Effects of time delay on symmetric two-species competition subject to noise

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(Received 27 April 2007; revised manuscript received 24 January 2008; published 6 March 2008)

Noise and time delay act simultaneously on real ecological systems. The Lotka-Volterra model of symmetric two-species competition with noise and time delay was investigated in this paper. By means of stochastic simulation, we find that (i) the time delay induces the densities of the two species to periodically oscillate synchronously; (ii) the stationary probability distribution function of the two-species densities exhibits a transition from multiple to single stability as the delay time increases; (iii) the characteristic correlation time for the sum of the two-species densities squared exhibits a nonmonotonic behavior as a function of delay time. Our results have the implication that the combination of noise and time delay could provide an efficient tool for understanding real ecological systems.

I. INTRODUCTION

The Lotka-Volterra model (LVM), originally introduced by Volterra for the description of struggle for existence among species [1,2], has been paid considerable attention in many fields, such as medicine [3], biology [4], ecology [5–9], and mathematics [10,11], etc. Its paramount contribution to biology lies in understanding the diversity of species in the process of biological evolution, where environmental noise plays a beneficial role [12], and the species are able to coexist in a common environment, whether inferior or superior in terms of competitiveness. In ecosystems, noise, through its interaction with the nonlinear ecosystem, can induce many novel phenomena such as stochastic resonance [13,14], noise-delayed extinction [15], and spatial patterns [13,14,16]. In chaotic systems, noise can enhance phase synchronization [17,18] and induce coherence resonance [19]. Less effort, however, has been devoted to the study of synchronization and coherence resonance occurring in ecosystems.

In realistic systems, however, inclusion of time delay is natural. Several authors have investigated the effects of time delay, and have found resulting dynamic phenomena such as multistability [20–22], desynchronization [21,22], clustering [20], amplitude death [23,24], anticipated synchronization [25–27], and slow switching [28]. It was recently found that noise and delay can actually be an integral part of biological information processing [29–31]. In the field of pure statistical physics, systems with noise and time delay have been investigated in detail [32–37]. We have studied the effects of time delay on a mutualism system and found that the combination of the noise and the time delay completely suppresses its population explosion [38]. In competitive systems in the ecological field, the effects of time delay combined with noise is not fully understood yet.

In this paper, based on the research work of Vilar and Solé [13], we further investigate the effects of including time delay into the LVM of symmetric two-species competition. In

Sec. II, the time evolution of population densities, the stationary probability distribution function, and the characteristic correlation time of the system with time delay are simulated. In Sec. III, conclusions are drawn.

II. THE STATISTICAL PROPERTIES OF SYMMETRIC TWO-SPECIES COMPETITION WITH TIME DELAY

A. The time evolution of population densities with time delay

The time evolution of symmetric two-species competition is obtained within the formalism of the Lotka-Volterra equations [39] in the presence of multiplicative noise [9,40]. On the basis of Ref. [13], according to Refs. [40,41], and introducing a time delay into the LVM of the symmetric two-species competition, one obtains the following equations:

$$\frac{dx(t)}{dt} = \mu x(t)[1 - x(t-\tau) - \beta(t)y(t-\tau)] + x(t)\xi_x(t), \quad (1)$$

$$\frac{dy(t)}{dt} = \mu y(t)[1 - y(t-\tau) - \beta(t)x(t-\tau)] + y(t)\xi_y(t), \quad (2)$$

where x and y denote the population densities, μ is their growth rate, $\beta(t)$ represents the interaction parameter between two species, τ is the delay time, and $\xi_i(t)$ is Gaussian white noise with zero mean and correlation function $\langle \xi_i(t)\xi_j(t')\rangle = \sigma\delta(t-t')\delta_{ij}$ $(i,j=x,y)$; here σ denotes the strength of the multiplicative noise $\xi_i(t)$. $x(t)\xi_x(t)$ and $y(t)\xi_y(t)$ express the contributions of random forces due to external environmental fluctuation. Here the contribution of internal fluctuation in the system is neglected. $\tau=0$ means that all the members of the species survive to the same age, and the egg is instantaneously converted into an adult. In this model, it is assumed that the birth rate coefficient is diminished by the population of the preceding generation, τ being the generation time (the time required in going from an egg stage to the adult stage) [40]. The interaction parameter $\beta(t)$ is affected by geological factors. Analysis of the experimental data of planktonic foraminifera by Caruso and Gargano
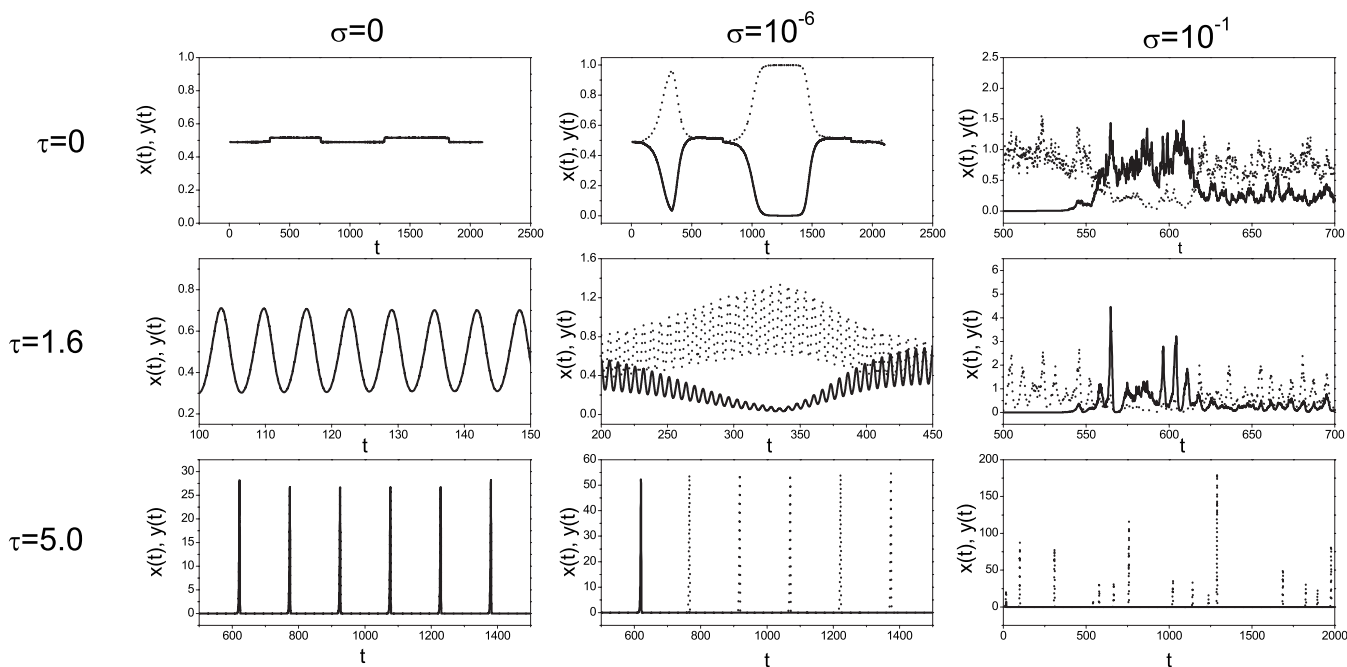
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FIG. 1. Time evolution of two populations at different levels of multiplicative noise and different delay times. One is represented by a dotted and the other by a solid line. The values of parameters are $\mu=1$, $\gamma=0.1$, and $\omega_0/(2\pi)=10^{-3}$. The strength of the additive noise is fixed at the value $\sigma_\beta=1.78\times10^{-3}$. The initial values are $\beta(0)=0.94$, $x(0)=y(0)=1$, and $x(t-\tau)=y(t-\tau)=1$ as $t<\tau$, with time step 0.001.

[42] indicated that geological events produce "time windows" characterized by quasiperiodic fluctuations with almost constant noise intensity. Therefore, the dynamics of β is determined by an environmental noise and a periodic driving force [14],

$$\frac{d\beta}{dt} = -\frac{dU(\beta)}{d\beta} + \gamma\cos(\omega_0 t) + \xi_\beta(t), \qquad (3)$$

where $U(\beta)$ is a bistable potential

$$U(\beta) = h[\beta-(1+\rho)]^4/\eta^4 - 2h[\beta-(1+\rho)]^2/\eta^2; \qquad (4)$$

here h is the height of the potential barrier, $\xi_\beta(t)$ is the Gaussian white noise with the usual statistical properties $\langle\xi_\beta(t)\rangle=0$ and $\langle\xi_\beta(t)\xi_\beta(t')\rangle=\sigma_\beta\delta(t-t')$, where σ_β denotes the strength of additive noise $\xi_\beta(t)$. The parameters $h=6.25\times10^{-3}$, $\eta=0.05$, $\rho=-0.01$, $\gamma=0.1$, and $\omega_0/(2\pi)=10^{-3}$ are the same as those in Ref. [14].

The analytical expressions for x and y are difficult to obtain. But Eqs. (1) and (2) can be stochastically simulated by means of Euler arithmetic with a time step ($\Delta t=0.001$) [43], where the Box-Mueller algorithm is used to generate Gaussian noise from two random numbers which are uniformly distributed on the unit interval [44]. For the initial values in the condition of time delay, it is rational to let $x(t-\tau)=y(t-\tau)=x(0)=y(0)$ as $t<\tau$.

The results of the simulations of x and y at different levels of multiplicative noise and different delay times are plotted in Fig. 1. From Fig. 1, one can see that the delay time strongly affects the time series of species. A pronounced feature is that the time delay induces periodically synchronized

oscillations of the population densities, which lead to the reduction of the total number of species (extinction of some species); however, there this feature does not occur in symmetric two-species competition without time delay, where the total number of species is basically conservative or remains near its equilibrium value at a small level of multiplicative noise [13].

In the process of simulation, we found that the effects of time delay on the time series of the species densities become obvious when τ is greater than about 1.5. For the case of $\sigma=0$, i.e., there is no noise in the system, the time delay brings about the Hopf bifurcation of x and y due to their sinusoidal oscillations; what is more, their amplitude increases with delay time. The critical value τ_c of bifurcation equals about 1.5. When the delay time is greater than τ_c, a stable limit cycle appears in the phase diagram of x versus $\frac{dx}{dt}$ (or y versus $\frac{dy}{dt}$), i.e., the topological properties of the solutions of Eqs. (1) and (2) exhibit a transition, or the structure of the system becomes unstable. For the case of $\sigma=10^{-6}$, i.e., there is noise in the system, the time coherence of x and y because of the competition without time delay is seriously disturbed by the time-delay-induced oscillations, which are very likely to affect to some degree the stochastic resonance corresponding to $(x-y)^2$. However, at a higher level of multiplicative noise (e.g., $\sigma=10^{-1}$), the time series of x and y become more regular in the presence of time delay, and the disorder introduced by noise is replaced by delay oscillations.

In Fig. 1 there are simultaneously two types of spikelike behavior. One is the time coherence caused by noise, which exhibits a stochastic resonance corresponding to the periodic signal in Eq. (3). The other is the synchronous oscillation caused by the time delay, whose period is not equal to that of the signal in Eq. (3) and depends on intrinsic characteristics

of the system. The first type was investigated in Refs. [13,14]. The second one will be addressed in Sec. II C.

B. Stationary probability distribution function with time delay

Recently, the one-dimension Langevin equation with time delay was investigated [33,45]. However, its exact solution is so difficult to find that one has to search for another approach, e.g., perturbation theory in the condition of small delay time, to get the stationary probability distribution function (SPDF) of the dynamic variable. As mentioned above, only when the delay time is greater than about 1.5 does the time delay effect in the system become obvious. Therefore, the small delay time approximation is not suitable for this system. Stochastic simulation is likely to be a more desirable approach to deal with it. By the same method used in simulating the results of Fig. 1, large numbers of x and y data for long time evolution will be obtained. By using the statistics of the number ratios of data belonging to different value zones of the variables and normalizing them, we can get the SPDF of x and y at different levels of multiplicative noise and different delay times. The simulation results are shown in Figs. 2 and 3.

For the case of $\tau=0$ and the lower level of noise $\sigma=10^{-6}$, there is a three-peak structure in the SPDF, the middle peak corresponding to coexistence and the other two peaks corresponding to exclusion [see Fig. 2(a)]. For the case of $\tau=1.6$ and $\sigma=10^{-6}$, each of the peaks for the case of $\tau=0$ is split into two peaks along the line $x+y=1$ [see Fig. 2(b)]. For the case of $\tau=2$ and $\sigma=10^{-6}$, the peaks away from the origin disappear and another peak gradually shifts to the origin [see Fig. 2(c)]. That is, the structure of the SPDF exhibits the transitions three peaks→six peaks→one peak as the delay time increases at the lower level of noise.

For the case of $\tau=0$ and the higher level of noise $\sigma=10^{-1}$, there is a two-peak structure in the SPDF, two peaks corresponding to exclusion [see Fig. 3(a)]. For the case of $\tau=1.6$ and $\sigma=10^{-1}$, the peak of the coexistence appears and there is a three-peak structure in the SPDF [see Fig. 3(b)]. For the case of $\tau=2$, only one coexistence peak is left at the origin [see Fig. 3(c)]. That is, the structure of the SPDF exhibits the transitions two peaks→three peaks→one peak as the delay time increases at the higher level of noise, namely, the time delay induces a first-order-like transition in the system.

C. The characteristic correlation time as a function of delay time

The state variable autocorrelation function is an important quantity to measure the ordering of a time series; it is defined as

$$C(\tau') = \frac{\langle \tilde{u}(t)\tilde{u}(t+\tau') \rangle}{\langle \tilde{u}^2 \rangle}, \qquad (5)$$

where τ' is the autocorrelation time, $u(t)$ is the state variable considered, $\tilde{u}(t)=u(t)-\langle u(t) \rangle$, and $\langle u(t) \rangle$ is the statistical average of $u(t)$ over time. C describes the fluctuation decay of
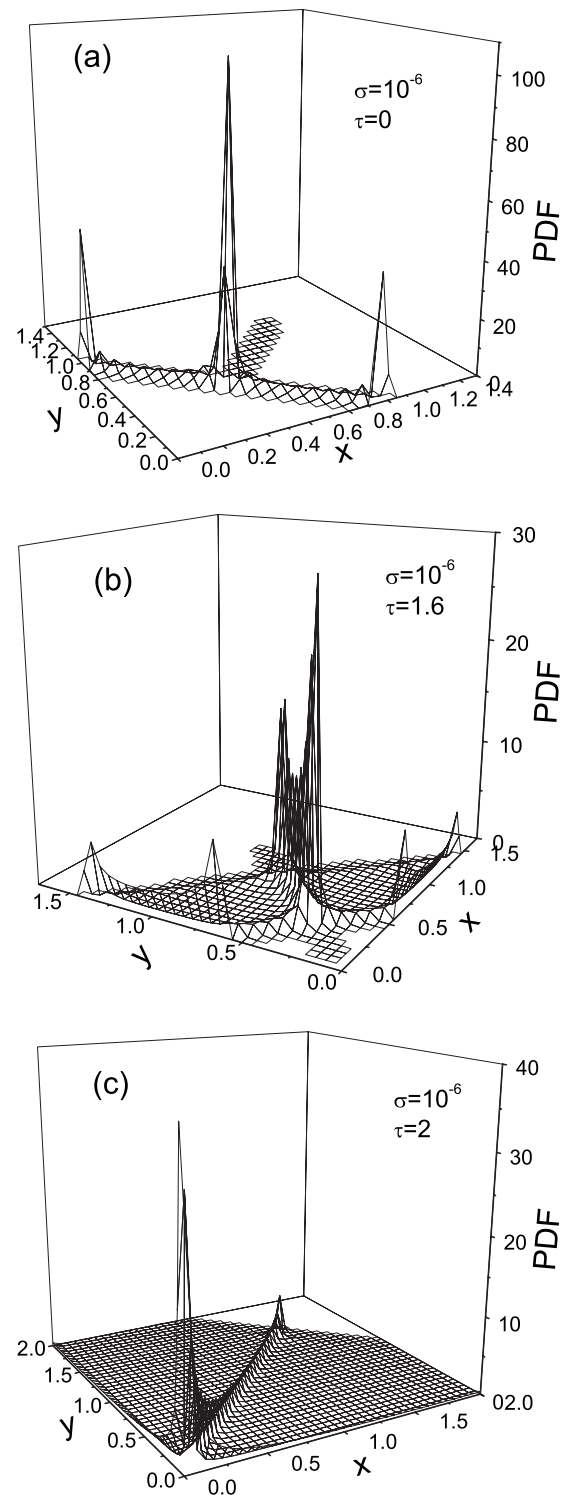

FIG. 2. Stationary probability distribution function (PDF) as a function of x and y at lower level of multiplicative noise $\sigma=10^{-6}$, for different delay times: $\tau=$ (a) 0, (b) 1.6, and (c) 2. The other parameter values are the same as in Fig. 1.

a dynamical variable $\tilde{u}(t)$ in the stationary state. At certain levels of noise and delay time, the autocorrelation function generally displays two types of motion with autocorrelation times: overdamped and underdamped motions. The underdamped motion may have better correlation than the over-
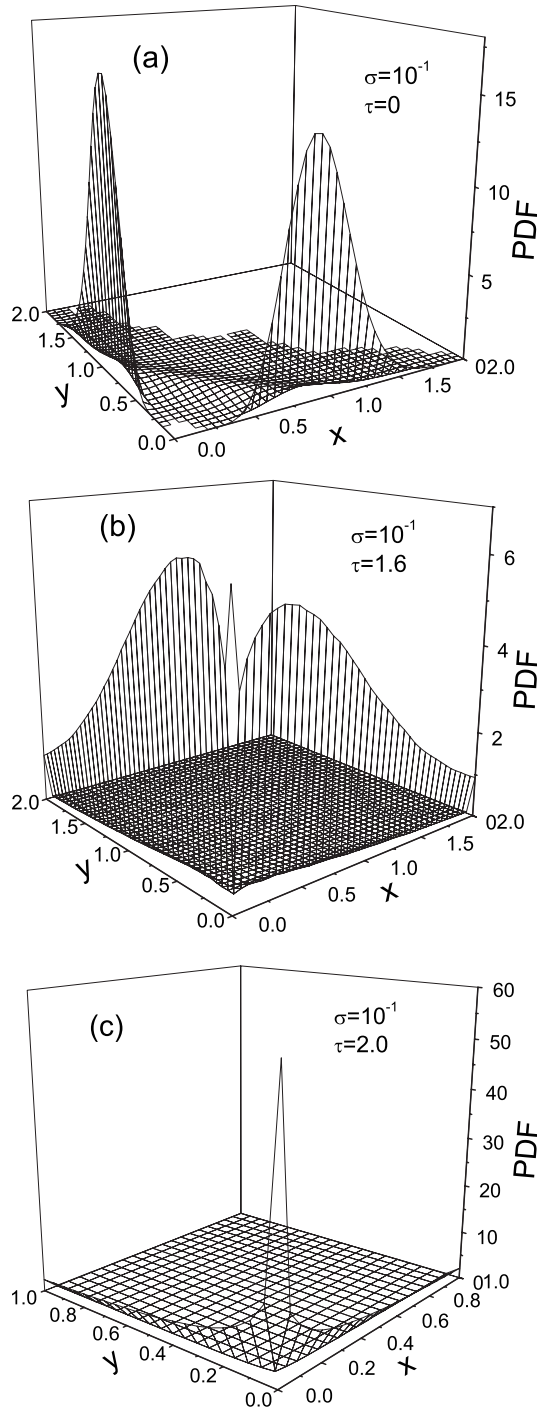
FIG. 3. Stationary PDF as a function of x and y at higher level of multiplicative noise $\sigma = 10^{-1}$, for different delay times: τ = (a) 0, (b) 1.6, and (c) 2. The other parameter values are the same as in Fig. 1.

FIG. 4. Autocorrelation function C of $(x+y)^2$ as a function of correlation time at $\sigma = 10^{-1}$ and different delay times. The other parameter values are the same as in Fig. 1.

the characteristic correlation time, the more pronounced the correlation, and the more orderly the time series.

In Ref. [47], Pikovsky and Kurths used this method to study the coherence resonance in an excitable Fitz Hugh-Nagumo system under external noisy driving, and demonstrated that for a certain noise amplitude the noise-excited oscillation appears to be rather regular, and its characteristic correlation time has a maximum. For the two-species competition system, although there is not an optimal noise amplitude at which Λ has a maximum, we found that the Λ of $(x+y)^2$ exhibits nonmonotonic behavior with respect to delay time. Thus, we let the dynamic variable of Eq. (5) take the form

$$u(t+\tau) = [x(t+\tau) + y(t+\tau)]^2 \qquad (7)$$

in the case of time delay, where τ is the delay time.

By means of Eqs. (1), (2), (5), and (7), we simulated the normalized autocorrelation function C and the characteristic correlation time Λ of $[x(t+\tau)+y(t+\tau)]^2$ at fixed levels of multiplicative and additive noise, and the results are plotted in Figs. 4 and 5, respectively. Figure 4 indicates that (i) with no time delay or large delay time, C shows an overdamped motion with autocorrelation time, and decays quickly to zero; (ii) with a medium delay time, i.e., $\tau = 1.6$, C shows an underdamped motion with slow decay. Therefore, at fixed levels of multiplicative and additive noise, there may be an optimal delay time which makes the time series of $(x+y)^2$ the most regular. This can be confirmed by the nonmonotonic behavior of the characteristic correlation time as a function of delay time (see Fig. 5). For a certain delay time, Λ has a maximum, which means that a coherence resonance with respect to delay time occurs in the system. The maximum depends on the multiplicative noise intensity, and the lower the multiplicative noise intensity, the greater the maximum. If there is a correlation between $\xi_x(t)$ and $\xi_y(t)$, the value of Λ will increase to some degree. For an effective delay time, however, Λ increases with decreasing σ because the very regular oscillation of $\tau = 0$ is gradually spoiled by increasing

damped one for the same dynamic variable. Quantitatively, the integral [46]

$$\Lambda = \int_0^\infty C^2(t)dt \qquad (6)$$

can reflect the correlation, where Λ is termed the characteristic correlation time of the dynamic variable $u(t)$. The larger
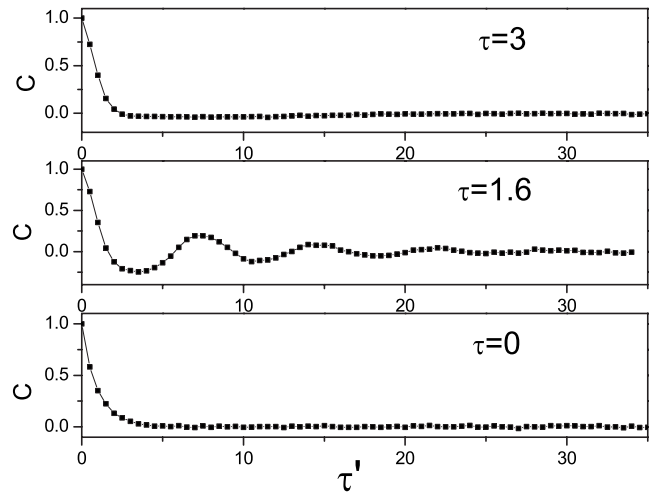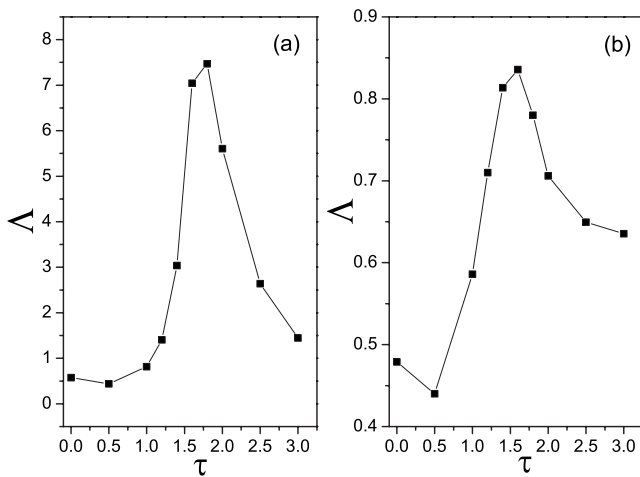
FIG. 5. Characteristic correlation time Λ vs delay time at the levels of noise: $\sigma = 10^{-2}$ for (a) and 10^{-1} for (b). The other parameter values are the same as in Fig. 1.

σ. Yet noise can enhance the antiphase synchronization of x and y below the threshold of the delay time (see Fig. 1). A similar circumstance also appears in Ref. [48].

III. CONCLUSIONS

In this paper, we studied the effects of time delay on symmetric two-species competition subjected to noise. By means of stochastic simulations, the time evolution of population densities, the two-dimensional SPDF, and the charac-teristic correlation time with the delay time are calculated. The results indicate that the time delay causes the noise-induced competition system to exhibit many peculiar charac-teristics. First, the time delay effect starts to become more and more obvious as τ becomes greater than about 1.5. Sec-ond, the time delay induces the species densities to synchro-nously periodically oscillate with time, which causes a tran-sition of the system's structure, i.e., symmetry breaking. Third, the stationary probability distribution function of the two-species densities exhibits a transition from multiple to single stability as the delay time increases. Finally, the char-acteristic correlation time of $(x+y)^2$ displays a nonmonotonic behavior with respect to delay time.

From the above findings, we can obtain further under-standing of the intrinsic properties in the system. It is gener-ally known that when the generation time (or delay time) is close to infinity, i.e., the reproducibility of species is com-pletely lost, the species will go to extinction ultimately. But at some delay times the system possesses a stable state with higher species density. This makes a large contribution to sustaining ecological equilibrium. In addition, the oscilla-tions of x and y caused by the time delay are strictly syn-chronous, unlike the oscillations caused by the noise. At an optimal delay time, the system exhibits a coherence reso-nance.

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