

Colored-noise-induced discontinuous transitions in symbiotic ecosystemsRomi Mankin,¹ Ako Sauga,¹ Ain Ainsaar,^{1,*} Astrid Haljas,^{1,2} and Kristiina Paunel¹¹*Department of Natural Sciences, Tallinn Pedagogical University, 25 Narva Road, 10120 Tallinn, Estonia*²*Institute of Theoretical Physics, Tartu University, 4 T  he Street, 51010 Tartu, Estonia*

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A symbiotic ecosystem is studied by means of the Lotka-Volterra stochastic model, using the generalized Verhulst self-regulation. The effect of fluctuating environment on the carrying capacity of a population is taken into account as dichotomous noise. The study is a follow-up of our investigation of symbiotic ecosystems subjected to three-level (trichotomous) noise [R. Mankin, A. Ainsaar, A. Haljas, and E. Reiter, *Phys. Rev. E* **65**, 051108 (2002)]. Relying on the mean-field theory, an exact self-consistency equation for stationary states is derived. In some cases the mean field exhibits hysteresis as a function of noise parameters. It is established that random interactions with the environment can cause discontinuous transitions. The dependence of the critical coupling strengths on the noise parameters is found and illustrated by phase diagrams. Predictions from the mean-field theory are compared with the results of numerical simulations. Our results provide a possible scenario for catastrophic shifts of population sizes observed in nature.

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I. INTRODUCTION

One of the key issues in ecology is how environmental fluctuations and species interactions determine variability in population densities [1,2]. Ecologists have mainly been interested in the dynamical consequences of population interactions, often ignoring environmental variability altogether. However, the essential role of environmental fluctuations has recently been recognized in theoretical ecology. Notably, the noise-induced effects on population dynamics have been the subject of intense theoretical investigations [3,4]. Moreover, ecological investigations suggest that population dynamics is sensitive to noise color [5]. Noise, via its interaction with nonlinearity of the system, has given rise to new counterintuitive phenomena: stochastic resonance [6], noise-enhanced stability [7], resonant activation [8], noise-induced nonequilibrium transitions [9–11], noise-induced multistability, and nonequilibrium phase transitions [12,13], etc.

It is recognized that gradual secular changes in environmental parameters may lead to discontinuous changes in ecosystems [14,15]. Such catastrophic transitions have also been noted in various theoretical models, assuming that the deterministic counterpart of the model is multistable [1,14,16–18]. The dominant model explaining such changes includes alternative attractors and their basins. Inspired by the fact that external multiplicative noise can induce multistability as well as first-order phase transitions in some complex systems (see Ref. [13]), the authors of Ref. [19] have investigated whether the catastrophic shifts occurring in ecosystems could be regarded sometimes as induced by multiplicative colored noise. The answer is again positive, as in a symbiotic ecosystem, described by an N -species generalized Lotka-Volterra model with logistic self-regulation, colored fluctuations of the carrying capacities of populations have been shown to produce discontinuous changes from a stable

state to an unstable one. Note that symbiotic Lotka-Volterra models with the true Verhulst (logistic) self-regulation have some special properties, such as transitions from stability to instability, even in the absence of noise [3,19,20]. When there are no transitions from stability to instability, as is true for most natural ecosystems, the features of the system can be different. A more fundamental question is, both from theoretical and practical viewpoints, whether colored fluctuations of the carrying capacities can also induce bistability of such systems and produce abrupt changes between the corresponding stable states.

In this paper we consider a broad class of N -species Lotka-Volterra models of symbiotic ecological systems with the generalized Verhulst self-regulation mechanism. The effect of fluctuating environment on the growth of a population is modeled as colored fluctuations of the carrying capacity. Since one of the characteristic quantities of an ecosystem, perhaps the most fundamental one, is its average species density [1] ($\sum_{i=1}^N x_i/N$, where x_i is the population density of the i th species), we consider average species density as the state parameter of the ecosystem. Although both logistic and generalized Verhulst mechanisms for self-regulation are useful in modeling actual ecological systems, the latter is more flexible, including the case of logistic self-regulation, and in some cases it may fit the population data better than a logistic law [1]. We study the model using a mean-field approach, focusing on exact stationary solutions of the self-consistency equation and on colored-noise-induced nonequilibrium transitions. For the sake of mathematical simplicity, it is useful to look for types of colored noise such that enable, in the case of the mean-field theory at least, the stationary probability density to be evaluated exactly for any value of the correlation time. The simplest noise of this kind is the dichotomous Markovian noise, also known as the random telegraph signal [9]. Thus motivated, in this work the fluctuations of the carrying capacity are modeled as dichotomous Markovian noise.

We mainly consider the generalized Verhulst self-regulation with an exponent $\beta > 1$ [cf. also Eq. (2)]. We

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would like to emphasize that our previous models with logistic self-regulation ($\beta=1$) [19] are qualitatively different from the present one with $\beta>1$. For the sake of clarity we note the following: (i) In the case of $\beta=1$ considered in Ref. [19], a coupling-induced transition from stability to instability occurs even if the system is deterministic (i.e., in the absence of noise). In the present model with $\beta>1$, however, the corresponding deterministic system is always monostable, i.e., there are no transitions from stability to instability. (ii) The deterministic counterpart of the modified model with $\beta=1$ in Ref. [19] is also monostable. But, in this modification the phenomenon of monostability is realized by means of introducing an artificial competing interaction. In the present model such a modification is absent; the relationship between species is but symbiotic. (iii) In comparison with Ref. [19], here the effect of fluctuating environment on the carrying capacity of a population is modeled in a more natural way — by the inclusion of an additive noise term for the carrying capacity. In Ref. [19] the immediately fluctuating quantity is the reciprocal of the carrying capacity.

The purpose of this article is twofold: First, to provide exact analytical results for colored-noise-induced first-order-like phase transitions in the model of symbiotic ecosystems over extended dichotomous noise parameters and interaction strengths. Second, the testing of models based on the generalized Verhulst self-regulation raises the important issue of how different self-regulation mechanisms can influence the behavior of stochastic complex systems. We show that dichotomous fluctuations can induce bistability of the ecosystem (with respect to the average species density), and that related discontinuous transitions can be controlled by noise parameters. We also establish the exact conditions under which abrupt transitions occur, and analyze the role of the parameters of the generalized Verhulst mechanisms in such transitions.

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 stationary stable phases, a low density phase and a high density phase of populations, and first-order-like phase transitions are established. The dependence of the critical noise parameters and the critical coupling parameter on the other system parameters is investigated. In the case of a finite number of interacting species ($N=500$) the mean-field results are compared with results of computer simulations. Section V contains brief concluding remarks.

II. MODEL

As in our previous work [19], the present model is based on the N -species generalized Lotka-Volterra equation

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

where $X_i(t)$ ($i=1, \dots, N$) is the population density of the i th species at time t [clearly $X_i(t) \geq 0$]. The function $f_i(X)$ de-

scribes the development of the i th 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]. These are taken into account by applying the generalized Verhulst model

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

with $\beta \geq 0$, where K_i is the saturation point of population density (the carrying capacity) and δ_i is the growth rate parameter of the i th species [1]. The matrix (J_{ij}) ($i, j = 1, \dots, N$) is the interaction (or coupling) matrix. If $J_{ij} > 0$ and $J_{ji} > 0$, the i th species is in a symbiotic relationship with the j th species, i.e., the presence of other species increases the growth rate of each species [3]. On the basis of Refs. [3,20] we consider all species to be equivalent, so that the characteristic parameters of the ecosystem (or metapopulation) are independent of the species, i.e., $\delta_i = \delta, K_i = K > 0, J_{ij} = J/N > 0$.

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

$$K_i = K[1 + a_0 Z_i(t)], \quad (3)$$

where the colored noise $Z_i(t)$ is assumed to be a dichotomous Markovian stochastic process [9]. A dichotomous process is a random stationary Markovian process consisting of jumps between two values $z = -1, 1$. The jumps follow in time according to a Poisson process, while the values occur with the stationary probability $1/2$. The transition probabilities between the states $Z(t) = \pm 1$ can be obtained as follows:

$$P(\pm 1, t + \tau | \mp 1, t) = \frac{1}{2}(1 - e^{-\nu\tau}), \quad \tau > 0, \quad \nu > 0. \quad (4)$$

The mean values of $Z_i(t)$ and the correlation function are

$$\langle Z_i(t) \rangle = 0, \quad \langle Z_i(t), Z_j(t') \rangle = \delta_{ij} \exp(-\nu|t - t'|). \quad (5)$$

It can be seen that the switching rate ν is the reciprocal of the noise correlation time, $\nu = 1/\tau_c$. Moreover, the following identities are true:

$$(Z_i(t))^{2k} = 1, \quad (Z_i(t))^{2k-1} = Z_i(t), \quad (k = 1, 2, \dots). \quad (6)$$

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

$$a_0 < 1. \quad (7)$$

It is practicable, by applying the properties (6) of the dichotomous process, to convert the term $K_i^{-\beta}$ in Eq. (2) to the form

$$K_i^{-\beta} = K^{-\beta} \gamma(1 + aZ_i(t)), \quad (8)$$

in which we have introduced

$$\gamma = \frac{1}{2(1-a_0)^\beta} [(1+a_0)^\beta + (1-a_0)^\beta], \quad (9)$$

and the amplitude of the dichotomous fluctuations

$$a = \frac{(1+a_0)^\beta - (1-a_0)^\beta}{(1+a_0)^\beta + (1-a_0)^\beta}. \quad (10)$$

By substituting identity (8) into Eq. (2) and applying a scaling of the form

$$\tilde{X}_i = \frac{X_i}{K}, \quad \tilde{t} = \delta t, \quad \tilde{J} = \frac{KJ}{\delta}, \quad \tilde{\nu} = \frac{\nu}{\delta}, \quad (11)$$

we get a dimensionless formulation of the dynamics

$$\frac{d\tilde{X}_i(\tilde{t})}{d\tilde{t}} = \tilde{X}_i(\tilde{t}) \left\{ 1 - \gamma [1 + a\tilde{Z}_i(\tilde{t})] \tilde{X}_i^\beta(\tilde{t}) + \frac{\tilde{J}}{N} \sum_{j \neq i} \tilde{X}_j(\tilde{t}) \right\}, \quad (12)$$

where $\tilde{Z}_i(\tilde{t})$ is a dichotomous noise with an amplitude 1 and a switching rate $\tilde{\nu}$. Note that an analogous system of equations with a trichotomous noise in the particular case of $\beta = 1$ is investigated in Ref. [19].

We emphasize that Eqs. (12) are mathematically equivalent to the initial system (1)–(3) and have been derived without any approximation. For brevity, in what follows we shall omit the tilde throughout this paper.

III. MEAN-FIELD APPROXIMATION

To proceed further with the analytical examination of model (1) with the generalized Verhulst self-regulation mechanism with arbitrary β , we follow the mean-field approximation scheme described in the case of $\beta = 1$ in Ref. [19]. We assume that $N \rightarrow \infty$. This means that we are interested in the case of infinitely many interacting species. Following Shiino [21], one can reach the mean-field approximation by replacing the site average $(1/N) \sum_{j(\neq i)} X_j(t)$ by the statistical average $\langle X(t) \rangle$ in Eq. (12). Hence, each stochastic differential equation (12) can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{dX(t)}{dt} = X(t) \{ 1 + J\langle X(t) \rangle - \gamma X^\beta(t) [1 + aZ(t)] \}. \quad (13)$$

The corresponding composite master equation is

$$\begin{aligned} \frac{\partial P_n(x,t)}{\partial t} = & - \frac{\partial}{\partial x} \{ x[r(t) - x^\beta \gamma(1+a_n)] P_n(x,t) \} \\ & + \sum_m U_{nm} P_m(x,t), \end{aligned} \quad (14)$$

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

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

Many significant inequalities follow from Eq. (13) to characterize the stationary states of the system. First, as for a stationary case, $x_1 = [r/\gamma(1-a)]^{1/\beta}$ and $x_2 = [r/\gamma(1+a)]^{1/\beta}$ are stable fixed points of the deterministic equations (13) with $Z(t) = -1$ and $Z(t) = 1$, respectively, and all trajectories $X(t)$ satisfy the following inequalities:

$$\left[\frac{r}{\gamma(1-a)} \right]^{1/\beta} > X(t) > \left[\frac{r}{\gamma(1+a)} \right]^{1/\beta}. \quad (15)$$

Second, as the mean value $\langle X \rangle$ must also satisfy the inequalities (15), it follows that if $\beta \leq 1$ and if

$$J > J_1 = \frac{\beta}{1-a_0} (1-\beta)^{(1/\beta)-1},$$

then no stationary state with a positive finite mean value can exist. It is remarkable that in the case $\beta > 1$ such a restriction of the coupling intensity J disappears.

The deterministic behavior of Eq. (13) with $\beta = 1$ neglecting noise $Z(t)$ is investigated in Ref. [20]. When $J < \gamma$, the deterministic potential associated with Eq. (13) with $Z = 0$, $\beta = 1$ causes the species to approach the equilibrium state $\langle X \rangle = 1/(\gamma - J)$, 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.

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. (14), taking as the boundary condition that there is no probability current at the boundary (15). This way we get the stationary probability distribution in the x space, $P(x, r) = \sum_n P_n^s(x)$, where $P_n^s(x)$ is the stationary probability density for the state (x, a_n) . After quite simple calculations one can find

$$P(x, r) = \frac{\beta r x^{-(1+\beta)}}{\gamma a B(1/2, \nu/2r\beta)} \left| 1 - \frac{r^2}{\gamma^2 a^2} \left(\frac{\gamma}{r} - \frac{1}{x^\beta} \right)^2 \right|^{(\nu/2r\beta)-1}, \quad (16)$$

where $r = 1 + J\langle X \rangle$, $B(\lambda, \kappa) \equiv \Gamma(\lambda)\Gamma(\kappa)/\Gamma(\lambda+\kappa)$ is the beta function, and Γ is the gamma function. The probability density $P(x, r)$ is normalized to restrict x within the interval

$$x_2 \equiv \left[\frac{r}{\gamma(1+a)} \right]^{1/\beta} < x < x_1 \equiv \left[\frac{r}{\gamma(1-a)} \right]^{1/\beta}.$$

Note that in the particular case of $\beta = 1$ the formula (16) for the stationary probability distribution coincides with the stationary probability distribution considered in Ref. [19] with $q = 1/2$ (see also Ref. [22]). The self-consistency equation for the Weiss mean-field approach, whose solution yields the

dependence of $\langle X \rangle$ on the system parameters, is

$$\langle X \rangle = \int_{x_2}^{x_1} xP(x,r)dx. \quad (17)$$

For the sake of simplicity, we shall introduce the “order parameter”

$$m := \frac{\nu}{2\gamma\beta} \left\langle \frac{1}{X^\beta} \right\rangle = \frac{\nu}{2\beta(1+J\langle X \rangle)}. \quad (18)$$

Defining the parameters ϱ and κ as

$$\varrho = \left(\frac{2\gamma\beta}{\nu} \right)^{1/\beta} \frac{\nu}{2\beta J}, \quad \kappa = \left(\frac{2\gamma\beta}{\nu} \right)^{1/\beta} \frac{1}{J}, \quad (19)$$

we get a dimensionless formulation of the self-consistency equation (17). The corresponding equation is

$$\varrho - \kappa m = m^{1-(1/\beta)} {}_2F_1 \left(\frac{1}{2\beta}, \frac{1}{2\beta} + \frac{1}{2}; m + \frac{1}{2}; a^2 \right) = g(m), \quad (20)$$

where ${}_2F_1$ is the hypergeometric function.

With the help of the stationary probability distribution (16), one can easily calculate the moments of population densities

$$\langle X^k \rangle = \left(\frac{r}{\gamma} \right)^{k/\beta} {}_2F_1 \left(\frac{k}{2\beta}, \frac{k}{2\beta} + \frac{1}{2}; m + \frac{1}{2}; a^2 \right). \quad (21)$$

IV. RESULTS

As the deterministic behavior of systems with $\beta \leq 1$ and $\beta > 1$ differs, we will restrict ourselves in this section to such systems in which the condition $\beta > 1$ holds. It is just with $\beta > 1$ that new, biologically important effects can be expected in comparison with the model with $\beta = 1$ presented in Ref. [19].

It seems convenient to introduce graphical representations of Eq. (20) to have a better understanding of 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-hand and left-hand sides of Eq. (20). We can see that there are two possible situations. (i) There is just one solution of Eq. (20) if the function $g(m)$ increases monotonically from zero to infinity as m increases. (ii) In the case of nonmonotonic dependence of $g(m)$ on m there occur either one or three solutions of Eq. (20). In the case of fixed values of β there is a lower limit for the noise amplitude $a_{0c}(\beta)$, below which $a_0 \leq a_{0c}$, $g(m)$ increases monotonically. If $a_0 > a_{0c}$, then for increasing values of m , the function $g(m)$ starts from zero, growing to a local maximum; next it decreases, attaining a local minimum, and then grows to infinity as $m \rightarrow \infty$. The critical noise amplitude $a_{0c}(\beta)$ is given by the system of transcendental equations

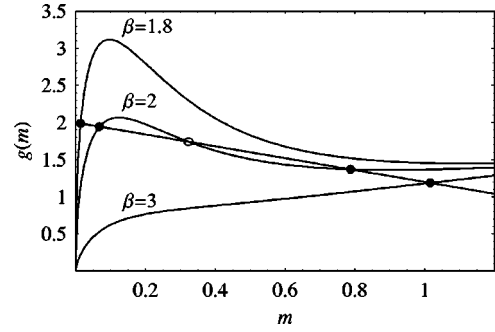


FIG. 1. Solutions of the self-consistency equation (20) at different parameters β . The amplitude parameter $a^2 = 0.995$ and the straight line is determined by $\varrho = 2, \kappa = 0.8$. The mean-field solutions are given by the intersection points of different curves with a straight line. Two typical cases are shown: there is just one stable solution (full circles on curves $\beta = 1.8$ and $\beta = 3$), or two stable solutions and one unstable solution (empty circle on curve $\beta = 2$).

$$\left. \left(\frac{dg(m)}{dm} \right) \right|_{a_0=a_{0c}} = 0, \quad \left. \left(\frac{d^2g(m)}{dm^2} \right) \right|_{a_0=a_{0c}} = 0. \quad (22)$$

The dependence of $a_{0c}^2(\beta)$ on β is represented in Fig. 2. It is remarkable that the critical parameter a_{0c}^2 increases monotonically from zero to $a_{0c}^2(\infty) \approx 0.9248$ if the parameter $\beta \in (1, \infty)$ increases. For $\beta - 1 \ll 1$ we can make do with the approximate equation $a_{0c}^2 \approx 4(\beta - 1)$.

Figure 3 shows different solutions of the self-consistency equation (20) for the mean field m as a function on the coupling constant J and the noise correlation time τ_c at the amplitude parameter $a_0^2 = 0.980$. The existence of alternative stable states (Fig. 3, the curve $\tau_c = 0.5$) indicates that there is a coexistence region, $J_1 < J < J_2$, where two stable phases are possible. Notably, coexistence does not mean that the two phases are present simultaneously; however, either is possible depending on the initial distribution. The situation described represents a typical case of first-order phase transitions. If the value of the “order parameter” m (describing the stationary stable state of the system at $J < J_2$ close to the point J_2) is on the upper branch, a slight growth of the coupling parameter may bring it beyond the bifurcation point J_2 and induce a discontinuous transition to the other stable state of the system with the value of m on the lower branch.

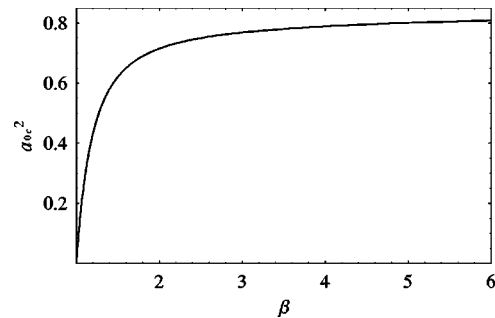


FIG. 2. The critical noise amplitude parameter a_{0c}^2 vs the system parameter β . In the case of large values of β the critical noise amplitude saturates up to the value $a_{0c}^2 \approx 0.9248$.

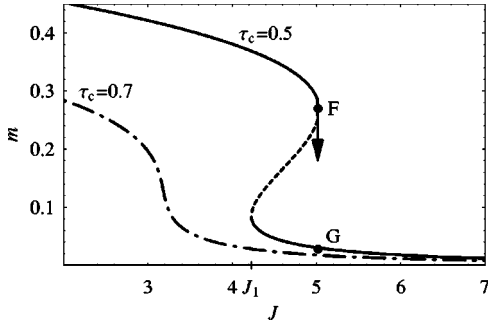


FIG. 3. Stationary mean field m vs coupling strength J at different correlation times τ_c . The system parameter $\beta=2$ and the noise amplitude $a_0=0.99$. In the case of $\tau_c=0.5$ the system shows hysteresis. Solid and dashed lines are stable and unstable solutions of the self-consistency equation (20), respectively. If the value of the mean field lies on the upper branch close to the point F with $J=J_2$, a slight growth of J induces a catastrophic transition of the system to another stable state with the value of the mean field corresponding to the point G .

Figure 4 shows a phase diagram in the $J-\tau_c$ plane at $a_0^2=0.980$ and $\beta=2$. The shaded region in the figure corresponds to the coexistence region of two phases. As the correlation time τ_c increases, the multiphase region narrows down and disappears at the value of the correlation time $\tau_c^*=0.655$. Hence, there is an upper limit $\tau_c^*(a_0, \beta)$ for the correlation time τ_c at greater values of which the system is monostable.

The curve of the boundary of the coexistence region, $J_i(\tau_c)$, is given by a parametric formula as

$$\tau_c(m) = \frac{1}{2\beta} \left[m + \frac{g(m)}{|g'(m)|} \right]^{-1}, \tag{23}$$

$$J_i(m) = \frac{1}{|g'(m)|} \left[\frac{1}{\gamma} \left(m + \frac{g(m)}{|g'(m)|} \right) \right]^{-1/\beta}, \quad i=1,2,$$

where the prime denotes a differentiation with respect to m , $m \in (m_1, m_2)$ for $i=1$, and $m \in (m_2, m_3)$ for $i=2$. The

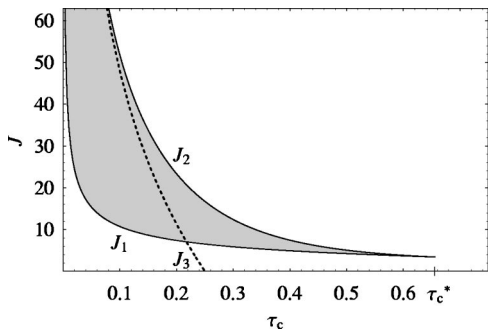


FIG. 4. A plot of the phase diagram in the $J-\tau_c$ plane at $a_0^2=0.980, \beta=2$. The shaded region in the figure corresponds to the coexistence region of two phases. The critical correlation time $\tau_c^*=0.655$. The borders of the coexistence region $J_1(\tau_c)$ and $J_2(\tau_c)$ are computed from Eq. (23). The dotted line J_3 corresponding to Eq. (24) separates the domains of the phase space, where the shapes of the probability density $P(x, r)$ are qualitatively different.

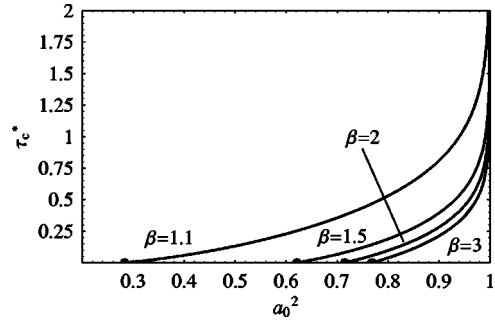


FIG. 5. The critical correlation time τ_c^* vs the noise amplitude a_0 for some values of the system parameter β . The filled dots on the a_0^2 axis correspond to values of the critical noise amplitude $a_{0c}(\beta)$: $a_{0c}^2(1.1)=0.2828, a_{0c}^2(1.5)=0.6208, a_{0c}^2(2)=0.7148,$ and $a_{0c}^2(3)=0.7686$. At the point $a_0=1$ the critical correlation time approaches infinity.

points m_1 and m_3 correspond to the points in which the function $g(m)$ achieves the local maximum and local minimum, respectively. The point m_2 corresponds to the minimum of the function $g'(m)$. From Eq. (23) a monotonic dependence of $J_i(\tau_c)$ on τ_c follows: if τ_c increases from 0 to τ_c^* , then J_i decreases from ∞ to $J^*(a_0, \beta)$. Notably, the coexistence region exists only if the coupling parameter J is sufficiently large: $J > J^*$. The critical correlation time $\tau_c^* = \tau_c(m_2)$ and the critical coupling parameter $J^* = J_i(m_2)$ can be evaluated from Eq. (23) by numerical methods or by using approximate equations.

As $\tau_c < 1/2\beta$, noise-induced transitions different from those considered can be observed on the phase diagram in the $J-\tau_c$ plane. These transitions are reflected in changes in the shape of the probability distribution (16): if $J < J_3(\tau_c)$, then the probability density $P(x, r)$ exhibits a bell-shaped form; for $J > J_3(\tau_c)$ the two-value structure of noise is still immediately reflected in the form of $P(x, r)$, i.e., $P(x, r)$ exhibits a U-shaped form. The critical curve $J_3(\tau_c)$ is determined by

$$J_3(\tau_c) = \left(1 - \frac{1}{\beta} \right) \left(1 - \frac{a_0}{a} \right)^{-1} (1 - 2\beta\tau_c)(2\beta\tau_c)^{(1/\beta)-1}. \tag{24}$$

The curve $J_3(\tau_c)$ in Fig. 4 demonstrates that, in the model considered, the phenomenon of noise-induced bistability does not depend on the shape of the stationary probability distribution $P(x, r)$, as in the coexistence region of the two phases $P(x, r)$ can exhibit either bell-shaped or U-shaped forms. Discontinuous transitions can also occur between stationary states with probability densities of qualitatively identical forms.

In Fig. 5 we have plotted the critical correlation time τ_c^* as a function of the parameters a_0^2 and β . In the case of fixed values of β the critical parameter τ_c^* increases monotonically from zero to infinity if the noise amplitude a_0 increases from $a_{0c}(\beta)$ to 1. In the vicinity of the maximal noise amplitude $a_0=1, 1 > a_0^2 > 1 - \exp(-\lambda)$, with a constant $\lambda \gg 1$; the value of τ_c^* can be estimated by the following equation:

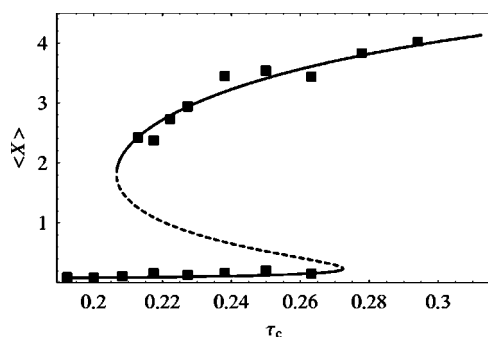


FIG. 6. Plot of the mean value of the population density $\langle X \rangle$ as a function of the noise correlation time τ_c at $a_0^2=0.939$, $\beta=2$, and $J=6$. The solid and dashed lines correspond to the stable and unstable solutions of Eq. (20), respectively. Hysteresis of the mean value $\langle X \rangle$ appears. The squares are obtained by means of computer simulations of the system (12) with $N=500$.

$$\tau_c^*(\beta, a_0) \approx \frac{1}{2} \left(1 + \sqrt{1 - \frac{1}{\beta}} \right)^{-2} \ln \left(\frac{1 + a_0}{1 - a_0} \right). \quad (25)$$

Note that for $\beta=1$ the critical correlation time can be exactly expressed by elementary functions (cf. Ref. [19])

$$\tau_c^*(1, a_0) = \frac{a_0}{2} \ln \left(\frac{1 + a_0}{1 - a_0} \right).$$

At the critical noise amplitude, $a_0 \geq a_{0c}$, we can see that τ_c^* approaches zero as $\tau_c^* \sim (a^2 - a_c^2)$, where $a_c^2 := a^2|_{a_0=a_{0c}}$ [see Eq. (10)]. As the noise amplitude $a_0 > a_{0c}$ increases, the critical coupling parameter J^* decreases monotonically from infinity to the value

$$J^*(1, \beta) = \left(1 - \frac{1}{\beta} \right)^{(1/2)[(1/\beta)-1]} \left[\left(1 - \frac{1}{\beta} \right)^{1/2} + 1 \right]^{-1/\beta} \times \exp \left[1 - \frac{1}{\beta} + \left(1 - \frac{1}{\beta} \right)^{1/2} \right] \quad (26)$$

at $a_0=1$. In the vicinity of the critical amplitude $a_0 \approx a_{0c}$, $a_0 > a_{0c}$, the parameter J^* decreases as $J^* \sim (a^2 - a_c^2)^{(1/\beta)-1}$. It is remarkable that in the case of fixed values of β there is a lower limit for the coupling parameter $J^*(1, \beta)$, below which, $J < J^*(1, \beta)$, the system is monostable at all values of the noise parameters.

Hysteresis can also occur in the case of either noise parameter, τ_c or a_0 , being chosen as the control parameter. For example, in Fig. 6 hysteresis is exposed for the mean value of the population densities $\langle X \rangle$ 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 one occurs at smaller correlation times than the opposite jumps.

The mean-field solution $\langle X \rangle$ is also compared with computer simulation of the system (12) with the finite number of interacting species, $N=500$, using the numerical methods described in Refs. [10,11]. The mean value of the population densities \bar{X} is computed by

$$\bar{X} = \frac{1}{TN} \int_{t_0}^{t_0+T} \sum_{j=1}^N X_j(t) dt. \quad (27)$$

The averaging time T was chosen to be sufficiently longer than the correlation time; for example, $T \approx 1$ near the coexistence region. The time evolution of the average value is carefully monitored until the stationary state is reached ($t_0 > 5$). The squares in Fig. 6 show \bar{X} obtained by numerical calculations as we gradually change the correlation time τ_c during integration of Eqs. (12), i.e., the solution X_i for the previous value $\tau_{ck} = \tau_{ck+1} - \Delta\tau$ is taken as the initial condition for the next point τ_{ck+1} and τ_{ck} is varied monotonically in two cases: as τ_c increases and as τ_c decreases. It can be seen that the numerical data satisfactorily coincide with the analytical stable solutions for $\langle X \rangle$. Notably, the coexistence region exists also in the case of a finite number of interacting species. As can be expected, the bistable region shrinks as the number N of species decreases. As was mentioned before, hysteresis appears also at a change of the noise amplitude. In these cases jumps to lesser numbers of individuals occur at larger amplitudes than the opposite jumps.

Perhaps the most important new result, in an ecological context, is the existence of the critical noise amplitude $a_{0c}(\beta)$. The value of $a_{0c}(\beta)$ is the lowest value of the noise amplitude for the phenomenon of hysteresis to occur, i.e., discontinuous transitions are possible if $a_0 > a_{0c}(\beta)$. It should be pointed out that the threshold amplitude $a_{0c}(\beta)$ depends only on the exponent β describing the generalized Verhulst self-regulation (see Fig. 2). This circumstance may, in principle, provide vital information to maintain ecosystem stability in a technogeneous environment. Yet, this conjecture remains to be verified by further studies. Let us note that in the case of $\beta=1$ discontinuous transitions from a stable state to an unstable one, where the mean population size grows without limit (a biologically meaningless situation), occur, however, at small noise amplitudes (see also Ref. [19]).

Finally, the modified model with $\beta=1$ in Ref. [19], exhibiting noise-induced hysteresis, is able to display discontinuous transitions similar to those represented in Figs. 3 and 6. But, in this modification the phenomenon of hysteresis is realized by the inclusion of an artificial competing interaction in the form of a dependence of the carrying capacity K on the average number of individuals of all populations. Note that the present model is qualitatively different, for such a competing interaction is absent but the mean population density nevertheless exhibits hysteresis as a function of noise parameters and the symbiotic coupling strength for all values of $\beta > 1$.

V. CONCLUDING REMARKS

In the present work, we extended our previous N -species Lotka-Volterra stochastic model of a symbiotic ecological system with a simple logistic self-regulation mechanism [19] to a version with the generalized Verhulst self-regulation [see Eq. (2), with $\beta > 1$]. We would like to emphasize that our previous model [19], where an interaction-strength-induced transition from stability to instability takes place, even if the

system is deterministic (i.e., in the absence of noise), is qualitatively different from the present model. In the latter the corresponding deterministic system is always monostable, i.e., there are no transitions from stability to instability.

The presence of colored fluctuations of the carrying capacities of populations has a profound effect on an ecosystem described by Eqs. (9)–(12) with $\beta > 1$, rearranging its parameter space so that in a certain region colored noise can induce bistability of the ecosystem. Moreover, hysteresis for the mean field and related discontinuous transitions can sometimes be found as functions of noise parameters as well as of the coupling constant. As the coupling-induced two-phase coexistence region does not exist in the system without noise, it is a colored-noise effect. The results indicate that the effect of noise is not merely restricted to the shift of the mean population density, but the whole nature of the dynamics changes. Notably, the coexistence region exists only at bounded values of the noise correlation time $\tau_c < \tau_c^*$ [see Eq. (25) and Fig. 4]. Let us note that there are lower limits for the coupling parameter, $J > J^*(1, \beta)$ [see Eq. (26)], and for the noise amplitude, $a_0 > a_{0c}$ [see Eq. (22)], at lower values of which the hysteresis of the mean field disappears. This interesting circumstance demonstrates that both agents — the symbiotic coupling of species and the colored fluctuations of the carrying capacities — act in unison to generate discontinuous transitions of the mean population density.

The following characteristic regions can be discerned for the exponent β in the formula (2), describing the generalized Verhulst self-regulation. (i) For $\beta \leq 1$ and as the coupling strength J exceeds some critical value, dichotomous noise-induced discontinuous transitions from a stable stationary phase of the system to an unstable phase can appear. In the unstable phase an explosive increase of populations occurs. Of course, the growth of any expanding population must eventually be limited by shortage of resources. Thus, in ecological contexts unstable states of a system can be interpreted variously: extinction of populations, presence of additional interaction between species that the model has not taken into account, etc. (for $\beta = 1$ see also Ref. [19]). (ii) In case $\beta > 1$ there is no unstable state of the system, and the deterministic counterpart of the system is monostable. However, environmental fluctuations can induce bistability of the ecosystem, and the system presents abrupt (first-order-like) transitions between the low and high density phases of populations. The phenomenon is robust enough to survive a modification of the noise as well as the coupling mechanism. Calculations analogous to those given in Secs. III and IV show that in the case of a trichotomous noise [19,22] most of the results of Sec. IV are qualitatively valid. It is remarkable that for a trichotomous noise Z , the flatness parameter $\varphi = \langle Z^4 \rangle / \langle Z^2 \rangle^2$, contrary to the case of the symmetric dichotomous noise

($\varphi = 1$), can be anything from 1 to ∞ . Notably, variations of the trichotomous noise flatness can also induce discontinuous transitions. We can also modify the model with $\beta > 1$ by including a term that mimics a competing interaction described in Ref. [19]. Though the concrete formulas are different, the general picture of the colored-noise-induced hysteresis is the same as that encountered in Sec. IV.

Our major result is that, for symbiotic ecological systems (or metapopulations) with the generalized Verhulst self-regulation ($\beta > 1$), colored fluctuations of the environment can cause bistability and also abrupt transitions of mean population densities. Therefore, an increase of noise amplitude or a decrease of noise correlation time can, under certain conditions, cause a catastrophic fall in the size of the populations. Moreover, as in Eq. (11) the growth rate δ and the deterministic carrying capacity K of species have been absorbed into the time scale and into the coupling strength \tilde{J} ; thus, in the original (unscaled) setup, discontinuous transitions can occur also by a gradual change of the parameters δ, K , and J .

We emphasize that for $\beta > 1$ abrupt changes of mean population densities appear only if the noise amplitude is greater than the threshold value $a_{0c}(\beta)$. As the critical noise amplitude a_{0c} increases relatively rapidly if β increases (see Fig. 2), it seems reasonable to assume that in symbiotic ecosystems with the generalized Verhulst self-regulation abrupt transitions appear with a greater probability if the exponent β is lower. It remains to be seen whether such a trend has a meaning for problems in natural sciences.

The mean-field results considered correspond to an infinite number of globally coupled species. Bearing in mind the results of computer simulations presented in Fig. 6, one can assume that this scenario is not much different from more realistic ecosystems, where the number of species is finite, at least in the case when the number of species is great enough.

It is worth emphasizing that the deterministic counterpart of most ecological models exhibiting noise-induced discontinuous transitions is able to display transitions similar to those induced by noise for a certain range of the values of the parameters [14,16,17]. In our model, however, these transitions occur only when colored noise is present.

We believe that the obtained results are of interest also in other fields where symbiotic interaction and generalized Verhulst self-regulation are relevant by modeling the system, e.g., in the dynamics of human world population [23], coupled chemical reactions, some laser systems [9], and business [24].

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