Chaos, Solitons and Fractals 91 (2016) 421–429

Contents lists available at ScienceDirect

Chaos, Solitons and Fractals

Nonlinear Science, and Nonequilibrium and Complex Phenomena

journal homepage: www.elsevier.com/locate/chaos

Turing patterns induced by cross-diffusion in a predator-prey system in presence of habitat complexity

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ARTICLE INFO

Article history:
Received 10 March 2016
Revised 1 July 2016
Accepted 8 July 2016

Keywords:
Habitat complexity
Cross diffusion
Two parameter bifurcation
Turing pattern formation
Control of pattern

ABSTRACT

In this paper, we have investigated the phenomena of Turing pattern formation in a predator-prey model with habitat complexity in presence of cross diffusion. Using the linear stability analysis, the conditions for the existence of stationary pattern and the existence of Hopf bifurcation are obtained. It is shown analytically that the presence of cross diffusion in the system supports the formation of Turing pattern. Two parameter bifurcation analysis are done analytically and corresponding bifurcation diagrams are presented numerically. A series of simulation results are plotted for different biologically meaningful parameter values. Effects of variation of habitat complexity and the predator mortality rate and birth rate of prey on pattern formation are also reported. It is shown that cross-diffusion can lead to a wide variety of spatial and spatiotemporal pattern formation. It is found that the model exhibits spot and stripe pattern, and coexistence of both spot and strip patterns under the zero flux boundary condition. It is observed that cross-diffusion, habitat complexity, birth rate of prey and predator's mortality rate play a significant role in the pattern formation of a distributed population system of predator-prey type.

1. Introduction

Predator-prey dynamics have been continuing as one of the dominant themes in mathematical ecology since the pioneer work of Lotka [1] and Volterra [2]. The main goal of mathematical ecology is to understand the relationship between different species and their living environment. The crucial components of a mathematical model of the predator prey system are the growth function of prey species, the mortality function of predator species and the functional response. Several types of functional responses such as Holling type I -IV [1–5], Beddington–Deangelis [6] etc. have been used for modeling predator prey systems. The existence of habitat complexity in an eco-system reduces the probability of capturing a prey by reducing the searching efficiency of predator and habitat complexity affects the attack coefficient [7] as a result the functional response will be modified. Habitat complexity is the structural complexity of habitats. Habitat complexity can strongly mediate predator-prey interactions, affecting not only total predation rates, but also modifying selectivities for different prey species [8–11]. Pennings [12] and Grabowski [13] reported that habitat complexity reduces encounter rates of predators with prey. Aquatic habitat becomes structurally complex in presence of submerged vegetation or aquatic weeds. It is observed that structural complexity of the habitat stabilizes the predator-prey interaction between piscivorous perch (predator) and juvenile perch and roach (prey) by reducing predator foraging efficiency. Luckinbill prolonged the coexistence of Paramecium aurelia (prey) and Didinium nasutum (predator) in laboratory system by increasing strength of habitat complexity using methyl cellulose in the Cerophyl medium (nutrient)[14]. Therefore, it is important to incorporate the effect of habitat complexity in predator-prey functional response for theoretical models.

Reaction-diffusion (RD) systems have attracted increasing attention from the mathematical biologists in recent years to seek insights into the fascinating patterns that occur in living organisms and in ecological systems. Turing instability constitutes a universal paradigm for the spontaneous generation of spatially organized patterns. Alan Turing [15] proposed a dynamical mechanism, which has been extensively used to explain how Turing patterns are formed and is now known as Turing bifurcation or Turing instability. Turing pointed out that to generate spatial patterns, a reaction diffusion system should contain at least two reactive species that diffuse at very different rates: one slowly diffusing substance and other rapidly diffusing substance. Based on the pioneer work of Turing [15], Segel and Jackson [16] first introduced the reaction diffusion system in ecology. Under some ecological settings, diffusion should be thought of as dispersal of population density and often be considered as a stabilizing process, thus it is the diffusion

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http://dx.doi.org/10.1016/j.chaos.2016.07.003
0960-0779/

results in spatial patterns [17–20]. Existence of non-Turing shown the pattern under the self diffusion was reported [21–23] when the homogeneous state is unstable but all those investigations are based on the consequence of Turing concept.

Effects of migration (directed movement) and diffusion (random movement) in a predator-prey system with Holling-Tanner form was reported by Sun et al. [24]. Recently an epidemic model with spatial diffusion is considered by Li [25] to understand the patterns in disease spreading. To reveal the relationship between inducible defenses and herbivore outbreak, a reaction diffusion model was proposed and analyzed by Sun et al. [26]. Periodic solutions in a herbivore-plant system with time delay and spatial diffusion was first reported by Li et al. [27]. Relationship between pattern structures and ecosystems collapse was investigated by Sun et al. [28] formulating a reaction diffusion model.

Systems with cross-diffusion are widespread in nature and play an important role, in biophysical and biomedical situations. The escaping-chasing phenomena was described of cross-diffusion by Kerner (1959) [29], and first applied in competitive systems by Shigesada et al. (1979) [30]. An important example of cross-diffusion is chemotaxis, in which a field (e.g., an insect population) diffuses towards regions of high concentrations of another field (e.g., a chemically desirable substance). The escaping velocity of preys may be considered as dispersive velocity of the predators and the chase velocity of predators may be considered as dispersive velocity of prey. The presence of cross-diffusion in reaction process yields a large variety of pattern-forming instabilities. In case of cross-diffusion, the gradient in the concentration of one species induces a flux of another species which is very significant in generating spatial structures. After worked of Kerner [29], Shigesada [30], the study of in ecological models with cross diffusion has attracted attention of biologists [31–35]. The resulting governing system is a reaction-diffusion equation of the linear form can be written in the following form :

$$\frac{\partial \mathbf{U}}{\partial t} = \mathbf{G}(\mathbf{U}) + \mathbf{D}\nabla^2\mathbf{U}.$$

Where $\mathbf{U}$ is the n dimensional vector with components $u_i(x, t)$, (i=1,2, $\cdots$, n) as the species- densities. $\mathbf{D}$ is the $n \times n$ matrix of the diffusion coefficients, where the diagonal elements are called the self-diffusion coefficient and the off-diagonal elements are called cross-diffusion coefficients, $\mathbf{G}$ is the reaction term indicating the interaction between the involved species and ∇^2 be Laplacian operator. Recently cross-diffusion driven instabilities have gained a considerable attention in population dynamics [32–36], mainly due to their ability to predict some important features in the study of the spatial distribution of species in ecological systems [30,37,38], in epidemic system [39].

Despite recognition of the significance of habitat complexity in community dynamics, current reaction diffusion models of theoretical ecology have rarely considered its effects. In this paper, we consider a mathematical model of predator prey system in presence of habitat complexity [40]. The effects of cross diffusion term together with self diffusion term in the pattern forming instability are investigated both analytically and numerically. The effects of variation of habitat complexity parameter, birth rate of prey, mortality rate of predator and cross diffusion term are investigated. The goal of this paper is to show that cross-diffusion can drive the emergence of Turing pattern and the impact of variation of cross-diffusion coefficients in the spatially inhomogeneous distribution of population density. Our analyze reveal that the cross-diffusion may induce spatial patterns and different cross-diffusion coefficient may lead to transition between spot and stripe patterns.

The paper is organized as follows. In Section 2, we introduce a diffusive predator-prey model with habitat complexity in presence of the linear cross diffusion term. In Section 3, the analysis of the local model is carried out. In Section 4, the bifurcation is done. The possibility of existence of Turing pattern in presence of cross diffusion is shown analytically. The result of Turing pattern formation through extensive numerical simulations are presented in Section 5. In Section 6 the controllability aspect of spatiotemporal pattern are discussed. Finally, conclusions are drawn in Section 7.

2. Mathematical model

Habitat complexity exists in every terrestrial or aquatic ecological systems. In our model, we assume the logistic growth of prey linear mortality rate of predator. The existence of habitat complexity reduces the probability of capturing a prey by reducing the searching efficiency of predator and habitat complexity affects the attack coefficient [41]. Now following the Jana and Bairagi [40], Sahoo and Poria [42] and introducing a dimension less parameter $c(0 < c < 1)$ that measures the strength of habitat complexity we obtain the following model,

$$\begin{aligned} \frac{dX}{dt} &= RX\left(1 - \frac{X}{K}\right) - \frac{A(1-c)XY}{B + (1-c)X} \\ \frac{dY}{dt} &= \frac{\xi A(1-c)XY}{B + (1-c)X} - \delta Y. \end{aligned} \tag{1}$$

where $X(t)$ and $Y(t)$ stand for the prey and predator densities at time t, respectively. The parameter R is the growth rate of the prey, K is its carrying capacity, ξ is the conversion rate of prey into the predator and δ is the death rate of the predator in the absence of prey. In absence of habitat complexity, i.e. when $c = 0$ the system (4) becomes the well known Rosenzweig–MacArthur model [43].

Now re-defining

$$X_{new} = \frac{X_{old}}{K}, \quad t_{new} = R\, t_{old}, \quad Y_{new} = \frac{AY_{old}}{BR}$$

the model (1) can be transformed to the following non-dimensional form,

$$\begin{aligned} \frac{dX}{dt} &= X(1-X) - \frac{XY}{a+bX} \\ \frac{dY}{dt} &= \frac{\xi XY}{a+bX} - \delta Y \end{aligned} \tag{2}$$

where

$$a = \frac{1}{1-c}, \quad \xi_{new} = \frac{AK\xi_{old}}{BR}, \quad \delta_{new} = \frac{\delta_{old}}{R}, \quad b = \frac{K}{B}.$$

The new parameter a is the new habitat complexity dependent parameter and notice that the model has habitat complicity if $a > 1$ and in case of no habitat complexity $a = 1$.

In presence of spatial diffusion of species the model (2) takes the following form,

$$\begin{aligned} \frac{\partial X}{\partial t} &= X(1-X) - \frac{XY}{a+bX} + D_{11}\nabla^2 X \\ \frac{\partial Y}{\partial t} &= \frac{\xi XY}{a+bX} - \delta Y + D_{22}\nabla^2 Y. \end{aligned} \tag{3}$$

where $D_{11} > 0$ and $D_{22} > 0$ are the diffusion coefficients for prey and predator respectively and $\nabla^2 = \frac{\partial}{\partial x^2} + \frac{\partial}{\partial y^2}$ is the Laplacian operator.

We now focus on the following predator-prey model considering the presence of linear cross-diffusion in our model :

$$\begin{aligned} \frac{\partial X}{\partial t} &= X(1-X) - \frac{XY}{a+bX} + D_{11}\nabla^2 X + D_{12}\nabla^2 Y \\ \frac{\partial Y}{\partial t} &= \frac{\xi XY}{a+bX} - \delta Y + D_{21}\nabla^2 X + D_{22}\nabla^2 Y. \end{aligned} \tag{4}$$

The coefficient D_{12} and D_{21} are called the cross-diffusion coefficient describe the respective population fluxes of preys and predators resulting from the presence of the other species, respectively,