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Addendum to "Colored-noise-induced discontinuous transitions in symbiotic ecosystems"

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A symbiotic ecosystem with Gompertz self-regulation and with adaptive competition between populations is studied by means of a *N*-species Lotka-Volterra stochastic model. The influence of fluctuating environment on the carrying capacity of a population is modeled as a dichotomous noise. The study is a follow up of previous investigations of symbiotic ecosystems subjected to the generalized Verhulst self-regulation [Phys. Rev. E **69**, 061106 (2004); **65**, 051108 (2002)]. In the framework of mean-field approximation the behavior of the solutions of the self-consistency equation for a stationary system is examined analytically in the full phase space of system parameters. Depending on the mutual interplay of symbiosis and competition of species, variation of noise parameters (amplitude, correlation time) can induce doubly unidirectional discontinuous transitions as well as single unidirectional discontinuous transitions of the mean population size.

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The catastrophic shifts sometimes observed in natural ecosystems, which are due to gradual secular changes in environmental parameters are currently being actively investigated (for a review, see [1]). Inspired by the fact that external multiplicative noise can induce multistability as well as first-order phase transitions in some complex systems [2], the authors of Refs. [3,4] have shown that in a symbiotic ecosystem, described by a *N*-species Lotka-Volterra model with the generalized Verhulst self-regulation mechanism (GVM), with an exponent $\beta \geqslant 1$, colored fluctuations of carrying capacities of populations can induce bistability and produce abrupt changes between the corresponding stable states.

Although the GVM with $\beta \geqslant 1$ is useful in modeling many actual ecological communities, there are some biologically important systems, such as bacterial populations, where the Gompertz law fits population data better than the GVM [5]. Moreover, the long generation times of most organisms and the complexity of the natural environment have fostered interest in ecological experiments based on bacterial populations [6], (see also [7] for a review), where the Gompertz law may be essential.

Thus motivated, in this paper we consider an *N*-species Lotka-Volterra model of a symbiotic ecological system with the Gompertz self-regulation mechanism. For the sake of mathematical simplicity, the effect of fluctuating environment on the growth of populations is modeled as dichotomous fluctuations of the carrying capacity. We study the model using a mean-field approach, focusing on colored-noise-induced discontinuous transitions. In addition, we show that the behavior of models with the GVM $\beta < 1$ resembles that with the Gompertz law in many features—e.g., the qualitative picture of noise-induced discontinuous transitions is the same.

The main contributions of this paper are as follows: (i) The dependence of noise-induced discontinuous transitions on the intensities of symbiosis and adaptive competition is investigated in detail and illustrated by a phase diagram. (ii) We establish two types of noise-induced discontinuous transitions—doubly unidirectional transitions (DUT) and single unidirectional transitions (SUT)—and give the necessary and sufficient conditions for the appearance of such effects. To our knowledge, the appearance of a noise-induced SUT (e.g., an increase in noise amplitude can cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude no opposite transitions can occur) in models of ecosystems without extinction is a new noise-induced effect. (iii) We also show that, as compared with models with GVM $\beta > 1$, models with Gompertz law, as well as with the GVM $\beta < 1$, display a more sensitive response to environmental fluctuations, at that the vulnerability of the modeled ecosystems to variations of fluctuations' amplitude is higher at lower noise correlation times.

As in our previous works [3,4], the present model is based on the *N*-species generalized Lotka-Volterra equation with symbiotic interaction

$$\frac{d}{dt}X_i(t) = f_i(X_i(t)) + \frac{J}{N}X_i(t)\sum_{j\neq i} X_j(t), \tag{1}$$

where $X_i(t)(i=1,\ldots,N)$ is the population density of the *i*th species at time *t* (clearly $X_i(t) \geqslant 0$) and $J > 0$ is the coupling constant that describes the intensity of the symbiotic interaction. The function $f_i(X)$ describes the development of the *i*th species without any interaction with other species. As discussed above, we consider the Gompertz model for self-regulation

$$f_i(x) = -\delta_i x \ln\left(\frac{x}{K_i}\right), \tag{2}$$

where $K_i > 0$ is the saturation point of population density (the carrying capacity) and δ_i is the growth parameter of the *i*th species [8]. On the basis of Refs. [3,4,9] we consider all species to be equivalent, so that the parameters of the ecosystem (or metapopulation) are independent of the species, i.e., $\delta_i = \delta$. Random interaction with the environment (climate, diseases, etc.) is taken into account by introducing a

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dichotomous noise in $f_i(X)$. From now on we shall use fluctuations of the carrying capacity

$$K_i = K\left(1 - \frac{\epsilon}{N}\sum_{j\neq i} X_j(t)\right)[1 + aZ_i(t)], \qquad (3)$$

where the noise $Z_i(t)$ is assumed to be a dichotomous Markovian process [10] consisting of jumps between two values $z=-1$, 1, and $\epsilon>0$ is the adaptation parameter. The mean value of $Z_i(t)$ and the correlation function are $\langle Z_i(t)\rangle = 0, \langle Z_i(t), Z_j(t')\rangle = \delta_{ij}\exp(-\nu|t-t'|)$, where the switching rate ν is the reciprocal of the noise correlation time $\nu = 1/\tau_c$. Obviously, model (1) with Eqs. (2) and (3) is biologically meaningful only if $|a|<1$ (the carrying capacity K_i is nonnegative). The factor $[1-(\epsilon/N)\Sigma X_j(t)]$ in Eq. (3) mimics the decrease of the carrying capacity caused by adaptive competition of populations for common resources, such as food or living space (see also [11]). A need for the consideration of interspecies adaptive competition in models with Gompertz self-regulation of biological relevance arises from the following circumstance: In the absence of adaptation ($\epsilon=0$), for all $J>0$ the corresponding deterministic model (without noise) is characterized by instability; that means that within a finite time the site average $\bar{X} = (1/N)\Sigma X_i(t)$ grows to infinity [9]. More particularly, if $J < J_c = \delta/(eK)$, there are two possible regimes, depending on the initial distribution of the species: Either the system evolves to an equilibrium state with a finite $\bar{X}$, or to an unstable state; if $J > \delta/(eK)$, then the system is unstable at all initial distributions, i.e., $\bar{X}\to\infty$. For biologically relevant models any growth of an expanding population must eventually be stopped by shortage of resources. The addition of adaptation to the model would regulate the behavior of the system so that an unstable state of the system will be replaced by a stable stationary state. Notably, an interplay between competition and symbiosis can cause bistability in a deterministic case, i.e., if $4\epsilon\delta < J < 4\delta/(e^2K)$. Note that a qualitatively analogous situation takes place in models with the GVM, $f_i(x) = \delta x[1-(x/K_i)^\beta]$, with $0<\beta<1$. In this case, in the absence of adaptation ($\epsilon=0$) no stable state occurs when $J > J_c = \delta\beta K^{-1}(1-\beta)^{(1/\beta)-1}$, while the presence of adaptation of the form (3) can cause bistability in $4\delta\beta\epsilon < (1-\beta)^2 J < 4\delta\beta K^{-1}[(1-\beta)/(1+\beta)]^{(1/\beta)+1}$. In what follows, we will, without loss of generality, use dimensionless units with $K=1$, $\delta=1$ and $0<a<1$. As the parameter a can be interpreted as the noise amplitude, the behavior of the model does not depend on sign of a.

We follow the mean-field approximation scheme described in Ref. [4]. The mean-field approximation can be reached by replacing the site average $\bar{X}$ by the statistical average $\langle X\rangle$. Now, with the help of calculations analogous to those considered in Ref. [4] we get, in the stationary case, the self-consistency equation in the following form:

$$\langle X\rangle = (1 - \epsilon\langle X\rangle)F(\nu,a)\exp(J\langle X\rangle), \qquad (4)$$

where

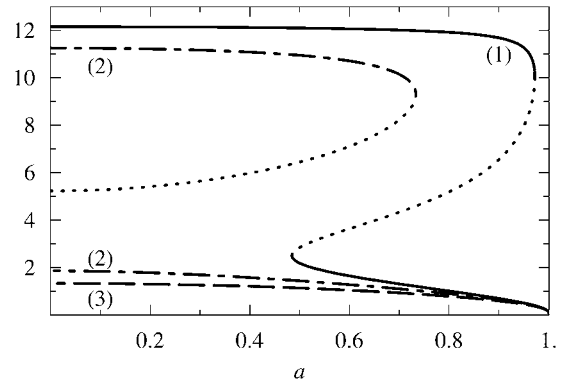

FIG. 1. Mean value of the population density $\langle X\rangle$ versus the noise amplitude a at different values of the system parameter J. The noise correlation time $\tau_c = 1/\nu = 0.2$ and the adaptation parameter $\epsilon=0.08$. Solid line (1): $J=0.5$. Dashed-dotted line (2): $J=0.42$. Dashed line (3): $J=0.3$. For all curves the dotted lines depict the unstable solutions of the self-consistency Eq. (4), the other lines depict the stable solutions of Eq. (4).

$$F(\nu,a) := (1-a)\Phi\left(\frac{\nu}{2}, \nu; \ln\left|\frac{1+a}{1-a}\right|\right) \qquad (5)$$

and Φ is the confluent hypergeometric function.

In Fig. 1 we have plotted different solutions of the self-consistency Eq. (4) for the mean value $\langle X\rangle$ as a function of the noise amplitude a and the coupling constant J at the system parameters $\nu=5$, $\epsilon=0.08$, showing that three types of graphs $\langle X\rangle$ versus a emerge. In the case of curve (a) a hysteresis for $\langle X\rangle$ appears. There are two critical values for the noise amplitude, $a_1=0.485$ and $a_2=0.972$, at which a slight variation of a induces discontinuous transitions of the mean population density $\langle X\rangle$. In this case a variation of the noise amplitude can cause discontinuous transitions of $\langle X\rangle$ in both directions, i.e., a jump from a state with a bigger number of individuals to that with a lesser one and *vice versa*. Curve (c) is described with a monotonically decreasing function as the noise amplitude a increases. Obviously the system is monostable and discontinuous transitions cannot occur. Another interesting example admitting discontinuous transitions is the case depicted in Fig. 1 with curve (b). A variation of a can cause an abrupt transition from a stable state of a bigger number of individuals to one of a lesser number, while the opposite cannot occur.

Figure 2 shows phase diagrams in the $J-a$ plane at $\nu=10$. It is remarkable that the qualitative forms of phase diagrams [see Figs. 2(a) and 2(b)] depend only on the value of the adaptation parameter ϵ. Notably the shaded common region of the two stable phases in Fig. 2(a) demonstrates a phenomenon of noise-induced bistability; in this case $\epsilon > 1/e^2$ and the corresponding deterministic system (i.e., without noise) is monostable. As the noise amplitude a decreases, the multiphase region narrows down and disappears at the value of the amplitude $a_c=0.451$. The critical value a_c of the noise amplitude is the solution of the transcendental equation $F(\nu,a)=1/(\epsilon e^2)$, [see Eq. (5)]. In the case of fixed values of ϵ the critical parameter a_c^2 increases monotonically

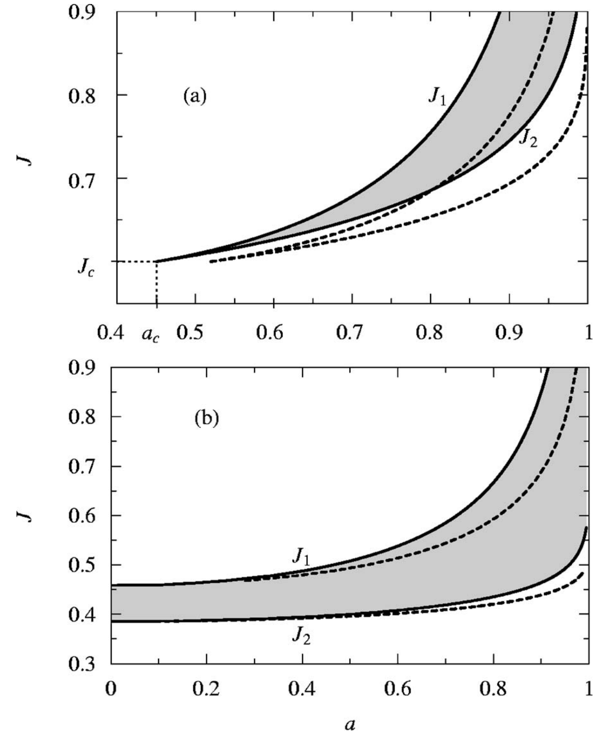

FIG. 2. (J,a) phase diagrams at different values of the adaptation parameter ϵ. The noise correlation time $\tau_c=0.1$. The shaded regions correspond to the common regions of two phases. The borders of the common region $J_1(a)$ and $J_2(a)$ are computed from Eqs. (5) and (6). Both functions $J_1(a)$ and $J_2(a)$ tend to infinity as noise amplitude increases $(a\rightarrow 1)$. In the panels the dashed lines depict the borders of the common regions at the noise correlation time $\tau_c=0.5$. (a) The case of $\epsilon>1/e^2$, $\epsilon=0.15$. (b) The case of $\epsilon<1/e^2$, $\epsilon=0.08$.

from $a^2_{c\ \mathrm{min}}=1-1/(e^4\epsilon^2)$ to 1 if the noise correlation time $\tau_c=1/\nu$ increases from zero to infinity. The tendency apparent in Fig. 2 as we compare the borders of the common regions in the case $\nu=10$ with those of the case $\nu=2$, namely, a decrease of the values of noise amplitude at which the discontinuous transitions occur as the switching rate ν grows, also takes place in the general case, i.e., for an arbitrary ν. The boundary of the common region of the two stable phases $J_i(a)$ and $i=1$, 2 is given by the following equations:

$$J_i(a)=\frac{\epsilon(\rho_i+1)^2}{\rho_i},\ \rho_i e^{-\rho_i}=\epsilon e F(\nu,a), \tag{6}$$

where $\rho_1\in(0,1)$ and $\rho_2\in(1,\infty)$. Relying on the $J-a$ phase diagram and on the formulas (5) and (6), one can find the necessary and sufficient conditions for the emergence of discontinuous transitions due to noise amplitude variations. (i) SUT occur only if $\epsilon<1/e^2$ and $J_2(0)<J<J_1(0)$. The critical values of the coupling parameter $J_1(0)$ and $J_2(0)$ are determined by Eq. (6). (ii) The sufficient and necessary conditions for DUT are $J>J_1(0)$ if $\epsilon<1/e^2$, and $J>4\epsilon$ if $\epsilon>1/e^2$. (iii) Discontinuous transitions disappear, i.e., the system is monostable for all values of noise amplitude, in the cases $\epsilon<1/e^2$, $J<J_2(0)$ and $\epsilon>1/e^2$, $J<4\epsilon$. It is remarkable that the sufficient and necessary conditions for the existence of discontinuous transitions versus a are independent of correlation time.

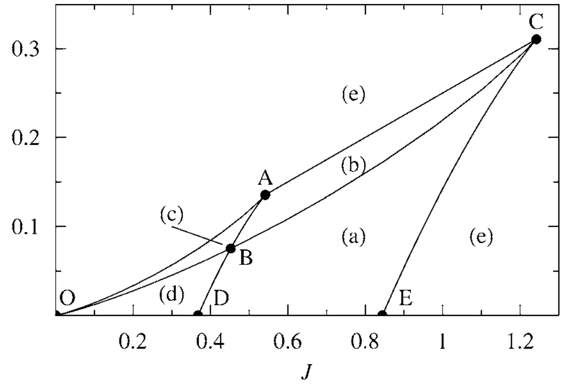

FIG. 3. (ϵ,J) phase diagram for the dependence of the population density $\langle X\rangle$ on ν in the case of $a=0.9$. Discontinuous transitions occur in the regions (a), (b), and (c). The borders of the domains are determined by Eqs. (5) and (6). More details in the text (see also Ref. [12]).

Discontinuous transitions can also occur when the noise correlation time $\tau_c=1/\nu$ is chosen as the control parameter. When using Eq. (4) to investigate the dependence of $\langle X\rangle$ on the correlation time τ_c, five different types of the graphs $\langle X\rangle$ versus ν emerge. We interpret these five qualitatively different shapes of the graphs as different "phases" in the phase space (ϵ,J) [the phases (a)–(e) in Fig. 3]. Phase (a): The system exhibits SUT from a lesser number of individuals to a bigger number. Phase (b): The phenomenon of DUT appears. Phase (c): The system also exhibits SUT, but from a bigger number of individuals to a lesser one. Phase (d): The system is bistable for all values of ν. No transitions between stable states occur. Phase (e): The system is monostable for all values of ν.

Note that the coordinates (ϵ,J) of point B monotonically decrease from $(1/e^2,4/e^2)$ to $(0,1/e)$ as the noise amplitude a increases from 0 to 1. Therefore an increase of the noise amplitude causes an increase of the domain (c), where a SUT from a stable state of a bigger numbers of individuals to a lesser number takes place. An important observation now is that the growth of noise amplitude will increase the region of the phase space (ϵ,J), where discontinuous transitions in ν are possible [12]. In particular, the necessary condition for the appearance of discontinuous transitions is $4\epsilon<J<4/(e^2\sqrt{1-a^2})$.

In stationary mean-field approximation, the influence of fluctuations on an ecosystem can be biologically interpreted as a reduction of the carrying capacity K of a single species in the original (unscaled) setup. The reduced (effective) carrying capacity K_{eff} reads: $K_{\mathrm{eff}}(\nu,a)=KF(\nu/\delta,a)$, where $F(\nu,a)$ is given by Eq. (5). Thus, our model with noise is equivalent to a deterministic model with the carrying capacity K_{eff}, where the nonlinear interplay between symbiosis and competition can cause bistability if $4\epsilon\delta<J<4\delta/[e^2K_{\mathrm{eff}}(\nu,a)]$. The possibility of a noise-induced transition is now obvious.

Bearing in mind Eq. (21) presented in Ref. [4], it can be shown that in symbiotic ecosystems with adaptive competition the general picture of noise-induced SUT and DUT (see also the phase diagram in Fig. 3) is restricted not only to models with Gompertz self-regulation, but is qualitatively true for a broad class of models with the GVM, $0<\beta<1$. The phenomenon of colored-noise-induced bistability in symbiotic ecosystems has been studied in [3,4]. However, in contrast to ours, in those models the authors have chosen a GVM with $\beta\geqslant 1$. Perhaps the most fundamental difference is that the corresponding deterministic models (without noise) are monostable, at any values of the parameters J and ϵ. As a consequence the discontinuous transitions versus noise amplitude (or correlation time) are doubly unidirectional—the effect of SUT disappears. Moreover, we emphasize that for the GVM with $\beta>1$ DUT appear only if the noise amplitude is greater than the threshold value $a_{0c}(\beta)>0$; in the model presented here such a restriction is absent. Hence, ecosystems with the Gompertz law (or with the GVM $\beta<1$) are more sensitive to environmental fluctuations than ecosystems with the GVM $\beta>1$.

In the case considered here nonlinear interplay between symbiosis and competition is important, and an increase of noise amplitude can, under certain conditions, cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude an opposite transition cannot be brought about. As in long time interval, low sizes of populations face a high probability of extinction, the consequence of SUT can prove fatal to the ecosystem. This feature of symbiotic ecosystems can provide a possible scenario for some catastrophic shifts of population sizes observed in nature [1], e.g., in the case of coral reefs, where symbiosis is essential [13]. Furthermore, the next interesting finding is that critical noise amplitudes (the amplitudes at which discontinuous transitions appear) decrease if noise correlation time decreases. On the basis of this result, one may formulate the conjecture that in symbiotic ecosystems with Gompertz law, as well as with the GVM $\beta<1$, discontinuous transitions appear with a greater probability if the noise correlation time is shorter.

Finally, we believe that the model and the results discussed here are of interest also in other fields where Gompertz self-regulation is relevant in system modeling, e.g, in market forecasting [14], in oncology [15], in bioeconomics [16], and in sociology, e.g., in the theory of cultural diffusion [17].

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