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Fluctuations and correlations in lattice models for predator-prey interaction

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Including spatial structure and stochastic noise invalidates the classical Lotka-Volterra picture of stable regular population cycles emerging in models for predator-prey interactions. Growth-limiting terms for the prey induce a continuous extinction threshold for the predator population whose critical properties are in the directed percolation universality class. We discuss the robustness of this scenario by considering an ecologically inspired stochastic lattice predator-prey model variant where the predation process includes next-nearest-neighbor interactions. We find that the corresponding stochastic model reproduces the above scenario in dimensions $1<d\leq 4$, in contrast with the mean-field theory, which predicts a first-order phase transition. However, the mean-field features are recovered upon allowing for nearest-neighbor particle exchange processes, provided these are sufficiently fast.

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In 1920 and 1926, respectively, Lotka [1] and Volterra [2] devised a simple coupled set of differential equations to describe an autocatalytic reaction model and the statistics of fish catches in the Adriatic. The Lotka-Volterra model (LVM) has since become one of the central paradigms for the emergence of periodic oscillations in nonlinear systems with competing constituents [3], and features prominently in textbooks, from undergraduate-level population biology [4] to ecology [5,6] and mathematical biology [7] as, for instance, it can also be formulated as a host-pathogen model [8]. Yet it has often been severely criticized as being biologically unrealistic and mathematically unstable [4,7,9]. Recent investigations of zero-dimensional [10] and spatial stochastic models [8,11–15] have shown that this criticism definitely pertains to the original deterministic rate equations; however, it turns out that the stochastic, or lattice, two-species predator-prey model variants display quite robust properties, rather insensitive to the details of the underlying microscopic processes (for a recent overview, see Ref. [16]). In particular, the lattice predator-prey models (LPPM) display the following features: (i) The population densities typically display erratic (rather than regular periodic) oscillations, with amplitudes that vanish in the thermodynamic limit [13], caused by persistent and recurrent predator-prey activity waves that form complex spatiotemporal structures [17]; (ii) when the prey population growth is limited (finite carrying capacity, local site restrictions), there exists an extinction threshold for the predator population [14,15]; this constitutes a nonequilibrium active-to-absorbing-state phase transition with the critical exponents of *directed percolation* (DP) [18,19]. Also, for host-pathogen models with two types of pathogens, the invasion of the system by one pathogen (the other becoming extinct) through oscillatory behavior was reported using mean-field (MF) and pair-approximation treatments [8].

As noted by various authors [13–15,17], a more realistic description of the predator-prey interaction should include the possibility for the agents to move. In fact, in real ecosystems prey tend to evade the predators, while the predators aim to pursue the prey. One approach to account for the motion of the agents is to consider *diffusion* [nearest-neighbor (NN) hopping] of predators and/or prey, which, however, does not really affect the global properties of the LPPM [14]. Another approach, to be considered, is to assume a NN exchange process (among any two agents: predators, prey, and empty sites) in the following referred to as "stirring." It has to be noted that both diffusion and stirring processes are not taken into account at the (MF) rate equation level. In addition, some recent investigations have included long-range processes in two-dimensional LPPM, reporting quite different results on the existence [15] or absence [14] of "self-sustained oscillations" (in the thermodynamic limit). We also note that for spatial host-pathogen models (with NN interactions), the rate equations include algebraic nonlinear terms of power $2d+1$ in dimensions d [8]. Thus, an understanding of the joint effect of long-range interactions and of the agents' motion is desirable and relevant from ecological and statistical physics points of view.

In this Rapid Communication, we aim to shed further light on the remarkable robustness of the LPPM scenario. To this end, we study an ecologically inspired stochastic lattice predator-prey model with a *next-nearest-neighbor* (NNN) interaction (NNN-LPPM), both in the presence and absence of a *NN exchange process* (stirring). We will demonstrate a subtle interplay between the correlations generated by the NNN interaction and the stirring process. As a result, there is a regime where the NNN-LPPM phase diagram, indeed, follows the LPPM scenario outlined above, with a *continuous* predator extinction transition in the DP universality class. On the other hand, we shall also see under which unexpected conditions a *first-order* phase transition can occur as a consequence of the competition between the short-range ex-

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change and the NNN predator-prey interactions.

To begin, we outline the main properties of the deterministic LVM and then of the corresponding LPPM [3,4,7]. Consider two chemical species subject to the reactions $A \to \oslash$ (decay rate $\mu > 0$), $B + \oslash \to B + B$ (branching rate $\sigma > 0$), and $A + B \to A + A$ (predation rate $\lambda > 0$). Neglecting any spatial variations and fluctuations of the concentrations $a(\boldsymbol{x},t)$ and $b(\boldsymbol{x},t)$ of "predators" A and "prey" B, one obtains the classical LVM rate equations: $\dot{a}(t) = \lambda a(t) b(t) - \mu a(t)$ and $\dot{b}(t) = \sigma b(t) - \lambda a(t) b(t)$. These deterministic equations have as stationary states $(a^*, b^*) = (0,0)$ (extinction), $(0,\infty)$ (predators extinct, prey proliferation), and $(a_c^*, b_c^*) = (\sigma/\lambda, \mu/\lambda)$ (species coexistence). The unstable fixed points $(0,0)$ and $(0,\infty)$ constitute *absorbing* states of the dynamics. The existence of a conserved first integral of the deterministic rate equation, $K(t) = \lambda[a(t) + b(t)] - \sigma \ln a(t) - \mu \ln b(t) = \text{constant}$, implies oscillatory kinetics around (a_c^*, b_c^*).

Since this center singularity is *unstable* with respect to introducing model modifications [5,7], the LVM rate equations are often rendered more "realistic" by introducing growth-limiting terms [4,7]. For the LVM, this amounts to replacing the rate equation for species B with $\dot{b}(t) = \sigma b(t)[1 - \rho^{-1} b(t)] - \lambda a(t) b(t)$ (ρ is the prey "carrying capacity"; growth-limiting terms for the predators do not induce any qualitative changes). The three fixed points are now shifted to $(a^*, b^*) = (0,0)$ (extinction), $(0,\rho)$ (predators extinct, system saturated with prey), and (a_r^*, b_r^*) with $a_r^* = (1 - \mu/\lambda\rho)\sigma/\lambda$, which is in the physical region ($0 < a_r^* \leqslant 1$) if $\lambda > \mu/\rho$, and $b_r^* = \mu/\lambda$. Linear stability analysis reveals $(0,0)$ to be a saddle point, whereas $(0,\rho)$ is stable (node) if $\lambda < \mu/\rho$ (when $a_r^* < 0$), and a saddle point (stable in the b direction) otherwise. When $\lambda > \mu/\rho$, the coexistence state (a_r^*, b_r^*) is stable; it is either a node or a focus, associated with spiral trajectories in the (a,b) phase plane [7]. Thus, at the rate equations level, $\lambda_c = \mu/\rho$ is the critical predation rate. The global stability of (a_r^*, b_r^*) is established by the existence of a Lyapunov function $\mathcal{L}(a,b) = \lambda\{a_r^* \ln a(t) + b_r^* \ln b(t) - a(t) - b(t)\}$ [7]. Many of these features re-emerge in *stochastic* LPPM with site restriction. Indeed, Monte Carlo simulations [11,13] yield that as in mean-field theory, the coexistence fixed point is either a node or a focus. In the latter case, amazingly rich spatiotemporal patterns of persistent predator-prey "pursuit and evasion" waves [7,9] emerge, inducing erratic correlated population density oscillations. In *finite* systems, these quasiperiodic fluctuations appear on a global scale, but the amplitude of the density oscillations decreases with system size [13]. A completely different picture emerges when the active fixed point is a node just above the predators' extinction threshold λ_c: Instead of the intricate front patterns, small predator "clouds" effectively diffuse in a sea of prey [16]. If the value of λ is reduced further (keeping the other rates fixed), at the critical value λ_c the system reaches the absorbing state. This active-to-absorbing phase transition is found to be in the DP universality class [19]; this is also true for many LPPM variants [13–15]. These results can be understood from the master equation: For the above reactions one may derive an equivalent field-theory action [20], which near λ_c can be mapped onto Reggeon field theory [16], known to describe the asymptotic DP scaling laws [19–21].

In most LPPM (see, e.g., Refs. [14,13]), the "predation" process subsumes *NN* interaction and the effects on both the prey and the predators in a *single* reaction. More realistically, one should split this into two processes, and thereby introduce *two* independent time scales. This leads to the following stochastic reaction scheme that incorporates a *three-site* NNN process: (a) A predator reproduces in the vicinity of a prey (*favorable* environment) according to the triplet reaction $A + \oslash + B \to A + A + B$ [with rate $\delta/z(z-1)$; $z = 2d$ is the coordination number of a d-dimensional hypercube]; (b) a predator consumes a neighboring prey (rate η/z), leaving an empty site, according to the binary process $A + B \to \oslash + A$; (c) we shall also allow for an efficient *mixing* process, through particle exchange with rate $\mathcal{D}/z$ (stirring) between two *neighboring* sites regardless of their content [12]. Besides these reactions, we still consider the processes $B + \oslash \to B + B$ (rate σ/z) and $A \to \oslash$ (rate μ). Assuming full site restriction, i.e., allowing at most one particle per site, the MF rate equations now read

$$\dot{a}(t) = \delta a(t) b(t)[1 - a(t) - b(t)] - \mu a(t), \tag{1}$$

$$\dot{b}(t) = \sigma b(t)[1 - a(t) - b(t)] - \eta a(t) b(t). \tag{2}$$

These equations can be obtained from the master equation of our NNN-LPPM upon factorizing the three-point correlators as products of the corresponding densities a, b. In contrast with the LVM, the nonlinear term in Eq. (1) is *cubic* (NNN interaction); the site restriction appears through the growth-limiting factors $1 - a - b$. Note that the mixing parameter $\mathcal{D}$ does not enter the rate equations (but would appear in the equations for the three-point and higher correlation functions). Equations (1) and (2) admit *four* fixed points, provided $\delta > \delta_c = 4\mu(\sigma + \eta)/\eta$. In addition to the previous absorbing states, $(a^*, b^*) = (0,0)$ and $(0,1)$, the two new nontrivial steady states $(k = 1,2)$ are given by

$$a_k^* = [\sigma/2(\sigma + \eta)][1 - (-1)^k \sqrt{1 - \delta_c/\delta}] \tag{3}$$

and $b_k^* = \frac{1}{2}[1 + (-1)^k \sqrt{1 - \delta_c/\delta}]$. These active fixed points $(a_{1,2}^*, b_{1,2}^*)$ correspond to two *distinct* predator-prey coexistence phases. From linear stability analysis, we infer that the absorbing state $(0,1)$ is *always* a stable node: The associated Jacobian eigenvalues read $\epsilon_+(0,1) = -\mu$ [with eigenvector $\boldsymbol{v}_+ = (\{\mu - \sigma\}/\{\sigma + \eta\}, 1)$] and $\epsilon_-(0,1) = -\sigma$ [eigenvector $\boldsymbol{v}_- = (0,1)$]. On the other hand, $(0,0)$ is an unstable saddle point, with eigenvalues $\epsilon_+(0,0) = \sigma$ [with unstable eigendirection $\boldsymbol{v}_+ = (0,1)$] and $\epsilon_-(0,1) = -\mu$ [stable eigendirection $\boldsymbol{v}_- = (1,0)$]. Without loss of generality, we just discuss the stability of the active fixed points (3) when $\eta = \mu = \sigma = 1$. In this case, $\delta_c = 8$ and the eigenvalues of the Jacobian, respectively, read $(k = 1,2)$: $\epsilon_\pm(a_k^*, b_k^*) = -\frac{1}{4}[3 + (-1)^k \sqrt{1 - 8/\delta}] \pm \frac{1}{4}\sqrt{22(-1)^k \sqrt{1 - 8/\delta} + 10 - 8/\delta}$. Thus, the active fixed point (a_1^*, b_1^*) is stable, $\text{Re}[\epsilon_\pm(a_1^*, b_1^*)] < 0$, while (a_2^*, b_2^*) is a saddle point. More generally, for fixed μ, σ, η there exists a value $\delta_s > \delta_c$ such that (a_1^*, b_1^*) is a stable node if $\delta_c < \delta \leqslant \delta_s$, and a stable focus, i.e., $\text{Im}[\epsilon_\pm(a_1^*, b_1^*)] \neq 0$, if $\delta > \delta_s$. When $\eta = \mu = \sigma = 1$, $\delta_s = (29 + 11\sqrt{7})/6 \approx 9.683\,88$. Typical phase portraits

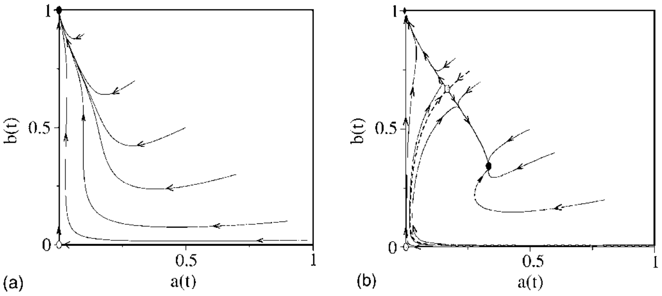

FIG. 1. Flows in the phase plane from integrating Eqs. (1) and (2) for $\mu=\sigma=\eta=1$, with $\delta=4$ (a) and $\delta=9$ (b). (a): $(0,1)$ is the only stable fixed point (node). (b): There is an additional stable (node) active fixed point $(a_1^*,b_1^*)=(1/3,1/3)$; while $(0,0)$ and $(a_2^*,b_2^*)=(1/6,2/3)$ are unstable. The slopes of the separatrices at (a_2^*,b_2^*) are ≈ 1.126 (dashed line) and ≈ -1.568 (see text).

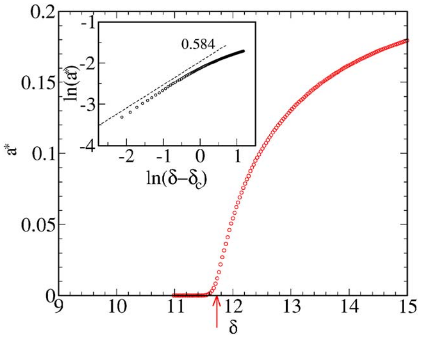

FIG. 3. (Color online) Average stationary density of predators in the absence of stirring on a 512×512 lattice with $\eta=\sigma=2\mu=2$ and $\mathcal{D}=0$: Existence of a DP-like phase transition at $\delta_c\approx 11.72$ with exponent $\beta\approx 0.584$ (see inset).

as predicted by Eqs. (1) and (2) are illustrated in Fig. 1. The eigenvectors associated with (a_2^*,b_2^*) give the slope of the separatrices in its vicinity: $4(\sqrt{\delta}-\sqrt{\delta-8})/[\sqrt{\delta}-\sqrt{\delta-8}\pm\sqrt{10\delta+22\sqrt{\delta(\delta-8)}-8}]$. It follows from this discussion that, at the MF level, the introduction of a triplet interaction changes the behavior of the system dramatically: For $\delta>\delta_c$, the system can reach the absorbing state full of prey or, alternatively, a phase where the prey population, with stationary density $b^*<1/2$, coexists with the predators. Hence, the rate equations predict the possibility of a *first-order* phase transition.

Motivated by these predictions, quite different from those of other LPPM, we have studied the properties of our NNN-LPPM through Monte Carlo simulations on periodic hypercubic lattices. We have first considered the case of slow ($\mathcal{D}\approx 0$) and fast stirring and noted the emergence of quite different behavior. In fact, for no (or slow) stirring, instead of a discontinuous phase transition, we have observed a *continuous* active-to-absorbing phase transition as for the LPPM in dimensions $d=2$, 3 and even $d=4$, see Fig. 2(a). (Of course, in dimensions $d>3$ the model is biologically irrelevant: these cases have only been considered to assess the validity of the MF theory.) To ascertain the properties of the NNN-LPPM, we have employed the dynamical Monte Carlo technique [18]. Near the extinction threshold, one expects power-law behavior for the survival probability $P(t)\sim t^{-\delta'}$ and the number of active sites $N(t)\sim t^{\theta}$. By averaging over 3×10^6 independent runs, performed on a 512×512 lattice, each with a duration of 10^5 Monte Carlo steps, for fixed rates $\eta=\sigma=2\mu=2$ and $\mathcal{D}=0$, we have estimated the critical point to be at $\delta_c\approx 11.72$ (the MF prediction is $\delta_c=8$), and measured $\delta'\approx 0.451$ and $\theta\approx 0.230$, very close to the established two-dimensional DP exponents [18]. As illustrated in Fig. 3, we have also determined the order parameter critical exponent defined via $a(t\to\infty)\sim(\delta-\delta_c)^{\beta}$ as $\beta\approx 0.584$. We have checked that the exponent values are consistent with the DP universality class for several choices of the rates η,μ,σ. Qualitatively, the features of the NNN-LPPM remain similar in $d=3$ and 4 [Fig. 2(a)]: We observe continuous phase transitions (for different values of δ_c) with $\beta\approx 0.81$ for $d=3$ and $\beta\approx 1.0$ for $d=4$ (upper critical dimension of DP) in agreement with DP values [18].

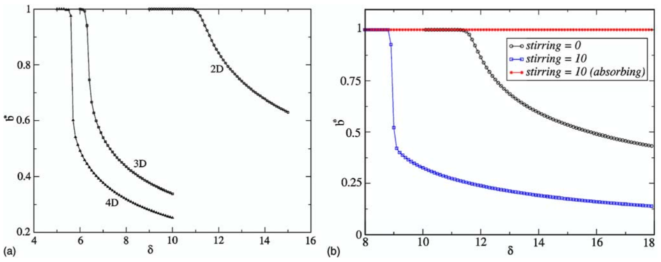

FIG. 2. (Color online) Average stationary prey density b^* vs δ for $\eta=\sigma=2\mu=2$. (a): DP-like transitions on 256^2, 50^3, and 20^4 lattices when $\mathcal{D}=0$. (b): Effect of the stirring on a 512^2 lattice. For $\mathcal{D}=0$, there is a *continuous* transition (center curve, black), while for $\mathcal{D}=10$ (sufficient stirring) two stable branches emerge, and there is a *first-order* transition; the top (red) branch corresponds to predator extinction, and the bottom (blue) branch is associated with a coexistence phase.

In the absence of stirring, the phase diagram changes qualitatively when $d\geqslant 5$: Even for $\mathcal{D}=0$, one then observes the first-order phase transition predicted by the MF approximation. The situation turns out to be completely different when the stirring is sufficiently fast, as illustrated in Fig. 2(b): A first-order phase transition occurs in low dimensions as well, and, depending on the initial condition with respect to the separatrices [see Fig. 1(b)], the flows in the phase portrait end either at the absorbing fixed point $(0,1)$, or reach a stationary state where both predators and prey coexist (with $b^*<1/2$). This scenario, in the presence of sufficiently fast stirring, therefore recovers the MF behavior, at least qualitatively. It is quite remarkable that the rate equations (1) and (2) describe the NNN-LPPM already for mere NN exchanges at *finite* rates; one would rather expect the MF regime to emerge in the limit of infinitely fast exchange processes involving the swap of *all* particles (not restricted to NN partners) [12].

As illustrated in Fig. 4, the intriguing properties of the NNN-LPPM with NN exchange process can be summarized as follow: (i) For vanishing mixing ($\mathcal{D}$ small compared to the other rates), in dimensions $1<d\leqslant 4$ the system undergoes an active-to-absorbing state transition, which belongs again to the DP universality class; only for $d\geqslant 5$, a first-order phase

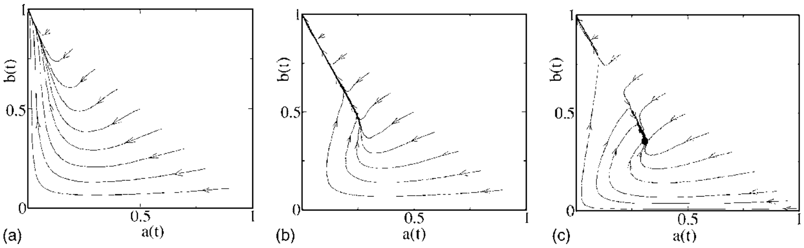

FIG. 4. Phase portrait of the generalized "NNN" lattice predator-prey model (on a 256×256 lattice) with rates $\eta = \mu = \sigma = 1$, $\delta = 10$ and different exchange rates. From (a) to (c): stirring rate $\mathcal{D} = 0, 2, 5$. (See text).

transition appears. Stochastic fluctuations clearly have a drastic effect here, invalidating the MF picture in dimensions $d \leqslant 4$. (ii) When one allows for random short-range particle mixing ($\mathcal{D} > 0$), the dynamics and the phase portrait flows change dramatically [Fig. 4(b)]. (iii) When the exchange processes become sufficiently fast (typically, when $\mathcal{D} \approx \delta$), a new fixed point associated with a coexistence phase is available (this holds even in $d = 1$), as demonstrated in Fig. 4(c), and the system undergoes a first-order phase transition as predicted by the MF theory. As expected, when there is "fast" stirring ($\mathcal{D}$ much larger than the other rates) the MF predictions become very accurate. We have also checked that the NNN-LPPM stable active fixed point is, in agreement with the MF analysis and generic properties of the other LPPM [13,14], either a node or a focus. When it is a focus, the coexistence phase is again characterized by population oscillations originating in moving activity fronts but, as the system is more mixed, these "rings" appear less prominent than in the LPPM with NN interactions [16].

In this paper, we have first outlined the main properties of the LPPM with NN interactions: namely, the existence of erratic oscillations and complex patterns deep in the coexistence phase and a directed percolation type phase transition. We have then further tested this scenario by considering a perhaps more realistic model variant with *NNN* interaction. Upon introducing a short-range stirring mechanism together with this longer-range interaction, an intriguing interplay emerges: When the NN exchange process is "slow," the NNN reaction induces subtle correlations that completely invalidate the MF treatment and the system still undergoes a DP-type phase transition (for $1 < d \leqslant 4$). In this regime, the generic LPPM scenario is thus fully confirmed. However, when the value of the mixing rate $\mathcal{D}$ is raised, the simple NN exchange process "washes out" the NNN correlations and the system reproduces the MF behavior, displaying a *first-order* phase transition. This is to be viewed in contrast with the standard LPPM, for which even the fast diffusion of predators and prey generally does not qualitatively affect its properties [14].

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