heaviside unit step function. From this equation and applying the self consistent condition we can calculate the steady state average population and its variance. Specifically we have...
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\[
< n_i > = \langle (\gamma + h_i) \Theta(\gamma + h_i) \rangle = \frac{1}{\sqrt{2\pi}\sigma_{h_i}^2} \exp \left[ \frac{\gamma^2}{2\sigma_{h_i}^2} \right] + \frac{\gamma \sqrt{2\sigma_{h_i}^2}}{\sqrt{2\pi}} \left( 1 + erf \left( \frac{\gamma}{\sqrt{2\sigma_{h_i}^2}} \right) \right),
\]

(21)

and

\[
< n_i^2 > = \langle (\gamma + h_i)^2 \Theta^2(\gamma + h_i) \rangle = \left[ \frac{\gamma^2 + \sigma_{h_i}^2}{2} \right] \left( 1 + erf \left( \frac{\gamma}{\sqrt{2\sigma_{h_i}^2}} \right) \right) + \frac{\gamma^2 \sigma_{h_i}^2}{\sqrt{2\pi}} \exp \left[ \frac{\gamma^2}{2\sigma_{h_i}^2} \right].
\]

(22)

For an interaction strength \( J = 1 \) and an intrinsic growth parameter \( \gamma = 1 \) we obtain: \( < n_i > = 1.4387, < n_i^2 > = 4.514, \) and \( \sigma_{n_i}^2 = 2.44. \) These values are in good agreement with those obtained from numerical simulation of Eq. (1). The choice of this particular value for the interaction strength, based on a preliminary investigation on the stability-instability transition of the ecosystem, ensures that the ecosystem is stable.

The stationary probability distribution of the populations is the sum of a delta function and a truncated Gaussian

\[
P(n_i) = n_{ei} \delta(n_i) + \Theta(n_i) \frac{\exp \left[ -\frac{(n_i - n_{i0})^2}{2J^2\sigma_{h_i}^2} \right]}{\sqrt{2\pi}J^2\sigma_{n_i}^2}.
\]

(23)

In Fig. (1) we report the stationary probability distribution of the population densities, without the extinct species, in comparison with the computer simulations for systems with \( N = 1000 \) species and for an interaction strength \( J = 1, \) and \( \gamma = 1. \)

As in the previous case we focus on the statistical properties of the time integral of the \( i \)-th population \( N_i(t) \)

\[
N_i(t) = \int_0^t dt' n_i(t'),
\]

(24)

in the asymptotic regime. From Eq. (3) we have

\[
N_i(t) = \ln \left[ 1 + n_i(0) \int_0^t dt' \exp \left[ \gamma t' + \sqrt{\epsilon} w_i(t') + \sum_{J \neq i} J_{ij} N_j(t') \right] \right],
\]

(25)

In Eq. (25) the term \( \sum_j J_{ij} N_j \) gives the influence of other species on the differential growth rate of the time integral of the \( i \)-th population and represents a local field acting on the \( i \)-th population.

\[
h_i = \sum_j J_{ij} N_j(t) = J n_{ei}.
\]

(26)

We use the same approximation of the Eq. (8) and, after differentiating, we get the asymptotic solution of Eq. (25).
where \( w_{\text{max}_i}(t) = \sup_{0 < t' < t} w(t') \) and \( \eta_{\text{max}_i}(t) = \sup_{0 < t' < t} \eta(t') \). The Eq. (27) is valid for \( \gamma \geq 0 \), that is when the system relaxes towards an equilibrium population and at the critical point. Evaluating Eq. (27) for \( \gamma \geq 0 \), after making the ensemble average, we obtain for the time average of the \( i \)-th population \( \bar{N}_i \)

\[
\langle \bar{N}_i \rangle \simeq \frac{1}{t} \left[ N_w \sqrt{\epsilon \ell} + \ln t + \langle \ln [n_i(o)] \rangle \right], \quad \gamma = 0,
\]

and

\[
\langle \bar{N}_i \rangle \simeq \frac{1}{t} \left[ N_w \sqrt{\epsilon \ell} + (\gamma + N_\eta) + \langle \ln \left[ \frac{n_i(o)}{\gamma} \right] \rangle \right], \quad \gamma > 0,
\]

where \( N_w \) and \( N_\eta \) are variables with a semi-Gaussian distribution \( \mathbb{F} \) and \( N_\eta \) must be determined self-consistently from the Eq. (26). These asymptotic behaviours are consistent with those obtained using a mean field approximation. We obtain in fact the typical long time

![Figure 1: The stationary probability distribution (Eq.(23)), without the extinct species, in comparison with the histograms arising from numerical simulations (open circles). The system parameters are: \( N = 1000 \) species, \( J = 1 \) and \( \gamma = 1 \).](image)
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tail behaviour \((t^{-1/2})\) dependence, which characterize nonlinear relaxation regimes when \(\gamma \geq 0\). Besides the numerical results confirm these analytical asymptotic behaviours of \(\bar{N}_i\). When the system relaxes towards the absorbing barrier \((\gamma < 0)\) we get from Eq. (25) in the long time regime

\[
\langle \bar{N}_i \rangle \simeq \frac{1}{t} \left[ \ln(n_i(0)) + \ln \left[ \int_0^t dt' e^{\gamma t' + \sqrt{\tau} w_i(t') + j \eta_i(t')} \right] \right].
\]  

(30)

In this case the time average of the \(i\)-th population \(\langle \bar{N}_i \rangle\) is a functional of the local field and the Wiener process, and it depends on the history of these two stochastic processes.

We have also analyzed the dynamics of the ecosystem when one species is absent. Specifically we considered the cavity field, which is the field acting on the \(i\)-th population when this population is absent. In Fig.(2) we report the probability distributions of the local and of the cavity fields obtained by our simulations after a time \(t = 100\) (expressed in arbitrary units) in absence of external noise and for two species (namely species 1 and 33). We note that the probability distributions of the cavity fields differ substantially from that of the local fields for the same species unlike the spin glasses dynamics, where the two fields coincide. We calculate also the same quantities in the presence of the external noise. The results of our simulations are reported in Figs (3) and (4). The effect of the external noise

![Figure 2: The probability distribution of the cavity fields \(P(h_c)\) (open circles) and of the local fields \(P(h_l)\) (black circles) for the species 1 and 33 after time \(t = 100\). The system parameters are the same of Fig.(1).](image)
is to overlap the two fields in such a way that for some particular species they coincide. Specifically this happens for the species 1 (see Fig. (3)). For the species 33 we obtain a partial overlap (see Fig.(4)).

We found this interesting phenomenon, which is reminiscent of the phase transition phenomenon, for some populations. The main reasons for this behaviour are: (i) all the populations are positive; (ii) the particular structure of the attraction basins of our ecosystem; (iii) the initial conditions, which differ for the value of one population, belong to different attraction basins. Some populations have a dynamical behaviour such that after a long time they influence in a significant way the dynamics of other species. While in the presence of noise all the populations seem to be equivalent from the dynamical point of view. We found also that for strong noise intensity (namely $\epsilon = 1$) all species extinguish on a long time scale ($t \approx 10^6$ a. u.). Whether extinction occurs for any value of noise intensity or not is still an open question, because of time-consuming numerical calculations.

5. CONCLUSIONS

![Figure 3: The probability distribution $P(h_1)$ of the local (black circles) and of the cavity (open circles) fields for the species 1 after time $t = 100$, in the presence of external noise. The noise intensity is $\epsilon = 0.1$. The other system parameters are the same of Fig.(1).](image-url)
We studied a stochastic model of an ecosystem of $N$ interacting species. By means of an approximation of the integral equation, which gives the stochastic evolution of the system, we obtain analytical results reproducing very well almost all the transient. We investigate the role of the noise on the stability-instability transition and on the transient dynamics. For random interaction we obtain asymptotic behaviour for three different nonlinear relaxation regimes. We obtain the stationary probability distribution of the population, which is the sum of two contributions: (i) a delta function around $n = 0$ for the extinct species and (ii) a truncated Gaussian for the alive species. When we switch on the external noise an interesting phenomenon is observed: the local and the cavity fields, whose probability distributions are different in the absence of noise, coincide for some populations. This phenomenon can be ascribed to the peculiarity of the attraction basins of our ecosystem. We have also investigated the overlap between the asymptotic values of the populations and the eigenvector of the interaction matrix with the maximum eigenvalue and we have not found any ordering regime phenomenon like in the spin glasses system. A more detailed investigation concerning the probability distribution of the populations and the local fields in the presence of noise is the subject of work in progress.

![Figure 4: The probability distribution $P(h_{33})$ of the local (black circles) and of the cavity (open circles) fields for the species 33 after time $t = 100$ in the presence of external noise. The noise intensity is $\epsilon = 0.1$. The other system parameters are the same of Fig.(1).](image-url)
6. ACKNOWLEDGMENTS

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7. REFERENCES

1. Yu. M. Svirezhzv and D. O. Logofet, *Stability of Biological Communities* (Mir, Moscow, 1983).
2. S. Ciuchi, F. de Pasquale and B. Spagnolo, *Phys. Rev.* E54 (1996) 706.
3. F. de Pasquale and B. Spagnolo, in *Chaos and Noise in Biology and Medicine*, ed. M. Barbi and S. Chillemi (World Scientific, Singapore, 1998), p. 305.
4. M. A. Cirone, F. de Pasquale and B. Spagnolo, in *Nuclear and Condensed Matter Physics*, ed. A. Messina (AIP, New York, 2000), p. 365.
5. G. Abramson, *Phys. Rev.* E55 (1997) 785.
6. G. Abramson and D. H. Zanette, *Phys. Rev.* E57 (1998) 4572.
7. M. Mezard, G. Parisi and M. A. Virasoro, *Spin Glasses Theory and Beyond* (World Scientific Lect. Notes in Physics 9, Singapore, 1987), p. 65.