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Sensitive Response of a Model of Symbiotic Ecosystem to Seasonal Periodic Drive

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Abstract. A symbiotic ecosystem (metapopulation) is studied by means of the stochastic Lotka-Volterra model with generalized Verhulst self-regulation. The effect of variable environment on the carrying capacities of populations is taken into account as an asymmetric dichotomous noise and as a deterministic periodic stimulus. In the framework of the mean-field theory an explicit self-consistency equation for the system in the long-time limit is presented. Also, expressions for the probability distribution and for the moments of the population size are found. In certain cases the mean population size exhibits large oscillations in time, even if the amplitude of the seasonal environmental drive is small. Particularly, it is shown that the occurrence of large oscillations of the mean population size can be controlled by noise parameters (such as amplitude and correlation time) and by the coupling strength of the symbiotic interaction between species.

Keywords: Symbiotic ecosystem, dichotomous noise, mean-field approximation, Verhulst self-regulation, stochastic amplification

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INTRODUCTION

The dynamical stability of populations and ecosystems is known to govern their responsiveness to fluctuating environmental conditions, which determine with what reliability natural resources provide life-sustaining services to society. Therefore, population and ecosystem dynamics is a major structuring theme in ecology [1]. Fluctuations, via interaction with nonlinearity in physical, chemical, and biological systems, have given rise to several counterintuitive phenomena: stochastic resonance [2–4], noise-enhanced stability [5, 6], stochastic transport in ratchets [7–9], memory generated resonance [10, 11], and so forth. Recently, the essential role of environmental fluctuations has been recognized in theoretical ecology. Noise-induced effects on population dynamics have been subject to intense theoretical investigations [12, 13]. Those include, for example, noise-induced oscillations in two competing species [14], stochastic resonance in population dynamics [15], extinction statistics in N random interacting species [16], transient dynamics of ecosystems in the presence of colored noise [17, 18], and noise-controlled oscillations in predator-prey models [19]. The problem how environmental fluctuations and species interaction may determine oscillations in population sizes, displayed by many organisms in nature as well as in laboratory cultures [1, 20, 21], is one of the central issues in ecology.

Inspired by the fact that external multiplicative noise can induce multistability as well as first-order phase transitions in some complex systems [22], the authors of Refs. [18, 23] have shown that in a symbiotic ecosystem, described by a N-species Lotka-Volterra model with a generalized Verhulst self-regulation mechanism (GVM) colored fluctuations of carrying capacities (a limiting factor on the population growth, which is imposed by environmental factors, basically food and space limitations) of populations can induce bistability and produce abrupt changes between different states of the ecosystem. Although the effect of environmental colored noise on the carrying capacity, and thus also on metapopulation (or ecosystem) dynamics have been subject to intense theoretical investigations [18, 23], it seems that proper analysis of the potential consequences of an interplay of colored fluctuations and a time-periodic seasonal drive of the carrying capacity in population growth models with a GVM is still missing in literature.

Thus motivated, we consider the Lotka-Volterra stochastic model with a GVM for a N-species symbiotic ecosystem. For the sake of mathematical simplicity, the effect of time-variable environment on the carrying capacities of species is modeled by a deterministic periodic stimulus and by an asymmetric dichotomous noise. Although both symmetric and asymmetric dichotomous noises may be too rough approximations of environmental fluctuations, the latter is more flexible to model actual fluctuations [24]. We study the model using a mean-field approach, focusing on the behavior of the statistical moments of a population size.

The main contributions of this paper are as follows: (i) For the described model, in the long-time limit exact formulas for the analytical treatment of the dependence of the probability distribution and the statistical moments
of the population size on system parameters are found. (ii) We establish that in some cases an interplay of a small periodic seasonal forcing and colored noise causes large oscillations of the mean population size in time. (iii) We also show that this phenomenon is sensitive to variations of the coupling strength of symbiotic interaction – the amplitude of oscillations of the mean population size increases rapidly as the coupling strength increases.

**MODEL**

We consider the model of a symbiotic ecosystem (metapopulation), which is slightly different from the model considered in [23]. The major advantage of this model (perhaps more realistic that in [23]) is that it enables to find, in the mean-field approximation, exact moments of a population size for all values of the system parameters. Our starting point is the $N$-species generalized Lotka-Volterra equation [18, 23, 25, 26]

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

where $X_i(t) i = 1, ..., N$ is the population density of the $i$-th species at time $t$ (clearly $X_i(t) \geq 0$). The function $g_i(X)$ describes the development of the $i$-th species without any interaction with other species, i.e., the self-regulation of population $i$. The matrix $(J_{ij}) (i, j = 1, ..., N)$ is the interaction (or coupling) matrix. On the basis of Refs. [25, 26] we consider a symbiotic relationship between the species ($J_{i1} > 0$ and $J_{j2} > 0$), i.e., the presence of other species increases the growth rate of each species. We also assume that all species are equivalent, so that the characteristic parameters of the ecosystem (or metapopulation) are independent of the species, i.e., $J_{ij} = J/N > 0$. A typical mechanism for self-regulation consists of territorial breeding requirements and the crowding effect caused by competition for resources [27, 28]. These are taken into account by applying the generalized Verhulst mechanism

$$g_i(X) = \delta_0 - \gamma(t)X^\beta, \quad (2)$$

with $\beta > 0$, where $\gamma(t)$ characterizes the carrying capacity for the $i$th population and $\delta_0 > 0$ is the growth rate parameter of the species. The effect of time-variable environment on the dynamics of the population is taken into account as a variable carrying capacity in the model including a time-periodic deterministic part and an asymmetric dichotomous noise. More precisely, we assume that

$$\gamma(t) = \gamma(1 + A_0 \sin \Omega t + Z_i(t)), \quad (3)$$

where the constant $\gamma$ determines the carrying capacity $K$ for a single population without any temporal perturbations:

$$K = \left( \frac{\delta_0}{\gamma} \right)^{\frac{1}{\beta}}. \quad (4)$$

The periodic term with an amplitude $A_0$ and frequency $\Omega$ in the right side of Eq. (3) mimics the time dependence of the availability of a resource whose dynamics is forced by diverse environmental factors and climatic oscillations. Random interaction with the environment (climate, disease, etc.) is taken into account by introducing a colored noise $Z_i(t)$ in $\gamma(t)$. The symbol $\bar{X}_i(t)$ in Eq. (1) denotes the time average of $X_i(t)$ over the period $T = 2\pi/\Omega$ of the deterministic seasonal drive of the carrying capacity

$$\bar{X}_i(t) = \frac{1}{T} \int_{t-T}^{t} X_i(t')dt'. \quad (5)$$

The use of $\bar{X}_i(t)$ instead of $X_i(t)$ in Eq. (1) mimics the fact that in real ecosystems the influence of symbiotic interaction between species on the population growth rate is seasonal rather than instantaneous. The stationary random process $Z_i(t)$ is assumed as a statistically independent asymmetric dichotomous Markovian process consisting of jumps between two values $z_1 = \varepsilon a$ and $z_2 = -(1-\varepsilon)a$, where $0 < \varepsilon < 1$ is the asymmetry parameter [24]. The jumps follow in time according to a Poisson process, while the values $z_1$ and $z_2$ occur with the stationary probabilities $1-q$ and $q$ ($0 < q < 1$), respectively. The mean value of $Z_i(t)$ and the correlation function are

$$\langle Z_i(t) \rangle = (\varepsilon - q)a, \quad \langle Z_i(t + \tau)Z_j(t) \rangle = (\varepsilon - q)^2a^2 + \delta_{ij}q(1-q)^2ae^{-\nu \tau}, \quad (6)$$
where $\delta_j$ is the Kronecker symbol.

It can be seen that the switching rate $\nu$ is reciprocal to the noise correlation time, $\nu = 1/\tau_c$. As a biologically meaningful carrying capacity is always positive, then in what follows we shall assume that

$$0 \leq A_0 < 1, \quad 0 \leq (1 - \varepsilon)a < 1 - A_0. \quad \tag{7}$$

**MEAN-FIELD APPROXIMATION**

To proceed further with the analytical examination of model (1) with a GVM with an arbitrary $\beta$, we follow the mean-field approximation scheme described in Refs. [23, 29]. We assume that $N \to \infty$. This means that we are interested in the case with a very large number of interacting species. One can reach the mean-field approximation by replacing the site average $(1/N) \sum_{j \neq i} \tilde{X}_j(t)$ by the statistical average $\langle \tilde{X}(t) \rangle$ in Eq. (1). Hence, each stochastic differential equation (1) can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{d}{dt} X(t) = X(t) \left\{ \delta_0 + J\langle \tilde{X}(t) \rangle - \gamma X^2(t) \left[ 1 + (\varepsilon - q)a + A_0 \sin \Omega t + \tilde{Z}(t) \right] \right\}, \quad \tag{8}$$

where $\tilde{Z}(t)$ is the zero-centred asymmetric dichotomous noise defined as

$$\tilde{Z}(t) = Z(t) - \langle Z(t) \rangle. \quad \tag{9}$$

Using that in the long-time limit ($t \to \infty$), the mean population size $\langle X(t) \rangle$ is a periodic function of $t$ with the period $T = 2\pi/\Omega$ we obtain

$$\langle \tilde{X}(t) \rangle = \frac{1}{T} \int_{t-T}^{t} X(t') dt' = \frac{1}{T} \int_{0}^{T} \langle X(t) \rangle dt, \quad t \to \infty, \quad \tag{10}$$

i.e., $\langle \tilde{X}(t) \rangle$ is a positive constant. Thus, the equation (8) can be reduced to a linear stochastic equation by means of the transformation

$$Y = \frac{1}{X^2}, \quad \tag{11}$$

which leads to the equation

$$\frac{d}{dt} Y(t) = -\beta \frac{\delta}{Y(t)} + \beta \gamma \left[ 1 + (\varepsilon - q)a + A_0 \sin \Omega t + \tilde{Z}(t) \right], \quad \tag{12}$$

where

$$\delta := \delta_0 + J\langle \tilde{X} \rangle. \quad \tag{13}$$

Due to the linearity of Eq. (12) the solution $Y(t)$ can be represented as a superposition of the deterministic part $y_1(t)$ and the stochastic part $Y_2(t)$:

$$Y(t) = y_1(t) + Y_2(t), \quad \tag{14}$$

which are solutions of the equations

$$\frac{d}{dt} y_1(t) = -\beta \frac{\delta}{y_1(t)} + \beta \gamma (1 + (\varepsilon - q)a + A_0 \sin \Omega t) \quad \tag{15}$$

and

$$\frac{d}{dt} Y_2(t) = -\beta \frac{\delta}{Y_2(t)} + \beta \gamma \tilde{Z}(t), \quad \tag{16}$$

respectively. The solution of Eq. (15) reads as

$$y_1(t) = Ce^{-\beta \delta t} + \frac{\gamma}{\delta} \left[ 1 + a(\varepsilon - q) - \frac{A_0 \beta \delta}{\sqrt{(\beta \delta)^2 + \Omega^2}} \cos(\Omega t + \phi) \right], \quad \tag{17}$$

where the phase shift $\phi$ is given by

$$\tan \phi = \frac{\beta \delta}{\Omega} \quad \tag{18}$$
and $C$ is determined by an initial condition. It is obvious that in the long-time limit ($t \to \infty$) the memory about the initial condition will vanish and the deterministic part of the solution can be represented in the form

$$y_1(t) = \frac{\gamma}{\delta} \left[ 1 + a(e - q) - \frac{A_0 \beta \delta}{\sqrt{(\beta \delta)^2 + \omega^2}} \cos(\Omega t + \varphi) \right], \quad t \to \infty.$$  

(19)

As the noise $\tilde{Z}(t)$ is a stationary process, the solution $Y_2(t)$ of the stochastic differential equation (16) in the long-time limit is also a stationary process. The master equation corresponding to Eq. (16) is

$$\frac{\partial P_n(y_2,t)}{\partial t} = \beta \frac{\partial}{\partial y_2} \left\{ \left[ \delta y_2 - \gamma \bar{a} \right] P_n(y_2,t) \right\} + \nu(-1)^n [qP_1(y_2,t) - (1 - q)P_2(y_2,t)],$$  

(20)

where $n = 1, 2$; $\tilde{z}_1 = qa$, $\tilde{z}_2 = -(1 - q)a$, and $P_n(y_2,t)$ denotes the probability density for the combined process $(y_2, \tilde{z}_a,t)$. As for a stationary case, $y_2^+ = (\gamma/\delta)qa$ and $y_2^- = -(\gamma/\delta)(1 - q)a$ are stable fixed points of the deterministic equations (16) with $\tilde{Z}(t) = aq$ and $\tilde{Z}(t) = -a(1 - q)$, respectively, while all trajectories $y_2(t)$ satisfy the following inequalities:

$$\frac{\gamma}{\delta} qa > y_2(t) > -\frac{\gamma}{\delta}(1 - q)a.$$  

(21)

For a stationary state we can solve Eq. (20), taking as the boundary condition that there is no probability current at the boundary determined by (21). This way we get the stationary probability distribution in the $y_2$ space

$$\tilde{P}(y_2) = P_n(y_2) + P_2(y_2),$$  

(22)

where $P_n(y_2)$ is the stationary probability density for the state $(y_2, \tilde{z}_a)$. After quite simple calculations one can find

$$\tilde{P}(y_2) = \frac{(\gamma a / \delta)^{1-\frac{1}{\beta}}} {B(\nu(1 - q)/\beta, \nu/(\beta \delta))} \left| y_2 + \frac{\gamma(1 - q)a}{\delta} \right|^{\frac{\nu(1 - q)}{\beta} - 1} \left| y_2 - \frac{\gamma qa}{\delta} \right|^{\frac{\nu}{\beta} - 1},$$  

(23)

where $B(\lambda, \kappa) = \Gamma(\lambda) \Gamma(\kappa) / (\Gamma(1 + \kappa))$ is the beta function and $\Gamma$ is the gamma function.

Now, using Eqs. (11), (14), (19), and (23) we obtain, in the long-time limit, for the probability density $P(x,t)$ in the $x$ space

$$P(x,t) = \frac{\beta}{x^+ + 1} \tilde{P}(y_2(x,t)), \quad y_2(x,t) = \frac{1}{x^+} - y_1(t), \quad t \to \infty.$$  

(24)

Note that $P(x,t)$ is normalized to restrict $x$ within the interval $(x^+, x^-)$, where

$$x^+ = \left[ y_1(t) + \frac{aq \gamma}{\delta} \right]^{-\frac{1}{\beta}}, \quad x^- = \left[ y_1(t) - \frac{a(1 - q) \gamma}{\delta} \right]^{-\frac{1}{\beta}}.$$  

(25)

With the help of the probability distribution (24), one can easily calculate the moments of the population size

$$\langle X^k \rangle = \int_{x^+}^{x^-} x^k P(x,t) dx = \left( \frac{\delta}{\gamma y^*(t)} \right)^{\frac{k}{\beta}} \text{ }_2F_1 \left( \frac{k}{\beta}, \frac{\nu}{\beta \delta}, \frac{\nu}{\beta \delta}; y^*(t) \right),$$  

(26)

where $_2F_1$ is the hypergeometric function and

$$y^*(t) = 1 + a e - \frac{A_0 \beta \delta}{\sqrt{(\beta \delta)^2 + \omega^2}} \cos(\Omega t + \varphi).$$  

(27)

The self-consistency equation for the Weiss mean-field approach, whose solution yields the dependence of $\langle X \rangle$ on the system parameters, is

$$\langle X \rangle = \frac{1}{T} \int_0^T \left( \frac{\delta}{\gamma y^*(t)} \right)^{\frac{k}{\beta}} \text{ }_2F_1 \left( \frac{1}{\beta}, \frac{\nu}{\beta \delta}, \frac{\nu}{\beta \delta}; y^*(t) \right) dt,$$  

(28)

with $\delta = \delta_0 + J \langle X \rangle$.

The analytical expressions (26)-(28) belong to the main results of this work. These equations fully determine the behavior of the average population abundance in response to system parameters in the long-time limit.
RESULTS

As the deterministic behavior of Eq. (1), if temporal perturbations of the carrying capacity are neglected, differs qualitatively for $\beta \leq 1$ and $\beta > 1$ [18, 23], we will restrict ourselves in this section to such systems in which the condition $\beta > 1$ holds. By use of Eqs. (26)-(28) we can now explicitly obtain the behavior of $\langle X(t) \rangle$ for any combination of the system parameters $\gamma$, $\delta_0$, $\beta$, $\Omega$, $A_0$, $a$, $\epsilon$, $q$, and $v$. Next we consider, in brief, the phenomenon of stochastic amplification (SA) – a relatively small periodic forcing of the carrying capacity can be amplified by noise and cause strong oscillations of the mean population abundance $\langle X(t) \rangle$ – in the model system (1)-(3) (cf. also Figure 1). To show this effect, we assume that the amplitude $A_0$ of the periodic forcing is small

$$A_0 \ll 1.$$  \hspace{1cm} (29)

As the noise is absent, i.e., $a = 0$, the population size $x$ oscillates also with a small amplitude in comparison with its time average $\bar{x}$

$$x \approx \bar{x} \left[ 1 + \frac{A_0 \delta}{\sqrt{(\beta \delta)^2 + \Omega^2}} \cos (\Omega t + \varphi) \right],$$  \hspace{1cm} (30)

where $\bar{x}$ can be found from the equation

$$\bar{x} \approx \left( \frac{\delta_0 + J \bar{x}}{\gamma} \right)^\frac{1}{\beta}.$$  \hspace{1cm} (31)

It should be noted that Eq. (31), in a slightly modified form, is also applicable for $\langle X \rangle$ in the fast-noise limit, $\nu \to \infty$. In this case, i.e., at very high frequencies of colored fluctuations, the dynamics of the system is under the influence of the average

$$\langle \gamma(t) \rangle = \gamma (1 + (\epsilon - q) a + A_0 \sin \Omega r)$$  \hspace{1cm} (32)

and thus behaves as the corresponding deterministic system, i.e.,

$$x \approx \bar{x} \left[ 1 + \frac{A_0 \delta}{(1 + (\epsilon - q) a) \sqrt{(\beta \delta)^2 + \Omega^2}} \cos (\Omega t + \varphi) \right],$$  \hspace{1cm} (33)

with $\gamma$ replaced by $\gamma' = (1 + (\epsilon - q) a) \gamma$. SA is possible if the noise switching rate $\nu$ satisfies the inequality

$$\nu < \frac{\delta}{1 - q}.$$  \hspace{1cm} (34)

Namely, by the condition (34) the hypergeometric function $\Gamma_1$ in Eq. (26) tends to infinity as $a$ tends to the minimum of the function $\gamma'(t)$; in the case of the opposite inequality, i.e., $\nu > \delta/(1 - q)$, $\Gamma_1$ remains finite in such a limit process.

FIGURE 1. Plots of the mean population size $\langle X \rangle$ vs time $t$, computed from Eqs. (26)-(28). All quantities are dimensionless with $\gamma = \delta_0 = 1$, $\Omega = 0.2$, $\nu = 1.2$, $A_0 = 0.22$, $q = 0.4$, $\epsilon = 0.2$, and $a = 0.974$. Panel (a): $\beta = 1.25$; solid line, $J = 0.6$; dashed line, $J = 0.3$; dotted line, $J = 0$. Panel (b): $J = 0.45$; solid line $\beta = 1.2$; dashed line, $\beta = 1.3$; dotted line, $\beta = 2$.
In Figure 1 we depict the behavior of $\langle X(t) \rangle$ for various values of the coupling intensity $J$ and the self-regulation exponent $\beta$. This figure demonstrates that the amplification of oscillations gets more and more pronounced as the coupling intensity increases or as the exponent $\beta$ decreases. From Eq. (26) it follows that strong SA appears if the noise amplitude $(1 - \varepsilon)a$ is greater than a “threshold value” which increases relatively rapidly as the self-regulation exponent $\beta$ increases (cf. Figure 2). To clarify the previous statement, we shall now study the behavior of $\langle X(t) \rangle$ in the limit (see also Eq. (34))

$$\delta \gg \max \{\nu, \Omega\}. \quad (35)$$

By condition (35) Eq. (26) gives for the first moment of the population size

$$\langle X(t) \rangle \approx \left(\frac{\delta}{\gamma}\right)^{\frac{1}{\beta}} \left[(1 - q) (y^* (t))^{\frac{1}{\beta}} + q (y^* (t) - a)^{-\frac{1}{\beta}}\right]. \quad (36)$$

Let us note that condition (35) has a distinct physical meaning. At the long-correlation-time limit $\nu \ll \delta$, Eqs. (20) for $P_1 (y_2, t)$ and $P_2 (y_2, t)$ are decoupled and the mean population size is given by the average of two deterministically formed population sizes which correspond to noise states $\bar{z}_1$ and $\bar{z}_2$, i.e., the time intervals between noise-state switchings are large enough to form the long-time limit of deterministic dynamics. The second term $(y^* (t) - a)^{-1/\beta}$ in the right side of Eq. (36) corresponds to the noise state $\bar{z}_2$. Obviously, the maximum of this term increases rapidly (as does the maximum value of $\langle X(t) \rangle$) as the noise amplitude $(1 - \varepsilon)a$ tends to $1 - A_0$ (see Eq. (27)).
It should be noted that the phenomenon of SA is qualitatively different from conventional stochastic resonance [2, 3, 30]. In the case of stochastic resonance, the amplification of a small input signal means a nonmonotonic dependence of the output signal or some function thereof on noise parameters, but in the case considered here the amplification of the output signal depends monotonically on noise parameters (cf. also Figure 3).

Figure 3 illustrates that the phenomenon of SA gets more pronounced as either the correlation time \( \tau_c \) or the parameter \( q \) increases.

**CONCLUSION**

We have presented some results for the mean-field dynamics of an \( N \)-species stochastic symbiotic Lotka-Volterra system subjected to generalized Verhulst self-regulation. The influence of a time-variable environment on the carrying capacities of species subpopulations is modeled as a periodic deterministic part and an asymmetric dichotomous noise. Our main conclusion is that a nonlinear interplay between seasonal periodic drive and colored noise can, under certain conditions, cause large oscillations of the mean population sizes, even if the amplitude of the seasonal environmental drive is small.

The phenomenon is robust enough to survive a modification of the noise as well as of the coupling mechanism. Calculations analogous to those given in the present paper show that in the cases of a trichotomous noise [6] and by including a term that mimics an additional competing interaction described in Ref. [18] most of the results of the present paper remain qualitatively valid. Furthermore, the next interesting finding is that the amplitude of the oscillations of the population sizes increases rapidly as the coupling strength of the symbiotic interaction increases or as the self-regulation exponent decreases. On the basis of this result, one may formulate the conjecture that the models of symbiotic ecosystems (or metapopulations) with a greater coupling strength display a more sensitive response to the time-variability of the environment, i.e., the vulnerability of the modeled ecosystems to variations of the fluctuations amplitude is higher at a stronger symbiosis. These features of the model can provide a possible scenario for large oscillations or for some catastrophic shifts of population sizes observed in nature [31], e.g., in the case of coral reefs, where symbiosis is essential [32]. It remains to be seen whether the mechanism of the noise-induced amplification of oscillations of the population size considered here can play some role in natural ecosystems (or in metapopulations) dominated by a symbiotic relationship or by cooperation between species. Undoubtedly, ultimate verification of this phenomenon lies with experimentalists-ecologists.

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