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Trichotomous-noise-induced catastrophic shifts in symbiotic ecosystems

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An *N*-species Lotka-Volterra stochastic model of a symbiotic ecological system with the Verhulst self-regulation mechanism is considered. The effect of fluctuating environment on the carrying capacity of a population is modeled as the colored three-level Markovian (trichotomous) noise. In the framework of the mean-field theory an explicit self-consistency equation for stationary states is presented. Stability and instability conditions and colored-noise-induced discontinuous transitions (catastrophic shifts) in the model are investigated. In some cases the mean field exhibits hysteresis as a function of the noise parameters. It is shown that the occurrence of catastrophic shifts can be controlled by noise parameters, such as correlation time, amplitude, and flatness. The dependence of the critical coupling strengths on the noise parameters is found and illustrated by phase diagrams. Implications of the results on some modifications of the model are discussed.

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I. INTRODUCTION

Modeling of the dynamics of interacting species is central in ecological theory, and there is a vast literature describing deterministic and stochastic models for such interactions (for a reference survey see [1]). Usually the process is so complex that the dynamics of such webs of coevolving species, especially in the case of a great number of interacting species, can be successfully represented by means of a dynamical system with stochastic elements [2,3].

Ecological systems are usually assumed to smoothly respond to a gradual change of environmental parameters. However, studies have shown that the smooth change can be interrupted by catastrophic shifts leading to a new state of the ecosystem [4]. Furthermore, recent results exhibit existence of alternative stability domains in different natural ecosystems [4,5]. Such catastrophies have also been noted in various theoretical models, assuming that the effective deterministic potential is multistable [1,4]. Typical examples are models in which a prey-predator relationship dominates [6] and models of competing communities [7].

Motivated by the modeling of the idiotopic network in the immune system, which works as a regulation scheme for idiotope recognition [8], the authors of Refs. [3,9] have investigated such requirements concerning the self-regulation and interaction strength of a complex ecosystem, at which the transition from stability to instability takes place. For example, if in a complex ecosystem, described by the generalized Lotka-Volterra model with the Verhulst self-regulation mechanism and with symbiotic interaction among species, the interaction strength exceeds some critical value, an explosive increase in population occurs [9]. Note that the models considered in Refs. [3,9] have a uniquely determined steady state that does not depend on the initial conditions and, as a result, no catastrophic shifts occur.

Physical environments, however, are rarely static, and variability in important environmental parameters, such as temperature and rainfall, have widely recognized impacts on natural populations of plants and animals. It is generally acknowledged that an important characteristic of environmental variability, or noise, is its correlation time (color). Theoretical investigations suggest that population dynamics is sensitive to noise color [10]. In spite of the obvious significance of this circumstance, the role of colored noise that is characteristic to the changes of the environmental parameters, i.e., to the dynamics of ecosystems, has not been much investigated.

Recently, noise-induced nonequilibrium transitions (as well as colored-noise-induced transitions) in spatially extended nonlinear systems with multiplicative noise have been the topic of a number of physical investigations [11]. The initial motivation in this field has come from studies of phase transitions, in particular, from the discovery of a noise-induced reentrant second-order phase transition for an artificial spatially extended model [12]. Afterwards, noise-induced nonequilibrium transitions (either continuous or discontinuous) were found in systems of coupled oscillators [13] and also in some other systems [14,15]. The fact that external multiplicative noise can induce multistability as well as discontinuous transitions in some complex systems (see, e.g., Ref. [15]) inspired us to apply an analogous approach to analyze ecological models. It is of interest, both from theoretical and practical viewpoints, to know whether the catastrophic shifts sometimes occurring in ecosystems [4,5] can be regarded as induced by multiplicative colored noise.

In this paper we consider an *N*-species Lotka-Volterra model of an ecological system with the Verhulst self-regulation mechanism. The effect of fluctuating environment on the growth of a population is modeled as trichotomous fluctuations of the carrying capacity. The trichotomous process is a symmetric three-level stationary telegraph process characterized by three parameters: amplitude $a_0 \in (0,\infty)$, correlation time $\tau_c \in (0,\infty)$, and flatness $\varphi \in (1,\infty)$ [16,17]. The study is restricted to systems in which the interaction between species is symbiotic [3,9]. As a first step to get some

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insight into the behavior of such complex ecosystems and in order to set a firm basis for further work, we addressed the model using a mean-field approach, focusing on the exact stationary solutions of the self-consistency equation and on the colored-noise-induced nonequilibrium transitions. The purpose of this paper is to provide exact analytical results for colored-noise-induced first-order-like phase transitions (discontinuous ones) over extended trichotomous noise parameters and interaction strengths. We show that the existence and value of catastrophic shifts of the mean field can be controlled by noise parameters. We have also succeeded in reaching exact conditions bring forth the discontinuous transitions. Since such transitions do not exist in systems without noise, these are pure colored-noise effects.

A major virtue of the models with trichotomous noise is that they constitute a case admitting exact analytical solutions for some nonlinear stochastic problems, such as colored noise-induced transitions [17] and the reversals of noise-induced flow [16]. Furthermore, it is remarkable that for trichotomous noises, the flatness parameter φ, contrary to cases of the Gaussian colored noise ($\varphi=3$) and symmetric dichotomous noise ($\varphi=1$), can be anything from 1 to ∞. This extra degree of freedom can prove useful at modeling actual fluctuations. Although both dichotomous and trichotomous noises may be too rough approximations of environmental fluctuations, the latter is more flexible, including all cases of dichotomous noises and, as such, revealing the essence of its peculiarities.

The structure of the paper is as follows. Section II presents the basic model investigated in this work. In Sec. III a mean-field description of the model is given and the corresponding exact self-consistency equation is found. Section IV analyzes the behavior of the self-consistently determined stationary mean field. In the phase space of the system parameters a coexistence region of two phases, a stationary stable phase and an unstable one, and first-order-like phase transitions are established. The dependence of the critical coupling parameters on the noise parameters is investigated. In Sec. V, motivated by the knowledge of a possible hysteresis, we generalize the model introduced in Sec. II by adding an attractive term, which mimics a decrease of the carrying capacity caused by competition between the populations. Section VI contains brief concluding remarks. Some calculations are delegated to the Appendix.

II. MODEL

Our starting point is the N-species generalized Lotka-Volterra equation

$$\frac{d}{dt}X_i(t)=X_i(t)\left[f_i(X_i(t))+\sum_{j\neq i}J_{ij}X_j(t)\right], \tag{1}$$

where $X_i(t)(i=1,\ldots,N)$ is the population density of the ith species at time t [clearly $X_i(t)\geqslant 0$]. The function $f_i(X)$ describes the development of the ith species without any interaction with other species. Typical mechanisms for self-regulation in ecosystems are, for example, a territorial breeding requirement and the crowding effect caused by competition for resources [1]. It is convenient to consider

$$f_i(x)=\delta_i\left[1-\left(\frac{x}{K_i}\right)^{\beta}\right] \tag{2}$$

with $\beta\geqslant 0$, where K_i is the saturation point of population density (the carrying capacity) and δ_i is the growth rate parameter of the ith species. Throughout this paper we take $\beta=1$, which corresponds to the Verhulst model for self-regulation [1,3]. The matrix $(J_{ij})(i,j=1,\ldots,N)$ is the interaction (or coupling) matrix. If $J_{ij}>0$ and $J_{ji}>0$, the ith species is in a symbiotic relationship with species j, i.e., the presence of other species increases the growth rate of each species [3]. On the basis of Refs. [3,9] we consider all species equivalent, so that the characteristic parameters of the ecosystem are independent of the species, i.e., $\delta_i=\delta,\ K_i=K,\ J_{ij}=J/N>0$.

Random interaction with the environment (climate, disease, etc.) is taken into account by introducing a colored noise in $f_i(X)$. From now on we shall use only fluctuations of the carrying capacity K_i:

$$\frac{\delta}{K_i}=\gamma+Z_i(t), \tag{3}$$

where $\gamma\equiv\delta\langle 1/K_i\rangle$ and the colored noise $Z_i(t)$ is assumed to be a zero-mean trichotomous Markovian stochastic process [16,17]. A trichotomous process is a random stationary Markovian process that consists of jumps between three values $a=a_0,0,-a_0$. The jumps follow in time according to a Poisson process, while the values occur with the stationary probabilities

$$P_s(a_0)=P_s(-a_0)=q,\quad P_s(0)=1-2q. \tag{4}$$

The transition probabilities between the states $Z(t)=\pm a_0$ and 0 can be obtained as follows:

$$\begin{aligned}P(\pm a_0,t+\tau|0,t)&=P(-a_0,t+\tau|a_0,t)\\&=P(a_0,t+\tau|-a_0,t)\\&=q(1-e^{-\nu\tau}),\end{aligned} \tag{5}$$

$$P(0,t+\tau|\pm a_0,t)=(1-2q)(1-e^{-\nu\tau}),$$

$$\tau>0,\quad 0<q<1/2,\quad \nu>0.$$

The process is completely determined by Eqs. (4) and (5). The mean value of $Z_i(t)$ and the correlation function are

$$\langle Z_i(t)\rangle=0, \tag{6}$$

$$\langle Z_i(t),Z_j(t')\rangle=\delta_{ij}2qa_0^2e^{-\nu|t-t'|}.$$

It can be seen that the switching rate ν is the reciprocal of the noise correlation time, $\nu=1/\tau_c$. The flatness parameter φ proves to be a very simple expression of the probability q:

$$\varphi = \frac{\langle Z^4(t)\rangle}{\langle Z^2(t)\rangle^2} = \frac{1}{2q}. \tag{7}$$

Obviously, model (1) with Eqs. (2) and (3) is biologically meaningful only if

$$a_0 < \gamma. \tag{8}$$

III. MEAN-FIELD APPROXIMATION

To proceed further with the analytical examination of model (1) with the Verhulst self-regulation, mechanism, we assume that $N \to \infty$. This means we are interested in the case of infinitely many interacting species. Following Shiino [18], one can reach the mean-field approximation by replacing the site average $(1/N)\Sigma_{j(\neq i)}X_j(t)$ by the statistical average $\langle X(t)\rangle$ in Eq. (1). Hence, each stochastic differential equation (1), where Eqs. (2) and (3) are assumed, can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{dX(t)}{dt} = X(t)[\delta + J\langle X(t)\rangle - X(t)\{\gamma + Z(t)\}]. \tag{9}$$

The corresponding composite Fokker-Planck master equation is

$$\frac{\partial P_n(x,t)}{\partial t} = -\frac{\partial}{\partial x}\{x[r(t) - x(\gamma + a_n)]P_n(x,t)\} + \sum_m U_{nm}P_m(x,t) \tag{10}$$

with $r(t) \equiv \delta + J\langle X(t)\rangle, P_n(x,t)$ denoting the probability density for the combined process $(x,a_n,t); n,m = 1,2,3; a_1 \equiv -a_0, a_2 \equiv 0, a_3 \equiv a_0$; and

$$\mathbf{U} = \nu \begin{pmatrix} q-1 & q & q \\ 1-2q & -2q & 1-2q \\ q & q & q-1 \end{pmatrix}.$$

Many significant inequalities follow from Eq. (9) to characterize the stationary states of the system. First, as for a stationary case, $x_1 = r/(\gamma - a_0)$ and $x_2 = r/(\gamma + a_0)$ are stable fixed points of the deterministic equations (9) with $Z(t) = -a_0$ and $Z(t) = a_0$, respectively, all trajectories $X(t)$ satisfy the following inequalities:

$$\frac{r}{\gamma - a_0} > X(t) > \frac{r}{\gamma + a_0}. \tag{11}$$

Second, as the mean value $\langle X\rangle$ must also satisfy inequalities (11), it follows that if $J < \gamma - a_0$, then $\delta/(\gamma - J + a_0) < \langle X\rangle < \delta/(\gamma - J - a_0)$, if $\gamma + a_0 > J > \gamma - a_0$, then $\langle X\rangle > \delta/(\gamma + a_0 - J)$, and if $J > \gamma + a_0$, then no stationary state with a positive finite mean value can exist.

The deterministic behavior of Eq. (9), neglecting noise Z, is investigated in Ref. [9]. For different values of the parameter $\delta > 0$, when $J < \gamma$, the deterministic potential associated with Eq. (9) with $Z = 0$ causes the species to approach the equilibrium state $\langle X\rangle = \delta/(\gamma - J)$, while when interaction between the species is greater than the saturation effect ($J > \gamma$), an instability occurs. That means that at a finite time t_c, the mean value $\langle X\rangle$ grows to infinity and the system becomes unstable. This transition time t_c depends on the parameters of the dynamical system and on the initial distribution of the populations [9].

Next we consider the role of fluctuations due to a noise in the population dynamics. As is evident from the deterministic behavior, asymptotic stationary state solutions exist if $J < \gamma - a_0$. If $J > \gamma + a_0$, then the system becomes unstable, as in finite time the statistical average $\langle X(t)\rangle$ would grow to infinity. The case $\gamma + a_0 > J > \gamma - a_0$ needs extra investigation, as depending on the system parameters and on the initial distribution of the populations, the system can either admit a stationary state or remain unstable.

The behavior of a stationary system can be analytically studied by means of a standard mean-field theory procedure [11]. For a stationary state we can solve Eq. (10), taking as the boundary condition that there is no probability current at the boundary. This way we get the stationary probability distribution in the x space, $P(x,r) = \Sigma_n P_n^s(x)$, where $P_n^s(x)$ is the stationary probability density for the state (x,a_n). After quite simple but voluminous calculations one can find

$$\begin{aligned} P(x,r) = {} & \frac{r2^{1-\nu/r}}{x^2 a_0 B(q\nu/r,[1-q]\nu/r)} \\ & \times\left(1 - \frac{(\gamma x - r)^2}{a_0^2 x^2}\right)^{(1-q)\nu/r - 1} \\ & \times F\left(\frac{\nu(1-2q)}{2r}, \frac{\nu(1-2q)}{2r} \right. \\ & \left. + \frac{1}{2}; \frac{\nu(1-q)}{r}; 1 - \frac{(\gamma x - r)^2}{a_0^2 x^2}\right), \end{aligned} \tag{12}$$

where $B(\lambda,\kappa) \equiv \Gamma(\lambda)\Gamma(\kappa)/\Gamma(\lambda + \kappa)$ is the beta function, F is the hypergeometric function (also known as ${}_2F_1$), and Γ is the gamma function (see also Ref. [17]). $P(x,r)$ is normalized to restrict x within $(r/[\gamma + a_0], r/[\gamma - a_0])$. The self-consistency equation for the Weiss mean-field approach, whose solution yields the dependence of $\langle X\rangle$ with the system parameters, is

$$\langle X\rangle = \int_{r/(\gamma + a_0)}^{r/(\gamma - a_0)} xP(x,r)dx, \tag{13}$$

where $r \equiv \delta + J\langle X\rangle$.

For the sake of simplicity, we shall introduce the "order parameter"

$$m := \frac{\nu}{2\gamma}\left\langle \frac{1}{X}\right\rangle = \frac{\nu}{2(\delta + J\langle X\rangle)}. \tag{14}$$

By applying a scaling of the form

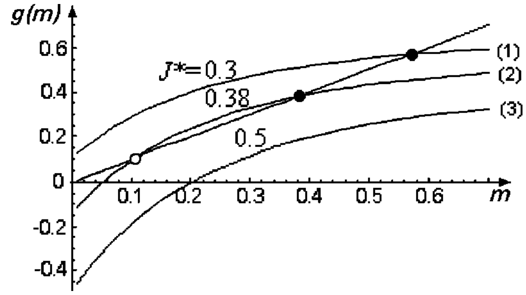

FIG. 1. Solutions of the self-consistency equation (16) at different coupling strengths J^*. The flatness parameter equals $\varphi = 1/2q = 2$, the amplitude parameter $\alpha = 0.8$, and the growth rate $\delta^* = 1$. The mean-field solutions are given by the intersection points of different curves with a straight line. Three typical cases are shown: (1) there is just one stable solution (full circle), (2) one stable solution and one unstable solution (empty circle) appear, and (3) there are no solutions.

$$\delta^* = 2\delta/\nu, \quad J^* = J/\gamma, \quad \alpha = a_0^2/\gamma^2, \tag{15}$$

we get a dimensionless formulation of the self-consistency equation (13). The corresponding equation is

$$\delta^* m = 1 - J^*{}_3F_2\left(1, \frac{1}{2}, 2qm; m, m + \frac{1}{2}; \alpha\right) = g(m), \tag{16}$$

where ${}_3F_2$ is the hypergeometric function.

The behavior of m at different asymptotics and the conditions of occurrence of the stationary state will be considered in Sec. IV.

IV. RESULTS

It seems convenient to introduce graphical representations of Eq. (16) to have a better understanding for the occurrence of this or that solution. Figure 1 shows a typical example of such representations. All self-consistently determined values of m are given by the intersection points of the two curves in Fig. 1 presenting the right-and left-hand sides of Eq. (16). We can see that under condition (8) the function $g(m)$ in Eq. (16) increases monotonically from $g(0) = 1 - J^*/J_1$ to $g(\infty) = 1 - J^*$ as m increases. The characteristic coupling parameter J_1 takes a remarkably simple form

$$J_1 = \frac{1 - \alpha}{1 - \alpha(1 - 2q)}. \tag{17}$$

The following three characteristic regions can be discerned for the coupling parameter J^* (see Fig. 1).

(i) There is just one solution of Eq. (16) if $J^* < J_1$, the solution is stable.

(ii) There is no solution if $J^* > 1$, the system is unstable, as in finite time the statistical average $\langle X(t) \rangle$ grows to infinity.

(iii) In the case of $J_1 < J^* < 1$ there are two possible situations in the long time limit. There is an upper limit δ_c^* for the growth rate parameter δ^*, at greater values of which there is no solution and the system is unstable. For $\delta^* < \delta_c^*$, another critical value of the coupling parameter $1 > J_2 > J_1$ occurs. In the case $J^* > J_2$ the system is unstable, but at $J_1 < J^* < J_2$ there are two solutions. The bigger one (m_1) is stable and the smaller one ($m_2 < m_1$) is unstable (see the Appendix).

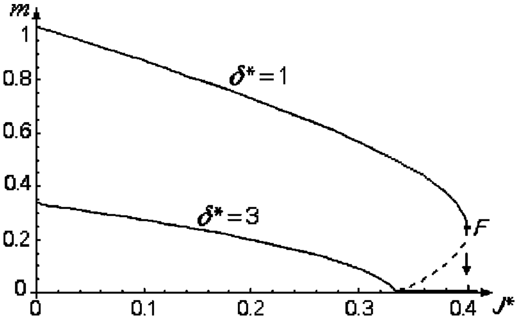

FIG. 2. Stationary mean field m vs coupling strength J^* at different growth rates δ^*. The flatness parameter equals $\varphi = 2$ and the amplitude parameter $\alpha = 0.8$. If J^* exceeds the critical coupling strength $J_1 = 1/3$, an unstable phase of the system occurs (marked by the bold line on the J^* axis). In the case of $\delta^* = 1$ another critical coupling strength $J_2 \approx 0.3998$ appears; the dashed line marks unstable solutions of the self-consistency equation (16). If the mean field lies on the upper branch close to the point F, a slight growth of J^* induces a catastrophic transition of the system to an unstable state.

Figure 2 shows different solutions of the self-consistency equation (16) for the mean field m as a function of the coupling constant J^* and the growth rate parameter δ^*. Existence of an unstable solution (Fig. 2, lower branch of curve $\delta^* = 1$) indicates that there is a coexistence region, $J_1 < J^* < J_2$, where two phases of the system — a stationary stable and an unstable one — are both possible. Notably, *coexistence* does not mean that the two phases are present simultaneously, however, either is possible depending on the initial distribution. In the Appendix we show that in the case $J^* > J_1$ an unstable phase really exists. The situation described represents a typical case of first-order phase transitions. If the value of the "order parameter" m (describing the stationary state of the system at $J^* < J_2$ close to the point J_2) is different from zero, a slight growth of the coupling parameter may bring it beyond the bifurcation point J_2 and induce a discontinuous transition to the unstable state of the system.

Figure 3 shows a phase diagram in the J^*-δ^* plane at $\alpha = 0.8$ and $q = 0.25$. The dashed region in the figure corresponds to the coexistence region of two phases. As δ^* increases, the multiphase region narrows down and disappears at the value of the growth rate parameter $\delta_c^* = 2.688\,52$. It should be noted that the critical coupling parameter J_1 can be described by an exact analytical formula [Eq. (17)], but for J_2 there is no such a formula. The latter can be evaluated from Eq. (16) by numerical methods or by using approximate equations. From Eq. (16) a monotonic dependence of J_2 on δ^* follows: if δ^* increases from 0 to δ_c^*, then J_2 decreases from 1 to J_1.

It is somewhat surprising that the critical growth rate parameter δ_c^* can be exactly expressed by elementary functions.

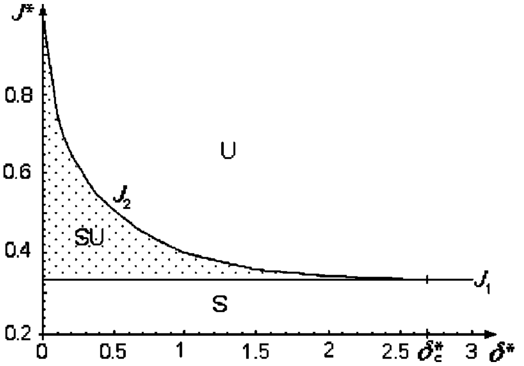

FIG. 3. A plot of the phase diagram in the δ^*-J^* plane at $\alpha = 0.8$, $q = 0.25$. The stable phase, unstable phase, and the coexistence region of two phases are marked by *S*, *U*, and SU, respectively. The critical growth rate parameter is $\delta_c^* \approx 2.6885$ and the critical coupling strength is $J_1 = 1/3$.

Equation (16) shows that the critical coupling parameter J_2 is given by the system of transcendental equations

$$\delta^* m = 1 - J_2\, {}_3F_2, \tag{18}$$

$$\delta^* = -J_2 \frac{d}{dm}\, {}_3F_2,$$

where the hypergeometric function ${}_3F_2$ is the same as in Eq. (16). At the critical point $\delta^* = \delta_c^*$, where $J_2 = J_1$ and $m = 0$ holds, from Eqs. (18) the following solution can be obtained:

$$\delta_c^* = -J_1 \left(\frac{d}{dm}\, {}_3F_2 \right) \Bigg|_{m=0} .$$

From this we can easily obtain an expression for the critical growth rate parameter

$$\delta_c^* = \frac{2q\sqrt{\alpha}}{1-(1-2q)\alpha} \ln \left| \frac{(1+\sqrt{\alpha})^{1-(1-2q)\sqrt{\alpha}}}{(1-\sqrt{\alpha})^{1+(1-2q)\sqrt{\alpha}}} \right| . \tag{19}$$

It is remarkable that in the case of fixed values of q the critical parameter δ_c^* increases monotonically from zero to infinity if the noise amplitude $\alpha \in (0,1)$ increases. We can also consider the solution (19) as a function of the flatness parameter $\varphi = 1/2q$. The typical forms of the graph of $\delta_c^*(q)$ are represented in Fig. 4. There is a lower limit for the noise amplitude $\alpha_c \approx 0.633\,01$, below which $\alpha \leqslant \alpha_c, \delta_c^*(q)$ increases monotonically. If $\alpha > \alpha_c$, then for increasing values of q, the critical growth rate starts from zero, growing to maximum at a certain value q_m of q, and δ_c^* approaches the value

$$\tilde{\delta}_c = \sqrt{\alpha} \ln \left| \frac{1+\sqrt{\alpha}}{1-\sqrt{\alpha}} \right|$$

as $q \to 1/2$. The parameter q_m at which the critical growth rate δ_c^* is maximized can be given the form

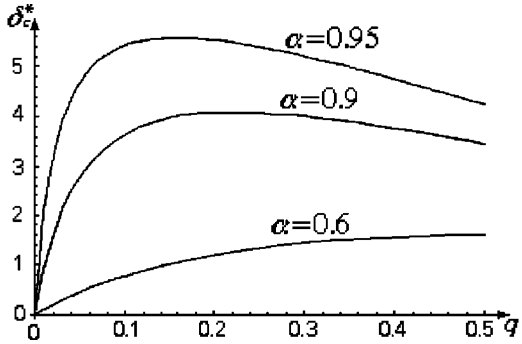

FIG. 4. The critical growth rate δ_c^* vs the noise parameter $q \in (0,0.5)$ for some values of the noise amplitude parameter α. Note a bell-shaped extremum of $\delta_c^*(q)$ at $\alpha > \alpha_c \approx 0.633\,01$. If $\alpha < \alpha_c$, then $\delta_c^*(q)$ increases monotonically as q increases.

$$q_m = \frac{\sqrt{1-\alpha}}{2\alpha} \left(\sqrt{1 - \frac{\tilde{\delta}_c}{\ln(1-\alpha)}} - \sqrt{1-\alpha} \right). \tag{20}$$

As the noise amplitude $\alpha > \alpha_c$ increases, q_m decreases monotonically from 1/2 to zero. In the case of a large amplitude $\alpha \approx 1$ one can find from Eqs. (19) and (20) that $\delta_c^*(q_m) \approx 2\tilde{\delta}_c$. It means that in the case of $\alpha > \alpha_c$ the value of the critical parameter δ_c^* induced by a trichotomous noise can up to twice exceed the value $\tilde{\delta}_c$ of the parameter δ_c^* induced by a dichotomous noise ($q = 1/2$) of the same amplitude. Notably, in the case of $\alpha < \alpha_c$, the parameter δ_c^* of trichotomous noise is always less than the corresponding parameter $\tilde{\delta}_c$ of a dichotomous noise.

In Fig. 5 we have plotted the width of the coexistence region of two phases $J_2 - J_1$ as a function of the parameter q. It can be seen that, if $\alpha > \alpha_c$, then the functional dependence of $J_2 - J_1$ on the parameter q is of a bell-shaped form that is associated with the behavior of $\delta_c^*(q)$.

In the vicinity of the critical point $\delta^* \approx \delta_c^*, \delta^* < \delta_c^*$, the values of J_2 and the "order parameter" $m(J_2)$ can be estimated by the following equations:

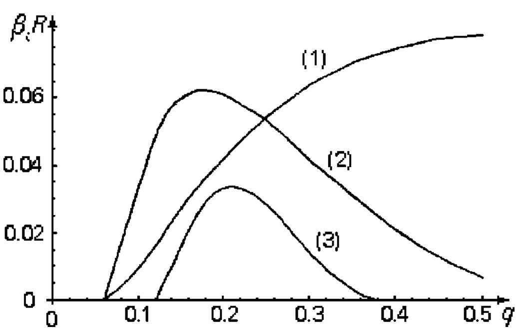

FIG. 5. The width of the phase coexistence region $R = J_2 - J_1$ vs noise parameter $q \in (0,0.5)$ at three typical cases. The curves (1)–(3) correspond to the following parameters: (1) $\delta^* = 0.5, \alpha = 0.6, \beta_1 = 1$; (2) $\delta^* = 3, \alpha = 0.9, \beta_2 = 10$; (3) $\delta^* = 3.8, \alpha = 0.9, \beta_3 = 100$. At fixed coupling strength, $J^* > 1 - \alpha$, the discontinuous transitions caused by changes of the noise flatness parameter $\varphi = 1/2q$ can occur only within the finite intervals of φ: (1) $1 < \varphi < 8.803$, (2) $1 < \varphi < 8.606$, (3) $1.283 < \varphi < 4.250$.

$$J_2 \approx J_1 + \frac{(\delta_c^* - \delta^*)^2}{2\rho}, \quad m(J_2) \approx \frac{(\delta_c^* - \delta^*)}{J_1\rho}, \tag{21}$$

where

$$\rho := \left[\frac{d^2}{dm^2}\ {}_3F_2\left(1,\frac{1}{2},2qm;m,m+\frac{1}{2};\alpha\right)\right]\Bigg|_{m=0}.$$

For $\alpha \ll 1$ (i.e., if the noise amplitude is small), we can do with the following approximate equations:

$$\delta_c^* \approx 4q\alpha, \quad \rho \approx 4\delta_c^*.$$

At large amplitudes, $1-\alpha \ll 2q$, the parameters δ_c^* and ρ can be given as $\delta_c^* \approx 2(1-q)|\ln(1-\alpha)|$, $\rho \approx \delta_c^{*2}/J_1$. Since the coupling-induced two-phase coexistence region does not exist in a system without noise, it is a pure colored-noise effect [see also Eq. (19)]. From Eq. (15) we can find that there is a coexistence region if the noise correlation time τ_c satisfies the condition $\tau_c < \delta_c^*/2\delta$. Evidently, if the system is in a stationary stable phase in the coexistence region, then a perturbation of the noise parameters can turn the system to the unstable phase. It is remarkable that variations of the noise correlation time can induce only abrupt transitions between the stable and unstable states of the system. In contrast, variations of the noise amplitude (and the flatness) can induce both discontinuous and continuous transitions.

V. HYSTERESIS

In ecological contexts unstable states of a system can variously be interpreted: extinction of populations, presence of additional interaction between species that the model has not taken into account, etc. In order to investigate the presence of a possible hysteresis induced by a noise we modify our model so that the unstable state of the system is replaced by a new stable state. We take into account that in case there is a competition for a common resource, such as food or living space, the growth of any expanding population must eventually be limited by the shortage of resources. Relying on Ref. [19], we introduce an adaptation in the above model [Eqs. (1)–(3)] by means of the dependence of the carrying capacity K_i on the numbers of individuals in the populations:

$$\frac{\delta}{K_i} = \gamma + \frac{\epsilon\gamma^2}{N}\sum_{j\neq i} X_j(t) + Z_i(t), \tag{22}$$

where the adaptation factor $\epsilon > 0$ is assumed independent of the species, i.e., the populations adapt themselves with respect to the total number of individuals of all populations. The mean-field approximation scheme presented in Sec. III can also be applied in this case by replacing the parameter γ in Eq. (9) by the following one:

$$\gamma^* = \gamma + \epsilon\gamma^2\langle X\rangle. \tag{23}$$

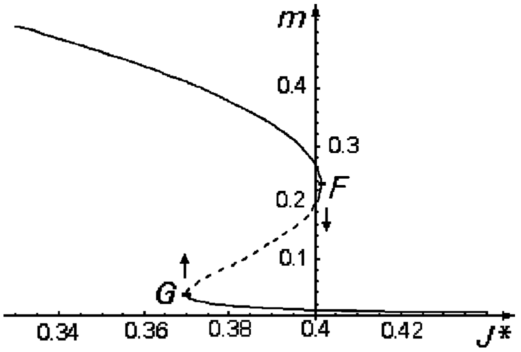

FIG. 6. The mean field m vs coupling constant J^* at $q=0.25, \alpha=0.8, \tau_c=0.5$, and $\epsilon=10^{-4}$ with time scaling $\delta=1$. Solid and dashed lines are stable and unstable solutions of the self-consistency equation (24), respectively. The system shows hysteresis — discontinuous transitions appear at the bifurcation points F and G.

The corresponding stationary self-consistency equation is

$$\delta^* m = 1 - \frac{J^{*2}m}{m(J^*-\delta\epsilon)+\epsilon/2\tau_c}\ {}_3F_2\left(1,\frac{1}{2},2qm;m,m+\frac{1}{2};\frac{\alpha m^2 J^{*2}}{[m(J^*-\delta\epsilon)+\epsilon/2\tau_c]^2}\right), \tag{24}$$

where the parameters δ^*, J^*, α, and m are given by Eqs. (14) and (15). Differently from what is presented in Sec. III, the stationary states at the conditions relevant in biology ($\delta > 0, J > 0, \gamma > 0, \epsilon > 0, \alpha < 1$, and $X_i \geq 0$) always exist, i.e., there is no unstable state. If noise is absent, the stationary state is monostable and

$$\langle X\rangle = \frac{1}{2\epsilon\gamma}\left[\sqrt{(J^*-1)^2+4\epsilon\delta} + J^* - 1\right].$$

In Fig. 6 the mean field m is shown as a function of the coupling intensity J^* satisfying the self-consistency equation (24) at $\tau_c=0.5, \delta=1, \alpha=0.8, q=0.25$, and $\epsilon=0.0001$. A hysteresis for the mean field appears and the discontinuous transition is doubly unidirectional. There are two critical values for the coupling intensity $\tilde{J}_1 = 0.3700$ and $\tilde{J}_2 = 0.4014$ at which the abrupt transitions occur. If the adaptation factor is rather small (ϵ is much less than the other parameters characteristic of the system), the critical parameters can be estimated as

$$\tilde{J}_1 \approx J_1, \quad \tilde{J}_2 \approx J_2.$$

Hysteresis can also be present in case any noise parameter, α, q, or τ_c, is chosen as the control parameter. For example, in Fig. 7 the hysteresis is exposed for the mean field m if the noise correlation time τ_c is considered as the control parameter. It can be seen that a jump from a state with a bigger number of individuals to that with a lesser

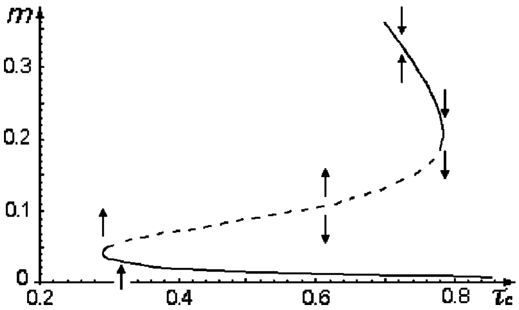

FIG. 7. Plot of the mean field m as a function of the noise correlation time τ_c at $q=0.25, \alpha=0.8, J^*=0.39$ with time scaling $\delta=0.7$ and $\epsilon=10^{-4}$. The solid and dashed lines correspond to the stable and unstable solutions of Eq. (24), respectively. Hysteresis of the mean field appears. The arrows show the direction of the change. The states in the dashed middle section lie on the border between the basin of attraction of the two alternative stable states on the upper and lower branches.

number occurs at smaller correlation times than opposite jumps. As was mentioned before, hysteresis appears at a change of the noise amplitude. In these cases the jump to bigger numbers of individuals occurs at larger amplitudes than the opposite jumps. Therefore a decrease of the noise amplitude (or of the correlation time) can under certain conditions cause a catastrophic fall in the size of the population.

VI. CONCLUDING REMARKS

The presence of colored noise has a profound effect on an ecosystem described by Eqs. (1)–(3), rearranging its parameter space so that in a certain region the system can be either in the unstable phase or in the stationary stable one and abrupt (first-order-like) transitions occur. Since the coupling-induced two-phase coexistence region does not exist in the system without noise, it is a pure colored-noise effect. The results indicate that the effect of noise is not merely restricted to the shift of the critical value of the interaction strength, but the whole nature of the transition changes. Notably, the coexistence region exists only at bounded values of the correlation time $\tau_c < \delta_c^*/2\delta$ [see Eq. (19)]. The phenomenon is robust enough to survive a modification of the noise as well as the coupling mechanism. Calculations analogous to those given in the Appendix show that in the case of a symmetric zero-mean exponentially correlated noise $\langle Z(t+\tau), Z(t)\rangle = \sigma \exp(-\nu\tau)$, if the dispersion is small enough $(\sigma \ll \gamma^2)$, all the results from Sec. IV are valid. In this case $\alpha (\alpha \ll 1)$ must be replaced by $\sigma/(2q\gamma^2)$ in the equations of Sec. IV. For example, the noise can also be a Gaussian stationary process. Evidently, a choice of a Gaussian noise implies the possibility of obtaining negative values of γ or the carrying capacity. Such a case has no biological meaning but, as the width of the Gaussian distribution is small enough, the small negative tail does not affect our results, if restricted to the first order in σ/γ^2.

Another interesting example admitting an exact analytical self-consistency equation is the case where the carrying capacity K_i fluctuates according to $K_i/\delta = (K/\delta) + Z_i$ [cf. Eq. (3)]. If Z_i means a dichotomous process $(q=1/2)$, then all mathematical results of Sec. III and IV are valid, just the parameters γ and α must be replaced by $\gamma^* = \tilde{\gamma}/(1-\alpha^*)$ and $\alpha^* = (\tilde{\gamma} a_0)^2 < 1$ (where $\tilde{\gamma} = \delta/K$) in the respective formulas. It is remarkable that, differently from what could be seen in Sec. IV, the rescaled critical coupling constant $\tilde{J}_1$ does not depend on the parameters of the noise and retains the value it has if noise is absent, $\tilde{J}_1 = J_c = \tilde{\gamma}$. The region of the coexistence of two phases is determined by the conditions $\tilde{\gamma} < J < \tilde{J}_2 \leqslant \tilde{\gamma}/(1-\alpha^*), \tau_c < \tilde{\delta}_c/2\delta$. This means that in the presence of noise, a symbiotic ecological system can have a stable stationary state also if the coupling parameter considerably exceeds the critical value of the coupling constant $J_c = \tilde{\gamma}$ characteristic of the deterministic case. Notably, in the cases considered in Secs. III and IV the values of the coupling parameter for stationary states are always less than J_c.

In Sec. V we have modified the model by including a term that mimics the decrease of the carrying capacity caused by the competition of populations for common resources. In this case there is no unstable state of the system and the mean field is characterized by one or two stable stationary solutions for every value of the coupling parameter $J^* \geqslant 0$. Moreover, hystereses for the mean field and related discontinuous transitions can sometimes be found as functions of the noise parameters as well as of the coupling constants. This is because colored noise can induce bistability of the ecosystem.

Our major result is that, in the case of ecological systems with a symbiotic interaction between the species, random interaction with the environment can cause discontinuous transitions in ecosystems, even if the system is monostable in the absence of noise. Such transitions can appear in two ways (both of which may depend on human activities). First, abrupt transitions can be caused by changes of control parameters, for example, the variations of the coupling constant or the noise correlation time (see Figs. 2 and 7). Second, some environmental fluctuations can affect the state directly, for example, by wiping out parts of the populations [4]. If there are alternative stable states, rather severe fluctuations may shift the system into a basin of attraction of another state (Fig. 7). Such catastrophies were also noted in different ecological models assuming that the deterministic potential in the absence of noise is multistable [4,6]. We would like to emphasize that these models are qualitatively different from these considered in our work. In the latter the deterministic potential is monostable and bistability is induced by the combined effects of multiplicative colored noise and symbiotic coupling (Sec. V).

The systems considered consist of infinite number of globally coupled species. When the number of species is finite, as is true for more realistic ecosystems, the features of the system can be different (see, e.g., [14]). Thus, the case of a finite number of interacting populations remains to be studied. It should be considered whether pure colored-noise-induced catastrophic shifts can play some role in natural ecosystems (or in metapopulations) dominated by a symbiotic relationship or by cooperation between species (see also

Ref. [20]). Undoubtedly, ultimate verification of these amazing phenomena lies with experimentalists—ecologists.

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APPENDIX

Since the self-consistency equation (16) for m yields, in general, more than one solution for the system and in addition the system can have an unstable state that Eq. (16) does not include, it is essential to ascertain which of the stationary states is realized in the course of time and to consider the transitions between stable and unstable states. For this purpose we investigate the behavior of $d\langle X(t)\rangle/dt$ in the long time regime ($t\to\infty$ for the stability region and $t\to t_c$ for the instability region, where t_c is the stability-instability transition time). For the sake of simplicity we confine ourselves to the case where the noise amplitude is small, $\alpha \ll 1$.

The solution of Eq. (9) is given by

$$X(t)=x_0 e^{M(t)}\left[1+x_0\int_{t_0}^{t} e^{M(t^*)}[\gamma+Z(t^*)]dt^*\right]^{-1} \tag{A1}$$

with

$$x_0=X(t_0)$$

and

$$M(t)=\int_{t_0}^{t}[\delta+J\langle X(t^*)\rangle]dt^*.$$

Taking into account that

$$\langle Z(t),Z(t')\rangle=2q\gamma^2\alpha\exp(-\nu|t-t'|)$$

and confining ourselves to the terms proportional to α, we get

$$\langle X(t)\rangle_0=x_0 e^{M(t)}[1+2qx_0^2\alpha\gamma^2 G(t)]\times\left[1+x_0\gamma\int_{t_0}^{t} e^{M(t^*)}dt^*\right]^{-1}+O(\alpha^2),$$

where

$$G(t)=\left(1+x_0\gamma\int_{t_0}^{t} e^{M(t^*)}dt^*\right)^{-2}\int_{t_0}^{t}dt'\times\int_{t_0}^{t}dt^* e^{M(t^*)+M(t')-\nu|t'-t^*|}$$

and the symbol $\langle\rangle_0$ denotes an average calculated over the realizations of the process $Z(t)$. Proceeding analogously from Eq. (A1) the formulas for both $\langle X^2(t)\rangle_0$ and $\langle Z(t)X^2(t)\rangle_0$ can be found.

From Eq. (9) follows

$$\frac{d\langle X\rangle_0}{dt}=\langle X\rangle_0\{\delta+J\langle X\rangle-\langle X\rangle_0[\gamma+2q\alpha x_0\gamma^2\{x_0\gamma G(t)-R(t)\}]\}+O(\alpha^2), \tag{A2}$$

where

$$R(t)=2e^{-\nu t}\left(1+x_0\gamma\int_{t_0}^{t}dt^* e^{M(t^*)}\right)^{-1}\int_{t_0}^{t}dt^* e^{M(t^*)+\nu t^*}.$$

In Eq. (A2) the following long time regime approximation can be applied:

$$R(t)-x_0\gamma G(t)\approx\frac{J\langle X\rangle+\delta}{x_0\gamma(\nu+\delta+J\langle X\rangle)}.$$

After averaging Eq. (A2) over the initial distribution we can reach in the long time regime the following asymptotic equation:

$$\frac{d\langle X\rangle}{dt}\simeq\frac{\gamma^2\langle X\rangle}{\nu+\delta+J\langle X\rangle}\left\{J^*(J^*-J_1)\langle X\rangle^2+\frac{1}{\gamma}[(2\delta+\nu)J^*-\nu-\delta J_1]\langle X\rangle+\frac{\delta(\nu+\delta)}{\gamma^2}\right\}, \tag{A3}$$

where $J^*=J/\gamma$ and $J_1=1-2q\alpha$.

Following the sign and zeros of the expression in the braces we can single out the following alternatives.

(i) For $J^*<J_1$ there is just one stationary stable solution of Eq. (A3) — the average size of the species saturates at this solution.

(ii) For $J^*>J_1$, if $\langle X\rangle$ is sufficiently large, unlimited growth of the mean value $\langle X\rangle$ occurs.

(iii) If $J^*>J_2=J_1+(\sqrt{2q\alpha}-\sqrt{\delta\tau_c})^2, \tau_c\delta<2q\alpha$ or if $J^*>J_1, \tau_c\delta>2q\alpha$, then the system is unstable and the mean value $\langle X\rangle$ grows to infinity.

(iv) In the case of $J_1<J^*<J_2$ and $\tau_c\delta<2q\alpha$ there occur two stationary solutions and a solution that grows to infinity in time. The bigger stationary solution is unstable and the smaller one is stable.

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