

# Statistical Properties of Multispecies Competition Ecosystems Subjected to Dichotomous Noises\*

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**Abstract** We investigate statistical properties of multispecies competition ecosystems subjected to both symmetric and asymmetric dichotomous noises. The expression of the stationary probability distribution function (SPDF) is analytically derived by means of mean-field approximation, and verified by stochastic simulations. The results indicate that: (i) A noise amplitude ( $a_0$ ), a noise autocorrelation time ( $\tau_0$ ) and a noise symmetry parameter ( $k$ ) all can affect the SPDF; (ii) There is an optimal  $\tau_0$ , which makes the mean value of population density be maximal, near which a transition takes place, i.e., the stationary mean value of species density ( $\langle x \rangle_{\text{st}}$ ) suddenly falls to a lower constant; (iii) As  $k$  decreases, the maximum of  $\langle x \rangle_{\text{st}}$  and the optimal  $\tau_0$  increase. The parameter planes of  $\tau_0 - a_0^2$  and  $\tau_0 - k$  for the transition are plotted.

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**Key words:** statistical properties, multispecies competition, dichotomous noise, transition

## 1 Introduction

The Lotka–Volterra model describing the populations of interacting biological species was verified by two categories of experiment: one is the observations in a natural ecological system and the other is the controlled experiments. In the first category, the data collected by Elton<sup>[1]</sup> on rodents and fur animals support the implication that physical environmental factors and interactions between various species probably contribute to the fluctuations of the species populations. In the second category, the experiments on flour beetle tribolium by Neyman, *et al.*,<sup>[2]</sup> point to the need of introduction of stochastic processes in the model. Hence, how environmental fluctuations and species interactions determine variability in population densities is the key issue in ecology.<sup>[3–5]</sup>

Noise is known to cause disturbing effects through additions of fluctuations and instability to the system. Noise, via its interaction with nonlinearity of the system, however, has given rise to new phenomena. In a symmetric two-species competition, noise is responsible for temporal oscillations, spatial patterns, and the enhancement of the response of the system via stochastic resonance.<sup>[6]</sup> For symbiotic ecosystems, noise induces discontinuous transitions and catastrophic shifts.<sup>[7–8]</sup> Noise and time delay together suppress population explosion of mutualism ecosystems,<sup>[9]</sup> and induce first-order-like

transition and coherence resonance in a symmetric two-species competition.<sup>[10]</sup> In predator-prey communities, colored noise induces Hopf bifurcations.<sup>[11]</sup> In addition, a noise also delays species extinction,<sup>[12]</sup> induces resonant activation,<sup>[13]</sup> stochastic resonance,<sup>[14–15]</sup> and enhances stability of metapopulation<sup>[16]</sup> and nonequilibrium phase transitions,<sup>[17–18]</sup> etc. The paper mainly study the effect of dichotomous noise on multispecies competition ecosystems.

The paper is structured as follows. In Sec. 2, the Lotka–Volterra model of  $N$ -species competition subjected to an asymmetric dichotomous noise is introduced. In Sec. 3, the mean-field approximation is applied to calculating stationary probability distribution function (SPDF) and mean value of species density. In Sec. 4, the results are presented. In Sec. 5, conclusions are made.

## 2 Model

Based on the  $N$ -species Lotka–Volterra equation,<sup>[19]</sup> we discuss the model

$$\frac{dx_i(t)}{dt} = x_i(t) \left[ f_i(x_i(t)) + \sum_{j \neq i} J_{ij} x_j(t) \right],$$

$$i, j = 1, 2, \dots, N, \quad (1)$$

where  $x_i(t)$  is the population density of the  $i$ -th species at time  $t$ , and  $J_{ij}$  denotes the interspecies interaction matrix that represents the environmental conditions.<sup>[20–21]</sup>

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As  $J_{ij} > 0$ , these species are symbiotic, i.e., the presence of other species increases the growth rate of each species, otherwise they are competitive.<sup>[22]</sup> Here we only consider the case of  $J_{ij} < 0$ . The function  $f_i(x_i)$  describes the development of the  $i$ -th species without any interaction with other species. Applying the generalized Verhulst model, one gets

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

where  $\beta$  is the model exponent, and as  $\beta \geq 0$  the system considered contains profuse biological information.  $K_i$  is the saturation point of population density (the carrying capacity) and  $\delta_i$  is the growth rate parameter of the  $i$ -th species.<sup>[4]</sup> On the basis of Refs. [22–23], we consider all species to be equivalent, so that the characteristic parameters of the ecosystem are independent, i.e.,  $\delta_i = \delta$ ,  $K_i = K$ ,  $J_{ij} = J/N < 0$ .

The environment (climate, diseases, etc.) can cause fluctuations in the carrying capacity  $K_i$ . This random interaction is taken into account by introducing colored noise  $Z_i$  in  $f_i(x_i)$ . Thus  $K_i$  reads<sup>[7–8]</sup>

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

where  $Z_i(t)$  is assumed to be a two-level stationary telegraph process, and takes two values  $-1$  and  $k$  ( $k$  is a noise symmetry parameter, the dichotomous noise is symmetric as  $k = 1$ ; otherwise it is asymmetric<sup>[24]</sup>), and  $a_0$  is the noise amplitude. The transition rate from  $-1$  to  $k$  is  $\nu_1$ , and the reverse transition rate is  $\nu_2$ . The mean value of  $Z_i(t)$  is assumed to be equal to zero

$$\langle Z_i(t) \rangle = \frac{k\nu_1 - \nu_2}{k\nu_1 + \nu_2} = 0. \quad (4)$$

Its autocorrelation rate is given by

$$\nu = \nu_1 + \nu_2, \quad (5)$$

thus its autocorrelation time  $\tau_0 = 1/\nu$ .

From Eqs. (4) and (5), we can easily obtain

$$\nu_1 = \frac{\nu}{k+1}, \quad \nu_2 = \frac{k\nu}{k+1}. \quad (6)$$

Thus the correlation function of  $Z_i(t)$  is

$$\langle Z_i(t)Z_i(0) \rangle = D\nu \exp(-\nu|t|), \quad (7)$$

where  $D$  is defined by

$$D = \frac{1}{\tau} \int_{-\infty}^{+\infty} \langle Z_i(\tau)Z_i(0) \rangle d\tau = \frac{k}{\nu}. \quad (8)$$

As the noise  $Z_i(t)$  is asymmetric, it means that the environment makes the carrying capacity  $K_i$  fluctuate between two values  $K(1 - a_0)$  and  $K(1 + ka_0)$ , with mean waiting times  $1/\nu_1$  and  $1/\nu_2$ , respectively.

In order to make the calculation of the following process be convenient, we transform the asymmetric dichotomous noise into one with values  $-c$  and  $c$ . Let

$$Z_i(t) = \eta_i(t) + g, \quad (9)$$

where  $\eta_i(t)$  is a dichotomous noise, which takes two values  $-c$  and  $c$ , and  $g$  is a constant. The transition rate from  $-c$  to  $c$  is  $\nu_1$ , and the reverse transition rate is  $\nu_2$ . The mean value and the correlation function of  $\eta_i(t)$  are respectively

$$\langle \eta_i(t) \rangle = -g, \quad (10)$$

$$\langle \eta_i(t)\eta_i(0) \rangle = g^2 + D\nu \exp(-\nu|t|). \quad (11)$$

Using the relation between  $Z_i(t)$  and  $\eta_i(t)$ , we have

$$c = \frac{k+1}{2}, \quad g = \frac{k-1}{2}. \quad (12)$$

Inserting Eq. (9) to Eq. (3),  $K_i$  reads

$$K_i = K[1 + a_0 g + a_0 \eta_i(t)] = K'[1 + a'_0 \epsilon_i(t)], \quad (13)$$

with

$$K' = K(1 + a_0 g), \quad a'_0 = \frac{a_0 c}{1 + a_0 g}, \quad (14)$$

where

$$\epsilon_i(t) = \frac{\eta_i(t)}{c}, \quad (15)$$

and takes two values  $-1$  and  $1$ . This means that the following equations are satisfied

$$K_i^{-\beta} = K'^{-\beta} \gamma [1 + a\epsilon_i(t)], \quad (16)$$

with

$$\gamma = \frac{1}{2(1 - a_0'^2)^\beta} [(1 + a'_0)^\beta + (1 - a'_0)^\beta], \quad (17)$$

$$a = \frac{(1 + a'_0)^\beta - (1 - a'_0)^\beta}{(1 + a'_0)^\beta + (1 - a'_0)^\beta}. \quad (18)$$

By substituting Eq. (16) into Eq. (2) and applying scaling forms of the following

$$\tilde{x}_i = \frac{x_i}{K'}, \quad \tilde{t} = \delta t, \quad \tilde{J} = \frac{K'J}{\delta}, \quad (19)$$

to Eq. (1), a new Langevin equation of multispecies competition is obtained

$$\begin{aligned} \frac{d\tilde{x}_i(\tilde{t})}{d\tilde{t}} = & \tilde{x}_i(\tilde{t}) \left\{ 1 - \gamma [1 + a\epsilon_i(\tilde{t})] \tilde{x}_i^\beta(\tilde{t}) \right. \\ & \left. + \frac{\tilde{J}}{N} \sum_{j \neq i} \tilde{x}_j(\tilde{t}) \right\}. \end{aligned} \quad (20)$$

### 3 Mean-Field Approximation

In order to study analytically the statistical properties of population densities, we consider the case of  $N \rightarrow \infty$ , in which the mean-field approximation can be used<sup>[25]</sup>

$$\sum_{j \neq i} J_{ij} x_j(t) = \frac{J}{N} \sum_{j \neq i} x_j(t) = J \langle x \rangle. \quad (21)$$

Hence, each equation in Eq. (20) can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{dx(t)}{dt} = x(t) \{ 1 + J \langle x(t) \rangle - \gamma [1 + a\epsilon(t)] x^\beta(t) \}. \quad (22)$$

The symbol  $\sim$  on the physical quantities of Eq. (20) are neglected here and afterwards.

The composite master equation corresponding to Eqs. (10)–(11), (15) and (22) is<sup>[26]</sup>

$$\frac{\partial P_n(x, t)}{\partial t} = -\frac{\partial}{\partial x} \{x[r(t) - \gamma(1 + a_n)x^\beta] \times P_n(x, t)\} + \sum_m U_{nm} P_m(x, t), \quad (23)$$

where  $r(t) = 1 + J(x(t))$ ,  $P_n(x, t)$  denotes the probability density of the combined process  $(x, a_n, t)$ ;  $n, m = 1, 2$ ;  $a_1 = -a_2 = a$ ; and

$$U = \frac{\nu}{k+1} \begin{pmatrix} -1 & k \\ 1 & -k \end{pmatrix}. \quad (24)$$

In the stationary state,  $r$  is independent of time. The stable fixed points of the deterministic equations (22) with  $\epsilon(t) = -1$  and  $\epsilon(t) = 1$  are  $x_1 = [r/\gamma(1-a)]^{1/\beta}$  and  $x_2 = [r/\gamma(1+a)]^{1/\beta}$ , respectively. All trajectories  $x(t)$  satisfy the following inequalities:

$$\left[ \frac{r}{\gamma(1+a)} \right]^{1/\beta} < x(t) < \left[ \frac{r}{\gamma(1-a)} \right]^{1/\beta}. \quad (25)$$

Taking the boundary condition that there is no probability current at the boundaries of Eq. (25) in the stationary state, we can solve Eqs. (23) and (24), and get the SPDF of  $x$

$$P_{\text{st}}(x) = \aleph x^{-(1+\beta)} \left| 1 - \frac{r^2}{\nu^2 a^2} \left( \frac{\nu}{r} - \frac{1}{x^\beta} \right) \right|^{\nu/2\beta r - 1} \times \left| \frac{r - \gamma x^\beta + ar/(1-a)}{r - \gamma x^\beta - ar/(1+a)} \right|^{[(k-1)/(k+1)][\nu/2\beta r]}, \quad (26)$$

where  $\aleph$  is a normalization constant. The stationary mean value of  $x$  is

$$\langle x \rangle_{\text{st}} = \int_{x_2}^{x_1} x P_{\text{st}}(x) dx. \quad (27)$$

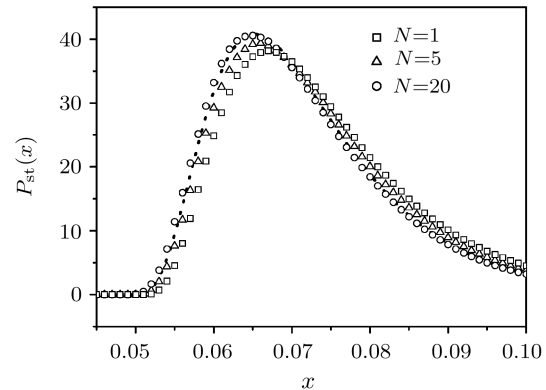
This is a self-consistency equation. The stationary mean value of  $x$  can be determined by solving numerically the Eq. (27). By means of graphical representations, the abscissa of the points at which the beeline  $y(\langle x \rangle_{\text{st}}) = \langle x \rangle_{\text{st}}$  intersects with the curve

$$y(\langle x \rangle_{\text{st}}) = \int_{x_2}^{x_1} x P_{\text{st}}(x) dx$$

is the solution of Eq. (27).

Based on Eq. (21), i.e., the result of the mean-field approximation, the SPDF of  $x$ , Eq. (26) is derived. Strictly speaking, the mean-field approximation is valid in the condition of species number  $N \rightarrow \infty$ . How do species numbers affect the SPDF? In order to understand it, we adopt stochastic simulations to study the change of the SPDF with species number, and further verify the analytical expression (26). Up to now, the method in Ref. [27] is the better one to simulate a dichotomous noise with the smaller error. The Taylor scheme of Ref. [27] is adopted to simulate stochastically the Langevin equation (20) to obtain the SPDFs at various species numbers in the parameter values:  $k = 1$ ,  $\beta = 2$ ,  $J = -1$ ,  $\tau_0 = 0.05$ ,  $a_0^2 = 0.9$ , 0.001 time step, and the results are shown in Fig. 1. From

Fig. 1, it can be seen that the result simulated in the case of  $N = 20$  is perfectly consistent with the one calculated through Eq. (26), however, the results simulated for the cases of a few species numbers (e.g.,  $N = 5$ ) also are good approximation results to the results calculated by the Eq. (26).



**Fig. 1** The stationary probability distribution function  $P_{\text{st}}(x)$  vs. population density  $x$  simulated by means of Eq. (20) for different species numbers:  $N = 1, 5, 20$ . The dot line represents the analytical result of  $P_{\text{st}}(x)$  in the case of  $N \rightarrow \infty$  through numerically calculating Eqs. (26) and (27) for the parameter:  $k = 1$ ,  $\beta = 2$ ,  $J = -1$ ,  $\tau_0 = 0.05$ ,  $a_0^2 = 0.9$ , and 0.001 time step.

## 4 Results

In this section, we will discuss the effect of the symmetric dichotomous noise and the asymmetric dichotomous noise on the SPDF and the stable average value of  $x$ .

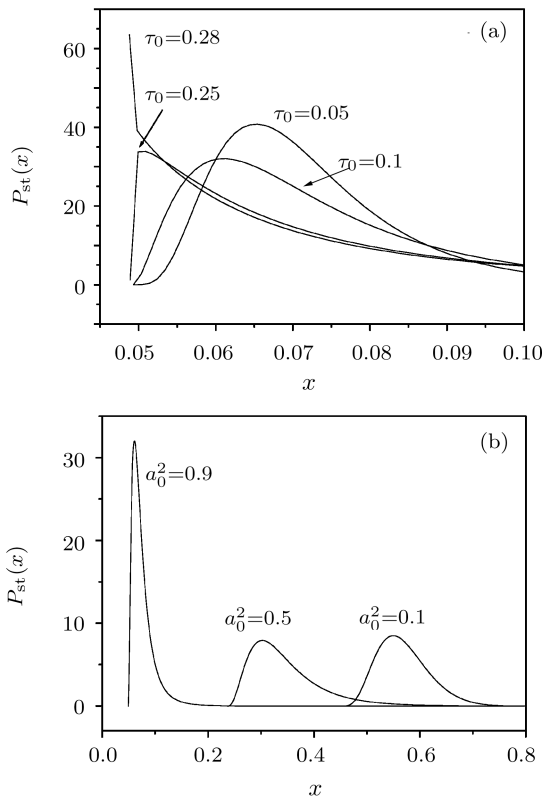
### 4.1 Case of Symmetric Dichotomous Noise

As  $k = 1$ , the system is driven by the symmetric dichotomous noise. By solving numerically the self-consistency equation (27), the SPDF at different autocorrelation times and different noise amplitudes are plotted in Figs. 2(a) and 2(b), respectively. From Fig. 2(a), it can be seen that as  $\tau_0$  is greater than about 0.27 (determined by the process of calculation), the  $P_{\text{st}}(x)$  decreases monotonously with increasing  $x$ . As  $\tau_0$  is lower than about 0.27, there appears a peak structure in  $P_{\text{st}}(x)$  curve and the peak shifts to the positive direction of  $x$  axis with decreasing  $\tau_0$ . Figure 2(b) shows that there a peak structure in the  $P_{\text{st}}(x)$  and that in the condition of constant autocorrelation time as the  $a_0$  increases, the peak moves to the negative direction of  $x$  axis and the fluctuation of  $x$  decreases. Thus the greater noise amplitude will result in the deduction of species population.

The stationary mean value of population density  $\langle x \rangle_{\text{st}}$  as a function of  $\tau_0$  for different values of  $a_0^2$  are obtained by numerically solving the self-consistency equation (27), and the calculative results are plotted on Figs. 3(a), 3(b), and 3(c). Figure 3(a) shows that for the case of smaller  $a_0$  (e.g.,  $a_0^2 = 0.1$ ),  $\langle x \rangle_{\text{st}}$  exhibits a platform structure as the  $\tau_0$  varies. From Figs. 3(b) and 3(c), it can be seen that

the platform structure becomes the peak structure and the peak shifts to the negative direction of  $\tau_0$  axis as  $a_0$  increases. Another feather in Fig. 3 is that near the peak position a transition takes place and the mean value of  $x$  suddenly falls to a lower constant. This can be explained from the SPDF of  $x$ . Figure 2(a) shows that the peak of the SPDF shifts to the stable fixed point  $x_2$  with the increment of  $\tau_0$ . As  $\tau_0$  is greater than some threshold value, the SPDF presents a characteristic of  $\delta$  function and the fluctuations of  $x$  contract to a point (namely,  $x_2$ ). Thus the lower constant mean value  $\langle x \rangle_c$  can be determined by

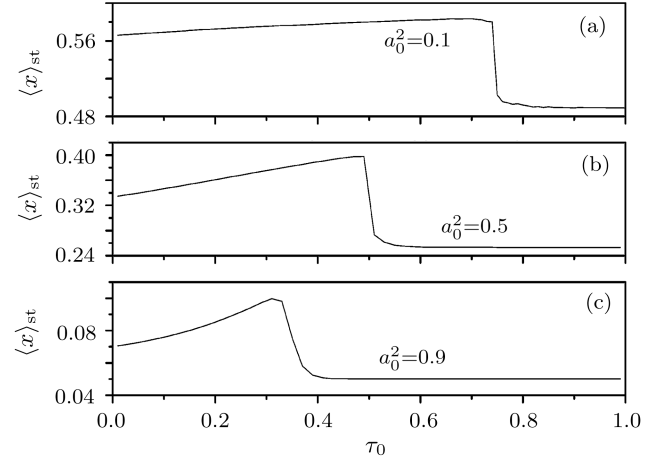
$$\left[ \frac{1 + J \langle x \rangle_c}{\gamma(1 + a)} \right]^{1/\beta} = \langle x \rangle_c. \quad (28)$$



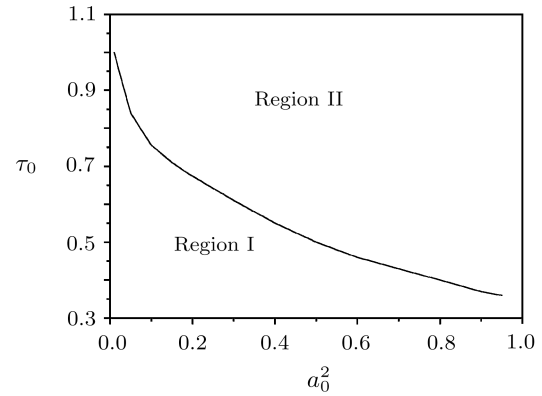
**Fig. 2**  $P_{st}(x)$  vs. population density  $x$  in the following parameter values:  $k = 1$ ,  $\beta = 2$ , and  $J = -1$ . (a)  $a_0^2 = 0.9$ ,  $\tau_0 = 0.05, 0.1, 0.25$ , and  $0.28$ ; (b)  $\tau_0 = 0.1$ ,  $a_0^2 = 0.9, 0.5$ , and  $0.1$ .

In terms of the onset of  $x$  failing to a lower constant, we draw the parameter plane of  $\tau_0 - a_0^2$  (see Fig. 4). One can easily see that the curve in Fig. 4 divides the plane into two regions, and in region I  $\langle x \rangle_{st}$  possesses higher values while lower constant values in region II. Figure 3 also indicates that at a fixed noise amplitude there is an optimal value of  $\tau_0$  which makes  $\langle x \rangle_{st}$  be maximal. The maximum  $\langle x \rangle_{max}$  monotonously decreases with the noise

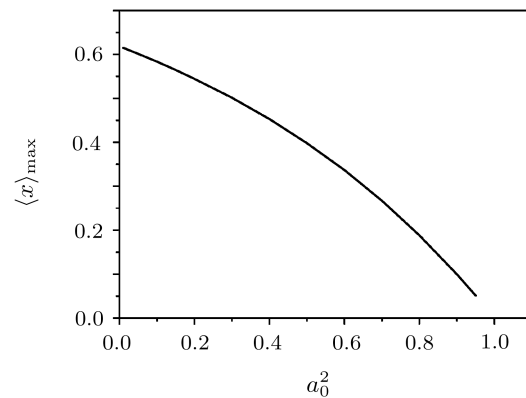
amplitude increasing (see Fig. 5).



**Fig. 3** The stationary mean value of population density  $\langle x \rangle_{st}$  as a function of autocorrelation time  $\tau_0$  for the parameter values:  $k = 1$ ,  $\beta = 2$ , and  $J = -1$ . (a)  $a_0^2 = 0.1$ ; (b)  $a_0^2 = 0.5$ ; (c)  $a_0^2 = 0.9$ .



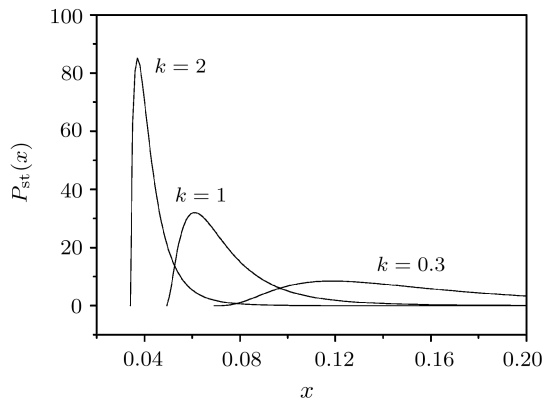
**Fig. 4** The parameter plane of  $\tau_0 - a_0^2$ . The parameter values are  $k = 1$ ,  $\beta = 2$ , and  $J = -1$ .



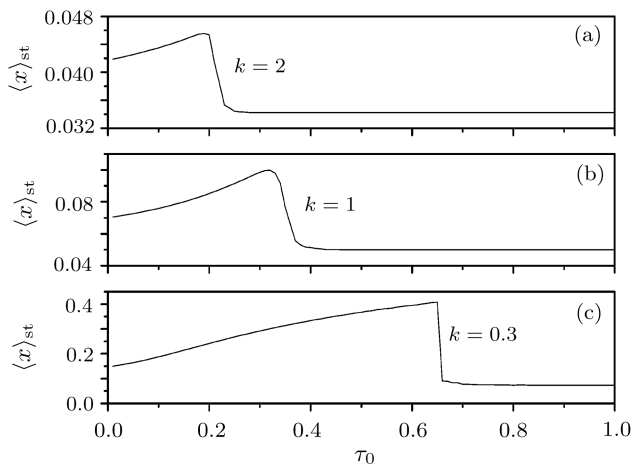
**Fig. 5** The mean density maximum  $\langle x \rangle_{max}$  vs.  $a_0^2$ . The parameter values are the same as Fig. 4.

#### 4.2 Case of Asymmetric Dichotomous Noise

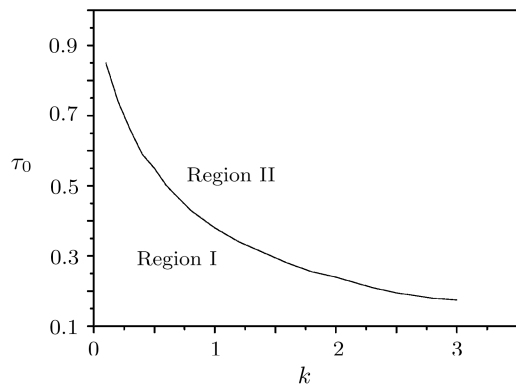
As  $k \neq 1$ , the system is subjected to the asymmetric dichotomous noise. The noise symmetry parameter  $k$  reflects the symmetry extent of the dichotomous noise, and  $k = 1$  belongs to a perfect symmetry.



**Fig. 6**  $P_{st}(x)$  vs. population density  $x$  for different noise symmetry parameters:  $k = 0.3, 1, 2$ , with  $\tau_0 = 0.1$ ,  $\beta = 2$ ,  $J = -1$ , and  $a_0^2 = 0.9$ .



**Fig. 7**  $\langle x \rangle_{st}$  vs. autocorrelation time  $\tau_0$  for different noise symmetry parameters:  $k = 0.3, 1, 2$ , with  $a_0^2 = 0.9$ ,  $\beta = 2$ , and  $J = -1$ .



**Fig. 8** The parameter plane of  $\tau_0 - k$ . The parameter values are  $a_0^2 = 0.9$ ,  $\beta = 2$ , and  $J = -1$ .

Figures 6 and 7 are plotted by solving numerically Eq. (27). First,  $k$  can influence on the SPDF of  $x$ . From

Fig. 6, one can see that as  $k$  increases, the SPDF peak moves to the origin of  $x$  axis and becomes sharper and sharper, i.e., the fluctuation of  $x$  is gradually decreasing. Obviously the stationary mean value of  $x$  also becomes lower and lower. Second,  $k$  can also affect the maximum of  $\langle x \rangle_{st}$ . Figure 7 indicates that with the decrement of  $k$  the peak of  $\langle x \rangle_{st}$  becomes higher and higher. Finally,  $k$  determines the transition position of  $\langle x \rangle_{st}$ . From Fig. 7, we can see that the smaller the value of  $k$ , the greater the transition autocorrelation time. In terms of the onset of  $\langle x \rangle_{st}$  failing to a lower constant, we equally draw the parameter plane of  $\tau_0 - k$  (see Fig. 8). In region I of Fig. 8  $\langle x \rangle_{st}$  takes higher values while lower constant values in region II.

## 5 Conclusions

Up to now we have investigated the statistical properties of the multispecies competition systems subjected to dichotomous noises. A major virtue of the models with dichotomous noise is that they constitute a case admitting an exact analytical solution for the stationary case for any value of the autocorrelation time  $\tau_0$ , the noise amplitude  $a_0$ , and the noise symmetric parameter  $k$ . In the case of infinite species, the analytical expression of SPDF was theoretically deduced through mean-field approximation, and verified by stochastic simulation.

In the process of solving the self-consistency equation (27), we found that there only exists one intersectant point between the beeline  $y(\langle x \rangle_{st}) = \langle x \rangle_{st}$  and the curve  $y(\langle x \rangle_{st}) = \int_{x_2}^{x_1} x P_{st}(x) dx$ . So the hysteresis behavior like Ref. [7] does not appear. This is because the systems considered are multispecies competition ecosystems, different from the symbiotic ecosystems investigated in Ref. [7]. In addition, we also studied the asymmetric effect of the dichotomous noise on the system, and obtained a series of interesting results: (i) The noise amplitude, the autocorrelation time and the noise symmetry parameter all can affect the SPDF; (ii) For the greater noise amplitude,  $\langle x \rangle_{st}$  can be maximized at an optimal autocorrelation time; (iii) Near the peak, there is the transition of  $\langle x \rangle_{st}$  that  $\langle x \rangle_{st}$  suddenly falls to a lower constant; (iv) As  $k$  decreases, the peak value of  $\langle x \rangle_{st}$  goes up and the optimal autocorrelation time increases; (v) For the lower noise amplitude,  $\langle x \rangle_{st}$  displays a platform with autocorrelation time, while for the greater noise amplitude the platform turns into a peak. From the above results, we conclude that the noise can effectively change the species density, meanwhile induce the transition of species population. Therefore, in order to make the species density keep at a higher level in the competitive fluctuating environments, it is a very important measure to select a smaller noise amplitude, a smaller noise symmetry parameter, and an optimal autocorrelation time.

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