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Population evolution in mutualistic Lotka–Volterra system with spatial diffusion

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HIGHLIGHTS

- We considered mutualistic Lotka–Volterra model with a $+/+$ interaction with spatial diffusions.
- Wave front solutions in one dimension are investigated analytically and numerically.
- The propagating wave profiles beyond the simple Fisher wave fronts are revealed.
- The presence of diffusion can bring two situations: win–win situation and dominating situation.

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ABSTRACT

We consider the population dynamics of two species described by the mutualistic Lotka–Volterra model with a $+/+$ interaction in the presence of spatial diffusions. The results demonstrate that diffusion does not affect the system's stability but it brings two situations: one is a win–win situation where both species propagate with the same largest speed; in the other situation the aggressive species has two propagating wave fronts and the other species travels with a single slow wave front. Our model may help to understand the evolution of mutualism.

1. Introduction

Mutualisms are not uncommon in nature. There are models attempting to describe mutualist interactions between two species [1–4]. The well-known Lotka–Volterra (LV) model was one of the classical models for studying the cross-linked populations [5–7]. The global stability analysis for the LV mutualistic systems has been well done by some authors [8–11]. They showed that the mutualistic populations would grow to unlimited quantities exceeding their carrying capacities. However the unlimited growth is biologically unrealistic. Obviously there are many factors such as limited spaces or food resources, which are closely related to the evolution of mutualism. So considering the motion or migration of interacting species would be more close to the reality.

In fact there have been several analytical studies focused on the effect of spacial diffusion on the competitive LV system. Vance and Allen showed that dispersal did not always promote the stability of the population [12,13]. Takeuchi and Hastings suggested that diffusion did not affect the system's stability [14,15]. However for the LV model with diffusion, the population dynamics resembles the Fisher–Kolmogorov equation [16]. So there exist traveling wave solutions propagating from one

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fixed point to another, which would give rise to interesting spatiotemporal dynamics. Thus from wave propagation, one could observe the evolution of the system directly. Previous research mainly focused on the competitive diffusive LV model. Most of them studied the existence of traveling Fisher's waves that connect two states (from the stable state to the unstable state) in certain region of the parameter space. Ref. [17] showed that the intermediate equilibrium state played an important role in the wave propagation as first mentioned by Tang and Fife in the uncoupled logistic growth model [18].

In this paper, considering the LV model of two mutual beneficial species with spatial diffusion we investigated the steady wave front propagation not limited to the simple Fisher's waves. We examined the effect of intermediate equilibrium on the wave front profiles and wave speeds. Analytical results for the wave front speeds are obtained and verified by numerical solutions. It was found that there exists a combination of two wave fronts with different speeds, which is different from the competitive LV model. Moreover in presence of diffusion the stability of the system does not make changes but there are two situations: one situation is a win–win situation where both species travel with the same speed and the total population has a large growth rate. In the other situation one species dominates. The aggressive species propagates with a combination of two wave fronts and the other species grows with a single slow wave front.

2. Models

We consider a two-species LV model in which each species undergoes spatial diffusion. The populations of the two species are denoted by $n_1(x, t)$ and $n_2(x, t)$. They obey the reaction–diffusion type PDEs:

$$\begin{cases} \dfrac{\partial n_1}{\partial t} = \mathrm{d}_1 \dfrac{\partial^2 n_1}{\partial x^2} + r_1 n_1 (1 - n_1 + a_{12} n_2) \\ \dfrac{\partial n_2}{\partial t} = \mathrm{d}_2 \dfrac{\partial^2 n_2}{\partial x^2} + r_2 n_2 (1 - n_2 + a_{21} n_1) \end{cases} \tag{1}$$

where $\mathrm{d}_\alpha > 0$ and $r_\alpha > 0 (\alpha = 1, 2)$ are the diffusion coefficients and proliferation rates respectively. $a_{12}, a_{21} > 0$ describes the strength of mutualism, the environmental carrying capacity was taken to be 1. There are two types of interactions between the individuals in the system: intraspecific competition and interspecific mutual benefits. The parameters $a_{\alpha\beta}$ determines the mutual interaction strengths between two species. In this paper, we consider systems in one dimension and investigate the associated wave propagations.

In the presence of diffusion, Eqs. (1) resemble the well studied Fisher–Kolmogorov equation [16]. In the corresponding kinetic ODEs, steady states occur at the fixed points: $(0, 0)$, $(1, 0)$, $(0, 1)$, $(n_1{}^*, n_2{}^*)$, where $n_1{}^* = \frac{1+a_{12}}{1-a_{12}a_{21}}$, $n_2{}^* = \frac{1+a_{21}}{1-a_{12}a_{21}}$. The last steady state exists only when $a_{12}a_{21} < 1$ and the global stability analysis for this case has been done by several authors [8–11]. Notice in the last steady state the species populations exceed their carrying capacities. These positive interactions benefited all individuals in the system.

According to the phase plane analysis for the non-diffusive LV model with mutualistic interactions, there were two cases in this mutualistic Lotka–Volterra system [19]. When $a_{12}a_{21} < 1$ the non-zero steady state $(n_1{}^*, n_2{}^*)$ exists, all interior orbits converged to this fixed point as shown in Fig. 1(a). On the other hand, when $a_{12}a_{21} > 1$, all steady states lay on the coordinate axes, and all interior orbits diverge to infinity as shown in Fig. 1(b). In this article we mainly focus on the first case. The wave fronts in Eq. (1) has been studied by many groups [12–16]. Most results demonstrated the existence of Fisher's wave fronts that connect two equilibrium fixed points. In this paper, using analytical and numerical methods, we study the stable propagating behavior beyond the simple Fisher's wave profiles.

3. Analytical results for wave speeds

Assuming local plane wavefronts with $n_1(x, t) = U_1(x - c_1 t)$ and $n_2(x, t) = U_2(x - c_2 t)$, then Eqs. (1) can be expressed as a four dimensional ODE dynamical system [20]:

$$\begin{cases} U_1{}' = V_1 \\ U_2{}' = V_2 \\ \mathrm{d}_1 V_1{}' = -c_1 V_1 - r_1 U_1 (1 - U_1 + a_{12} U_2) \\ \mathrm{d}_2 V_2{}' = -c_2 V_2 - r_2 U_2 (1 - U_2 + a_{21} U_1). \end{cases} \tag{2}$$

This ODE system always has three fixed points $X_0 = (0, 0, 0, 0)$, $X_1 = (1, 0, 0, 0)$, $X_2 = (0, 1, 0, 0)$ and another fixed point $X_3 = (n_1{}^*, n_2{}^*, 0, 0)$ exists only when $a_{12}a_{21} < 1$. Nonlinear dynamic was employed to analyze these fixed points one by one. Refer to the competitive Lotka–Volterra model we could analytically get the wavefront speed at each fixed point [17]:

In the (U_1, U_2, V_1, V_2) phase space there are three unstable steady states X_0, X_1, X_2 and a stable one X_3. From the experience gained from the analysis of Fisher–Kolmogorov equation, there is thus the possibility of a traveling wave solution from unstable points to stable one. So we should look for solutions $(U_1(x), U_2(x))$ of Eqs. (2) with the boundary conditions. For $X_0 = (0, 0, 0, 0)$, the boundary condition is: $U_1(-\infty) = n_1{}^*$, $U_2(-\infty) = n_2{}^*$, $U_1(\infty) = 0$, $U_2(\infty) = 0$, we consider