



## Research paper

## Complex patterns in a space- and time-discrete predator-prey model with Beddington-DeAngelis functional response



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## ABSTRACT

The spatial pattern formation of predator-prey systems is an important issue widely concerned. In this research, we address this issue by developing a new space- and time-discrete predator-prey model, with predation relationship described by Beddington-DeAngelis functional response. The discrete model is given by a coupled map lattice, taking a nonlinear relationship between predator-prey “reaction” stage and dispersal stage. Through analysis of Turing instability and Hopf instability for the discrete model, the parametric conditions for pattern formation are determined. Numerical simulations reveal a surprising variety of spatiotemporal patterns, including regular and irregular patterns of spots, stripes, labyrinth, gaps, mosaics, spirals, circles, and many intermediate patterns in-between. These patterns cover a majority of predator-prey pattern types recorded in literature. Besides, the discrete model predicts the occurrence of spatiotemporal chaos, which is responsible for the formation of irregular patterns. This research demonstrates that the nonlinear mechanisms of the discrete model better capture the complexity of pattern formation of predator-prey systems.

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## 1. Introduction

Spatial pattern formation is one of the important and timely central topics in biological science [1–3]. It explains the self-organized spatial heterogeneity of populations and communities and plays a key role in understanding the dynamical complexity of biological systems. As recorded in literature, the spatial patterns widely exist in reality and manifest in a variety of complex types, such as vegetation stripes in semiarid regions, spots in vertebrate skins, and spiral waves in population distributions [3–6]. In recent decades, the complexity of spatial patterns has aroused more and more interests of theoretical and experimental biologists [7–9].

Predator-prey system is a type of basic biological system in nature. Due to its universal existence and importance, the dynamical behaviors of predator-prey system are investigated by a great number of researchers [10–14]. For a predator-prey system characterized by nonlinear interactions and spatial heterogeneity, spatiotemporal complexity of the system often exhibits [8,15,16]. Various approaches to modeling have been developed to enable the understanding of spatial pattern formations ranging from plant distributions to plankton aggregation [11,16,40–42]. According to the results of former research works [15–19], complex spatial predator-prey patterns are found, such as patterns of spots, stripes, labyrinth, and so on. The complexity of pattern formation in the predator-prey systems may arise in part from the diversity of predation relationships,

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and also from the complexity of nonlinear mechanisms. Predictably, the spatiotemporal complexity of predator-prey systems will continue to be one of the dominant themes in biology.

In the previous studies, most of the spatially extended models recorded in literature researching the predator-prey pattern formations are time- and space-continuous. However the continuous dynamic models hardly describe the discontinuity in the predator-prey systems, which may result from, for example, patchy environment or fragmented habitat [8,20]. For discontinuous predator-prey systems, applying discrete models should be more reasonable and adequate [8]. It is widely recognized that discrete dynamic models have advantage in describing nonlinear characteristics and complexity of natural ecological systems, compared with the continuous models. Domokos and Scheuring [21] found that the discrete model can be more accurate than corresponding continuous model in describing population dynamics. Complex nonlinear characteristics can emerge in the discrete model, including flip bifurcation, quasiperiodic behavior, chaos, and so on [22–24]. A lot of research works have demonstrated that the application of discrete dynamic models can lead to better results in studying predator-prey systems [25]. As found by Neubert et al., in comparing with the continuous reaction-diffusion models in which the conditions for diffusive instability are surprisingly severe, the discrete models exhibit dispersal-driven instability under a broader set of ecological conditions [37]. Such result can also be supported by the research of Han et al. [33].

The most common discrete models in literature developed for spatially extended systems are cellular automata and coupled map lattices [8,26,38,39,43,44]. In this research, the space- and time-discrete predator-prey model will be given by a coupled map lattice. The coupled map lattices are characterized by discrete time, discrete space, and continuous states. Compared with cellular automata, the coupled map lattices have great advantages in describing the spatiotemporal chaos and are widely applied in many fields [27]. In biology, the application of coupled map lattices results in a better understanding and prediction of biological complexity of pattern formations [8,9,27]. However, few coupled map lattice models are documented in literature for quantitatively describing the pattern formation of predator-prey systems. Applying the coupled map lattice models favours the understanding on the formation of complex patterns in predator-prey systems.

In this research, a space- and time-discrete predator-prey model, which is given by a coupled map lattice, is developed to study the pattern formation of a predator-prey system. The research is organized as follows. Section 2 gives the development of the discrete model, in which the predation relationship is described by Beddington-DeAngelis functional response. Section 3 provides the pattern formation conditions, via analyzing Hopf instability and Turing instability of the discrete model. In Section 4, numerical simulations are performed to show the complex patterns. Section 5 discusses the ecological significances of the results obtained, and finally, conclusions are made in Section 6.

## 2. Development of space- and time-discrete predator-prey model

The development of the space- and time-discrete predator-prey model is based on two aspects, (1) discretization of a continuous predator-prey model which is described by reaction-diffusion equations, and (2) application of the framework of a coupled map lattice. Accordingly, the former continuous predator-prey model should be introduced at first.

Generally, a classical spatially extended predator-prey model, which is mostly widely applied in literature, can be described by the following reaction-diffusion equations [15,16,28]:

$$\frac{\partial N}{\partial t} = Nf(N) - Pg(N, P) + d_1 \nabla^2 N, \quad (1a)$$

$$\frac{\partial P}{\partial t} = \varepsilon Pg(N, P) - \eta P + d_2 \nabla^2 P, \quad (1b)$$

in which  $N$  and  $P$  are both spatiotemporal variables, meaning prey and predator densities, respectively;  $t$  denotes time;  $f(N)$  describes the prey growth rate;  $g(N, P)$  is the functional response describing the predation relationship, e.g., the prey consumption rate by an average single predator;  $\varepsilon$  is the conversion rate of eaten prey into new predator abundance;  $\eta$  is the per capita predator death rate;  $\nabla^2 N$  and  $\nabla^2 P$  express the diffusion of the prey and the predator in space,  $d_1$  and  $d_2$  are diffusion coefficients; specially,  $\nabla^2 = \partial/\partial x^2 + \partial/\partial y^2$  is the usual Laplacian operator in two-dimensional space,  $x$  and  $y$  give the space coordinates of  $N$  and  $P$ .

Many functions for  $f$  and  $g$  can be found in literature [29]. In this research, we focus on the following  $f$  and  $g$ :

$$f(N) = r \left( 1 - \frac{N}{K} \right), \quad (2a)$$

$$g(N, P) = \frac{\beta N}{B + N + wP}, \quad (2b)$$

which have been studied by many researchers [15–19]. In Eqs. (2),  $r$  stands for maximum per capita growth rate of the prey;  $K$  is the carrying capacity;  $\beta$  is the maximum consumption rate;  $B$  is a half-saturation constant;  $w$  is the predator interference parameter. With such  $f$  and  $g$ , Eqs. (1) describe a spatially extended predator-prey model with Beddington-DeAngelis functional response. According to the investigation in literature, this model exhibits a few spatial patterns, such as spotted pattern, labyrinth pattern, pattern of labyrinth with spots, and so on [15].

The new discrete model is developed based on discretizing the above continuous predator-prey model. For discretizing the continuous model, we consider a time interval  $\tau$  and a space interval  $h$ , and a two-dimensional rectangular domain

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