

Self-regulation mechanism of an ecosystem in a non-Gaussian fluctuation regime

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(Received 26 February 1996)

We study a dynamical model for an ecological network of many interacting species. We consider a Malthus-Verhulst type of self-regulation mechanism. In the framework of the mean field theory we study the nonlinear relaxation in three different cases: (a) towards the equilibrium state, (b) towards the absorbing barrier, (c) at the critical point. We obtain asymptotic behavior in all different cases for the time average of the process. The dynamical behavior of the system, in the limit of infinitely many interacting species, is investigated in the stability and instability conditions and theoretical results are compared with numerical simulations. [S1063-651X(96)09606-7]

PACS number(s): 05.40.+j, 02.50.-r, 05.20.-y

I. INTRODUCTION

In recent times some work has been devoted to the study of population dynamics of a large number of species randomly interacting each other [1]. The main motivation arises from the study of complex ecosystems such as the idiotopic network in the immune system, which works as a regulation scheme for idiotopes recognition [2]. In a natural ecosystem, typical mechanisms for self-regulation are the territorial breeding requirement, the crowding effect caused by competition between the species for the same growth limiting resources [3], etc. We study an N -species generalization of the usual Lotka-Volterra model with a Malthus-Verhulst modelization of the self-regulation processes. In this model the species extinction is not prevented as in a similar model: the Gompertz model, studied recently in an interesting paper by Rieger [1], where the function of the population density, which describes the development of the i th species without interacting with the other species, is a logarithmic one. Moreover, in this model the stability domain is enlarged with respect to the Gompertz model. In fact, the critical interaction strength J_c , where the transition from stability to instability takes place, is very low (typically smaller than one), while in our model the interaction strength can assume any value due to the value of the population saturation parameter only. In our model we consider mean field interaction between the species, as a first step to get some insight into the behavior of complex ecosystems, and a multiplicative noise to take into account the influence of the environment (i.e., climate, disease, etc.).

Nonmonotonic growth of fluctuations in a nonlinear relaxation during the decay towards the equilibrium state, in the presence of the multiplicative noise, has been investigated very recently in Ref. [4], if the initial state is far away or close to the absorbing barrier. The fluctuation behavior has been easily obtained by means of a small-noise approximation.

In this paper we analyze the dynamical behavior and the

stability of the system by using methods developed in the above-mentioned Ref. [4]. The species interaction is introduced by a mean field approximation, i.e., assuming that the growth parameter is proportional to the species average.

The deterministic behavior of our system shows a stability-instability transition driven by the typical interaction strength J and the saturation parameter γ of the population, which gives a divergency of the time integral $M(t)$ in a finite time t_c .

The different modality of nonlinear relaxation is analyzed in the stability region ($\gamma > J$) and in the instability region ($J > \gamma$). For small noise intensity, when $\delta > 0$ and the system is in the instability region, the noise moves the system towards the instability beforehand. Moreover, the system keeps the memory of the initial state configuration, unless the distribution is extremely peaked around the mean value.

In the large n limit, with n being the species number, the average of the species concentration has negligible fluctuations. In this limit the stochastic evolution of the system can be solved exactly. The solution is given by a somewhat involved integral equation. The main result of this paper is to introduce an approximation for the time integral of the average species concentration, which greatly simplifies both the deterministic and the noise affected evolution of the system. This approximation is valid in all cases in which there exists a time range wherein the time integral of the average concentration becomes very large. This happens in a finite time when the system is unstable or asymptotically if the system is stable. When the system decays towards an absorbing barrier, the time integral of the average species concentration becomes asymptotically constant and as a consequence a different approximation scheme must be developed. We use the above-mentioned approximation together with the small-noise approximation [4]. We emphasize that in the previous cases the approximation scheme takes into account the noise influence in a nonperturbative way.

In this paper we investigate the nonlinear relaxation of the system in three different regions of the control parameter

δ , which describes the development of the i th species without interacting with other species.

(a) The region with $\delta > 0$, where the decay occurs towards the equilibrium state (equilibrium population) and where we find a linear asymptotic behavior in time for the time integral of the site population concentration average $M(t)$ in the stability region (i.e., when the saturation effect of the resources prevails over the growth parameter due to the interaction between the populations), and an exponential growth in the instability region.

(b) The critical point $\delta = 0$, where we find a long tail behavior for $M(t)$ [namely $M(t) \sim \sqrt{t}$], when the nonlinear term γ is greater than the interaction strength between species, like the behavior at the critical point in the zero dimensional case [4], and an interesting modified behavior [$M(t) \sim \sqrt{t}e^{\sqrt{t}}$] in the instability region, which is an intermediate one between the long tail behavior and the exponential growth.

(c) The region with $\delta < 0$, where the decay occurs towards the absorbing barrier, corresponding to a hostile environment, and where the time integral $M(t)$ becomes a constant in the asymptotic regime in the stability region, because there is no spontaneous growth (all the species are eliminated). When the system is unstable the growing behavior of $M(t)$ can be put in terms of exponential and error functions.

The paper is organized as follows. The model is described in the next section (Sec. II), where we give the integral equation for the time integral process and the mapping between the linear process and the time integral of the i th population. In this section we discuss also the deterministic behavior and the instability transition.

In Sec. III we study the fluctuations in this ecological model of interacting populations, in the asymptotic regime, and the effect of the noise on the time t_c . The different behaviors of the deterministic potential associated with the asymptotic evolution of the site population average $m(t)$ give rise to a growing transition time t_c from $\delta > 0$ to $\delta < 0$. This means that when the interaction population prevails over the resources, the presence of a hostile environment ($\delta < 0$) causes a late start of the divergence of some population.

In Sec. IV the analysis of the asymptotic regime for the three different values of the parameter δ is studied by means of an approximation of the integral equation for the time integral of the site average $M(t)$. The time integral $M(t)$ is weakly dependent on the initial state only for $\delta \geq 0$ and $J < \gamma$. It is worth noting that we study the nonlinear relaxation in both the stability and instability regions by approximating directly the integral equation for $M(t)$, unlike the zero dimensional model previously studied [4], where we approximate the stochastic process.

Besides, we note that the asymptotic behaviors obtained with the approximation of the integral equation for $M(t)$ are the same as those obtained with the process approximation of [4], in the stability region. In this section our theoretical results are compared with numerical simulations of the original stochastic differential equation (SDE). Finally in Sec. V we give the conclusions.

II. THE MODEL

We consider the Malthus-Verhulst stochastic model originally introduced to take into account a self-regulation

mechanism which prevents exponential growth of a single population in the absence of interaction with other species. Our starting point is the following stochastic differential equation:

$$d\varphi_i = \left[\left(Jm + \delta + \frac{\epsilon}{2} \right) \varphi_i - \gamma \varphi_i^2 \right] dt + \sqrt{\epsilon} \varphi_i dw_i, \quad (2.1)$$

where the parameters J , γ , and δ identify the interaction between species, the saturation effects, and the growth of the population; w_i is the Wiener process whose increment dw_i satisfies the properties

$$\langle dw_i(t) \rangle = 0; \quad \langle dw_i(t) dw_j(t') \rangle = \delta_{ij} \delta(t - t') dt \quad (2.2)$$

and

$$m(t) = \frac{1}{n} \sum_i \varphi_i(t) \quad (2.3)$$

is the site average. We adopt in Eq. (2.1) the Ito prescriptions [5]. In this model the interaction among species is a symbiotic one for $J > 0$, i.e., the presence of other species increases the growth rate of each species.

A. Stationary analysis and stability

The steady-state properties of the multiplicative process of Eq. (2.1) are well known for the zero dimensional model [6] and give for the Fokker-Planck equation associated to the SDE (2.1) two different solutions. Asymptotic, steady state, solutions exist only if $\gamma > J$. We obtain

$$P(\varphi_i) = \delta(\varphi_i) \quad \text{for } \delta^* \leq 0. \quad (2.4)$$

This is the case in which population extinction occurs, and

$$P(\varphi_i) = \mathcal{N} \varphi_i^{(2\delta^*/\epsilon) - 1} \exp\left(\frac{-2\gamma\varphi_i}{\epsilon}\right) \quad \text{for } \delta^* > 0 \quad (2.5)$$

when populations survive, with

$$P_{tot} = \prod_i P(\varphi_i), \quad (2.6)$$

where $\delta(\varphi_i)$ is the Dirac delta function, $\mathcal{N} = (2\gamma/\epsilon)^{2\delta^*/\epsilon(\gamma-1)}/\Gamma(2\delta^*/\epsilon)$ is the normalization constant, and $\delta^* = \delta\gamma/(\gamma - J)$.

The function defined by Eq. (2.5) shows another transition besides that for $\delta^* = 0$, when the most probable value is for vanishing small population concentration. This is the well known noise-induced phase transition [7], which is characterized by the qualitative change of the probability distribution profile for $\delta^* = \epsilon/2$. In fact the most probable value is given by $\varphi_p = (\delta^* - \epsilon/2)/(\gamma - J)$.

Let us remark that because of the instability-stability transition of our system the steady-state distribution [Eq. (2.5)] is an effective one in the case $\delta > 0$ and $\gamma > J$ (stability region), but it is only a formal steady-state distribution in the instability case where $J > \gamma$ and consequently $\delta < 0$. This means

that any small disturbance with respect to the state of Eq. (2.5) will grow exponentially in time.

The solution of Eq.(2.1) is given by

$$\varphi_i(t) = \frac{\varphi_i(0)e^{JM(t)+\delta t+\sqrt{\epsilon}w_i(t)}}{1+\gamma\varphi_i(0)z_i(t)}, \quad (2.7)$$

where

$$z_i(t) = \int_0^t dt' e^{JM(t')+\delta t'+\sqrt{\epsilon}w_i(t')} \quad (2.8)$$

and

$$M(t) = \frac{1}{n} \sum_i \int_0^t dt' \varphi_i(t') = \int_0^t dt' m(t'). \quad (2.9)$$

We note that the dynamical behavior of the i th population depends on the time integral of the process $\exp[JM(t)+\delta t+\sqrt{\epsilon}w_i(t)]$ and the time integral process $M(t)$ of the site average $m(t)$, which is, in the large n limit, a not fluctuating quantity.

In fact, the integral equation determining $M(t)$ is

$$\begin{aligned} M(t) &= \frac{1}{n\gamma} \sum_i \ln \left(1 + \gamma\varphi_i(0) \int_0^t dt' e^{JM(t')+\delta t'+\sqrt{\epsilon}w_i(t')} \right) \\ &= \frac{1}{\gamma} \langle \ln[1 + \gamma\varphi_i(0)z_i(t)] \rangle, \end{aligned} \quad (2.10)$$

where the angular brackets stand for the site average. It is interesting to note that the time integral of the i th population in the linear regime (i.e., in the early stages of evolution) is given by

$$\phi_i^L(t) = \int_0^t dt' \varphi_i^L(t') = \varphi_i(0)z_i(t) \quad (2.11)$$

and its knowledge completely determines the time evolution of the time integral of the population process $\phi_i(t)$. In fact, this process is simply related to the linear process $z_i(t)$ via the mapping

$$\phi_i(t) = \int_0^t dt' \varphi_i(t') = \frac{1}{\gamma} \ln[1 + \gamma\phi_i^L(t)]. \quad (2.12)$$

In other words the time evolution of the system has a simpler interpretation in terms of the time integral process $\phi_i(t)$ of Eq. (2.12) and of its site average $M(t)$ [Eq. (2.10)]. Both quantities are given in terms of the linear process $\phi_i^L(t)$. It is worth noting that Eqs. (2.10) and (2.12) are actually a system of stochastic integral equations. Moreover, the only way to solve the stochastic integral equation (2.10) involves a numerical procedure as complex as the numerical solution of the original stochastic differential equation (2.1). The main effort of our work is to introduce suitable approximation in various regimes in the parameter space, which allows us to obtain analytical results for the transient behavior.

B. Deterministic behavior and instability

We consider first the system evolution in the absence of noise, outside ($\delta > 0$ and $\delta < 0$) and at the critical point ($\delta = 0$). From Eq. (2.10), neglecting the noise, we have the following deterministic integral equation for $M(t)$:

$$M(t) = \frac{1}{\gamma} \left\langle \ln \left(1 + \gamma\varphi_i(0) \int_0^t dt' e^{JM(t')+\delta t'} \right) \right\rangle. \quad (2.13)$$

In the long time regime ($t \rightarrow \infty$ for $J < \gamma$ and $t \rightarrow t_c$ for $J > \gamma$, where t_c is the stability-instability transition time) we can approximate Eq. (2.13) as

$$\gamma M(t) \simeq \langle \ln(\gamma\varphi_i(0)) \rangle + \ln \left(\int_0^t dt' e^{JM(t')+\delta t'} \right). \quad (2.14)$$

By differentiating Eq. (2.14) we easily obtain a deterministic evolution equation for $M(t)$,

$$M(t) \simeq \frac{1}{(\gamma-J)} \ln \left[1 + \left(\frac{\gamma-J}{\gamma} \right) e^{\langle \ln(\gamma\varphi_i(0)) \rangle} \int_0^t dt' e^{\delta t'} \right]. \quad (2.15)$$

For a distribution of the initial conditions $\varphi_i(0)$ well peaked around the mean value $m(0)$ [i.e., with $\sigma_{\varphi_i(0)}^2/m(0) \ll 1$] we get

$$\exp[\langle \ln(\gamma\varphi_i(0)) \rangle] \simeq \exp \left[+ \ln(\gamma m(0)) - \frac{\sigma_{\varphi_i(0)}^2}{2m(0)} \right] \simeq \gamma m(0) \quad (2.16)$$

and

$$M(t) = \frac{1}{(\gamma-J)} \ln \left(1 + m(0)(\gamma-J) \int_0^t dt' e^{\delta t'} \right). \quad (2.17)$$

By differentiating Eq. (2.17) we obtain the following differential equation for the site average $m(t)$:

$$\dot{m}(t) = [\delta + (J - \gamma)m]m. \quad (2.18)$$

This equation can be also obtained, in the linear deterministic regime, from Eq. (2.1), if the time behaviors of the species are nearly close to $m(t)$.

For different values of the parameter δ , when the saturation parameter γ is greater than the interaction parameter J , the deterministic potential associated with Eq. (2.18) causes the particle to approach the equilibrium state $m_\infty = \delta/(\gamma-J)$ for $\delta > 0$ or the absorbing barrier $m=0$ for $\delta \leq 0$ [see Fig. 1(a)], while when the interaction between the species is greater than the saturation effect ($J > \gamma$), an instability occurs.

It means that in a finite time t_c , the time integral of the site average $M(t)$ [Eqs. (2.15) and (2.17)] grows to infinity and the system becomes unstable. If $m(0)$ is less than $|\delta|/(J - \gamma)$ and $\delta < 0$ we have an absorbing barrier at $m=0$. This transition time t_c depends on the parameters of the dynamical system and on the initial population distribution according to the expressions

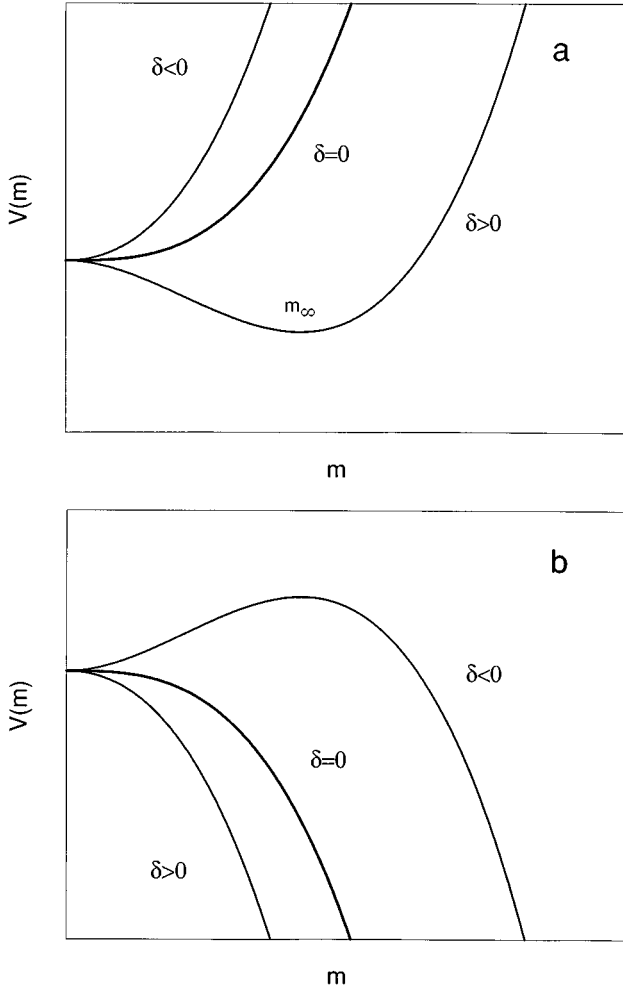


FIG. 1. (a) Schematic view of the potential of the deterministic equation of the site average $m(t)$ for different values of the parameter δ in the stability region ($J < \gamma$). (b) The same with $J > \gamma$ (instability region).

$$t_c = \frac{1}{\delta} \left\{ \ln \left[1 + \left(\frac{\delta \gamma}{(J - \gamma)} \right) e^{-\langle \ln(\gamma \varphi_i(0)) \rangle} \right] \right\} \quad \text{for } \delta \neq 0 \quad (2.19)$$

and

$$t_c = \left(\frac{\gamma}{(J - \gamma)} \right) e^{-\langle \ln(\gamma \varphi_i(0)) \rangle} \quad \text{for } \delta = 0. \quad (2.20)$$

In general from Eqs. (2.19) and (2.20) it is evident that the system keeps the memory of the initial distribution of the populations. However, for a peaked distribution of the initial conditions $\varphi_i(0)$ [see Eq. (2.16)], the system clearly loses memory of the initial state and the transition times become

$$t_c = \frac{1}{\delta} \ln \left(1 + \frac{\delta}{(J - \gamma)m(0)} \right), \quad \delta \neq 0 \quad (2.21)$$

and

$$t_c = \frac{1}{(J - \gamma)m(0)}, \quad \delta = 0. \quad (2.22)$$

It is worthwhile to note that in the instability region ($J > \gamma$) because of the different shapes of the potential of Eq. (2.18) [see Fig. 1(b)], the transition time increases from $\delta > 0$ to $\delta < 0$ according to

$$(t_c)_{\delta < 0} > (t_c)_{\delta = 0} > (t_c)_{\delta > 0}. \quad (2.23)$$

For $\delta > 0$ we have in the long time regime, from Eq. (2.10),

$$M(t) \simeq \frac{1}{\gamma} \ln(z_d(t)), \quad (2.24)$$

where $z_d(t)$ is the deterministic limit of the process of Eq. (2.8),

$$z_d(t) = \int_0^t dt' e^{JM(t') + \delta t'}. \quad (2.25)$$

We easily obtain the following asymptotic behavior:

$$M(t) \simeq \frac{\delta t}{(\gamma - J)} = m_\infty t \quad (2.26)$$

with $\gamma > J$ (stability region). At the critical point ($\delta = 0$) we obtain from Eq. (2.17) a logarithmic growth of $M(t)$,

$$\begin{aligned} M(t) &= \frac{1}{(\gamma - J)} \ln[1 + m(0)(\gamma - J)t] \\ &\simeq \frac{1}{(\gamma - J)} [\ln(m(0)(\gamma - J)) + \ln(t)]. \end{aligned} \quad (2.27)$$

When $\delta < 0$ we have a decay towards the absorbing barrier and the time integral $M(t)$ attains a constant value given by

$$M_\infty = \frac{1}{(\gamma - J)} \ln \left(1 + \frac{m(0)(\gamma - J)}{|\delta|} \right), \quad (2.28)$$

while for $J > \gamma$ we get (for $t \rightarrow t_c$)

$$M(t) \simeq \frac{m(0)}{|\delta|} (1 - e^{\delta t} J). \quad (2.29)$$

In the next section we shall study fluctuations with respect to the deterministic evolution due to the noise.

III. FLUCTUATIONS ($\delta > 0$)

We consider now the role of the fluctuations due to the noise on the population dynamics. We are able to discuss fluctuations on the population concentration process for $\delta > 0$, both in the stable and unstable regions. In particular, we calculate the asymptotic fluctuations of the time average of the i th population,

$$\bar{\phi}_i(t) = \frac{1}{t} \int_0^t dt' \varphi_i(t'). \quad (3.1)$$

We can introduce a fluctuation process $\Delta \bar{\phi}_i(t)$ with respect to the site average of the time average process

$$\Delta \bar{\phi}_i(t) = \bar{\phi}_i(t) - \langle \bar{\phi}_i(t) \rangle. \quad (3.2)$$

As is evident from Eq. (2.9), the time integral of the spatial average $M(t)$, in the limit of infinitely many interacting species, is the first moment of the time integral of the process $\phi_i(t)$, therefore we have

$$\Delta \bar{\phi}_i(t) = \frac{1}{\gamma t} \{ \ln[1 + \gamma \varphi_i(0) z_i(t)] - \langle \ln[1 + \gamma \varphi_i(0) z_i(t)] \rangle \}. \quad (3.3)$$

When the relaxation takes place towards the equilibrium population ($\delta > 0$), we approximate the integral equation (2.10), using the following asymptotic equation:

$$\begin{aligned} \int_0^t dt' e^{JM(t') + \delta t' + \sqrt{\epsilon} w_i(t')} &\simeq e^{\sqrt{\epsilon} w_{max_i}} \int_0^t dt' e^{JM(t') + \delta t'} \\ &= e^{\sqrt{\epsilon} w_{max_i}} f(t), \end{aligned} \quad (3.4)$$

where $w_{max_i}(t) = \sup_{0 < t' < t} w_i(t')$ [5], and

$$f(t) = \int_0^t dt' e^{JM(t') + \delta t'}. \quad (3.5)$$

This approximation [Eq. (3.4)] is based on the consideration that for $\delta J \geq 0$, $M(t)$ will grow in time, thus the integral appearing in Eq. (3.4) is dominated by the large time behavior of the integrand. As a consequence the time integral $M(t)$ is proportional to the process $w_{max_i}(t)$. In fact we have

$$M(t) \simeq \frac{1}{\gamma} \langle \ln[1 + \gamma \varphi_i(0) e^{\sqrt{\epsilon} w_{max_i}} f(t)] \rangle, \quad (3.6)$$

where $f(t)$ is independent of the population index. In the long time regime ($t \rightarrow \infty$ for $J < \gamma$ and $t \rightarrow t_c$ for $J > \gamma$) we obtain

$$M(t) \simeq \frac{1}{\gamma} [\langle \ln(\gamma \varphi_i(0)) \rangle + \sqrt{\epsilon} \langle w_{max_i}(t) \rangle + \ln(f(t))]. \quad (3.7)$$

So we can approximate Eq. (3.3) as

$$\Delta \bar{\phi}_i(t) \simeq \frac{1}{\gamma t} \{ \sqrt{\epsilon} [w_{max_i}(t) - \langle w_{max_i}(t) \rangle] \}. \quad (3.8)$$

The distribution of the process $w_{max_i}(t)$ is known [5], and we have

$$w_{max_i}(t) = l_i \sqrt{t}, \quad (3.9)$$

where each l_i is a random variable distributed according a *semi-Gaussian* distribution

$$P(l_i) = \begin{cases} 2(2\pi)^{-1/2} \exp(-l_i^2/2) & \text{for } l_i \geq 0, \\ 0 & \text{for } l_i < 0 \end{cases} \quad (3.10)$$

with moments λ_n given by

$$\lambda_n = \frac{(2)^{n/2}}{\sqrt{\pi}} \Gamma\left(\frac{n+1}{2}\right). \quad (3.11)$$

As a consequence the fluctuations of the time average $\bar{\phi}_i(t)$ are asymptotically determined by the statistical properties of the process $w_{max_i}(t)$,

$$\begin{aligned} \langle \Delta^2 \bar{\phi}_i(t) \rangle &= \langle \bar{\phi}_i^2(t) \rangle - \langle \bar{\phi}_i(t) \rangle^2 \\ &\simeq J \frac{1}{(\gamma t)^2} \{ \epsilon [\langle w_{max_i}^2(t) \rangle - \langle w_{max_i}(t) \rangle^2] \} \\ &\simeq \left(\frac{\epsilon(\pi-2)}{\pi \gamma^2} \right) \frac{1}{t} + O\left(\frac{1}{t^2}\right), \end{aligned} \quad (3.12)$$

which shows that we have smaller fluctuations as the system approaches the equilibrium population distribution. We can also find the effect of the noise on the time (t_c), in which the stability-instability transition occurs. For $\delta > 0$, using the same approximated integral equation (3.4), and after differentiating and neglecting the low order term $O(1/\sqrt{t})$, from Eq. (3.7), for large time we get

$$\gamma \dot{M}(t) \simeq \exp[\langle \ln(\gamma \varphi_i(0)) \rangle] \exp[(J - \gamma)M(t) + \delta t + \sqrt{\epsilon} N \sqrt{t}], \quad (3.13)$$

where $\langle w_{max_i}(t) \rangle = \sqrt{t} N$, and $N = \sqrt{2/\pi}$. This is a differential equation equivalent to Eq. (3.7), and it is useful to derive the time t_c . Solving Eq. (3.13) we obtain

$$\begin{aligned} M(t) &\simeq \frac{1}{(\gamma - J)} \ln \left[1 + \left(\frac{\gamma - J}{\gamma} \right) e^{\langle \ln(\gamma \varphi_i(0)) \rangle} \right. \\ &\quad \left. \times \int_0^{t_c} dt' e^{\delta t' + \sqrt{\epsilon} N \sqrt{t'}} \right]. \end{aligned} \quad (3.14)$$

The system becomes unstable earlier owing to the noise, as it is easily seen comparing Eq. (3.14) with (2.15). In fact, from Eq. (3.14) we obtain the instability time t_c ,

$$\begin{aligned} t_c &\simeq \frac{1}{\delta} \left\{ \left(\frac{\epsilon}{2\pi\delta} + \ln \left[1 + \left(\frac{\delta\gamma}{(J-\gamma)} \right) e^{-\langle \ln(\gamma \varphi_i(0)) \rangle} \right] \right)^{1/2} \right. \\ &\quad \left. - \sqrt{\frac{\epsilon}{2\pi\delta}} \right\}^2 \\ &\simeq \frac{1}{\delta} \left\{ \left(\ln \left[1 + \left(\frac{\delta\gamma}{(J-\gamma)} \right) e^{-\langle \ln(\gamma \varphi_i(0)) \rangle} \right] \right)^{1/2} \right. \\ &\quad \left. - \sqrt{\frac{\epsilon}{2\pi\delta}} \right\}^2, \end{aligned} \quad (3.15)$$

where the following approximation, valid for small noise intensity, has been used:

$$e^{y_c^2} \simeq \left[1 + \left(\frac{\delta\gamma}{(J-\gamma)} \right) e^{-\langle \ln(\gamma \varphi_i(0)) \rangle} \right] e^{y_o^2} \quad (3.16)$$

with $y_c = y_o + \sqrt{\delta t_c}$ and $y_o = \sqrt{\epsilon/(2\pi\delta)}$.

A small noise moves the system towards the instability, because the noise forces the system to sample more of the available range in the parameter space than otherwise occurs without noise.

From Eq. (3.15) we can also see that the effect of different species distributions of the initial conditions on the transition time t_c is quite analogous to the deterministic case previously discussed in Sec. II. Namely for values of $\varphi_i(0)$ equally distributed around a given mean value $m(0)$ it is easy to show that the time t_c increases because the factor $e^{-\langle \ln(\gamma\varphi_i(0)) \rangle}$ is greater than $e^{-\ln(\gamma m(0))}$, when all the species have the same initial condition equal to the mean value $m(0)$. This means that the system has not enough time to lose memory of the initial state, when it is in the instability region. However, for a peaked distribution of the initial conditions $\varphi_i(0)$ with $m(0) = 1$ [i.e., with $\sigma_{\varphi_i(0)}^2/m(0) \ll 1$], the system clearly loses memory of the initial state [see Eq. (2.16)] and the transition time becomes

$$t_c \approx \frac{1}{\delta} \left\{ \left[\ln \left(1 + \frac{\delta}{(J-\gamma)} \right) \right]^{1/2} - \sqrt{\frac{\epsilon}{2\pi\delta}} \right\}^2. \quad (3.17)$$

IV. ASYMPTOTIC REGIME

We consider now the asymptotic behavior of the time integral of the site average $M(t)$ for different values of the growth parameter δ in both stability and instability regions.

A. Relaxation towards the equilibrium state

For $\delta > 0$ using the approximation (3.4) and Eq. (3.13) we get the asymptotic solution of Eq. (3.6),

$$M(t) \approx \frac{1}{(\gamma-J)} \ln[1 + F(t)], \quad (4.1)$$

where

$$F(t) = \Gamma(\varphi_i(0)) \int_0^t dt' e^{\delta t' + \sqrt{\epsilon} N \sqrt{t'}} \quad (4.2)$$

and

$$\Gamma(\varphi_i(0)) = \left(\frac{\gamma-J}{\gamma} \right) e^{\langle \ln(\gamma\varphi_i(0)) \rangle}. \quad (4.3)$$

Explicit expression for $M(t)$ in the asymptotic regime is given in terms of complex error functions,

$$M(t) \approx \left(\frac{1}{(\gamma-J)} \right) \ln \left\{ 1 + \left(\frac{\Gamma(\varphi_i(0))}{\delta} \right) \left[e^{\delta t + \sqrt{(2\epsilon/\pi)t}} - 1 - \frac{\sqrt{\pi}}{i} y_o e^{-y_o^2} [\operatorname{erf}(i(\sqrt{\delta t + y_o})) - \operatorname{erf}(i y_o)] \right] \right\} \quad (4.4)$$

with $y_o = \sqrt{\epsilon/(2\pi\delta)}$. In terms of series expansions we obtain

$$M(t) \approx \left(\frac{1}{(\gamma-J)} \right) \ln \left\{ 1 + \left(\frac{e^{-y_o^2} \Gamma(\varphi_i(0))}{\delta} \right) \sum_{k=0}^{\infty} \left(\frac{1}{k!} \right) \left[y^{2k} \left(1 - \frac{2y_o y}{2k+1} \right) - (y_o)^{2k} \left(1 - \frac{2y_o^2}{2k+1} \right) \right] \right\}, \quad (4.5)$$

with $y = \sqrt{\delta t} + y_o$.

Case I. Stability region $J < \gamma$

In this region the asymptotic behavior is characterized by a divergence of the time integral $M(t)$ when the time goes to infinity. We can approximate Eq. (4.1) as follows:

$$M(t) \approx \frac{1}{\gamma-J} \left[\langle \ln(\gamma\varphi_i(0)) \rangle + \ln \left(\frac{\gamma-J}{\gamma} \right) + \ln \left(\int_0^t dt' e^{\delta t' + \sqrt{(2\epsilon/\pi)\sqrt{t'}}} \right) \right] \quad (4.6)$$

and using the mean value theorem to estimate the integral in Eq. (4.6) we have

$$M(t) \approx \left(\frac{\delta}{\gamma-J} \right) t + \frac{\sqrt{(2\epsilon/\pi)\sqrt{t}}}{(\gamma-J)} + \frac{\ln(t\beta(t))}{(\gamma-J)} + \frac{1}{(\gamma-J)} \left[\langle \ln(\gamma\varphi_i(0)) \rangle + \ln \left(\frac{\gamma-J}{\gamma} \right) \right] \approx \left(\frac{1}{\gamma-J} \right) \left[\delta t + \sqrt{\frac{2\epsilon t}{\pi}} + \ln(t\beta(t)) + \ln(\gamma-J) \right], \quad (4.7)$$

where

$$t\beta(t) = \frac{\int_0^t dt' e^{\delta t' + \sqrt{(2\epsilon/\pi)\sqrt{t'}}}}{e^{\delta t + \sqrt{(2\epsilon/\pi)\sqrt{t}}}} \quad (4.8)$$

is a function which diverges less than a linear function of time, and where we used $\sigma_{\varphi_i(0)}^2 \ll 1$ and Eq. (2.16) to calculate $\langle \ln(\gamma\varphi_i(0)) \rangle$. We see that, as expected, the system loses memory of the initial state. We obtain the same asymptotic behavior apart from the additive constant $(1/(\gamma-J)) \ln((\gamma-J)/\gamma)$ if we approximate directly the process $z(t)$ of Eq. (2.8) by

$$z(t) \approx \alpha(t) e^{JM(t) + \delta t \sqrt{\epsilon} w_{max}(t)}, \quad (4.9)$$

where $\alpha(t)$ is a function which, like $t\beta(t)$, diverges less than a linear function of time [4]. It is worthwhile to note that in the limit of the vanishing interaction strength J we recover the asymptotic constant value of the first moment of the multiplicative stochastic process, studied in Ref. [4], when the relaxation takes place towards the equilibrium state. Moreover, here we obtain the square root long time behavior as a preasymptotic term.

The main role of the fluctuations on the time average of the site averaged population process is related to the asymptotic decay towards the steady state with a square root long time tail. In the same asymptotic region the dispersion of the same quantity can be neglected because, according to Eq. (3.12), it vanishes with an inverse time law.

Analytical results obtained in the present approximation scheme are compared with numerical solutions of the Langevin equation (2.1), using $n = 1000$ species, in Figs. 2–7. In Fig. 2 we see the time behavior of the first moment of the site average $m(t)$ in the transient, obtained by time derivation from Eq. (4.7), for two different values of the nonlinear parameter γ . A growth of γ means an increasing saturation

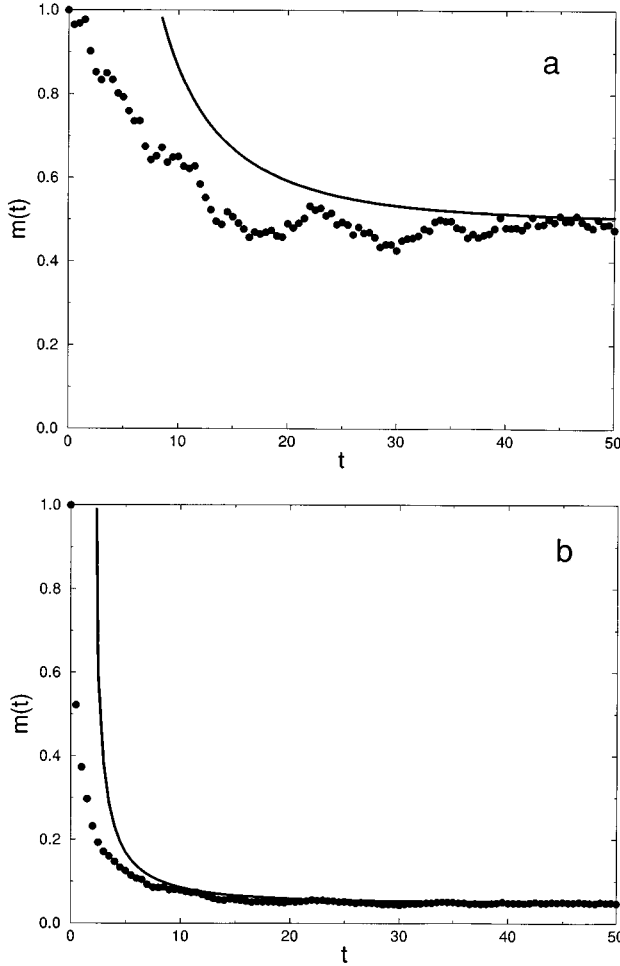


FIG. 2. Transient behavior of the first moment of the site average $m(t)$ for two values of the parameter γ in the stability region ($J < \gamma$): (a) $\gamma = 1.2$; (b) $\gamma = 3$. The solid lines are the results of the theory. The dotted lines are the results of numerical integration of the Langevin equation (2.1). As in Figs. 3, 4, and 5, data are obtained starting with the following parameter settings: $\delta = 0.095 > 0$, $J = 1$, $\epsilon = 0.01$, $m(0) = 1$, $\sigma_{\varphi_i(0)}^2 = 0.01$. The number of the species is $n = 1000$.

effect and the system settles down beforehand in the stationary regime. In Fig. 3 we report the transient behavior of the first moment of the time average of $m(t)$. We note that our approximation scheme works well for almost the full transient regime for high values of γ . Figure 4 shows the effect of different initial distributions on the transient behavior of the site average $m(t)$ and its time average $M(t)/t$. The effect of a large variance of the initial distribution of the species ($\sigma_{\varphi_i(0)}^2 = 1$) is to reduce only in the short time regime the values of $m(t)$ because of the term $\langle \ln(\gamma\varphi_i(0)) \rangle$, while the time average $M(t)/t$ keeps the memory of the initial conditions for all the transient. This is due to the memory effect of the integral operator [see Eq. (2.9)].

Case II. Instability region $J > \gamma$

In this region of parameters we note that $F(t)$, defined in Eq. (4.2), in a finite time t_c becomes equal to -1 . Therefore for times smaller than t_c , $F(t)$ is a small quantity. Particularly we have

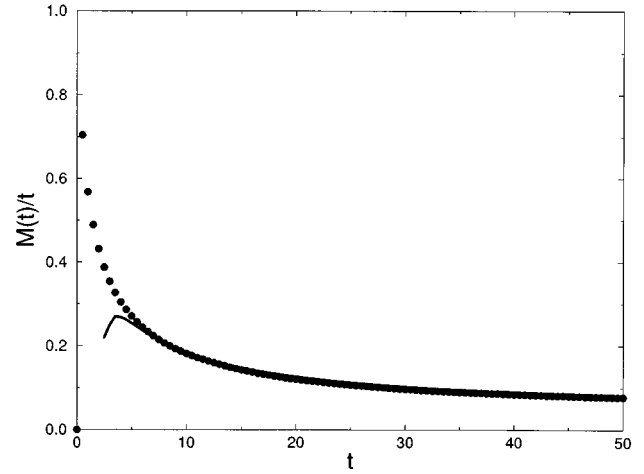


FIG. 3. Transient behavior of the first moment of the time average of $m(t)$ in the stability region ($\gamma = 3$). The solid line is the result of the theory.

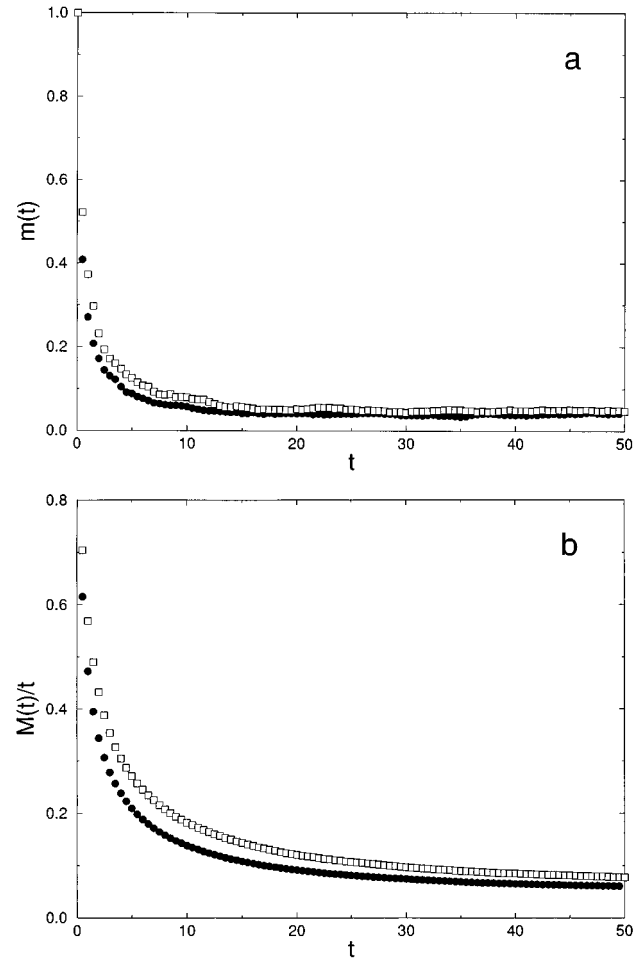


FIG. 4. Plots of $m(t)$ (a) and $M(t)/t$ (b) as a function of time for two values of the variance of the Gaussian initial distribution in the stability region ($\gamma = 3$). Namely, (a) $\sigma_{\varphi_i(0)}^2 = 0.01$ (squares); (b) $\sigma_{\varphi_i(0)}^2 = 1$ (dots).

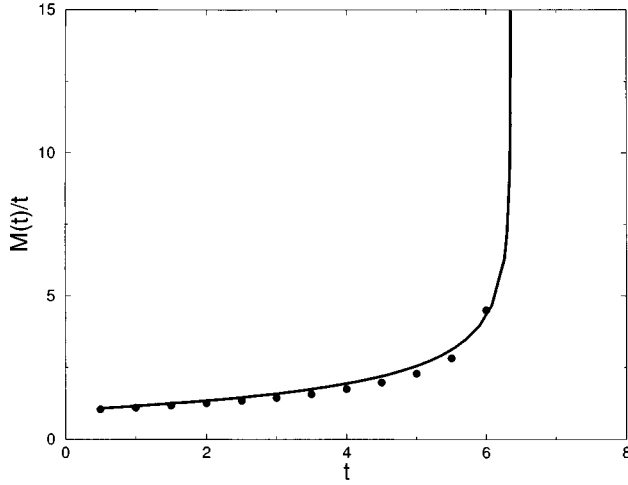


FIG. 5. Transient behavior of the first moment of the time average of $m(t)$ for $\gamma=0.9$ (instability region $J>\gamma$). The solid line is the result of the theory.

$$J|F(t)| \leq 1 \quad \text{for } t \leq t_c. \quad (4.10)$$

Because of the time cutoff t_c we can approximate the integral in Eq. (4.2) obtaining

$$M(t) < \frac{1}{(\gamma-J)} \ln \left[1 - A(t_c) \int_0^t dt' e^{\delta t'} \right], \quad (4.11)$$

where

$$\begin{aligned} A(t_c) &= \left(\frac{J-\gamma}{\gamma} \right) \exp[\langle \ln(\gamma\varphi_i(0)) \rangle + \sqrt{\epsilon N} \sqrt{t_c}] \\ &\simeq \left(\frac{J-\gamma}{\gamma} \right) \exp \left[\ln(\gamma m(0)) - \frac{\sigma_{\varphi_i(0)}^2}{2m(0)} + \sqrt{\frac{2\epsilon}{\pi}} \sqrt{t_c} \right]. \end{aligned} \quad (4.12)$$

Because of Eq. (4.10), from Eq. (4.11) we have

$$\left(\frac{A(t_c) e^{\delta t}}{\delta + A(t_c)} \right) < 1. \quad (4.13)$$

Now we obtain

$$\begin{aligned} M(t) &\simeq \frac{\ln(\delta)}{(J-\gamma)} + \frac{1}{(\gamma-J)} \ln \left[\delta \left(1 + \frac{A(t_c)}{\delta} \right) \right] + \frac{1}{(\gamma-J)} \ln \left[1 \right. \\ &\quad \left. - \left(\frac{A(t_c) e^{\delta t}}{\delta + A(t_c)} \right) \right], \end{aligned} \quad (4.14)$$

and for the leading term (for $t < t_c$)

$$M(t) \simeq \left(\frac{A(t_c)}{(J-\gamma)[\delta + A(t_c)]} \right) e^{\delta t} - \frac{\ln \left(1 + \frac{A(t_c)}{\delta} \right)}{(J-\gamma)}. \quad (4.15)$$

That is an exponential growth for the site population average $M(t)$. The plot of $M(t)/t$ (the solid line is the theo-

retical result) compared with simulation of Eq. (2.1) (dotted line) for this region of parameters is reported in Fig. 5.

B. Relaxation at the critical point

For $\delta=0$, i.e., with a zero growth of the population, we can use again the approximation (3.4) obtaining as asymptotic solution for $M(t)$

$$M(t) \simeq \frac{1}{(\gamma-J)} \ln \left[1 + \left(\frac{\gamma-J}{\gamma} \right) e^{\langle \ln(\gamma\varphi_i(0)) \rangle} \int_0^t dt' e^{\sqrt{\epsilon N} \sqrt{t'}} \right]. \quad (4.16)$$

For the stability region ($J < \gamma$), neglecting low order terms and using Eq. (2.16), we get

$$\begin{aligned} M(t) &\simeq \left(\frac{1}{\gamma-J} \right) \left[\left(\sqrt{\frac{2\epsilon}{\pi}} \right) \sqrt{t} + \ln \left(\frac{\sqrt{t}}{\sqrt{(2\epsilon)/\pi}} \right) \right. \\ &\quad \left. + \langle \ln(\gamma\varphi_i(0)) \rangle + \ln \left(\frac{2(\gamma-J)}{\gamma} \right) \right] \\ &\simeq \left(\frac{1}{\gamma-J} \right) \left[\left(\sqrt{\frac{2\epsilon}{\pi}} \right) \sqrt{t} + \ln \left(\frac{\sqrt{t}}{\sqrt{(2\epsilon)/\pi}} \right) \right. \\ &\quad \left. + \ln(\gamma\bar{\varphi}(0)) - \frac{\sigma_{\varphi_i(0)}^2}{2\bar{\varphi}(0)} + \ln \left(\frac{2(\gamma-J)}{\gamma} \right) \right], \end{aligned} \quad (4.17)$$

which is a result consistent with the zero dimensional case, previously studied [4]. Besides we note that the dominant term in Eq. (4.17) can be obtained using the approximation (4.9) [4].

While for the instability region ($J > \gamma$) we have

$$\begin{aligned} M(t) &\simeq \left(\frac{1}{\gamma-J} \right) \ln \left[1 + \left(\frac{\pi(\gamma-J)}{\gamma\epsilon} \right) e^{\langle \ln(\gamma\varphi_i(0)) \rangle} \right. \\ &\quad \left. \times \left(1 + \left(\sqrt{\frac{2\epsilon}{\pi}} \sqrt{t} - 1 \right) e^{\sqrt{(2\epsilon/\pi)} \sqrt{t}} \right) \right], \end{aligned} \quad (4.18)$$

and expanding the logarithm we obtain as a dominant behavior (for $t < t_c$)

$$M(t) \simeq \left\{ \left(\frac{\pi e^{\langle \ln(\gamma\varphi_i(0)) \rangle}}{\epsilon\gamma} \right) \left[1 + \left(\sqrt{\frac{2\epsilon}{\pi}} \sqrt{t} - 1 \right) e^{\sqrt{(2\epsilon/\pi)} \sqrt{t}} \right] \right\}, \quad (4.19)$$

which is an interesting behavior for the time averaged process $M(t)/t$, in fact we have a long time tail behavior ($t^{-1/2}$ dependence) modified by $e^{\sqrt{t}}$. Around the stability-instability transition the system goes from a purely long time tail behavior to a new long time regime modified by $e^{\sqrt{t}}$. In Fig. 6 we report the transient behaviors of $M(t)/t$ at the critical point.

C. Relaxation towards the absorbing barrier

The relaxation now is characterized by a constant asymptotic value for the time integral $M(t)$ as the system approaches the absorbing barrier, i.e., $J < \gamma$. In order to obtain

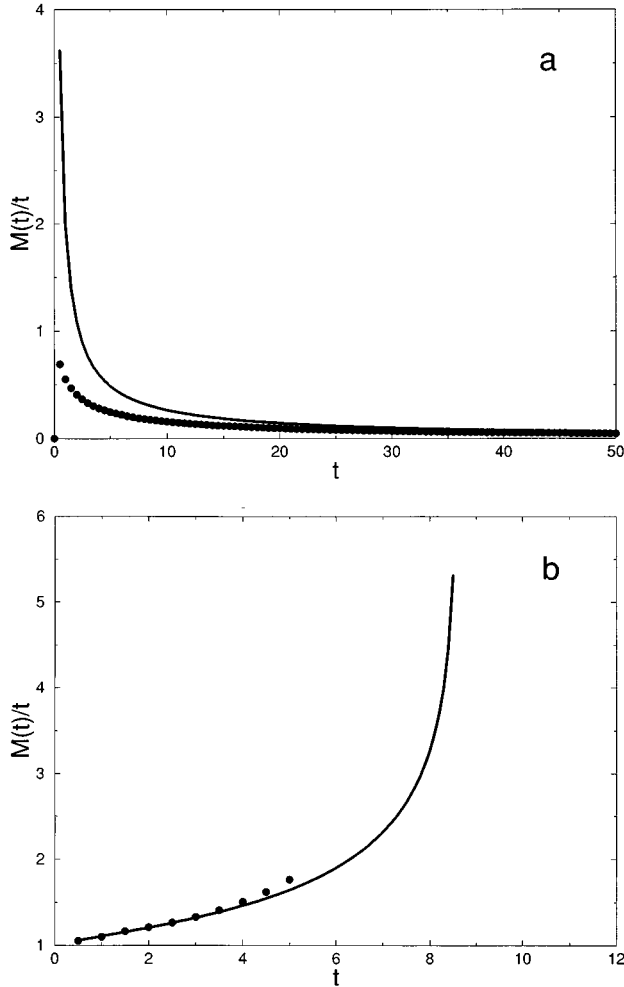


FIG. 6. Plot of the first moment of the site average $m(t)$ as a function of time at the critical point $\delta=0$. (a) Stability region ($\gamma=3$); (b) instability region ($\gamma=0.9$). The other parameters are the same as Fig. 2. The solid lines are the results of the theory.

the preasymptotic behavior in this regime, we approximate Eq. (2.10), taking into account that $M(t)$ is asymptotically constant. Therefore the approximation

$$\int_0^t dt' e^{JM(t') + \delta t' + \sqrt{\epsilon} w_i(t')} \simeq e^{JM(t)} \int_0^t dt' e^{\delta t' + \sqrt{\epsilon} w_i(t')} \quad (4.20)$$

is meaningful. Substituting Eq. (4.20) in Eq. (2.10) we obtain

$$M(t) \simeq \frac{1}{\gamma n} \sum_i \ln[1 + \gamma \varphi_i(0) e^{JM(t)} \bar{z}_i(t)], \quad (4.21)$$

where the process $\bar{z}_i(t)$ is given by

$$\bar{z}_i(t) = \int_0^t dt' e^{\delta t' + \sqrt{\epsilon} w_i(t')}. \quad (4.22)$$

Because of the expected small fluctuations for the time integral $M(t)$ we can use here the small noise expansion approximation used for a zero dimensional model recently

studied [4]. We can write for the process $\bar{z}_i(t)$, using the translation invariance properties of the Wiener process, the following multiplicative SDE:

$$d\bar{z}_i(t) = \left[\left(\delta + \frac{\epsilon}{2} \right) \bar{z}_i + 1 \right] dt + \sqrt{\epsilon} \bar{z}_i dw_i. \quad (4.23)$$

Therefore a mapping is introduced,

$$v_i(t) = \ln(\bar{z}_i(t)), \quad (4.24)$$

obtaining an additive noise process $v(t)$. In fact, from Eq. (4.23) and using Ito's rules of calculus we have the following SDE:

$$dv_i = (\delta + e^{-v_i(t)}) dt + \sqrt{\epsilon} dw_i. \quad (4.25)$$

We separate therefore the process v_i into a deterministic part v_d and a small fluctuating part \tilde{v}_i obeying an additive SDE,

$$d\tilde{v}_i = -e^{-v_d(t)} \tilde{v}_i dt + \sqrt{\epsilon} dw_i, \quad (4.26)$$

where

$$v_d(t) = \ln\left(\frac{1}{\delta}(e^{\delta t} - 1)\right) \quad (4.27)$$

and

$$\langle \tilde{v}_i \rangle = 0, \quad \sigma_{\tilde{v}_i}^2(t) = -\frac{\epsilon}{2\delta}(1 - e^{2\delta t}). \quad (4.28)$$

With this approximation Eq. (4.21) becomes

$$\begin{aligned} M(t) &\simeq \frac{1}{\gamma} \langle \ln[1 + \gamma \varphi_i(0) e^{JM(t)} \bar{z}_d(t) (1 + \tilde{v}_i)] \rangle \\ &\simeq \frac{1}{\gamma} \langle \ln[\gamma \varphi_i(0) e^{JM(t)} \bar{z}_d(t) (1 + \tilde{v}_i)] \rangle, \end{aligned} \quad (4.29)$$

where $\bar{z}_d(t)$ is the deterministic part of the process $\bar{z}_i(t)$. Therefore because of the zero mean of the process \tilde{v}_i , and neglecting all moments of order higher than 2 (small noise expansion) we obtain for $M(t)$

$$\begin{aligned} M(t) &\simeq \left(\frac{1}{\gamma - J} \right) [\langle \ln(\gamma \varphi_i(0)) \rangle + \langle \ln(1 + \tilde{v}_i) \rangle + \ln(\bar{z}_d(t))] \\ &\simeq \left(\frac{1}{\gamma - J} \right) \left[\langle \ln(\gamma \varphi_i(0)) \rangle + \ln\left(\frac{1}{\delta}(e^{\delta t} - 1)\right) \right. \\ &\quad \left. + \frac{\epsilon}{4\delta}(1 - e^{2\delta t}) \right]. \end{aligned} \quad (4.30)$$

From this equation we easily obtain the constant asymptotic value M_∞ of the time integral $M(t)$,

$$M_\infty \simeq \left(\frac{1}{\gamma - J} \right) \left[\langle \ln(\gamma \varphi_i(0)) \rangle + \ln\left(\frac{1}{|\delta|}\right) + \frac{\epsilon}{4J\delta} \right]. \quad (4.31)$$

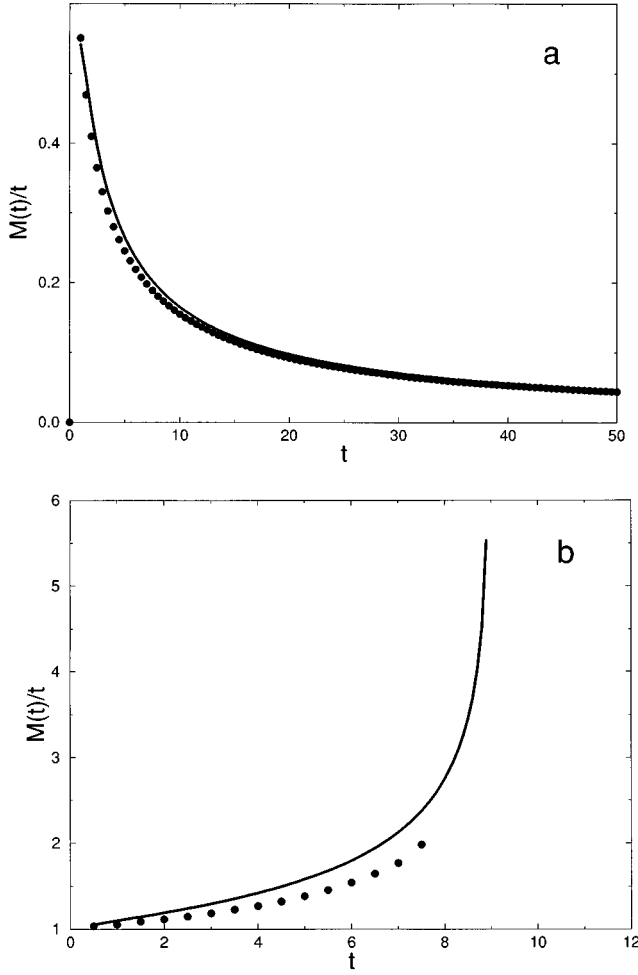


FIG. 7. Relaxation towards the absorbing barrier ($\delta = -0.01 < 0$): (a) stability region ($\gamma = 3$); (b) instability region ($\gamma = 0.9$). The other parameters are the same as Fig. 2. The solid lines are the results of the theory.

The plot of $M(t)/t$ is given in Fig. 7(a), where we see that our approximation scheme [Eqs. (4.20) and (4.29)] works well.

Finally we consider the instability region ($J > \gamma$), where in the long time regime [$t \rightarrow t_c$ and $M(t) \rightarrow \infty$] we can apply the asymptotic Eq. (3.4), obtaining

$$M(t) \approx \left(\frac{1}{\gamma - J} \right) \ln [J(1 - \bar{\Gamma}[\varphi_i(0)]) \{ e^{-y_o^2} - e^{-(\sqrt{|\delta|}t - y_o)^2} + \sqrt{\pi} y_o [\operatorname{erf}(\sqrt{|\delta|}t - y_o) + \operatorname{erf}(y_o)] \}], \quad (4.32)$$

where $y_o = \sqrt{\epsilon/(2\pi|\delta|)}$, erf is the error function, and

$$\bar{\Gamma}(\varphi_i(0)) = \left(\frac{(J - \gamma)e^{\epsilon/2\pi|\delta|}}{\gamma|\delta|} \right) e^{\langle \ln(\gamma\varphi_i(0)) \rangle}. \quad (4.33)$$

In Fig. 7(b) the asymptotic behavior (solid line) of the time average of $m(t)$ given by Eq. (4.32) is compared with the numerical simulation (dotted line) of Eq. (2.1). We see

that the approximation given by Eq. (3.4) works not as well as at the initial times. This is because to obtain Eq. (4.32) we perform an integration between the initial time $t=0$ and the time t of the asymptotic equation (3.13), thus extrapolating the asymptotic solution back to the initial time. In other words, we force the asymptotic behavior to cross the initial condition and as a consequence we obtain a worse behavior as the time t approaches the transition value t_c in this parameter region.

V. CONCLUSIONS

We have studied a stochastic model of interacting populations in the limit of a large number of interacting species. We have introduced an approximation for the time integral of the average species concentration which allows us to obtain analytical results for the transient behavior and the asymptotic statistical properties of the time average of the i th population process.

An interesting feature concerning the population dynamics is that the statistical properties of the time average of the i th population process are determined asymptotically from the statistical properties of the process $w_{max}(t) = \sup_{0 < t' < t} w(t')$ [5], where w is the Wiener process.

Our approximation scheme works for all cases studied [see Figs. 2–7(a)]. Results are less accurate in the instability region for the transient behavior when $\delta < 0$ [Fig. 7(b)], as compared with all other cases. This is because our approximation, which is accurate in the asymptotic regime ($t \rightarrow t_c$), needs also an extrapolation back to the initial time. This extrapolation is clearly less accurate when the $M(t)$ has a large slope variation in a finite time. A possible improvement should be achieved with a matching procedure between the asymptotic and a perturbative solution of Eq. (2.1) at an intermediate time.

On the other hand, in all the other different regimes of nonlinear relaxation our theoretical results reproduce not only the asymptotic behavior but almost all the transient evolution of the system. At the critical point we see that around the stability-instability transition, the system goes from a purely long time tail behavior for the time averaged process $M(t)/t$ to a new long time regime modified by e^{y_o} . For small noise intensity the transition time increases from $\delta > 0$ to $\delta < 0$ according to the same relation found for the deterministic evolution of the system

$$(t_c)_{\delta < 0} > (t_c)_{\delta = 0} > (t_c)_{\delta > 0} \quad \text{with } \epsilon \neq 0, \quad (5.1)$$

as we can see from Figs. 5, 6(b), and 7(b).

We investigated also the effect of a large variance of the Gaussian initial distribution of the populations (namely $\sigma_{\varphi_i(0)}^2 = 1$) on the transient behavior of the site average $m(t)$ and of the time average $M(t)/t$. We found that, apart from a short time regime where $m(t)$ is lower than the behavior obtained with the numerical solution of Eq. (2.1), the relaxation converges quickly to the right behavior. In the short time regime $m(t)$ keeps the memory of the initial distribution because of the term $\langle \ln(\gamma\varphi_i(0)) \rangle$. In fact the species with $\varphi_i(0) < m(0) = 1$ makes $\langle \ln(\gamma\varphi_i(0)) \rangle$ and therefore $m(t)$ lower. On the other hand, the behavior of the

process $M(t)/t$ is lowered for all the transient. The process $M(t)/t$ keeps the memory of the initial distribution because of the integral operator [see Eq. (2.9)].

A field of further investigation is the natural extension of this work to the study of populations dynamics with randomly interacting species.

ACKNOWLEDGMENTS

This work was supported in part by the Istituto Nazionale di Fisica della Materia (INFN) and the Ministero dell'Università e della Ricerca Scientifica e Tecnologica (MURST).

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