Dynamical effects of nonlocal interactions in discrete-time growth-dispersal models with logistic-type nonlinearities

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A B S T R A C T
The paper is devoted to the study of discrete time and continuous space models with nonlocal resource competition and periodic boundary conditions. We consider generalizations of logistic and Ricker’s equations as intraspecific resource competition models with symmetric nonlocal dispersal and interaction terms. Both interaction and dispersal are modeled using convolution integrals, each of which has a parameter describing the range of nonlocality. It is shown that the spatially homogeneous equilibrium of these models becomes unstable for some kernel functions and parameter values by performing a linear stability analysis. To be able to further analyze the behavior of solutions to the models near the stability boundary, a well-known method for continuous time systems, is employed. We obtain Stuart–Landau type equations and give their parameters in terms of Fourier transforms of the kernels. This analysis allows us to study the change in amplitudes of the solutions with respect to ranges of nonlocalities of two symmetric kernel functions. Our calculations indicate that supercritical bifurcations occur near stability boundary for uniform kernel functions. We also verify these results numerically for both models.

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1. Introduction
Diffusion driven instabilities in reaction-diffusion equations (RDE) have been studied since Turing’s seminal work (Turing, 1952) where he showed that diffusion combined with intra- and inter-specific interactions can lead to instability of space homogeneous equilibrium, and thus generate pattern formation. Segel and Stoeckly (1972) adopted the idea of diffusive instability to the ecology context. Since then there is an enormous literature on pattern formation in ecology (see e.g. Okubo and Levin, 2013; Murray, 2003).

Another important mechanism that generates pattern formation in continuous time systems is nonlocal interactions. The effect of such interactions has been studied in Britton (1989, 1990) and Gourley (2000). It was shown that the solutions to nonlocal Fisher equation exhibit instabilities of the space homogeneous solution (Genieys et al., 2006, 2009; Perthame and Génieys, 2007; Fuentes et al., 2003, 2004; Banerjee et al., 2017). Their model assumes that species disperses and at the same time competes for resources where the competition term is modeled via a contact distribution and diffusion can be local or nonlocal (Genieys et al., 2006; Aydogmus, 2015). Recently, the effects of nonlocal competition or interaction have been investigated for nonlocal RDEs (Segal et al., 2013; Tanzy et al., 2013; Banerjee and Volpert, 2016a,b). The study of Neubert et al. (1995) suggests that RDEs are not appropriate modeling tools for a large number of species that have discrete non-overlapping generations. Examples of such species consist of some plants (e.g., annual grass) and insects (e.g., paper wasps). Annual dispersal distances for these species are given by Neubert et al. (1995). In literature, such species have been modeled via integro-difference equations and analyzed in terms of traveling waves (Kot, 1992), spread and invasion (Kot et al., 1996), and pattern formation studied by Neubert et al. (1995) in an infinite domain. They considered integro-difference equations as discrete-time spatial contact models and showed that solutions to such systems exhibit dispersal driven instabilities.

As noted by Britton (1989), intra and interspecific growth terms (i.e. reaction terms) of RDEs depend only on the local population

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density. Similarly, if we use integro-difference equations as a modeling tool, we need to assume that the growth term depends on the local population density as well. However for mobile animals having non-overlapping generations such as paper wasps, the important factor for the growth term is the depletion of the common resource in their neighborhood. Therefore, the first aim of this paper is to study the effects of nonlocal interactions in discrete-time logistic and Ricker’s equations obtained by adding spatial effects (both dispersal and nonlocal competition for resources) to these models. We perform linear stability analysis of these models with periodic boundary conditions and show that the nonlocal interaction term with certain properties can destabilize the spatially homogeneous equilibrium. The linear stability analysis that we perform on two models is generally used to find pattern formation conditions, and the related technique is local in principle which could help us determine the value of the unstable wavenumbers and the parameters for which the space homogeneous solution becomes unstable.

The classical Stuart–Landau (SL) theory (Stuart, 1960), on the other hand, widely applied to RDE’s in biology (Murray, 2003), has been employed for the further investigation of the complex structure of the attractors. This method is also applied to nonlocal aggregation models (Topaz et al., 2006; Eftimie et al., 2009) and it was reported that the transition to instability is subcritical i.e. near the stability boundary, one can observe large oscillations depending on the initial condition. In other words, transition from disordered to ordered behavior is discontinuous. As a note, this method was also used in a recent work (Aydogmus, 2015) for the nonlocal Fisher equation with the nonlocal diffusion term.

Our second aim is to extend weakly nonlinear analysis to integro-difference equations. The multi-scale perturbation method has been used to obtain SL equations for the two proposed discrete-time integro-difference equations. Our computations show that transitions to instabilities are supercritical for symmetric nonlocal contact kernels. Thus one can observe that the amplitude of patterns near stability boundary is small. Hence using SL equations one can approximately compute the amplitudes of the patterns near stability boundary.

The paper is organized as follows. We begin by detailing our models in the next section, and relate these models to the existing RDEs. In Section 3, we perform linear stability analysis of two models with periodic boundary conditions, and obtain conditions on the nonlocal interaction kernel for which solutions to our models exhibit pattern formation. In Section 4, we perform weakly nonlinear analysis of patterns and obtain amplitude equations. In Section 5, we summarize our findings and discuss further extensions of the methods developed in the paper.

2. The model

Fisher (1937) proposed his famous equation to describe the spatial spread of an advantageous allele whose frequency is given below as a function of space and time $v(x,t)$:

$$v_t = D v + v (1 - v)$$

where $D$ is the Laplacian is used to model mobility of individuals and the reaction term is taken as logistic growth function.

We consider a discrete-time model possessing many of the attributes of RDEs (Kot and Schaffer, 1986). We assume that growth and dispersal occurs during different life cycles. First consider an organism with nonoverlapping generations. The growth of such a population is governed by a nonlinear map

$$u_{n+1} = f(u_n)$$

where $f$ can be taken as logistic or Ricker’s logistic growth functions.

Above given map does not allow spatial movements of individuals. To consider these movements, we denote the density of infective individuals at spatial location $x$ and time $n$ by $u_n(x)$. As mentioned above, in the sedentary step $u_n(x)$ is mapped into $f(u_n(x))$. The second stage is spatial shuffling. This stage is called dispersal stage and modeled by an integral operator. To be able to model such movements we use a probability kernel $K_1(x,y)$ describing the dispersal of individuals from $y$. In particular, it determines the probability that an infective individual in an interval of length $d$ about $y$ disperses to an interval of the same length about $x$. In a biological point of view, it is reasonable to assume that the dispersal weight depends on the relative distance $\hat{K}_1(x,y)$. Hence we obtain a classical integro-difference equation modeling these two steps as follows:

$$u_{n+1} = [K_1 * f(u_n)](x) = \int K_1(x,y) f(u_n(y)) dy$$

where $K_1$ is the distance dependent dispersal kernel. This equation models dispersing individuals with non-overlapping generations. For logistic and Ricker’s maps, (2) was studied by Kot and Schaffer (1986) and Kot (1992).

Recently Fisher equation (1) with a nonlocal interaction term was investigated by many authors (Britton, 1989; Gourley, 2000; Genieys et al., 2006; Fuentes et al., 2003) in terms of pattern formation and traveling waves. The model is given as follows:

$$v_t = Dv + v(1 - K_2 * v)$$

where the convolution term is as defined in (2) and $K_2$ models nonlocal interactions. It was shown that the space homogenous solution of (3) becomes unstable if the Fourier transform of the kernel function $K_2$ takes negative values. Thus, it was concluded that instability of space homogenous solution is driven by the nonlocal interaction term.

For derivation of the nonlocal reaction term in (3), one can consult with Genieys et al. (2006). Following the idea presented in Genieys et al. (2006), one can also include nonlocal competition term to density dependent growth functions governing the discrete time evolution of population densities. We will focus on the following two growth functions with nonlocal competition:

The logistic growth function:

$$f_l(u, K_2 * u) = ru(1 - K_2 * u)$$

and

The Ricker’s growth function:

$$f_R(u, K_2 * u) = u e^{-(1-K_2 * u)}.$$
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