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Boundary effects on population dynamics in stochastic lattice Lotka–Volterra models



PHYSICA

STATISTICAL MECHANIS

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HIGHLIGHTS

- The system is split in an active coexistence and a predator extinction domain.
- The predator density is enhanced at the boundary between these regions.
- The local predator correlation length displays a minimum at that boundary.
- The population oscillation attenuation rate attains its largest value there.
- Further subdivisions render the system similar to one with bimodal random disorder.

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ABSTRACT

We investigate spatially inhomogeneous versions of the stochastic Lotka-Volterra model for predator-prev competition and coexistence by means of Monte Carlo simulations on a two-dimensional lattice with periodic boundary conditions. To study boundary effects for this paradigmatic population dynamics system, we employ a simulation domain split into two patches: Upon setting the predation rates at two distinct values, one half of the system resides in an absorbing state where only the prey survives, while the other half attains a stable coexistence state wherein both species remain active. At the domain boundary, we observe a marked enhancement of the predator population density. The predator correlation length displays a minimum at the boundary, before reaching its asymptotic constant value deep in the active region. The frequency of the population oscillations appears only very weakly affected by the existence of two distinct domains, in contrast to their attenuation rate, which assumes its largest value there. We also observe that boundary effects become less prominent as the system is successively divided into subdomains in a checkerboard pattern, with two different reaction rates assigned to neighboring patches. When the domain size becomes reduced to the scale of the correlation length, the mean population densities attain values that are very similar to those in a disordered system with randomly assigned reaction rates drawn from a bimodal distribution.

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1. Introduction

Due to its wide range of applications and relative simplicity, variants of the Lotka–Volterra predator–prey competition model represent paradigmatic systems to study the emergence of biodiversity in ecology, noise-induced pattern formation in population dynamics and (bio-)chemical reactions, and phase transitions in far-from-equilibrium systems. In the classical

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deterministic Lotka–Volterra model [1,2], two coupled mean-field rate equations describe the population dynamics of a two-species predator-prey system, whose solutions display periodic non-linear oscillations fully determined by the system's initial state. Yet the original mean-field Lotka-Volterra rate equations do not incorporate demographic fluctuations and internal noise induced by the stochastic reproduction and predation reactions in coupled ecosystems encountered in nature. In a series of analytical [3-6] and numerical simulation studies [7-18], the population dynamics of several stochastic spatially extended lattice Lotka-Volterra model variants was found to substantially differ from the mean-field rate equation predictions due to stochasticity and the emergence of strong spatio-temporal correlations: Both predator and prey populations oscillate erratically, and do not return to their initial densities; the oscillations are moreover damped and asymptotically reach a guasi-stationary state with both population densities finite and constant on one- or twodimensional square lattices [7], whereas damping appears absent or is very weak in three dimensions [9]. Very similar dynamical properties are observed in other two-dimensional model variants, including a predator-prey system with added prey food supply and cover [12], and implementations on a triangular lattice [14]. In a non-spatial setting, the persistent nonlinear oscillations can be understood through resonantly amplified demographic fluctuations [19]. Local carrying capacity restrictions, representing limited resources in nature, can be implemented in lattice simulations by constraining the number of particles on each site [8,10,11,15–17]. These local occupation number restrictions cause the emergence of a predator extinction threshold and an absorbing phase, wherein the predator species ultimately disappears while the prey proliferate through the entire system. Upon tuning the reaction rates, one thus encounters a continuous active-to-absorbing state non-equilibrium phase transition whose universal features turn out to be governed by the directed percolation universality class [4.5.10-12.15.16.18].

Biologically more relevant models should include spatial rate variability to account for environmental disorder. The population dynamics in a patch surrounded by a hostile foe [20–22] is well represented by Fisher's model [23], which includes diffusive spreading as well as a reaction term capturing interactions between individuals and with the environment. For the stochastic Lotka–Volterra model, the influence of environmental rate variability on the population densities, transient oscillations, spatial correlations, and invasion fronts was investigated by assigning random reaction rates to different lattice sites [24,25]. Spatial variability in the predation rate results in more localized activity patches, a remarkable increase in the asymptotic population densities, and accelerated front propagation. These studies assumed full environmental disorder, as there was no correlation at all between the reaction rates on neighboring sites.

In a more realistic setting, the system should consist of several domains with the environment fairly uniform within each patch, but differing markedly between the domains, e.g., representing different topographies or vegetation states. In our simulations, we split the system into several patches and assign different reaction rates to neighboring regions. By tuning the rate parameters, we can force some domains to be in an absorbing state, where the predators go extinct, or alternatively in an active state for which both species coexist at non-zero densities. One would expect the influence of the boundary between the active and absorbing regions to only extend over a distance on the scale of the characteristic correlation length in the system. In this work, we study the local population densities, correlation length, as well as the local oscillation frequency and attenuation, as functions of the distance from the domain boundary. As we successively divide the system further in a checkerboard pattern so that each patch decreases in size, the population dynamics features quantitatively tend towards those of a randomly disordered model with reaction rates assigned to the lattice sites from a bimodal distribution.

2. Model description and background

The deterministic classical Lotka–Volterra model [1,2] is a set of two coupled non-linear dynamical rate equations that on a mean-field approximation level capture the following kinetic reactions of two species, respectively identified with predators *A* and prey *B*:

$$A \stackrel{\mu}{\to} \emptyset, \quad A + B \stackrel{\lambda}{\to} A + A, \quad B \stackrel{\sigma}{\to} B + B. \tag{1}$$

In these stochastic processes, μ corresponds to the spontaneous predator death rate, while σ denotes the prey reproduction rate. Finally, λ is the predation rate which describes the non-linear reaction through which the predator and prey species interact with each other. The simplified Lotka–Volterra model thus assumes that the prey population grows exponentially in the absence of predators, but becomes diminished with growing predator population. In the presence of the prey, the predator population will increase with the prey population, but is subject to exponential decay once all prey are gone. The configuration with vanishing predator number represents an absorbing state for this system, since there exists no stochastic reaction process that would allow recovery from it. For completeness, we mention that the total population extinction state of course represents another absorbing state. We also remark that one could add independent predator reproduction $A \rightarrow A + A$ (with rate $\bar{\sigma}$) and prey death $B \rightarrow \emptyset$ (rate $\bar{\mu}$) processes to the standard Lotka–Volterra kinetics (1). Yet this would induce no qualitative changes as long as $\bar{\sigma} < \mu$ and $\sigma > \bar{\mu}$; one then simply needs to replace μ with the rate difference $\mu - \bar{\sigma}$, and σ with $\sigma - \bar{\mu}$.

The associated rate equations, subject to mean-field mass action factorization for the non-linear predation process, and valid under well-mixed conditions for spatially homogeneous time-dependent particle densities a(t) and b(t), read

$$\dot{a}(t) = \lambda' a(t)b(t) - \mu' a(t), \quad \dot{b}(t) = -\lambda' a(t)b(t) + \sigma' b(t), \tag{2}$$

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