



Research paper

Hopf and steady state bifurcation analysis in a ratio-dependent predator–prey model

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ARTICLE INFO

Article history:

Received 25 March 2016

Revised 23 July 2016

Accepted 25 July 2016

Available online 29 July 2016

Keywords:

Prey–predator model

Turing instability

Pattern formation

Spatiotemporal bifurcation

Non-constant steady state

ABSTRACT

In this paper, we perform spatiotemporal bifurcation analysis in a ratio-dependent predator–prey model and derive explicit conditions for the existence of non-constant steady states that emerge through steady state bifurcation from related constant steady states. These explicit conditions are numerically verified in details and further compared to those conditions ensuring Turing instability. We find that (1) Turing domain is identical to the parametric domain where there exists only steady state bifurcation, which implies that Turing patterns are stable non-constant steady states, but the opposite is not necessarily true; (2) In non-Turing domain, steady state bifurcation and Hopf bifurcation act in concert to determine the emergent spatial patterns, that is, non-constant steady state emerges through steady state bifurcation but it may be unstable if the destabilising effect of Hopf bifurcation counteracts the stabilising effect of diffusion, leading to non-stationary spatial patterns; (3) Coupling diffusion into an ODE model can significantly enrich population dynamics by inducing alternative non-constant steady states (four different states are observed, two stable and two unstable), in particular when diffusion interacts with different types of bifurcation; (4) Diffusion can promote species coexistence by saving species which otherwise goes to extinction in the absence of diffusion.

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1. Introduction

A characteristic feature of ecological systems is the complex interactions among individuals and the interactions between individuals and their surrounding environment [25], which occur over a wide range of spatial and temporal scales. The spatial component has been identified as an important factor in determining the distribution of populations with the advancement of time and the structure of communities over their habitats. Experimental evidence suggests that movement rates of interacting individuals can dramatically affect population stability [12,20] and the composition of communities [8,21]. A consequence of individual movement behaviour is the spatial heterogeneity of individual abundance within the ecosystem which is observable at the macroscopic levels of population and community. Spatial pattern is a ubiquitous scenario in nature and often takes the role of modifying the temporal dynamics and regulating population stability [23,37]. In recent decades, a significant body of literature has explored the interactions between individual movement behaviours and spatial

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patterns with the ultimate goal of understanding how spatial component influences the dynamics of populations and the structure of communities.

A convenient approach to describe the spatiotemporal population dynamics is the reaction-diffusion framework [29], which is a way of relating dynamics at the individual level to the dynamics at the population level. In spite of its simple representation, reaction-diffusion systems can generate a wide variety of spatial patterns, giving this framework a powerful potential for application as an experimental hypothesis in a wide variety of biological phenomena [14]. Reaction-diffusion systems were first used to explain the formation of spatial patterns in ecological systems by Segel and Jackson [35], inspired by the seminal work of Turing [45]. Since then, numerous studies under the reaction-diffusion framework have been devoted to the description of spatial patterns [13,22], to the identification of its drivers [5,6,15,32,52], and to the implications for community dynamics [10,26,27,34]. Many important and interesting findings have been unrevealed. For instance, the author in [13] simulated both regular and irregular patterns in semiarid vegetation using reaction-diffusion system and found that the theoretically predicted patterns are in close agreement with field observations. Baurmann et al. [6] investigated different instability mechanisms behind the emergence of spatial patterns in an ecological prey–predator system.

Turing instability and Turing–Hopf bifurcation are two well known mechanisms behind the formation of spatial pattern [5,6,41]. The concept of Turing instability is that the locally stable homogeneous steady state becomes unstable due to small amplitude heterogeneous perturbation around the homogeneous steady states, leading to the formation of spatially heterogeneous distribution of population over their habitats [35,45]. The emergent spatial patterns due to Turing instability are stationary [3,9,48], which are also known as Turing patterns such as spots, strips or mixture of spots and strips. The basic idea of the Turing–Hopf bifurcation is that the locally unstable homogeneous steady state evolves into non-stationary spatial patterns under spatially inhomogeneous spatial perturbation. Non-stationary spatial patterns are characterized by periodic, quasi-periodic or even chaotic patterns as time advances. Besides these two mechanisms, other mechanisms such as biological invasion, turbulence, travelling wave, periodic travelling wave can also be responsible for spatial pattern formation [23,38,42,46].

The spatial patterns generated by the aforementioned two mechanisms can be obtained by numerical simulations, and the conditions for Turing and Hopf bifurcations can be reached by means of local stability analysis around the suitable homogeneous steady state [6,48]. These techniques can predict the regions in the targeted parametric space where we can observe spatial patterns but they are unable to predict the spatial patterns generated by large amplitude spatiotemporal perturbations. Non-constant steady states have been suggested as a fundamental argument for the existence of spatial patterns, and received great attention from various researchers [18,30,31,39,40,50]. However, the complexity of the (generally implicit) conditions for the existence of non-constant steady states makes it very hard to verify them numerically. Thus, the relationship between the emergent spatial patterns including Turing patterns and the non-constant steady states remains poorly understood. Undoubtedly, clear clarification of this relationship is of paramount importance in comprehensive understanding of spatiotemporal dynamics and spatial pattern formation as it bridges numerical results on emergent spatial patterns and theoretical predictions of non-constant steady states [4]. This paper is devoted to the clarification of this intimate relationship. To this aim, we consider a spatiotemporal prey–predator model with a ratio-dependent functional response in one dimensional spatial domain in order to derive precise and explicit conditions for the existence of non-constant steady state within the parametric restrictions that are satisfied for the stability and instability of constant steady state, an important and interesting aspect that has been overlooked by most of the researchers.

Predator–prey models with ratio-dependent functional response for predator consumption are widely implemented in ecological modelling and the ratio-dependent functional response has been strongly supported by numerous field and laboratory experiments [2,7,11,33]. A great number of theoretical works aim for understanding the formation of spatial patterns in ratio-dependent diffusive predator–prey models by means of the standard Turing–Hopf bifurcation analysis (e.g., [1,36,49]), the norm form and centre manifold theory for determining the direction and stability of Hopf bifurcation (e.g., [43,53]), and the technique of steady-state bifurcation (e.g., [4,47]). The former two approaches consider spatiotemporal dynamic models to derive the conditions under which purely spatially or temporarily periodic pattern occurs, while the last approach attempts to establish a link between the spatial patterns observed in the spatiotemporal models with the spatially heterogeneous steady state of the associated elliptic systems. The current paper combines the first and last approach by numerically comparing the parametric restrictions that are satisfied for existence of non-constant steady state and the conditions that are satisfied for Turing instability.

The paper is organised as follows. In the next section, we describe the temporal model and recall its basic dynamical features to understand the local stability of constant steady states with the help of complete global bifurcation analysis. In Section 3, we introduce the spatiotemporal model and present Turing instability results. Special attention is paid to the emergent stationary and non-stationary spatial patterns. Then we derive the general conditions in Section 4 ($\Omega \subset R^n$) and more explicit conditions in Section 5 ($\Omega \subset R$) for the existence of non-constant steady states in order to facilitate numerical analysis which is carried out in the coming section. In Section 6 we carry out detailed numerical simulations to verify the analytical findings obtained in Section 5 and most importantly cross verify the existence conditions of non-constant steady states and compare them to those conditions of Turing as well as Turing–Hopf bifurcations. The paper is closed with a conclusion section. The reason for Section 4 is to keep the completeness and generality of this paper and that part of the conclusions in that section will be referred to later in Section 5. However, readers who are interested in numerical analysis can skip Section 4 without causing any confusion.

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