



Viewpoint

Stationary, non-stationary and invasive patterns for a prey-predator system with additive Allee effect in prey growth



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ABSTRACT

This study deals with the pattern formation scenarios of a reaction-diffusion system of prey-predator interactions with Allee effect in prey growth, Holling type-II functional response and density dependent death rate for predator. The necessary conditions, such as the presence of Hopf and Turing bifurcations, to get pattern formation are rendered and exhaustive numerical simulations are performed to validate the analytical results. Numerical simulations affirm the existence of stationary patterns such as hot spot, cold spot, labyrinthine and mixture of spot and stripe patterns along with the non-stationary patterns such as spatiotemporal chaotic and quasi-periodic patterns in presence of both weak and strong Allee effects in prey growth. Numerical simulations also reveal the coexistence of both species (either stationary or chaotic in nature depending on the values for diffusion coefficients) in contrast to the extinction scenario for the corresponding temporal model. Further, we investigate the invasion of exotic species for the considered model for strong Allee effect. In this case, we find out the patchy invasion scenario apart from the invasion through propagation of continuous population fronts which is a common invasion scenario for deterministic prey-predator models. In the patchy invasion regime, we observe a striking patchy spatial distribution of species in the wake of an expanding population front as well as complete patchy invasion.

1. Introduction

Mathematical modeling of prey-predator interactions and their analysis have been attracting both ecologists and applied mathematicians over several decades since the introduction of famous Lotka–Volterra model in order to decipher key issues regarding ecological processes. However, large body of existing literature on modeling the prey-predator interactions rely on the logistic growth function for prey population. But there exist numerous instances in real ecosystems which confirm the existence of Allee effect in prey growth which was first introduced by Allee (1931). Allee effect in a certain species generally describes a positive correlation between any component of individual fitness and population size or density of the concerned species Allee (1931); Dennis (1989); Stephens et al. (1999). The Allee effect can be generally strong (growth rate becomes negative below a certain density of the species) or weak (growth rate remains positive at low density of the species) Dennis (1989); Lewis and Kareiva (1993); Odum and Barrett (2004). The Allee effect in prey growth can be incorporated in mathematical models generally through multiplicative Sen et al. (2012); Wang et al. (2011b) or additive Aguirre et al. (2009a,b); Stephens and Sutherland (1999) Allee effect term. Allee

effect can potentially lead to more rich temporal dynamics than the counterpart without it. Limit cycle arises in Rosenzweig–MacArthur model through Hopf bifurcation and, for a range of parameter values, a significant part of it stays very close to the axes. Therefore, demographic stochasticity can potentially lead to extinction of either species Rosenzweig and MacArthur (1963); Wang et al. (2011b). However, inclusion of Allee effect indicates this extinction threat explicitly through global bifurcations, such as homoclinic bifurcation for Rosenzweig–MacArthur model with strong multiplicative Allee effect Wang et al. (2011b). For example, Aguirre et al. (2009b) considered a temporal Leslie–Gower type prey-predator model with additive Allee effect in prey growth and showed the existence of a stable limit cycle surrounding an unstable limit cycle, which arises through Hopf bifurcation under certain parametric restrictions. They further demonstrated the existence of three limit cycles for this model under suitable parametric restrictions in Aguirre et al. (2009a), where two limit cycles arise through Hopf bifurcation and the other one arises due to homoclinic bifurcation.

Emergence of spatiotemporal patterns and their possible mechanisms in ecology have been attracting the attention of numerous researchers currently and from recent past. Study of pattern formations in

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prey-predator systems can be accomplished theoretically through the introduction of reaction-diffusion models for prey and predator interactions by taking into account the spatial mobility of both the species. This idea in population dynamics was initiated by Segel and Jackson (1972) following Turing's seminal work on chemical morphogenesis Turing (1952). This idea was further carried forward to explain the patchy spatial distribution in plankton ecosystem in Levin and Segel (1976) and the vegetation patterns in semiarid region in Klausmeier (1999). Spatiotemporal interactions of prey and predator can greatly impact the corresponding temporal dynamics and resulting spatial patterns are omnipresent in nature Malchow et al. (2008). For instance, Huffaker (1958) showed that two species of mite can exhibit long term persistence in an appropriate heterogeneous environment whereas small population size with homogeneous set up can lead to extinction of both the species. Generally, Turing and Hopf–Turing bifurcations act as two well-known mechanisms for spatiotemporal pattern formations Baurmann et al. (2007); Zhang et al. (2017). These bifurcations destabilize the homogeneous steady state but potentially lead to stationary or dynamic heterogeneous distribution of species within their habitat. Turing bifurcation gives rise to the formation of stationary in time, heterogeneous in space population distribution over natural habitat and the resulting patterns are usually termed as Turing patterns which are commonly classified as spots (hot and cold), labyrinthine, and mixture of stripes and spots Zhang et al. (2017). Turing bifurcation occurs when the locally stable spatially homogeneous equilibrium loses its stability due to small inhomogeneous perturbations on homogeneous steady state Murray (1989); Zhang et al. (2017). On the other hand, Hopf–Turing bifurcation can induce non-stationary periodic, quasi-periodic or even chaotic (spiral or spatiotemporal) patterns along with the above mentioned stationary patterns Zhang et al. (2017). Although empirical studies lack to provide widely accepted example for ecological chaos, there are few instances where chaotic behavior has been observed in ecological community. For example, Turchin and Ellner (2000) showed the recurrent short-term chaotic dynamics for vole population in northern Fennoscandia and Medvinsky et al. (2015) observed the chaotic dynamics of plankton community in the Naroch Lakes in Belarus with the horizon of predictability of about 2.5 months. In Banerjee and Petrovskii (2011), authors obtained both stationary and chaotic patterns inside the Hopf–Turing domain for a ratio-dependent prey-predator system. Banerjee and Banerjee (2012) found out that spatiotemporal chaos arises due to Hopf–Turing bifurcation with much higher value of diffusivity ratio of predator to prey for a ratio-dependent Holling–Tanner model. In both the articles Banerjee and Banerjee (2012); Banerjee and Petrovskii (2011), Hopf bifurcation has been identified as the necessary component in order to induce spatiotemporal chaos. Banerjee and Zhang (2016) argued that time delay is an important factor for enhancing spatiotemporal chaos in a prey-predator system. Apart from the above mentioned two mechanisms, there exist other types of mechanisms such as traveling wave, periodic traveling wave, biological invasion and turbulence which can eventually lead to spatial pattern formation Malchow et al. (2008); Zhang et al. (2017).

In recent years, several investigations have been conducted to understand the role of both diffusion and Allee effect together on the dynamics and spatiotemporal pattern formations for prey-predator interactions. Du and Shi (2007) examined the dynamics of a reaction-diffusion system of prey-predator interactions in heterogeneous environment by using mathematical techniques such as bifurcation theory, topological methods, comparison principles and elliptic estimates Berestycki and Lions (1980); Berestycki et al. (1994); Du (2005). They showed that spatial inhomogeneity of the environment can play a significant role for the presence of Allee effect when the prey growth is strong. Wang et al. (2011a) analyzed the spatiotemporal dynamics of a diffusive prey-predator model with strong Allee effect in prey growth and identified the ranges of parameters for spatial pattern formation by showing the non-existence of positive non-constant steady state.

Cai et al. (2012) considered and analyzed a diffusive prey-predator model with Holling type-II functional response and additive Allee effect in prey growth. They presented the conditions for stability of spatially homogeneous positive equilibrium and Hopf bifurcation in presence of both weak and strong Allee effect. In Cai et al. (2014), the authors further extended the model by incorporating density dependent death rate for predator and concentrated only on the weak Allee effect aspect. They provided rigorous mathematical results on the stability of positive constant steady state, existence and non-existence of positive non-constant steady state, and existence of Hopf bifurcation at the positive constant steady state. Further they demonstrated the Turing instability conditions with some numerical illustrations of stationary Turing patterns. They identified that density dependent death rate for predator plays an important role to induce Turing instability. Recently, Rao and Kang (2016) presented the complex dynamics exhibited by a diffusive prey-predator model with Michaelis–Menten type functional response and multiplicative Allee effect in prey growth. They performed similar type of mathematical analysis and presented numerical illustrations of pattern formations with and without Allee effect. They identified that the strength of the Allee effect plays a crucial role in the formation of different types of stationary and dynamic patterns.

Biological invasion of exotic species is an intriguing research area for both theoretical and field ecologists as it can be useful for designing an effective strategy in order to control and manage the invasive species Fagan et al. (2002); Morozov et al. (2006); Petrovskii et al. (2002). Generally, the spread of the invasive species from its initial area of introduction is determined by the propagation of continuous population fronts or patchy invasion Morozov et al. (2006); Petrovskii et al. (2002). For the sake of control and management of invasive species, an effective monitoring strategy can be employed very efficiently in case of continuous population front invasion but it becomes much harder to employ an effective monitoring strategy for patchy invasion Morozov et al. (2006). Earlier it was generally believed that reaction-diffusion type deterministic models can only predict the continuous population fronts invasion Holmes et al. (1994) and patchy invasion can be obtained by incorporating environmental stochastic factors in the model Lewis (2000); Lewis and Pacala (2000). In Morozov et al. (2006); Petrovskii et al. (2002), the authors found the patchy invasion in a fully deterministic model for prey-predator interaction by including multiplicative Allee effect in prey growth. Morozov et al. (2006) identified patchy invasion as the invasion at the verge of extinction.

Our objective in this paper is to provide a complete pattern formation scenario for the reaction-diffusion system of prey-predator interaction with additive Allee effect in prey growth presented in Cai et al. (2014). Cai et al. (2014) concentrated only on the weak Allee effect and entire scenario of non-Turing and spatiotemporal chaotic pattern formations remain unexplored. In this study, we focus on the all possible stationary and non-stationary pattern formations for this model in presence of both weak and strong Allee effect. We will also examine the possible patchy invasion produced by this model. Further, we want to explore whether the patchy invasive patterns are different from spatiotemporal chaotic patterns or not and what kind of temporal dynamics in presence of diffusion leads to invasive patterns and which varieties of invasive patterns can be obtained. We are also interested to explore the change in the characteristics of invasive patterns due to variation in the parameters involved in the local interactions between two species. The rest of this study is organized in the following manner. The next section presents the description of the model under consideration and the necessary conditions to get pattern formation are presented briefly in Section 3. In Section 4, we present extensive numerical results in order to illustrate possible spatiotemporal patterns within or outside of the Turing domain and possible patchy invasion. We end this study with a brief discussion in Section 5.

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