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Dynamics of two competing species in the presence of Lévy noise sources

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We consider a Lotka-Volterra system of two competing species subject to multiplicative α-stable Lévy noise. The interaction parameter between the species is a random process which obeys a stochastic differential equation with a generalized bistable potential in the presence both of a periodic driving term and an additive α-stable Lévy noise. We study the species dynamics, which is characterized by two different regimes, exclusion of one species and coexistence of both. We find quasiperiodic oscillations and stochastic resonance phenomenon in the dynamics of the competing species, analyzing the role of the Lévy noise sources.

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I. INTRODUCTION

Animal movement and dispersal, which are major drivers of spatiotemporal patterns in ecosystems, have solicited in ecology questions difficult to answer for two main reasons. First, quantifying the precise distributions of populations interacting in time and space could be hard. Recent technological advances have to some extent changed this scenario, opening new perspectives for the future. A second aspect, which represents, at the moment, a stronger hurdle, is the lack of concepts and/or technical tools for analyzing the feedbacks between the properties of macroscopic ecosystems and their elementary parts. A perspective which takes into account the time evolution of the system and the contemporary presence of different "ecological" approaches, i.e., behavioral, landscape, and spatial ecology [1–3], could play a key-role in this matter. In particular, identifying the components responsible for large-scale time evolution and understanding the long-term properties of the animal movements and dispersal allow to establish useful links across different scales, going from individuals to ecosystems and backward [4]. Moreover, random fluctuations of environmental variables in ecosystems increase the unpredictability in resource availability throughout time. Thus, environmental stochasticity, together with inevitable biological constraints, could introduce randomness in many relevant ecological contexts, such as foraging, mating, dispersal and habitat colonization [5]. Consequently, it is likely that an adaptive behavior has been the response to environmental randomness, playing a fundamental role in animal survival and contributing to determine the spatiotemporal dynamics of processes and patterns in real ecosystems [6]. Random walks describe stochastic trajectories obtained when the system is uniquely "driven" by random forces. However, random walks could participate in dynamics of systems where deterministic forces are also present. Therefore, it is possible to introduce stochastic trajectories as results of richer dynamics, where deterministic and random components are present. In this context, random walks appear to be essential tools to model and describe the dynamics of real ecosystems, whose dynamics are affected both by deterministic and random forces. In particular, noise-induced phenomena, such as stochastic resonance, noise-delayed extinction and coherence resonance are observed in many ecosystems [7,8]. Moreover, the combination of noise and time delay could provide an efficient tool for understanding real ecological systems [9]. Random walks can be categorized as Brownian, when the system is subject to Gaussian noise. Otherwise, the presence of non-Gaussian noise determines non-Brownian random walks. A particular class of non-Gaussian noises, whose statistics is given by the so-named Lévy (or α-stable) distributions, determines the non-Brownian motion known as Lévy walk that is characterized by Lévy flights (the turning points in a Lévy walk [10]). In short, Lévy flights are characterized by many small movements and few large displacements (see Fig. 1).

Lévy flights have been observed in many physical, natural and social complex systems [11–16], and in evolutionary game theory [17–20], where scale-invariance phenomena take place or can be suspected (for a recent review on Lévy flights see Ref. [15], and references there).

The Lévy flight theory has recently been borrowed by ecologists from the physical sciences to characterize the spa-

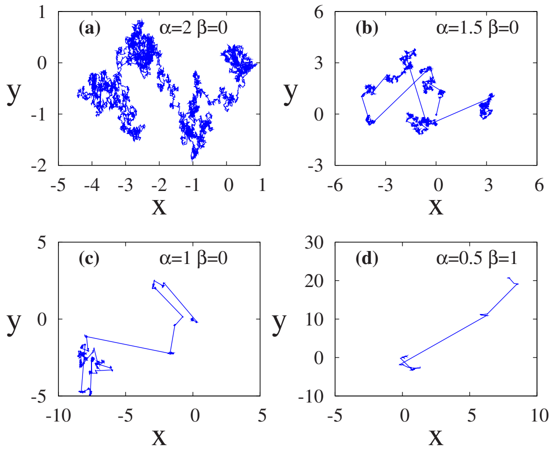

FIG. 1. (Color online) Two-dimensional trajectories of free diffusion of a particle subjected to noise sources with (a) Gaussian ($\alpha=2$, $\beta=0$); (b) Lévy ($\alpha=1.5$, $\beta=0$); (c) Cauchy-Lorentz ($\alpha=1$, $\beta=0$); (d) Lévy-Smirnov ($\alpha=0.5$, $\beta=1$) distributions. The values of the other parameters are $\mu=0$, $\sigma=1$. Arbitrary units are used in both axes.

tial distributions of predators or foragers. In particular, a big amount of empirical works showed that the spatial behavior of many animals exhibits scale-free characteristics [21], such as microzooplankton [22,23], fruit flies [24] and some marine predators [25], honey bees (*Apis mellifera*) [26,27], jackals (*Canis adustus*), spider monkeys (*Ateles geoffroyi*) [28,29]. The numerous evidences of faster than normal (Brownian) diffusion suggest that the investigation has to concern the origin of this superdiffusive behavior that can be, in principle, connected with Lévy walks or other mechanism.

Therefore, the theoretical study on Lévy noise and its role in model systems for population dynamics can be fundamental in view of better understanding the origin of power-law behavior in biological and social systems and eventually verifying whether the properties of the model can be observed in real ecosystems.

Recently, noise-induced ordering phenomena, such as dynamic hysteresis, stochastic resonance, resonant activation, and double stochastic resonance phenomenon were observed in a bistable system in the presence of Lévy noise [30–32]. In particular, we recall that noise-induced jumping between metastable states separated by potential barriers is common in physical systems.

The time scale to overcome the barrier depends on the noise source and potential profile. Most often the noise is Gaussian. However, non-Gaussian noises distributed with power-law tails are found not only in biological context but also in different physical systems such as turbulent diffusion, vortex dynamics, dynamical models and critical phenomena [33,34].

Also in these systems the distributions observed appear to be well described by Lévy noise sources. For example, the presence of Lévy statistics has been revealed in different climatic and geological events. In particular, anomalous diffusion in hydrological time series and α-stable statistics in atmospheric data have been observed [35,36]. Finally, in long paleoclimatic time series α-stable noise-induced jumping in a double-well potential has been revealed [37]. The two wells of the bistable potential correspond, in glacial times, to different climatic states. This indicates that the oceanic flow, in the presence of random fluctuations from the atmosphere, causes the system to jump between the two metastable states. Therefore, Lévy walks appear to be present both in a plenty of biological systems and in atmospheric and geological events. It is then worth to analyze and clarify some theoretical aspects of population dynamics in the presence of Lévy distributed random fluctuations. This can be done by using α-stable noise sources which affect the biological system both directly, by terms of multiplicative noise in the equations for the biological species, and indirectly considering Lévy noise sources, connected with climatic events, that influence the dynamics of some system parameters.

From a theoretical point of view, the Lévy flights can result from a Langevin equation driven by α-stable noise, giving rise to the scaling property $\Delta r(\lambda t) \sim \lambda^{\mu/2} \Delta r(t)$, with λ a positive parameter. The case $\mu=1$ corresponds to normal diffusion where D is the diffusion constant. The exponent μ is related to the scaling of the tail of the probability distribution for the increments of the random walk, $P(r \to \infty) \sim |r|^{-(1+\alpha)}$, with $\mu = 2/\alpha$. For $\mu > 1$ the process is superdiffusive, the probability density function follows a power law with heavy tails and the generalized central limit theorem is valid [38–40]; for $\mu=2$ and thus $\alpha=1$ the probability density function is a Cauchy-Lorentz function. For $\alpha=2$, the second moment exists and because of the central limit theorem the random walk reduces, in the continuum limit, to a Gaussian random process.

In this paper we focus on the stochastic resonance phenomenon in a model of population dynamics. In particular, we investigate the stochastic dynamics of a single compartment (spatially nonextended) system consisting of two competing species within the formalism of the generalized Lotka-Volterra equations. The choice of a single site model relies on the aim of this work, which is to study the local properties of two populations that experience Lévy distributed random fluctuations. Considering single site dynamics allows to analyze the time behavior in a pointlike space domain, interpreting sudden variations of the species concentrations as the local effect of an intensive spatial diffusion that occurs because of a long-pace migration (Lévy flight) into/from another spatial compartment. By this approach, we focalize on the characteristics induced by different Lévy noise sources on the dynamics of a model ecosystem, analyzing the system response to external random fluctuations by the knowledge of the signal-to-noise ratio (SNR) and signal power amplification (SPA). Monitoring these quantities in natural ecosystems can provide useful information for better understanding the dynamics of biological populations, especially when nontrivial response to the external noise are observed (nonmonotonic behavior of SNR or SPA).

In the model proposed here, the interaction parameter between the species is a stochastic process which obeys a stochastic differential equation with a term of additive α-stable Lévy noise, which mimics the effects that environmental noise produces on the dynamical regime of an ecosystem [41,42]. Moreover, we consider the generalized Lotka-Volterra equations in the presence of multiplicative α-stable Lévy noise, which models the direct interaction between species and environment. We analyze the role played by the Lévy noise on the system dynamics for different values of the index α. According to previous results obtained in the presence of Gaussian noise, we observe that the noise could have a constructive role. In particular, the additive noise is responsible for the generation of quasiperiodic oscillations in the time series of the species densities. Besides, the multiplicative noise, in the presence of two different dynamical regimes (coexistence and exclusion), produces the appearance of anticorrelated oscillations and stochastic resonance phenomenon.

II. LÉVY NOISE

The overdamped dynamics of a system subject to a Lévy white noise source is described by the following generalized Langevin equation [43–46]

$$\dot{x}(t) = f(x,t) + g(x,t)\chi(t), \tag{1}$$

which accounts for the time evolution of the system in the presence of both deterministic and random forces due to the mutliplicative interaction with the environment. In Eq. (1) $\chi(t)$ is the time derivative of the Lévy process $L(t)$, which is a generalized Wiener process [15].

Lévy flights are stochastic processes characterized by the occurrence of extremely long jumps, and their trajectories are not continuous. The length of these jumps is distributed according to a Lévy stable statistics with a power-law tail and divergence of the second moment. This peculiar property strongly contradicts the ordinary Brownian motion, for which all the moments of the particle coordinate are finite. The presence of Lévy flights can be explained as a deviation of the real statistics of fluctuations from the Gaussian law, giving rise to the generalization of the central limit theorem by Lévy and Gnedenko [47,48].

Lévy processes are characterized by stationary independent increments [49], which means that $\{L(t), t \geq 0\}$ is a Lévy process if, for every t, $\tau \geq 0$, the increment $L(t+\tau)-L(t)$ is independent of the process $\{L(t'), 0 \leq t' < t\}$ and follows the same law as $L(\tau)$, with $L(0)=0$. As it follows from the evident decomposition [15]

$$L(t) = L\left(\frac{t}{n}\right) + \left[L\left(\frac{2t}{n}\right) - L\left(\frac{t}{n}\right)\right] + \cdots + \left[L\left(\frac{nt}{n}\right) - L\left(\frac{(n-1)t}{n}\right)\right], \tag{2}$$

the random variable $L(t)$ can be divided into the sum of an arbitrary number of independent and identically distributed random variables. In other words, the probability distribution of $L(t)$ belongs to the class of infinitely divisible distributions (i.d.d.) [48,50–52].

A subclass of i.d.d. is that of the stable distributions. The general problem of determining the whole class of stable distributions has been solved by Lévy and Khintchine [47,51], that gave the most general expression for the characteristic function of the random variable $L(t)$ [40,52]

$$\varphi(k) = \exp\{ik\mu - |\sigma k|^{\alpha}[1 - i\beta\,\mathrm{sgn}(k)\Phi]\}, \tag{3}$$

where $\mathrm{sgn}(k)$ is the sign function with

$$\Phi = \tan(\pi\alpha/2), \quad \text{for all} \quad \alpha \neq 1,$$

and

$$\Phi = -(2/\pi)\log|k|, \quad \text{for} \quad \alpha = 1.$$

Such distributions form a four-parameter family of continuous probability distributions with location and scale parameters μ and σ, respectively, and two shape parameters β and α (see Fig. 2). In particular $0 < \alpha \leq 2$ is the index of stability or characteristic exponent and indicates the asymptotic behavior of the distribution (long-tail power law), σ is a scale factor, which for $\alpha=2$ provides a measure of the width of the distribution, and σ^{α} is the noise intensity, $\mu(\in \mathbb{R})$ is a location parameter, and $\beta(\in[-1,1])$ is an asymmetry parameter. Sample trajectories and probability distributions for different values of α and β are shown in Figs. 1 and 2, respectively. We note that for $\beta=0$, a Lévy symmetric α-stable distribution is obtained.

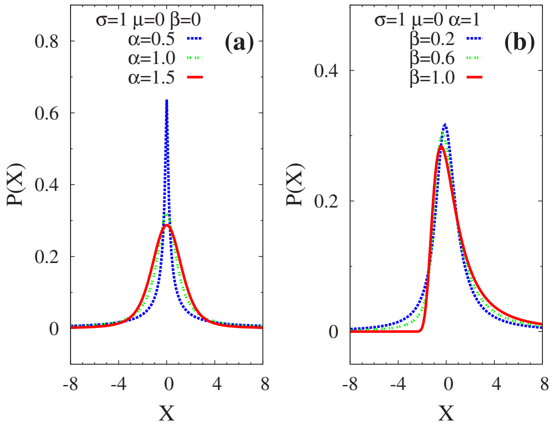

FIG. 2. (Color online) Probability density function, $P(X)$, of stable Lévy distribution for fixed values of μ and σ, and different values of α and β. Namely, (a) $\sigma=1$, $\mu=0$, $\beta=0$, and $\alpha=0.5, 1.0, 1.5$; (b) $\sigma=1$, $\mu=0$, $\alpha=1$, and $\beta=0.2, 0.6, 1.0$

By performing the inverse Fourier transform of the characteristic function $\varphi(k)$ we obtain the probability density function of the stable distribution,

$$l_{\alpha,\beta}(x;\sigma,\mu) = \frac{1}{\pi}\mathrm{Re}\left[\int_0^{\infty} e^{ik(x-\mu)} e^{-(\sigma k)^{\alpha}(1-i\beta\Phi)} dk\right], \tag{4}$$

where $\mathrm{sgn}(k)=1$ because $k>0$. By series expansion of the second exponential we have

$$l_{\alpha,\beta}(x;\sigma,\mu) = \frac{1}{\pi}\mathrm{Re}\left[\int_0^{\infty} e^{ik(x-\mu)} \sum_{n=0}^{\infty} \frac{(-qk^{\alpha})^n}{n!} dk\right], \tag{5}$$

where $q=\sigma^{\alpha}(1-i\beta\Phi)$. For $\mu=0$, $\beta=0$, and $\sigma=1$ a series expansion valid for large arguments $|x| \gg 0$ is [53]

$$l_{\alpha}(x) = -\frac{1}{\pi}\sum_{n=1}^{m} \frac{(-1)^n}{n!}\frac{\Gamma(\alpha n+1)}{|x|^{\alpha n+1}}\sin\left(\frac{n\pi\alpha}{2}\right) + R(|x|), \tag{6}$$

where $\Gamma(x)$ is the gamma function and $R(|x|) = O(|x|^{-\alpha(m+1)-1})$. The asymptotic expression of Eq. (6) for large values of x is characterized by a power-law behavior [40]

$$l_{\alpha,\beta}(x;1,0) \sim |x|^{-(1+\alpha)}, \quad x \to \infty, \tag{7}$$

which is deeply connected with the divergence of all moments $\langle x^n \rangle$ for $n>2$ and $\alpha<2$.

III. MODEL

Time evolution of two competing species is obtained by using a Lotka-Volterra model [54] based on two Ito stochastic differential equations in the presence of multiplicative Lévy noise [55]

$$\frac{dx}{dt} = mx[a - x - \gamma(t)y] + x\xi_x^{\alpha,\beta}(t), \tag{8}$$

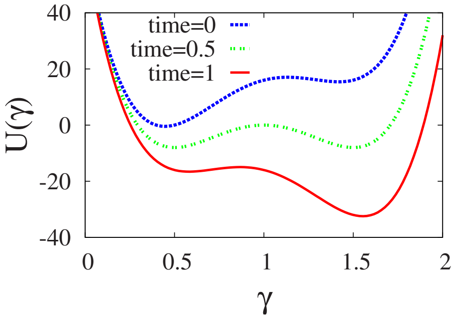

FIG. 3. (Color online) Three configurations of the time dependent bistable potential $U(\gamma,t)$ of Eq. (11) at times $t=0,0.5,1$. The values of the potential parameters are $h=8$, $\eta=0.5$, $A=2h$, $\omega_0=\pi$.

$$\frac{dy}{dt}=my[a-y-\gamma(t)x]+y\xi_y^{\alpha,\beta}(t), \tag{9}$$

where a is the growth parameter and $\gamma(t)$ is the time dependent interaction parameter between the species. Here $\xi_x^{\alpha,\beta}(t)$ and $\xi_y^{\alpha,\beta}(t)$ are statistically independent α-stable Lévy noises with zero mean ($\mu=0$) and intensity D equal for the two noise sources. We note that Langevin equations with multiplicative linear noise are ubiquitous in economics, optics, population dynamics, study of instabilities, with the multiplicative linear noise giving rise to behavior characterized by a power law, observed in economic and ecological systems, and known as the law of proportional effect [56–59]. The time series for the two populations are obtained setting $m=70$ and $a=1$. It is known that for $\gamma<1$ a coexistence regime takes place, while for $\gamma>1$ an exclusion regime is established. Coexistence of the two species and exclusion of one of them correspond to stable states of the Lotka-Volterra's deterministic model [60]. Real ecosystems are open systems, which implies that they are immersed in a noisy nonstationary environment. Therefore, the interaction parameter $\gamma(t)$ is affected both by deterministic periodical "forces," e.g., temperature, and random fluctuations of environmental and natural variables such as the temperature itself and food resources, whose variations produce a competition between the species. Therefore noise together with periodic forces determines the crossing from one dynamical regime ($\gamma<1\rightarrow$coexistence) to the other one ($\gamma>1\rightarrow$exclusion). This continuous and noisy behavior of the interaction parameter $\gamma(t)$ can be described by the stochastic differential equation

$$\frac{d\gamma(t)}{dt}=-\frac{\partial U(\gamma,t)}{\partial\gamma}+\xi_\gamma^{\alpha,\beta}(t), \tag{10}$$

where the time dependent bistable potential (see Fig. 3)

$$U(\gamma,t)=h(\gamma-1)^4/\eta^4-2h(\gamma-1)^2/\eta^2+A\gamma\cos(\omega_0 t) \tag{11}$$

represents the effects of deterministic forces, and the term of additive noise $\xi_\gamma^{\alpha,\beta}(t)$ mimics the random fluctuations of environmental variables and natural resources. The oscillating driving force takes into account, for example, periodic variations of the temperature. In Eqs. (10) and (11), $h=8$ is the height of the potential barrier, $A=2h$ and $\omega_0=\pi$ are the amplitude and the frequency of the driving force, respectively, and $\eta=0.5$. The noise source $\xi_\gamma^{\alpha,\beta}(t)$ is given by a Lévy process with zero mean and intensity D_γ.

Deterministic stationary states

In the absence of multiplicative noise ($D=0$) and for constant values of the interaction parameter γ, Eqs. (8) and (9) describe the deterministic dynamics of two competing species. In these conditions the stationary values of the two species densities are given by

$$x^{st}=y^{st}=\frac{a}{1+\gamma}. \tag{12}$$

In view of studying the system when a richer dynamics takes place, we introduced the interaction parameter $\gamma(t)$, as a stochastic process governed by Eq. (10). Here, $\gamma(t)$ takes values around the two minima (see Fig. 3), $\gamma=\gamma^{down}=0.5$ (left-side well) and $\gamma=\gamma^{up}=1.5$ (right-side well) corresponding to coexistence and exclusion regime, respectively. As a consequence, from Eq. (12) we get two different equilibrium points

$$x_1^{st}=y_1^{st}=2/3 \quad (\gamma=0.5\rightarrow\text{coexistence}),$$

$$x_2^{st}=y_2^{st}=2/5 \quad (\gamma=1.5\rightarrow\text{exclusion}).$$

In order to determine the conditions for which the stationary states given in Eq. (12) correspond to a point of stable equilibrium in the phase space, we perform a stability analysis. Therefore, we consider the Jacobian matrix of the system given in Eqs. (8) and (9)

$$J(\gamma)=\begin{pmatrix}-\dfrac{a}{1+\gamma} & -\dfrac{\gamma a}{1+\gamma}\\ -\dfrac{\gamma a}{1+\gamma} & -\dfrac{a}{1+\gamma}\end{pmatrix} \tag{13}$$

and obtain the corresponding eigenvalues

$$\lambda_1=\frac{a(\gamma-1)}{\gamma+1}, \tag{14}$$

$$\lambda_2=-a. \tag{15}$$

Therefore, for $\gamma=0.5$ we get

$$\lambda_1^s=-a/3, \quad \lambda_2^s=-a,$$

and for $\gamma=1.5$

$$\lambda_1^u=a/5, \quad \lambda_2^u=-a,$$

where the apices "s" and "u" indicate stable and unstable equilibrium, respectively. In fact, for $\gamma=0.5$ the two eigenvalues are negative, which causes the equilibrium point to be unconditionally stable, while for $\gamma=1.5$ one eigenvalue is positive and the other one negative, which implies that the equilibrium point corresponds to a saddle point in the phase space. Therefore, the stationary values $x_1^{st}=y_1^{st}=2/3$ obtained

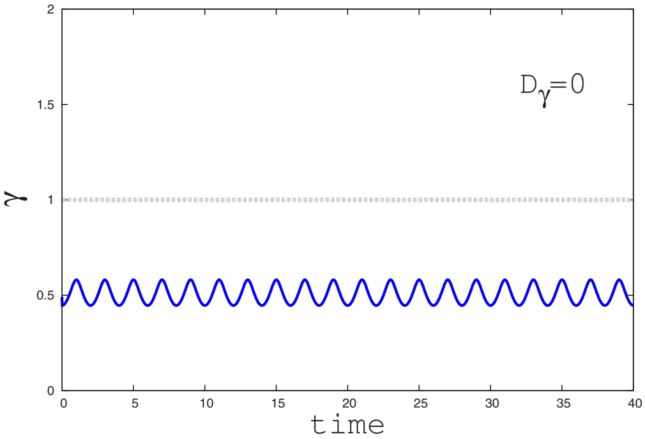

FIG. 4. (Color online) Time evolution of the interaction parameter $\gamma(t)$ (blue line), by numerical integration of Eq. (10) with zero noise intensity D_γ. The gray line indicates the threshold value $\gamma=1$: coexistence of both species ($\gamma<1$) and exclusion of one species ($\gamma>1$).

for $\gamma=0.5$ (coexistence regime) represent a stable equilibrium point for the Lotka-Volterra system considered [see Eqs. (8) and (9)]. Conversely, the stationary values $x_2^{st}=y_2^{st}=2/5$ obtained for $\gamma=1.5$ correspond to an unstable equilibrium (saddle point) and the system tends to exclude one of the two species (exclusion regime).

IV. INTERACTION PARAMETER

First, we investigate the effect of the noise on the time behavior of $\gamma(t)$. Since the dynamics of the species strongly depends on the value of the interaction parameter, we initially analyze the time evolution of $\gamma(t)$ for different values of both the intensity D_γ and index α, with $\beta=0$, of the Lévy source $\xi_\gamma^{\alpha,\beta}(t)$ [see Eq. (10)].

"Biological" stochastic resonance

Specifically, for $D_\gamma=0$ and $\gamma(0)=0.5$ we obtain a periodical behavior of $\gamma(t)$ in the coexistence region (see Fig. 4). In the presence of non-Gaussian noise ($\alpha\neq 2$), for low noise intensity ($D_\gamma=0.5 \ll h$), we can observe the effect of the noise on the time series of the interaction parameter (see Fig. 5). In particular, the noise is responsible not only for slight perturbations in the oscillating behavior of $\gamma(t)$, but also for the appearance of jumps (Lévy flights) between $\gamma=0.5$ (left well of the potential U) and $\gamma=1.5$ (right well). These jumps, distributed according to a Lévy stable statistics, are known as Lévy flights and represent the effect of the heavy tails which characterize these non-Gaussian distributions. It is also evident how the distribution of these jumps changes for different values of α. This indicates that the alternating coexistence/exclusion regime can be modulated by the specific Lévy noise source $\xi_\gamma^{\alpha,\beta}(t)$, varying both the intensity D_γ and the parameter α. It is then interesting to analyze the behavior of $\gamma(t)$ for different levels of noise. Therefore, setting again $\beta=0$, we obtain the time evolution of the interaction parameter for higher noise intensity ($D_\gamma \simeq h$). In particular, Fig. 6 shows the time series of $\gamma(t)$ with $D_\gamma=5,5.5,6$ and for different values of α ($\alpha=1.6,1.7,1.8,1.9$), compared with those obtained for Gaussian noise ($\alpha=2$) [42]. In the figure we see that the synchronization phenomenon between the Kramers time to overcome the potential barrier, starting from one of the two minima (see Fig. 3), and the periodical driving force is reduced in the presence of Lévy noise with respect to the Gaussian case. This indicates that the stochastic resonance effect, which can influence the dynamics of real ecosystems, results to be different in the presence of non-Gaussian noise source. A further increase of the noise intensity produces a loss of coherence and the dynamical behavior is strongly controlled by the noise (see Fig. 7).

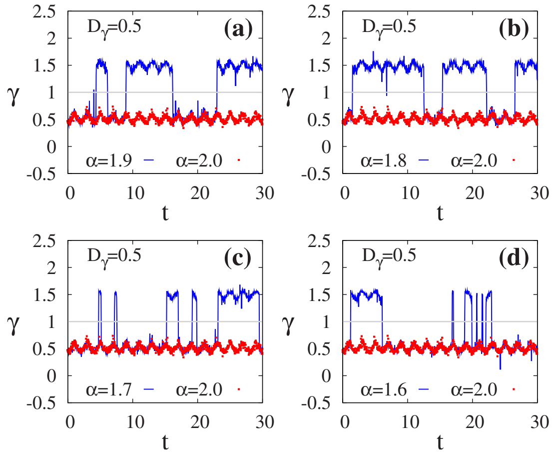

FIG. 5. (Color online) Time evolution of the parameter $\gamma(t)$, by numerical integration of Eq. (10) with noise intensity $D_\gamma=0.5$ and $\beta=0$, for five values of the index α, namely, (a) $\alpha=1.9$, (b) $\alpha=1.8$, (c) $\alpha=1.7$, (d) $\alpha=1.6$ (blue lines), and $\alpha=2.0$ (red points in all panels).

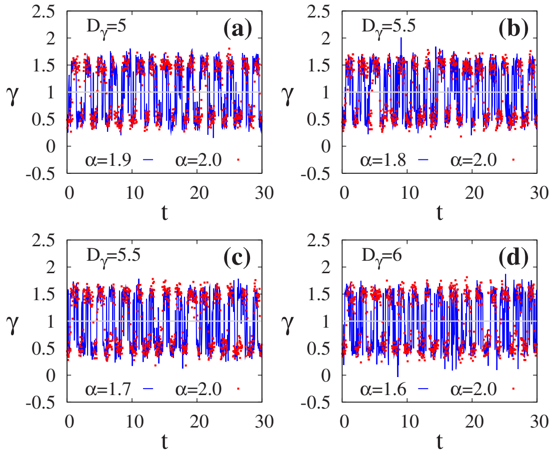

FIG. 6. (Color online) Time series of the parameter $\gamma(t)$ [from Eq. (10)], for suitable noise intensities ($D_\gamma=5,5.5,6$) and different values of the Lévy index α, namely, $\alpha=1.9,1.8,1.7,1.6$ (blue lines), compared with the Gaussian case ($\alpha=2.0$) (red points). The asymmetry parameter is $\beta=0$.

A measure of the stochastic resonance (SR) phenomenon and its intensity [61–64] is provided by the signal-to-noise ratio (SNR)

$$\mathrm{SNR}=\frac{2}{S_N(\Omega)}\lim_{\Delta\omega\to 0}\int_{\Omega-\Delta\omega}^{\Omega+\Delta\omega}S(\omega)d\omega. \tag{16}$$

Here, $\int_{\Omega-\Delta\omega}^{\Omega+\Delta\omega}S(\omega)d\omega$ represents the power carried by the signal $\gamma(t)$, and $S_N(\Omega)$ estimates the background noise level at

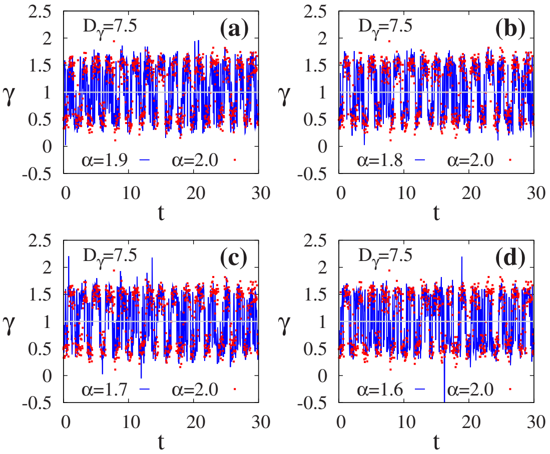

FIG. 7. (Color online) Time series of the parameter $\gamma(t)$ [from Eq. (10)], for noise intensity $D_\gamma=7.5$ and different values of the Lévy index α, namely, $\alpha=1.9,1.8,1.7,1.6$ (blue lines), compared with the Gaussian case ($\alpha=2.0$) (red points). The asymmetry parameter is $\beta=0$.

the driving frequency Ω. The SR effect observed indicates that an optimal level of noise exists for which the response of the system undergoes resonancelike behavior as a function of the noise level [61,62]. In this condition, it is established a quasiperiodical switching between $\gamma=\gamma^{down}=0.5$ and $\gamma=\gamma^{up}=1.5$, which is responsible for an alternating coexistence/exclusion regime in the dynamics of the two populations. Because the SR phenomenon observed affects the time behavior of $\gamma(t)$, which is a biological parameter responsible for the interaction of the two species, we name this effect "biological" stochastic resonance. In order to measure and better analyze the system response to the noise, we consider the spectral power amplification (SPA) [61,62], indicated by η and defined as the ratio of the power of the output signal $\gamma(t)$ sampled at the frequency Ω of the external driving, to the power of the driving signal. In Figs. 8 and 9 we show SNR and SPA, respectively, as a function of the noise intensity D_γ. The nonmonotonic behavior of the SNR indicates clearly the presence of stochastic resonance, characterized by a maximum whose value decreases as the index α approaches 1 (Cauchy distribution).

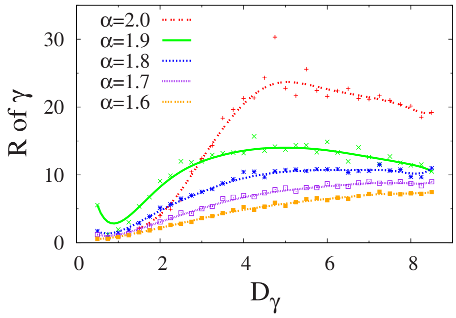

FIG. 8. (Color online) Signal-to-noise ratio R of $\gamma(t)$ as a function of the noise intensity D_γ, for different values of the index α of the stable Lévy distribution, namely, $\alpha=1.6,1.7,1.8,1.9,2.0$.

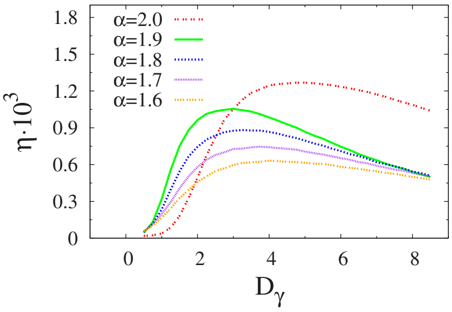

FIG. 9. (Color online) Spectral power amplification η of $\gamma(t)$ as a function of the noise intensity D_γ, for different values of the index α of the stable Lévy distribution, namely, $\alpha=1.6,1.7,1.8,1.9,2.0$.

V. STOCHASTIC RESONANCE WITHIN SPECIES DYNAMICS

In this section we analyze the dynamics of the two species densities. In particular, for different symmetrical ($\beta=0$) α-stable Lévy distributions, we calculate the noise intensity D_γ corresponding to the regime of "biological" stochastic resonance, that is the maximum of SNR. Afterwards, in Eq. (10) we set D_γ at this value and solve numerically Eqs. (8) and (9) for different values of the multiplicative noise intensity D. The results are shown in Figs. 10–13. In particular, from panels (a)–(c) of these figures it is evident that, for the values of index α considered in our simulations, the multiplicative noise induces anticorrelated periodical oscillations in the time series of the two species, breaking the symmetric dynamical behavior of the ecosystem [compare panels (a) with panels (b) and (c) of Figs. 10–13]. The anticorrelated oscillations of the two species are caused by the alternating dynamical regime (coexistence or exclusion) due to the quasiperiodical oscillations of the interaction parameter $\gamma(t)$ between the two potential wells. In particular, left and right potential wells correspond to coexistence [$\gamma(t)<1$] and exclusion [$\gamma(t)>1$] regime, respectively. For $\gamma(t)<1$ the coex-

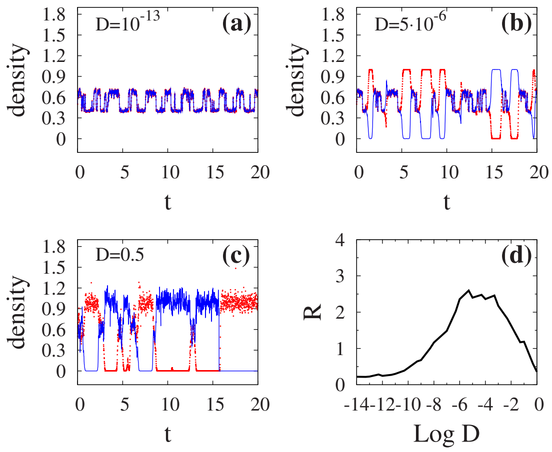

FIG. 10. (Color online) Panels (a), (b), (c): time series of the two species densities x (red points) and y (blue lines) obtained from Eqs. (8) and (9) with $\alpha=1.9$, $\beta=0$, $D_\gamma=5$ and (a) $D=10^{-13}$, (b) $D=5\times10^{-6}$, (c) $D=0.5$. Panel (d): SNR of $(x-y)^2$ as a function of the noise intensity D.

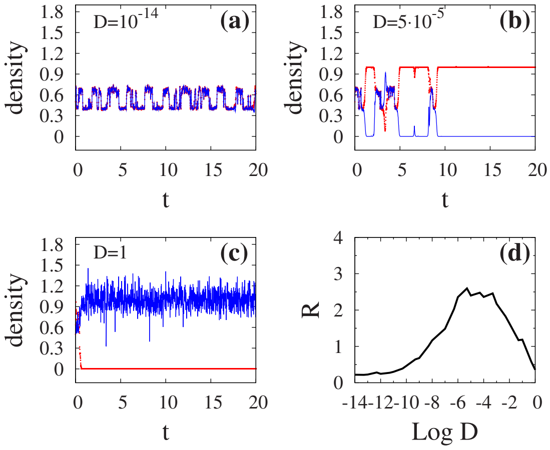

FIG. 11. (Color online) Panels (a), (b), (c): time series of the two species densities x (red points) and y (blue lines) obtained from Eqs. (8) and (9) with α=1.8, β=0, D_γ=5.3 and (a) D=10^{-14}, (b) D=5 $\times 10^{-5}$, (c) D=1. Panel (d): SNR of $(x-y)^2$ as a function of the noise intensity D.

istence of the two species is an equilibrium point in the phase space, so that, also in the presence of multiplicative noise, the two species tend to oscillate in phase (correlated behavior). Conversely, for $\gamma(t)>1$ exclusion of one species becomes an equilibrium point in the phase space, and one of the two species tends to disappear. The alternating dynamical regime, resulting from the quasiperiodical oscillation of $\gamma(t)$ between the two potential wells, determines the anticorrelated oscillating behavior of the two species [42]. Moreover, a multiplicative noise intensity exists that induces oscillating behavior with a maximum of anticorrelation between the two species [see panel (b) of Figs. 10–13]. This indicates the presence of a second SR effect. We check this by calculating the SNR of $(x-y)^2$ for different values of α [see panel (d) in Figs. 10–13]. Here, we can observe the presence of a nonmonotonic behavior characterized by the presence of a maximum. This confirms that the multiplicative noise is responsible for a further SR phenomenon affecting directly the dynamics of the two species. Because of this we name this effect “population” stochastic resonance. Finally, to better compare the SNR curves obtained we show them in one graph (see Fig. 14). Here, it is clear that the maximum of the SNR decreases as α approaches 1, according to the behavior of SNR observed for the interaction parameter γ (see Fig. 8).

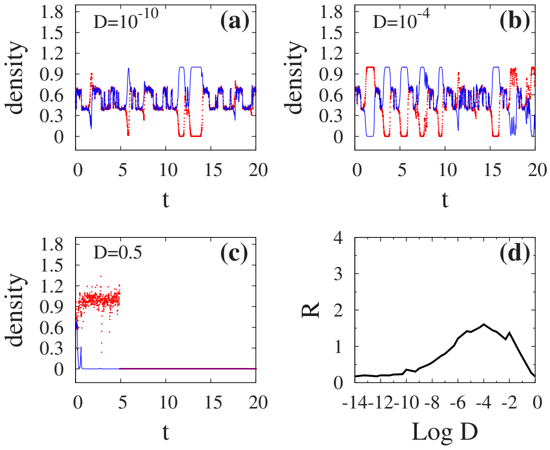

FIG. 12. (Color online) Panels (a), (b), (c): time series of the two species x (red points) and y (blue lines) obtained from Eqs. (8) and (9) with α=1.7, β=0, D_γ=5.5, and (a) D=10^{-10}, (b) D=10^{-4}, (c) D=0.5. Panel (d): SNR of $(x-y)^2$ as a function of the noise intensity D.

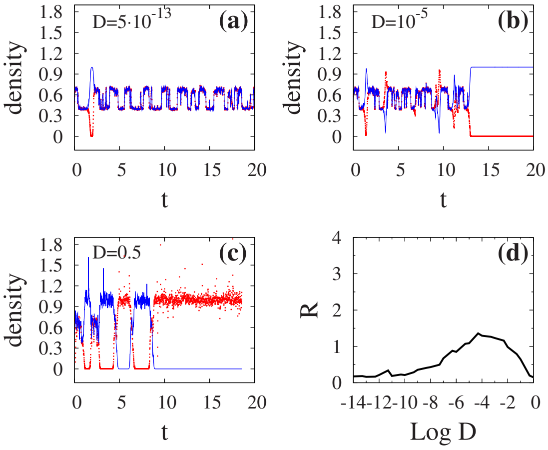

FIG. 13. (Color online) Time series of the two species x (red points) and y (blue lines) obtained from Eqs. (8) and (9) with α=1.6, β=0, D_γ=5.7 and D=5×10^{-13}, (b) D=10^{-5}, (c) D=0.5. Panel (d): SNR of $(x-y)^2$ as a function of the noise intensity D.

VI. CONCLUSIONS

We presented a study on the role of the Lévy noise in population dynamics. By using the Lotka-Volterra model in the presence of two symmetrical non-Gaussian α-stable noise sources, we analyzed the time behavior of an ecosystem consisting of two competing species and surrounding environment. In particular, an additive noise source affects the dynamics of the interaction parameter between the two species, $\gamma(t)$, which “moves” along a bistable potential in the presence of a periodical driving force. Depending on the values of the interaction parameter $\gamma(t)$, coexistence or exclusion regime takes place. By using different α-stable noise sources, stochastic resonance is always observed, with $\gamma(t)$ switching quasiperiodically between coexistence and exclusion regime. In this condition, we consider the second noise

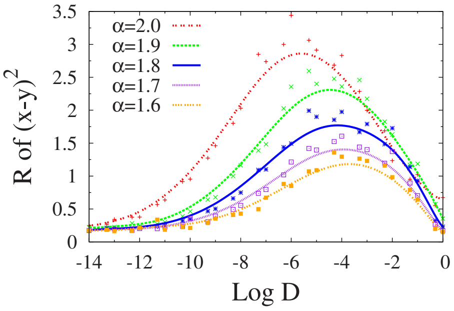

FIG. 14. (Color online) Signal-to-noise ratio R of $(x-y)^2$ as a function of the noise intensity D for different values of the index α.

source, inserting in the Lotka-Volterra equations a term of multiplicative Lévy noise, whose intensity is indicated by D. For different values both of the index α and intensity D, we study the time behavior of the two species densities, x and y, and find that noise is responsible for the generation of time series characterized by anticorrelated oscillations, whose amplitude is strictly dependent on the multiplicative noise intensity. To better analyze the response of the system to the multiplicative noise, we calculate the corresponding signal-to-noise ratio (SNR) of $(x-y)^2$. The results show that SNR is characterized by a nonmonotonic behavior with a maximum as a function of the noise intensity, which indicates the presence of a second stochastic resonance phenomenon. Finally, we observe that the values of this maximum in the SNR and the spectral power amplification is reduced as the Lévy index α decreases approaching 1 (more superdiffusive behavior).

We note that our model is useful to describe physical situations in which the amplitude of periodical driving forces, such as those connected with the temperature oscillations, is weak and therefore unable to produce considerable variations in the dynamical regime of the ecosystem. The synergetic cooperation between the nonlinearity of the system and the random and periodical environmental driving forces produces, therefore, a coherent time behavior of the ecosystem investigated. These noise-induced effects should be useful to explain the spatiotemporal behavior of species whose dynamics is strongly affected by environmental noise characterized by Lévy distribution [65,66].

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