Noise-induced effects in population dynamics

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Abstract

We investigate the role of noise in the nonlinear relaxation of two ecosystems described by generalized Lotka–Volterra equations in the presence of multiplicative noise. Specifically we study two cases: (i) an ecosystem with two interacting species in the presence of periodic driving; (ii) an ecosystem with a great number of interacting species with random interaction matrix. We analyse the interplay between noise and periodic modulation for case (i) and the role of the noise in the transient dynamics of the ecosystem in the presence of an absorbing barrier in case (ii). We find that the presence of noise is responsible for the generation of temporal oscillations and for the appearance of spatial patterns in the first case. In the other case we obtain the asymptotic behaviour of the time average of the ith population and discuss the effect of the noise on the probability distributions of the population and of the local field.

1. Introduction

The description and analysis of interacting populations with a discrete number of individuals is a common subject in several branches of physics and other sciences (Giardina *et al* 2000). Real ecosystems present a complex behaviour, which is characterized by two peculiarities: the interactions between components are nonlinear and their environment is noisy.

The noise can induce nontrivial effects in physical and biological systems. The presence of a noise source in fact can modify in an unexpected way the behaviour of the corresponding deterministic evolution of the system. Well known examples are stochastic resonance (Gammaitoni *et al* 1998), resonant activation (Mantegna and Spagnolo 2000) and noise-enhanced stability phenomena (Agudov and Spagnolo 2001).

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The dynamics of interacting biological species can be successfully represented by means of a dynamical system with stochastic elements. In particular the population dynamics of complex ecosystems is well described by the generalized Lotka–Volterra equations. Within this model the study of interacting populations of only two or three species extracted from an ecosystem seems to be ecologically justified in a number of important cases, because the nonlinearity of the model reproduces the typical phenomenology of population dynamics (Bazykin 1998). An N-species generalization of the usual Lotka–Volterra model with a Malthus–Verhulst modellization of the self-regulation processes with multiplicative noise seems to be an useful tool to study the population dynamics of interacting species in a timescale much shorter than the evolution time (Cirone *et al* 2001).

For these reasons in this paper we shall study the nonlinear relaxation of two ecosystems described by generalized Lotka–Volterra equations in the presence of multiplicative noise, namely

- a system with two interacting species in the presence of periodic driving;
- a system with a great number of interacting species with random interaction matrix.

In the first case we consider a symmetric two-species competition stochastic model which is suitable, with some improvements, to explain the spatial–time behaviours obtained from experimental data of fish populations collected by the Interdisciplinary Group of Oceanography of the IRMA-CNR on the Mediterranean Sea. We analyse how the interplay between the noisy environment, the periodic modulation of the interaction parameter and the nonlinearity of the system can change the population dynamics in an unexpected way. We find that the presence of noise is responsible for the generation of temporal oscillations and for the appearance of spatial patterns.

In the second case we focus on the statistical properties of the time integral of the ith population and on the distribution of the population and of the local field. We obtain asymptotic behaviour for three different nonlinear relaxation regimes and the stationary probability distribution of the population in the presence and in the absence of external noise. This analysis allow us to estimate characteristic timescales for which the consideration of random fluctuations significantly changes the usual picture obtained from deterministic differential equations. Moreover some populations have a dynamical behaviour such that after a long time they influence in a significant way the dynamics of other species. Specifically we find that the local field and the cavity field, which is the total interaction of all species in the ith population when this population is absent, are very different in absence of noise, contrary to what we expected. These fields, however, overlap quite well in the presence of noise.

2. Two interacting species

2.1. The model

We consider a generalized Lotka–Volterra model of symmetric two-species competition with a Malthus–Verhulst modellization of the self-regulation processes. The abundance of populations in nature is sensitive to fluctuations of the external environment and to periodic variations of the temperature. The interaction with the noisy and nonstationary environment is therefore taken into account with the introduction of two terms into the model: (i) multiplicative noise and (ii) a periodic variation of the interaction parameter among the species. The relative equations are

$$\dot{x} = \alpha x(\beta - x - \gamma(t)y) + x\xi_x(t) \tag{1}$$

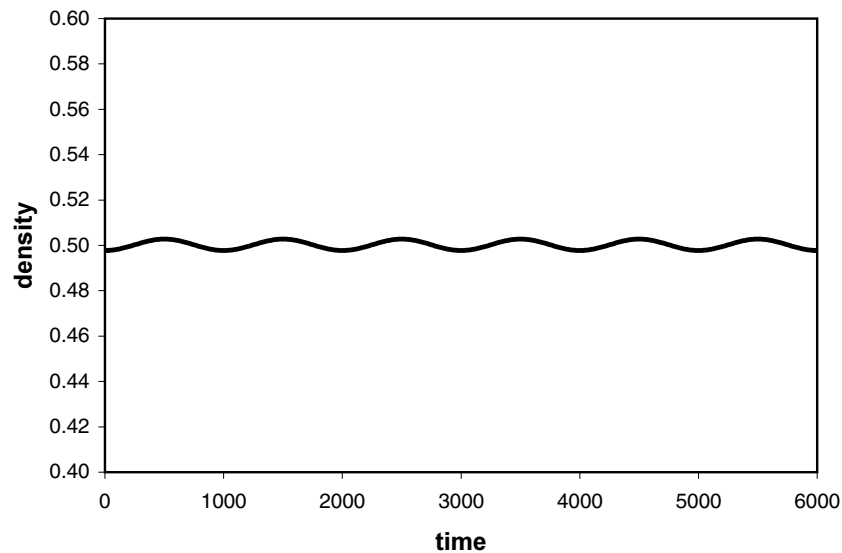$$\dot{y} = \alpha y(\beta - y - \gamma(t)x) + y\xi_y(t) \tag{2}$$

Figure 1. Time evolution of two competing populations in the absence of noise.

where x and y are the population densities, α is a coefficient which is proportional to the growth rate, β is the capacity of the ecological niche and $\gamma(t)$ modellizes the interactions among the species. The noise terms $\xi_i(t)$ are assumed to be Gaussian white-noise sources with zero mean and correlation function $\langle \xi_i(t)\xi_i(t+\tau)\rangle = \sigma\delta(\tau)\delta_{ij}$. To consider the effect of the periodic variations of the environment temperature on the abundances of populations we assume that the dynamics of the ecosystem is modulated through the interaction parameter $\gamma(t)$ as follows (Rinaldi *et al* 1993, Vilar and Solé 1998):

$$\gamma(t) = \beta + \delta + A\sin(\Omega t) \tag{3}$$

where the parameters δ, A and Ω are constants. In the absence of noise this functional form of the interaction parameter is a perturbation which moves the system periodically in time from a stable state (coexistence of the two species) to an unstable state (exclusion of one of the two species), depending on the value of the parameter δ. Specifically when $\delta > 0$ one of two species is eliminated (exclusion) while for $\delta < 0$ both species are present (coexistence).

2.2. Spatiotemporal patterns

We numerically integrate the stochastic differential equations (1) and (2), and we find that the presence of external multiplicative noise changes in a remarkable way the dynamics of the two species. In the absence of noise the result of the numerical solution of equations (1) and (2) is reported in figure 1. The values of the model parameter used for this simulation are $A = 0.1$, $\Omega = 2\pi \times 10^{-3}$, $\alpha = 1.0$, $\beta = 1.0$, $\delta = -0.01$.

We observe that the two species coexist and their evolution is in phase with the driving periodic external force. When we add the multiplicative noise we obtain a very interesting time behaviour (see figure 2), in which we observe (i) a transient behaviour with an enhancement of the temporal oscillation; (ii) anticorrelated oscillations of the two species, in such a way that, for particular values of the parameters, one species periodically predominates the other one; (iii) a random inversion of the temporal oscillations of the two species. These peculiarities of the temporal pattern are of course due to the presence of the noise.
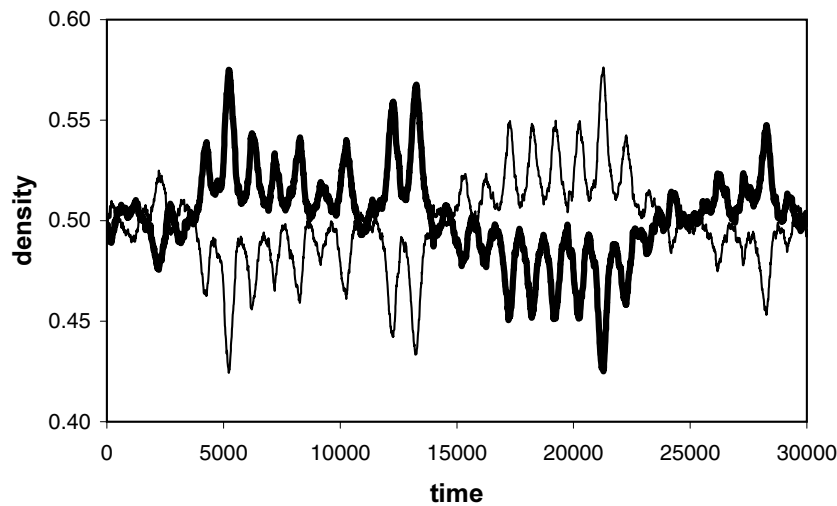
Figure 2. Time evolution of two competing populations in the presence of noise. The noise intensity is $\sigma = 10^{-6}$.

For appropriate values of the model parameters, namely $A = 0.2$, $\Omega = 0.035$, $\alpha = 1.0$, $\beta = 45.0$, $\delta = -0.45$, and with a noise intensity of $\sigma = 2$ we recover the qualitative time behaviour of the experimental data of some particular populations of the Mediteranean Sea: the foraminifera (Spagnolo *et al* 2001).

When we include in our model the spatial effects, new spatiotemporal patterns appear. These patterns, which are absent from the deterministic model, are due to the interplay between the noisy environment of the ecosystem and the spatial diffusion of the species. We take these effects into account by considering a discrete time evolution model, which is the discrete version of the equations (1) and (2) with diffusive terms, namely a couple map lattice (Kaneko 1992). These diffusive terms model the interaction between a site population with the four nearest neighbours. In this discrete model, spatial patterns arise when noise is present. In the deterministic time evolution we have a homogeneous spatial distribution of both populations. The results of our simulations for one species are shown in figure 3. The spatial pattern of the other species is anticorrelated with the first one. This means that each species prefers some spatial regions where the other species is absent. These peculiarities of the spatial patterns are the same as found by the Oceanography Group of the IRMA-CNR when they analysed the experimental data of small pelagians in the Mediterranean Sea (Spagnolo *et al* 2001). This means that our simple predictive model (equations (1) and (2)) can reproduce some of the basic features present in real ecosystems.

3. N interacting species

3.1. The model

Now we consider N interacting species of a fully connected ecological network. We use the same generalized Lotka–Volterra equations of the previous case but with random interaction among the species. The nonlinearity of the Lotka–Volterra equations complicates their analytical investigation, especially in the case of a great number of interacting species. Nevertheless some analytical approximation as well as numerical simulations give some
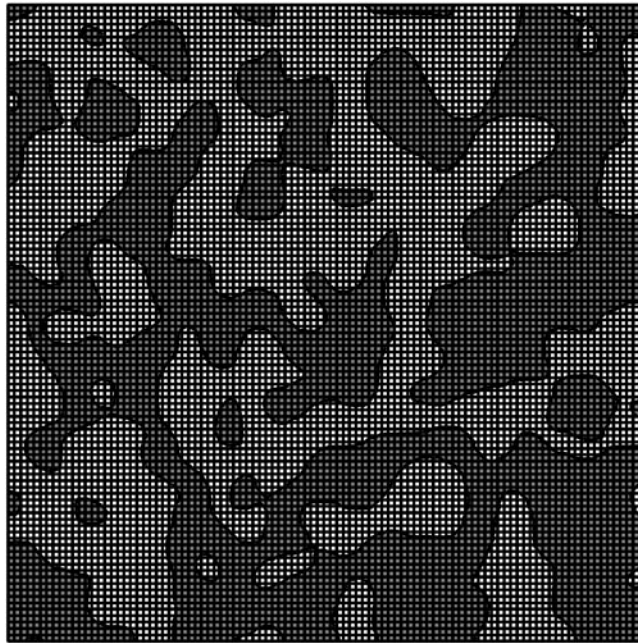
Figure 3. Spatial pattern of the density of a species. The intensity of the diffusion parameter is 0.01.

insight into the behaviour of complex ecosystems (Ciuchi *et al* 1996, Cirone *et al* 2001). The generalized Lotka–Volterra model has been explored in detail; however, a full characterization of the conditions under which a population extinguishes or survives in the competition process has not been achieved (Abramson and Zanette 1998).

Our starting point is the following Ito stochastic differential equation describing the dynamical evolution of the ecosystem:

$$dn_i(t) = \left[\left(\gamma + \frac{\epsilon}{2} \right) - n_i(t) + \sum_{j \neq i} J_{ij} n_j(t) \right] n_i(t) \, dt + \sqrt{\epsilon} n_i(t) \, dw_i \tag{4}$$

where $n_i(t) \geqslant 0$ is the number of elements of the ith species and $i = 1, \ldots, N$, with $N = 1000$, the number of the species of our ecosystem. In equation (4) γ is the growth parameter, the random interaction matrix J_{ij} modellizes the interaction between different species ($i \neq j$) and w_i is the Wiener process whose increment dw_i satisfies the usual statistical properties: $\langle dw_i(t) \rangle = 0$ and $\langle dw_i(t) \, dw_j(t') \rangle = \delta_{ij} \delta(t - t') \, dt$. We consider all species equivalent so that the characteristic parameters of the ecosystem are independent of the species. The solution of the dynamical equation equation (4) is given by

$$n_i(t) = \frac{n_i(0) \exp\left[\delta t + \sqrt{\epsilon} w_i(t) + \int_0^t dt' \sum_{j \neq i} J_{ij} n_j(t')\right]}{1 + \gamma n_i(0) \int_0^t dt' \exp\left[\delta t' + \sqrt{\epsilon} w_i(t') + \int_0^{t'} dt'' \sum_{j \neq i} J_{ij} n_j(t'')\right]}. \tag{5}$$

The interaction between the species is assumed to be random and it is described by a random asymmetric interaction matrix J_{ij}, whose elements are independently distributed according to a Gaussian distribution with $\langle J_{ij} \rangle = 0$, $\langle J_{ij} J_{ji} \rangle = 0$ and $\sigma_J^2 = J^2/N$, where J is the interaction strength. The initial values of the populations $n_i(0)$ also have Gaussian distribution with mean value $\langle n_i(0) \rangle = 1$ and variance $\sigma_n^2 = 0.01$.

3.2. Stationary analysis

In the absence of external noise ($\epsilon = 0$), the steady state solutions of equation (4) are obtained by the fixed-point equation

$$(\gamma - n_i + h_i)n_i = 0 \tag{6}$$

where $h_i = \sum_j J_{ij} n_j(t)$ is the local field, which we can assume to be Gaussian with zero mean and variance $\sigma_{h_i}^2 = \langle h_i^2 \rangle = J^2 \langle n_i^2 \rangle$, for a great number of interacting species. The solutions of equation (6) are

$$n_i = (\gamma + h_i)\Theta(\gamma + h_i) \qquad n_i > 0 \quad \text{and} \quad n_i = 0 \tag{7}$$

where Θ 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:

$$
\begin{aligned}
\langle n_i \rangle &= \langle (\gamma + h_i)\Theta(\gamma + h_i) \rangle \\
&= \frac{1}{\sqrt{2\pi\sigma_{h_i}^2}} \left[\sigma_{h_i}^2 \exp\left[\frac{\gamma^2}{2\sigma_{h_i}^2} \right] + \frac{\gamma\sqrt{2\sigma_{h_i}^2\pi}}{2} \left(1 + \text{erf}\left(\frac{\gamma}{\sqrt{2\sigma_{h_i}^2}} \right) \right) \right]
\end{aligned} \tag{8}
$$

and

$$
\begin{aligned}
\langle n_i^2 \rangle &= \langle (\gamma + h_i)^2 \Theta^2(\gamma + h_i) \rangle \\
&= \left[\left(\frac{\gamma^2 + \sigma_{h_i}^2}{2} \right) \left(1 + \text{erf}\left(\frac{\gamma}{\sqrt{2\sigma_{h_i}^2}} \right) \right) + \frac{\gamma}{2}\sqrt{\frac{2\sigma_{h_i}^2}{\pi}} \exp\left[\frac{\gamma^2}{2\sigma_{h_i}^2} \right] \right].
\end{aligned} \tag{9}
$$

The values obtained from these equations are in good agreement with that obtained from numerical simulation of equation (4) when the choice of the interaction strength and the growth parameter ensures that the ecosystem is stable. The stationary probability distribution of the populations is the sum of a delta function and a truncated Gaussian

$$P(n_i) = n_{e_i}\delta(n_i) + \Theta(n_i)\frac{\exp\left[-\frac{(n_i - n_{io})^2}{2J^2\sigma_{n_i}^2} \right]}{\sqrt{2\pi J^2\sigma_{n_i}^2}}. \tag{10}$$

In the presence of multiplicative noise ($\epsilon \neq 0$), in the asymptotic regime we obtain a quasi-stationary probability distribution of the populations. This distribution is a bivariate distribution with respect to the variables $n_i(t)$ and $h_i(t)$, and it is obtained by neglecting the fluctuations of the local field in the asymptotic regime:

$$P(n_i) = n_{e_i}\delta(n_i) + N_i\Theta(n_i)\exp\left[\left(\frac{2(\gamma + h_i)}{\epsilon} - 1 \right) \ln n_i \right] \exp\left[-\frac{2(n_i)}{\epsilon} \right]. \tag{11}$$

3.3. Asymptotic regime

We focus on the statistical properties of the time integral of the ith population $N_i(t)$ in the asymptotic regime:

$$
\begin{aligned}
N_i(t) &= \int_0^t dt' n_i(t') \\
&= \ln\left[1 + n_i(0) \int_0^t dt' \exp\left[\gamma t' + \sqrt{\epsilon} w_i(t') + \sum_{J \neq i} J_{ij} N_j(t') \right] \right].
\end{aligned} \tag{12}
$$

In equation (12) 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 ith population and represents a local field acting on the ith population $h_i = \sum_j J_{ij} N_j(t) = J\eta_i$.

We use the same approximation as considered for mean-field interaction (Ciuchi *et al* 1996) and, after differentiating, we obtain the asymptotic solution of equation (12)

$$N_i(t) \simeq \ln\left[n_i(0)\exp\left(\sqrt{\epsilon}w_{\max_i}(t) + J\eta_{\max_i}(t)\right)\int_0^t dt' e^{\gamma t'}\right] \qquad (13)$$

where $w_{\max_i}(t) = \sup_{0<t'<t} w(t')$ and $\eta_{\max_i}(t) = \sup_{0<t'<t}\eta(t')$. The equation (13) is valid for $\gamma \geqslant 0$, that is when the system relaxes towards an equilibrium population and at the critical point. Evaluating equation (13) for $\gamma \geqslant 0$, after making the ensemble average, we obtain for the time average of the ith population $\bar{N}_i$

$$\langle \bar{N}_i \rangle \simeq \frac{1}{t}\left[N_w\sqrt{\epsilon t} + \ln t + \langle \ln[n_i(0)]\rangle\right] \qquad \gamma = 0 \qquad (14)$$

and

$$\langle \bar{N}_i \rangle \simeq \frac{1}{t}\left[N_w\sqrt{\epsilon t} + (\gamma + N_\eta)t + \left\langle \ln\left[\frac{n_i(0)}{\gamma}\right]\right\rangle\right] \qquad \gamma > 0 \qquad (15)$$

where N_w and N_η are variables with a semi-Gaussian distribution (Ciuchi *et al* 1996) and N_η must be determined self-consistently from the variance of the local field. These asymptotic behaviours are consistent with those obtained using a mean-field approximation. We obtain in fact the typical long-time tail behaviour ($t^{-1/2}$) dependence, which characterizes nonlinear relaxation regimes when $\gamma \geqslant 0$. Moreover the numerical results confirm these analytical asymptotic behaviours of $\bar{N}_i$. When the system relaxes towards the absorbing barrier ($\gamma < 0$) we obtain from equation (12) in the long-time regime

$$\langle \bar{N}_i \rangle \simeq \frac{1}{t}\left[\ln(n_i(0)) + \ln\left[\int_0^t dt' \exp\left(\gamma t' + \sqrt{t'}w_i(t') + j\eta_i(t')\right)\right]\right]. \qquad (16)$$

In this case the time average of the ith 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 analysed the dynamics of the ecosystem when one species is absent. Specifically we considered the cavity field, which is the field acting on the ith population when this population is absent. 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 find that the probability distributions of the cavity fields differ substantially from that of the local fields for the same species. This peculiarity of our population dynamical model is different from the spin glass dynamics, where the two fields coincide. We also calculate the same quantities in the presence of external noise. The results of our simulations are reported in figures 4 and 5. The effect of the external noise is to overlap the two fields in such a way that for some particular species they coincide. Specifically this happens for species 1 (see figure 5). For species 33 we obtain a partial overlap. This suggests that, because all populations are positive and can grow during the dynamical process of the ecosystem, each population plays an important role in the total interaction among the species.

We have found this interesting phenomenon, which is reminiscent of the phase transition phenomenon, for some populations. The main reasons for this behaviour are as follows: (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. In the absence of noise some populations have a dynamical behaviour such
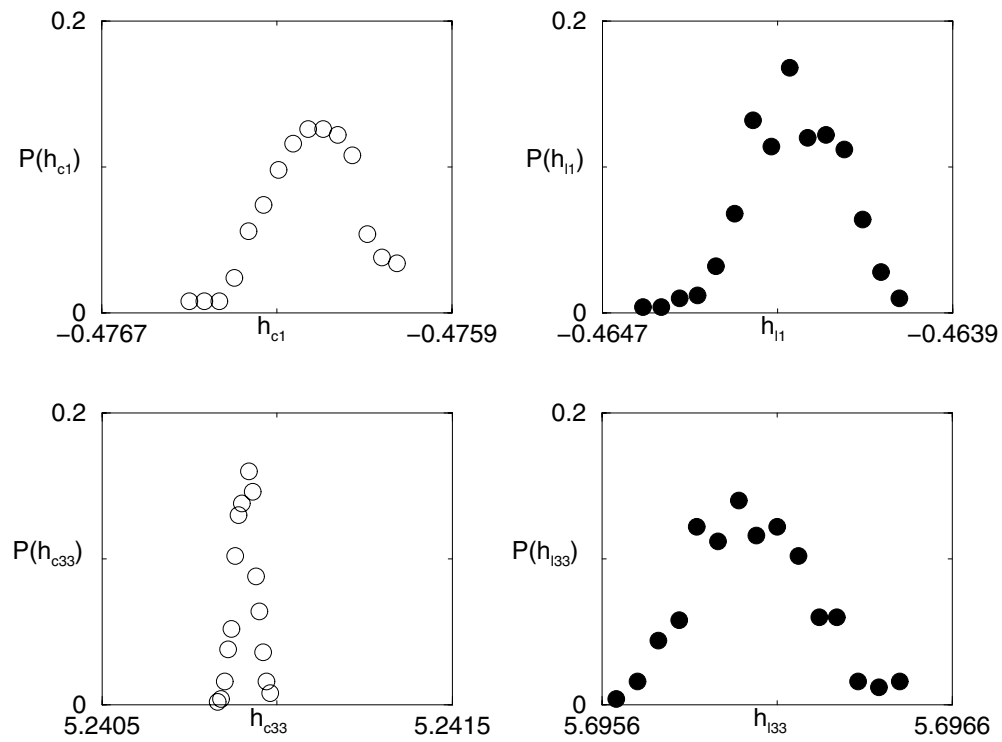
Figure 4. The probability distribution of the cavity fields $P(h_c)$ (open circles) and of the local fields $P(h_l)$ (black circles) for the species 1 and 33 after time $t = 100$. The system parameters are $N = 1000$ species, $J = 1$ and $\gamma = 1$.
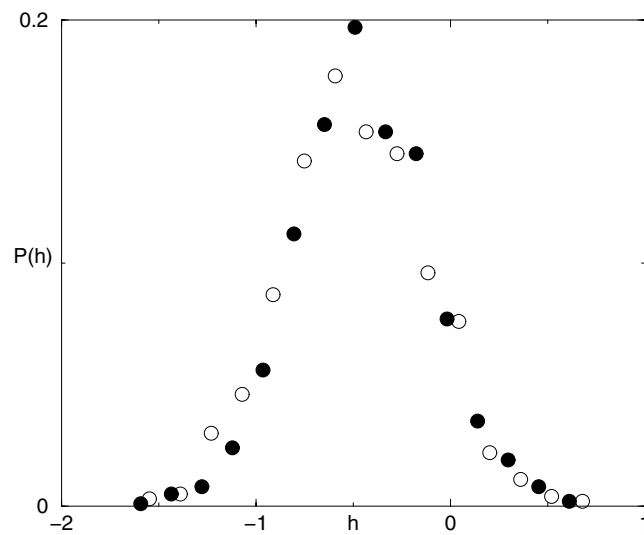

Figure 5. The probability distribution $P(h_1)$ of the local (black circles) and of the cavity (open circles) fields for species 1 after time $t = 100$, in the presence of external noise. The noise intensity is $\epsilon = 0.1$. The other system parameters are the same as those of figure 4.

that after a long time they influence in a significant way the dynamics of other species. Meanwhile, in the presence of noise all the populations seem to be equivalent from the dynamical point of view. We have found also that for strong noise intensity (namely $\epsilon = 1$) all species extinguish on a long timescale ($t \approx 10^6$ AU). Whether extinction occurs for any value of noise intensity or not is still an open question, because of time-consuming numerical calculations.

Acknowledgments

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