



Bifurcation, chaos and pattern formation in a space- and time-discrete predator–prey system



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ABSTRACT

The spatiotemporal dynamics of a space- and time-discrete predator–prey system is investigated in this research. The conditions for stable homogeneous stationary state of the system are derived via stability analysis. By using center manifold theorem and bifurcation theory, critical parameter values for flip bifurcation, Hopf bifurcation and Turing bifurcation are determined, respectively. Based on the bifurcation analysis, pattern formation conditions are also provided. Numerical simulations are performed not only to illustrate the theoretical results, but also to exhibit new and complex dynamical behaviors, including period-doubling cascade, invariant circles, periodic windows, chaotic dynamics, and pattern formation. Maximum Lyapunov exponents are calculated to distinguish chaos from regular behaviors. In the routes from bifurcation to chaos, flip-Turing instability and Hopf-Turing instability emerge, capturing the formation of diverse complex patterns, such as mosaic, circle, spiral, spatiotemporal chaotic patterns, and so on. The analysis and results in this research contribute to a new understanding on the relationship among bifurcation, chaos and pattern formation.

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1. Introduction

Predator–prey systems are a type of basic ecological system widely existing in nature. Since the pioneering work of Lotka and Volterra, the dynamical behaviors of predator–prey systems have aroused widespread interests of theoretical and experimental scientists [1–5]. With characteristics of nonlinear interactions and spatial heterogeneity, the predator–prey systems often exhibit spatiotemporal complexity [6,7]. Until now, the investigations on spatiotemporal complexity have formed a new research field, pattern dynamics, which is one of central topics in ecology [8–11]. As widely recognized, the pattern formation research fosters understanding on the dynamical complexity of predator–prey systems [12–15].

In order to theoretically investigate the spatiotemporal dynamics of predator–prey systems, various types of dynamical models have been developed, including cellular automata, games of cyclic dominance, reaction-diffusion models, coupled map lattices (CMLs), and so on. Cellular automata have played an important role in the research of ecological spatiotemporal complexity [26,37]. Characterized by discrete time, discrete space and discrete variables, cellular automata can exhibit many complex nonlinear behaviors of predator–prey systems, including fractals,

attractors, ergodicity, regular patterns, spatiotemporal chaos, and so on [26,38,39]. Moreover, cellular automata show advantage in describing a few special nonlinear population dynamics, such as outbreak or sudden extinction of populations [40,41]. The effective reproduction on nonlinear and complex characteristics of ecological systems evokes wide application of cellular automata in ecology field.

Recently, predator–prey systems with structured populations have been studied through games of cyclic dominance. Games of cyclic dominance not only play a prominent role in explaining the intriguing biodiversity in nature, but also are able to provide insights into Darwinian selection, as well as into structural complexity and prebiotic evolution [42,43]. It has been established that multiple species in a cyclic dominance can exhibit self-organizing behaviors in space [42,44]. As described in Perc et al. and Perc and Szolnoki, defensive alliances can emerge spontaneously on the spatial grid if the chain length of a predator–prey system is more than three [42,45]. Moreover, predator–prey interactions and spatiotemporal self-organization can also emerge spontaneously in evolutionary settings relevant to public goods, as reported in Szolnoki and Perc and Szolnoki et al. [46,47]. In evolutionary games, the spontaneous emergence of cyclic dominance acts one of the main driving forces behind complex pattern formation, which, in turn, is responsible for many differences between evolutionary outcomes reported in well-mixed and structured populations [43].

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Reaction-diffusion models are the mostly widely used theoretical models for studying spatially extended predator–prey systems [8–10,12–15,19]. Via the Turing instability mechanism, reaction-diffusion models have contributed greatly to explaining and revealing the spatial pattern formations ranging from plant distributions to plankton aggregation [2,14–17] and [18]. Many complex predator–prey patterns have been demonstrated, such as patterns of spots, stripes, labyrinth, spirals, gaps, and so on [8,12,15]. So far, the development of reaction-diffusion predator–prey models in literature mainly focuses on two aspects. First, many reaction functions are proposed to describe the dynamics of predator and prey. These reaction functions may incorporate particular growth function, functional response or predator numerical response [19–21]. Second, dispersal of predator and prey populations is described by different diffusion types, such as self-diffusion, cross-diffusion [21], and so on.

When considering spatially and temporally discrete forms of reaction-diffusion models, a new type of predator–prey model can be developed, i.e., coupled map lattices (CMLs) [7,29,30,35,36]. CMLs are a type of discrete model and can be used to study the spatiotemporal dynamics of space- and time-discrete predator–prey systems. In comparing with the continuous models, the CMLs show advantages in describing nonlinear characteristics and dynamical complexity. First, the CMLs can exhibit complex nonlinear characteristics, including frozen chaos, defect turbulence, chaotic Brownian motion of defect, spatiotemporal intermittency, fully developed spatiotemporal chaos and travelling wave [27,28]. Second, the CMLs may exhibit new dynamical behaviors, e.g., Turing instability and Turing patterns can occur in the discrete competitive Lotka–Volterra model rather than the continuous one [35]. Moreover, the CMLs show capability of describing discontinuous properties (e.g. patchy environment or fragmented habitat) of predator–prey systems [7].

Compared with other discrete models (such as cellular automata), the advantages of CMLs may reflect in the following aspects. First, the conditions for pattern formation can be theoretically determined and the effects of parameter variations on pattern formation can be quantitatively described [7]. Second, a CML itself describes a numerical algorithm, therefore, numerical simulations based on the CMLs often show high computational efficiency. Third, the application of CMLs may result to a better understanding and prediction of pattern formations [7,29,30]. Furthermore, the CMLs are very closely related to continuous spatiotemporal models and hence a few achieved theoretical results and methods can be taken to analyze the CMLs [22–25].

Although lots of works have been done on predator–prey systems, still few studies focus on applying the CMLs to explore the predator–prey dynamics. As described in previous research works, the CMLs further the understanding on the pattern formation of space- and time-discrete predator–prey systems [7,29,30,35,36]. However, these research works mainly investigate the case of pure Turing instability. An investigation on pattern formation related to various bifurcations is still seldom documented for the space- and time-discrete predator–prey systems. Therefore, the research on space- and time-discrete predator–prey systems so far still remains open. In this research, we will propose a new CML model and find new results for the spatiotemporal dynamics of predator–prey system. Moreover, due to the similarity of research problems, the potential applicability of the proposed approach in this research can also extend to broader areas of population dynamics and evolution, such as spatiotemporal complexity of competitive systems [35], physics of social systems [48] and statistical mechanics of evolutionary and coevolutionary games [49].

The research is organized as follows. Section 2 gives the development of the CML model and corresponding stability analysis. Section 3 analyzes the flip bifurcation, Hopf bifurcation and Turing

bifurcation, determining the pattern formation conditions. Section 4 provides numerical simulations to show the bifurcations and pattern formation, verifying and extending the theoretical results obtained in Section 3. And finally, Section 5 presents the discussion and conclusion.

2. Mathematical model and stability analysis

2.1. Development of the CML model

For developing the CML model, the reaction-diffusion models are introduced firstly. Generally, the governing equations for a reaction-diffusion predator–prey model can be described by the following:

$$\frac{\partial U}{\partial T} = Uf(U) - Vg(U, V) + D_1 \nabla^2 U, \tag{1a}$$

$$\frac{\partial V}{\partial T} = Vh(U, V) + D_2 \nabla^2 V, \tag{1b}$$

where U and V represent the densities of prey and predator, T denotes time; $f(U)$ describes per capita growth rate of the prey; $g(U, V)$ is a functional response for the predation relationship; $h(U, V)$ is known as the predator numerical response, expressing per capita growth rate of predators; ∇^2 is the Laplace operator describing the spatial dispersal of populations, and D_1 and D_2 are the diffusion coefficients corresponding to U and V ; $\nabla^2 = \partial^2/\partial x^2 + \partial^2/\partial y^2$, in which x and y are spatial coordinates in two-dimensional space describing the position of U and V .

In literature, a variety of functions for $f(U)$, $g(U, V)$ and $h(U, V)$ have been formulated to investigate the pattern formation of predator–prey systems in various situations [12,14]. $f(U)$ can be chosen to describe the prey growth in exponential or logistic form or under Alee effect. The functional response $g(U, V)$ can be chosen among lots of types, including Holling types [20], ratio-dependent type [21], Beddington–DeAngelis type [19], etc. Likewise, many possible choices can also be given for $h(U, V)$. The diversity of these functions raises the complexity of pattern formation of predator–prey systems. In this research, we focus on the following functions for $f(U)$, $g(U, V)$ and $h(U, V)$ [12,15]:

$$f(U) = r_1 \left(1 - \frac{U}{K} - \frac{m_1}{U + b_1} \right), \tag{2a}$$

$$g(U, V) \equiv g(U) = \frac{c_1 U}{U + K_1}, \tag{2b}$$

$$h(U, V) = r_2 - \frac{c_2 V}{U + K_2}, \tag{2c}$$

where r_1 is the intrinsic growth rate of the prey; K is the prey carrying capacity; $m_1/(U+b_1)$ is the term of additive Alee effect, m_1 and b_1 are the Alee effect constants; $g(U)$ describes the Holling type-II functional response, in which c_1 is the maximum predation rate and K_1 measures the extent to which environment provides protection to U ; $h(U, V)$ describes a modified Leslie-Gower type numerical response, in which r_2 is the growth rate of the predator, and c_2 and K_2 have similar meaning to c_1 and K_1 . With the functions described by Eqs. (2), a reaction-diffusion predator–prey model with modified Leslie-Gower and Holling-Type II schemes and additive Alee effect is described. According to Cai et al. [12], this model shows rich spatiotemporal dynamics.

In this research, the CML model is developed based on discretizing the dimensionless form of the above reaction-diffusion predator–prey model, which is described by the following equations:

$$\frac{\partial u}{\partial t} = u \left(1 - u - \frac{m}{u + b} - \frac{cv}{u + k_1} \right) + d_1 \nabla^2 u, \tag{3a}$$

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