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Research Article

Distinct Spreading Speeds in a Lotka–Volterra Cooperative System

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This paper deals with the spreading speeds in the classical Lotka–Volterra cooperative system, of which the bounds have been studied earlier. By introducing an auxiliary cooperative system and constructing an upper solution, we obtain a sufficient condition to confirm two distinct spreading speeds of unknown functions. Due to the different average moving speeds of different level sets, we find the existence of propagation terraces in such a cooperative system with constant coefficients. We also present some numerical results to illustrate our results.

1. Introduction

There are many examples where the interaction of two or more species is to the advantage of all, which is described by cooperative or mutualism models in population dynamics. Considering the limited carrying capacities for both species, one basic cooperative model is the following Lotka–Volterra type system:

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 (1 - N_1 + b_1 N_2), \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 (1 - N_2 + b_2 N_1), \end{cases} \tag{1}$$

in which all the parameters are positive and N_1, N_2 represent the densities of two cooperative species. We refer to Murray (Section 3.6 [1]) for the dynamics of (1). Introducing the spatial movement of individuals, one reaction-diffusion model is given by [2]

$$\begin{cases} \dfrac{\partial u_1(x,t)}{\partial t} = d_1 \Delta u_1(x,t) + r_1 u_1(x,t)[1 - u_1(x,t) + b_1 u_2(x,t)], \\ \dfrac{\partial u_2(x,t)}{\partial t} = d_2 \Delta u_2(x,t) + r_2 u_2(x,t)[1 - u_2(x,t) + b_2 u_1(x,t)], \end{cases} \tag{2}$$

in which $x \in \mathbb{R}, t > 0, \Delta = \partial^2/\partial x^2$ and all the parameters are positive. If $b_1 b_2 < 1$, then (2) admits a positive steady state that is spatially homogeneous and defined by

$$E = (e_1, e_2) = \left(\frac{1 + b_1}{1 - b_1 b_2}, \frac{1 + b_2}{1 - b_1 b_2} \right). \tag{3}$$

From the viewpoint of population dynamics, an important problem is to formulate the dynamics of (2) when the initial values satisfy proper conditions. In particular, assuming that $u_1(x,0), u_2(x,0)$ have nonempty compact supports, Li et al. [2] and Lin [3] studied the corresponding initial value problem of (2) by the following propagation threshold [4].

Definition 1. Assume that $u(x,t)$ is a nonnegative function for all $x \in \mathbb{R}, t > 0$. Then c_u is called the spreading speed of $u(x,t)$ if

(a) $\lim_{t \longrightarrow \infty} \sup_{|x| > (c_u + \varepsilon)t} u(x,t) > 0$ for any given $\epsilon > 0$

(b) $\liminf_{t \longrightarrow \infty} \inf_{|x| < (c_u - \varepsilon)t} u(x,t) > 0$ for any given $\epsilon \in (0, c_u)$

More precisely, Li et al. (Example 4.1 in [2]) estimated that

$$2\sqrt{d_i r_i} \le c_{u_i} \le 2\sqrt{d_i r_i e_i}, \quad i = 1, 2, \tag{4}$$

and some other bounds when $d_1r_1 > d_2r_2e_2$. Moreover, Lin (Theorem 3.1 in [3]) proved that if $d_1r_1 > d_2r_2e_2$, then $c_{u_2} \geq 2\sqrt{d_2r_2(1+b_2)}, c_{u_1} = 2\sqrt{d_1r_1}$. The purpose of this paper is to present some results such that $c_{u_2} = 2\sqrt{d_2r_2(1+b_2)}$ if $d_1r_1 > d_2r_2e_2$.

By Lin (Theorem 3.1 in [3]), it suffices to study the upper bounds of c_{u_2} if $d_1r_1 > d_2r_2e_2$. For this purpose, we introduce an auxiliary cooperative system that admits weaker irreducible property. The classical results in Weinberger et al. [5] imply the existence of constant speed of asymptotic spreading. However, this system is not subhomogeneous, and we cannot use some classical results of monotone semiflows to present the speed. In this paper, we present some sufficient conditions such that $c_{u_2} = 2\sqrt{d_2r_2(1+b_2)}$, which is based on proper upper and lower solutions and comparison principle. Furthermore, we give some numerical results to explore both the role of linear part and nonlinear part in the reaction term.

2. Main Results

Consider the initial value problem

$$\begin{cases} \dfrac{\partial u_1(x,t)}{\partial t} = d_1\Delta u_1(x,t) + r_1u_1(x,t) \\ \left[1 - u_1(x,t) + b_1u_2(x,t)\right], \\ \dfrac{\partial u_2(x,t)}{\partial t} = d_2\Delta u_2(x,t) + r_2u_2(x,t) \\ \left[1 - u_2(x,t) + b_2u_1(x,t)\right], \\ u_1(x,0) = \psi_1(x), u_2(x,0) = \psi_2(x), \end{cases} \tag{5}$$

in which $x \in \mathbb{R}, t > 0$, positive parameters satisfy

$$0 < b_1b_2 < 1, d_1r_1 > d_2r_2e_2. \tag{6}$$

The initial conditions ψ_1, ψ_2 are bounded and uniformly continuous functions admitting nonempty supports such that

$$0 \leq \psi_i(x) \leq e_i, \quad x \in \mathbb{R},\ i = 1, 2. \tag{7}$$

By the basic theory of reaction-diffusion systems [6, 7], we have the following conclusion.

Lemma 1. *Equation (5) has a global classical solution such that*

$$0 \leq u_i(x,t) \leq e_i, \quad x \in \mathbb{R}, t > 0,\ i = 1, 2. \tag{8}$$

Study the following auxiliary system

$$\begin{cases} \dfrac{\partial U_1(x,t)}{\partial t} = d_1\Delta U_1(x,t) + r_1\left[U_1(x,t) + 1\right] \\ \left[-U_1(x,t) + b_1U_2(x,t)\right], \\ \dfrac{\partial U_2(x,t)}{\partial t} = d_2\Delta U_2(x,t) + r_2U_2(x,t) \\ \left[1 + b_2 - U_2(x,t) + b_2U_1(x,t)\right], \\ U_1(x,0) = \phi_1(x), U_2(x,0) = \phi_2(x), \end{cases} \tag{9}$$

where $x \in \mathbb{R}, t > 0$, and

$$\begin{aligned} \phi_1(x) &= \max\{0, \psi_1(x) - 1\}, \\ \phi_2(x) &= \psi_2(x), \\ & x \in \mathbb{R}. \end{aligned} \tag{10}$$

The following existence of classical solutions of (9) is true by the theory in [6, 7].

Lemma 2. *Equation (9) has a global classical solution such that*

$$0 \leq U_1(x,t) \leq e_1 - 1, 0 \leq U_2(x,t) \leq e_2, \quad x \in \mathbb{R}, t > 0. \tag{11}$$

Moreover, the comparison principle implies that

$$\max\{u_1(x,t) - 1, 0\} \leq U_1(x,t), u_2(x,t) \leq U_2(x,t), \quad x \in \mathbb{R}, t > 0. \tag{12}$$

At the steady state $(0, 0)$, the linearizing system of (9) is

$$\begin{cases} \dfrac{\partial \mathcal{U}_1(x,t)}{\partial t} = d_1\Delta\mathcal{U}_1(x,t) - r_1\mathcal{U}_1(x,t) + r_1b_1\mathcal{U}_2(x,t), \\ \dfrac{\partial \mathcal{U}_2(x,t)}{\partial t} = d_2\Delta\mathcal{U}_2(x,t) + r_2(1+b_2)\mathcal{U}_2(x,t). \end{cases} \tag{13}$$

Evidently, (13) is not irreducible, but the hair-trigger effect in (9) occurs once $\phi_2(x)$ admits nonempty support even if $\phi_1(x) = 0, \quad x \in \mathbb{R}$. The phenomenon is similar to that in competition-exclusion process in diffusive competitive systems (see Weinberger et al. [5]). Again by the comparison principle and the results stated in Section 1 (Li et al. (Example 4.1 in [2]) and Lin (Theorem 3.1 in [3])), we have the following results on spreading speed.

Lemma 3. $c_{u_2} = 2\sqrt{d_2r_2(1+b_2)}$ *if* $c_{U_2} = 2\sqrt{d_2r_2(1+b_2)}$.

By Lemma 3, it suffices to give some sufficient conditions such that $c_{U_2} = 2\sqrt{d_2r_2(1+b_2)}$. Note that (9) is cooperative but not subhomogeneous; then Weinberger et al. [5] implies that

$$c_{U_2} \geq 2\sqrt{d_2 r_2 (1+b_2)},$$
$$c_{U_1} \geq 2\sqrt{d_2 r_2 (1+b_2)}, \tag{14}$$

which is also clear by utilizing the comparison principle and studying the following auxiliary equation [4]:

$$\frac{\partial w(x,t)}{\partial t} = d_2 \Delta w(x,t) + r_2 w(x,t)\left[1 + b_2 - w(x,t)\right], \quad x \in \mathbb{R}, t > 0. \tag{15}$$

Now, we prove that $c_{U_2} = 2\sqrt{d_2 r_2 (1+b_2)}$ by constructing upper and lower solutions. For the purpose, we introduce some notations. Define

$$c^* = 2\sqrt{d_2 r_2 (1+b_2)},$$
$$\lambda = \sqrt{r_2 \frac{(1+b_2)}{d_2}}. \tag{16}$$

We shall prove the following result on spreading speed.

Theorem 1. *Assume that* $\sup_{x\in\mathbb{R}} [\phi_1(x) + \phi_2(x)] e^{\lambda|x|} < \infty$. *If*

$$2r_2(1+b_2) \geq d_1 r_2 \frac{(1+b_2)}{d_2} + r_1(b_1 b_2 - 1), \tag{17}$$

then $c_{U_1} = c_{U_2} = 2\sqrt{d_2 r_2 (1+b_2)}$ *such that* $c_{u_1} = 2\sqrt{d_1 r_1} > c_{u_2} = 2\sqrt{d_2 r_2 (1+b_2)}$.

Proof. Define

$$\overline{U}_1(x,t) = \min\left\{ e^{\lambda(x+c^*t+x_0)}, e^{\lambda(-x+c^*t+x_0)}, e_1 - 1 \right\},$$
$$\overline{U}_2(x,t) = \min\left\{ b_2 e^{\lambda(x+c^*t+x_0)}, b_2 e^{\lambda(x+c^*t+x_0)}, e_2 \right\}, \tag{18}$$

in which $x_0 > 0$ is a constant such that

$$\overline{U}_1(x,0) \geq \phi_1(x),$$
$$\overline{U}_2(x,0) \geq \phi_2(x), \tag{19}$$
$$x \in \mathbb{R}.$$

If $(\overline{U}_1(x,t), \overline{U}_2(x,t))$ is an upper solution of (9), then the result is true by the comparison principle of cooperative systems. We now prove the definition of upper solutions.

We first prove that

$$\frac{\partial \overline{U}_2(x,t)}{\partial t} \geq d_2 \Delta \overline{U}_2(x,t) + r_2 \overline{U}_2(x,t)\left[1 + b_2 - \overline{U}_2(x,t) + b_2 \overline{U}_1(x,t)\right], \tag{20}$$

when $\overline{U}_2(x,t)$ is differentiable, which is clear if $\overline{U}_2(x,0) = e_2$. When $\overline{U}_2(x,t) = b_2 e^{\lambda(x+c^*t+x_0)}$ is differentiable, then

$$\frac{\partial \overline{U}_2(x,t)}{\partial t} = d_2 \Delta \overline{U}_2(x,t) + r_2 \overline{U}_2(x,t)(1+b_2)$$
$$\geq d_2 \Delta \overline{U}_2(x,t) + r_2 \overline{U}_2(x,t)\left[1 + b_2 - \overline{U}_2(x,t) + b_2 \overline{U}_1(x,t)\right], \tag{21}$$
$$d_2 \Delta \overline{U}_2(x,t) - \frac{\partial \overline{U}_2(x,t)}{\partial t} + r_2 \overline{U}_2(x,t)(1+b_2) = b_2 e^{\lambda(x+c^*t+x_0)}\left[d_2\lambda^2 - c^*\lambda + r_2(1+b_2)\right] = 0,$$

such that (20) is true by the definitions of λ, c^*. Similarly, if $\overline{U}_2(x,t) = b_2 e^{\lambda(-x+c^*t+x_0)}$ is differentiable, then we can obtain the same inequality (20).

On U_1, we need to prove that

$$\frac{\partial \overline{U}_1(x,t)}{\partial t} \geq d_1 \Delta \overline{U}_1(x,t) + r_1\left[\overline{U}_1(x,t) + 1\right] \cdot \left[-\overline{U}_1(x,t) + b_1 \overline{U}_2(x,t)\right], \tag{22}$$

when $\overline{U}_1(x,t)$ is differentiable, which is true if $\overline{U}_1(x,t) = e_1 - 1$ since

$$r_1\left[\overline{U}_1(x,t) + 1\right]\left[-\overline{U}_1(x,t) + b_1 \overline{U}_2(x,t)\right] \leq r_1 e_1\left[-(e_1 - 1) + b_1 e_2\right] = r_1 e_1\left[1 - e_1 + b_1 e_2\right] = 0. \tag{23}$$

When $\overline{U}_1(x,t) = e^{\lambda(x+c^*t+x_0)}$ is differentiable, then

$$\begin{aligned}\frac{\partial \overline{U}_1(x,t)}{\partial t} - d_1 \Delta \overline{U}_1(x,t) &= \left(c^*\lambda - d_1\lambda^2\right) e^{\lambda(x+c^*t+x_0)}, \\ &= \left[2r_2(1+b_2) - d_1 r_2 \frac{(1+b_2)}{d_2}\right] e^{\lambda(x+c^*t+x_0)}, \\ r_1[\overline{U}_1(x,t)+1][-\overline{U}_1(x,t) + b_1\overline{U}_2(x,t)] &\leq r_1(b_1b_2-1)[\overline{U}_1(x,t)+1] e^{\lambda(x+c^*t+x_0)}, \\ &\leq r_1(b_1b_2-1) e^{\lambda(x+c^*t+x_0)}.\end{aligned} \tag{24}$$

By $b_1b_2 < 1$, then (22) is true if (17) holds. Similarly, if $\overline{U}_1(x,t) = e^{\lambda(-x+c^*t+x_0)}$ is differentiable, then (22) holds. The proof is complete. □

Once the spreading speed is confirmed, we may obtain the convergence results in different moving intervals as time goes to infinity by the monotonicity and Fatou lemma, which is similar to that in the proof of Lin (Theorem 3.1 in [3]). □

Theorem 2. *Assume that Theorem 1 holds. Then for any given*

$$2\epsilon \in \left(0, 2\sqrt{d_1 r_1} - 2\sqrt{d_2 r_2(1+b_2)}\right), \tag{25}$$

we have $c_{u_1} = 2\sqrt{d_1 r_1}, c_{u_2} = 2\sqrt{d_2 r_2(1+b_2)}$ *and*

$$\begin{aligned}&\limsup_{t\longrightarrow\infty} \sup_{\left(c_{u_2}+\varepsilon\right)t<|x|<\left(c_{u_1}-\varepsilon\right)t} u_1(x,t) = \liminf_{t\longrightarrow\infty} \inf_{\left(c_{u_2}+\varepsilon\right)t<|x|<\left(c_{u_1}-\varepsilon\right)t} u_1(x,t) = 1, \\ &\limsup_{t\longrightarrow\infty} \sup_{|x|<\left(c_{u_2}-\varepsilon\right)t} u_i(x,t) = \liminf_{t\longrightarrow\infty} \inf_{|x|<\left(c_{u_2}-\varepsilon\right)t} u_i(x,t) = e_i, \quad i = 1,2, \\ &\limsup_{t\longrightarrow\infty} \sup_{|x|>\left(c_{u_1}+\varepsilon\right)t} u_1(x,t) = 0, \\ &\limsup_{t\longrightarrow\infty} \sup_{|x|>\left(c_{u_2}+\varepsilon\right)t} u_2(x,t) = 0.\end{aligned} \tag{26}$$

3. Numerical Simulation

In this section, we simulate several cases of spreading speeds of (2). Define

$$L_\lambda^u(t) = \inf\{x\colon u(x,t) = \lambda\}, \tag{27}$$

which is a special level set of $u(x,t)$. If $t_1 > t_2 > 0$, then $L_\lambda^u(t_1) - L_\lambda^u(t_2)/t_2 - t_1$ may formulate the average movement speed of the level sets in time interval $[t_2, t_1]$, of which the limit may further describe the spreading speed of $u(x,t)$ as $t_1 - t_2$ goes to infinity.

Example 1. We take

$$\begin{aligned}d_1 &= d_2 = 1, \\ r_1 &= 1, \\ r_2 &= 0.3, \\ b_1 &= 0.2, \\ b_2 &= 0.3,\end{aligned} \tag{28}$$

and initial value

$$\begin{aligned}\psi_1(x) = \psi_2(x) &= \cos x, |x| < \frac{\pi}{2}, \\ \psi_1(x) = \psi_2(x) &= 0, \ |x| \geq \frac{\pi}{2}.\end{aligned} \tag{29}$$

Evidently, (17) is true. By our theory, we have $c_{u_1} = 2, c_{u_2} = 1.2$. From Figures 1 and 2, we see that two species invade the habitat almost at two distinct constant speeds. Furthermore, $L_{0.1}^{u_1}(t)$ and $L_{1.1}^{u_1}(t)$ have different moving speeds, and the movement speed of $L_{0.1}^{u_1}(t)$ ($L_{1.1}^{u_1}(t)$ and $L_{1.1}^{u_2}(t)$) is close to c_{u_1} (c_{u_2}).

Example 2. We take

$$\begin{aligned}d_1 &= d_2 = 1, \\ r_1 &= 1, \\ r_2 &= 0.3, \\ b_1 &= b_2 = 0.2,\end{aligned} \tag{30}$$

and initial value

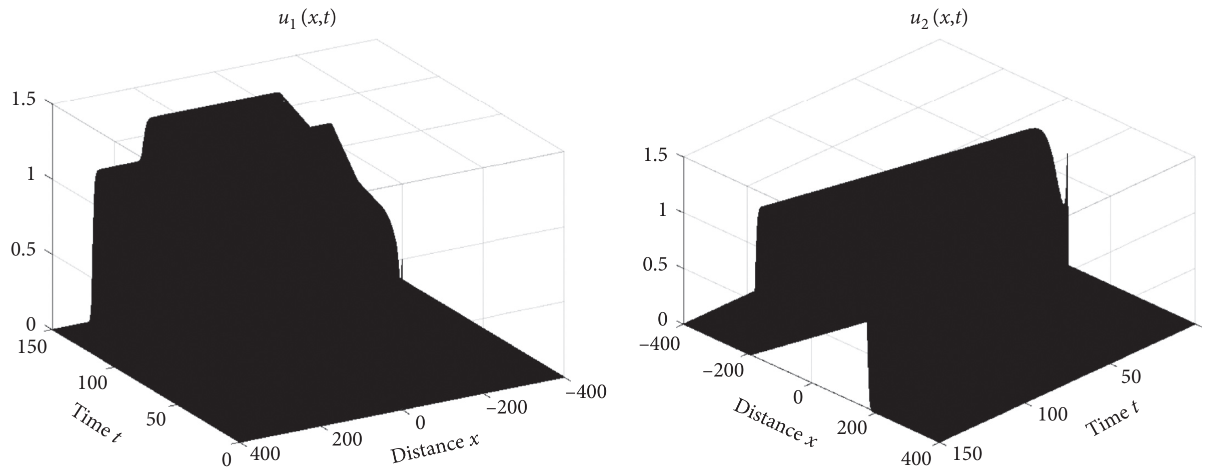

FIGURE 1: Simulation of $(u_1(x,t), u_2(x,t))$ defined by (2) with (28) and (29).

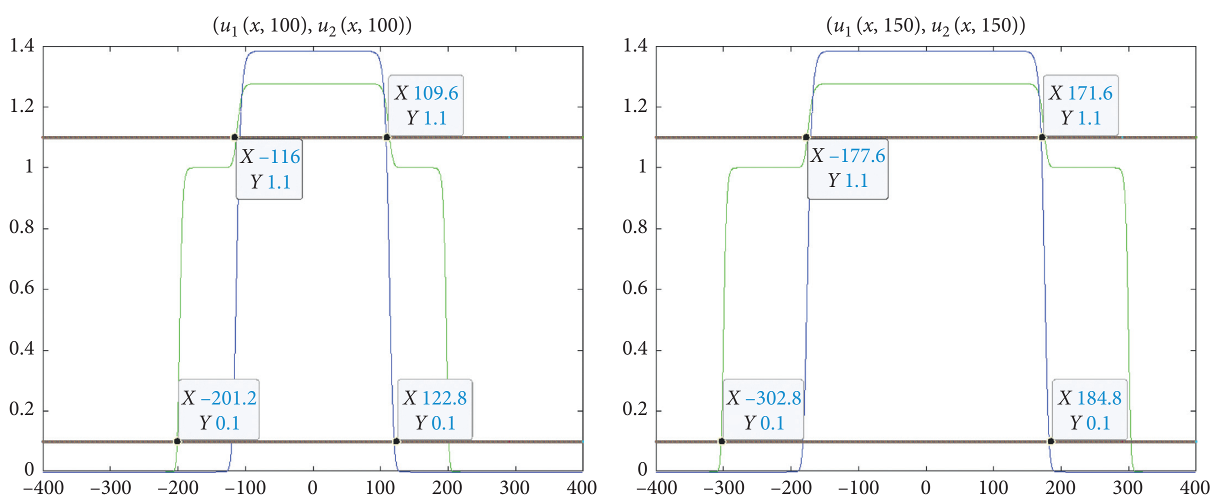

FIGURE 2: Spatial plots of $u_1(x,t)$ (green line) and $u_2(x,t)$ (blue line) at $t = 100, 150$ defined by (2) with (28) and (29).

$$\begin{aligned} &\psi_1(x) = 1, x \in \mathbb{R}, \\ &\psi_2(x) = \cos x, \ |x| < \frac{\pi}{2}, \\ &\psi_2(x) = 0, \ |x| \geq \frac{\pi}{2}. \end{aligned} \tag{31}$$

Evidently, (17) is true. By our theory, we have $c_{u_1-1} = 2$ and $c_{u_2} = 1.2$. Although $u_1(x,0)$ is not compactly supported, the spreading speed of u_2 is close to our results from Figures 3 and 4. Moreover, the movement speed of both $L_{1.1}^{u_1}(t)$ and $L_{1.1}^{u_2}(t)$ is close to c_{u_2}.

Example 3. We take

$$\begin{aligned} &d_1 = 1, \\ &d_2 = \frac{1}{3}, \\ &r_1 = r_2 = 1, \\ &b_1 = b_2 = 0.2, \end{aligned} \tag{32}$$

and initial value

$$\begin{aligned} &\psi_1(x) = \psi_2(x) = \cos x, |x| < \frac{\pi}{2}, \\ &\psi_1(x) = \psi_2(x) = 0, \ |x| \geq \frac{\pi}{2}. \end{aligned} \tag{33}$$

Evidently, (17) is not true. If our theory were true, then we have

$$\begin{aligned} &c_{u_1} = 2, \\ &c_{u_2} = \frac{2\sqrt{10}}{5} \approx 1.264. \end{aligned} \tag{34}$$

From numerical results (Figures 5 and 6), the threshold may be true.

4. Discussion

The cooperative systems have special dynamical features, for example, many cooperative systems do not admit nontrivial periodic solutions [8]. When the propagation dynamics is concerned, much attention has been paid to monotone semiflows (see Fang et al. [9], Liang and Zhao [10], Lui [11], and Weinberger et al. [5]). If a cooperative system is reducible at

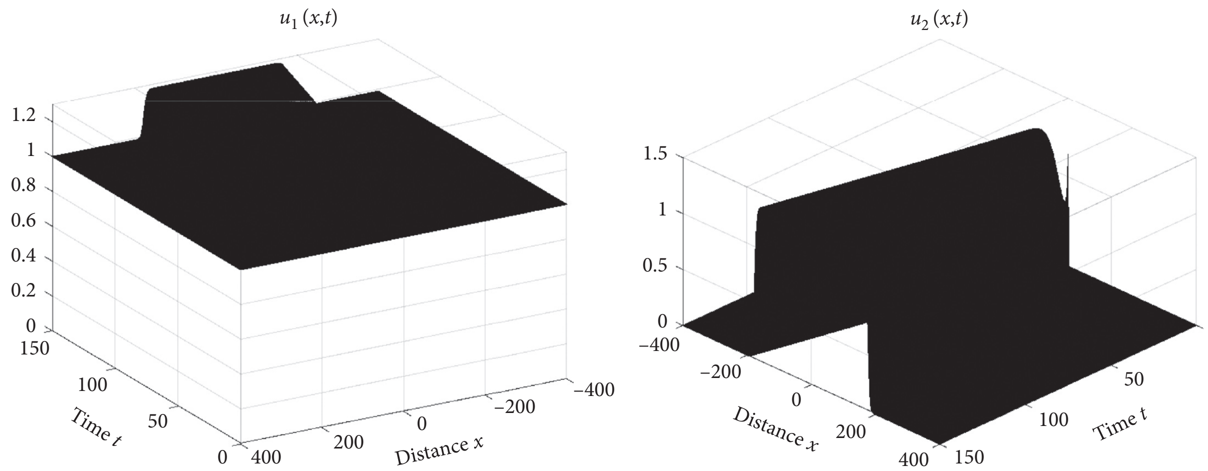

FIGURE 3: Simulation of $(u_1(x,t), u_2(x,t))$ defined by (2) with (28) and (29).

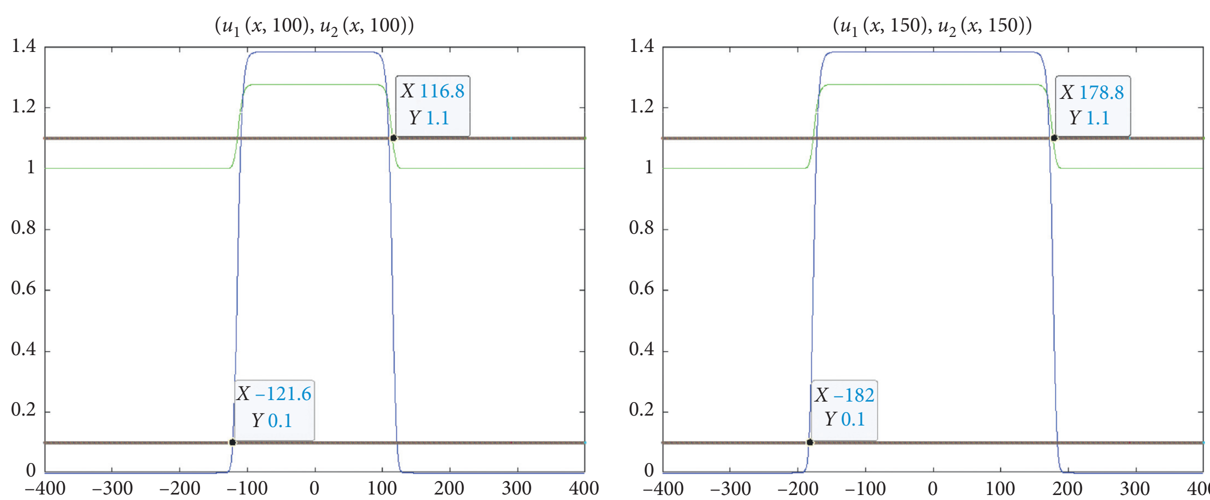

FIGURE 4: Spatial plots of $u_1(x,t)$ (green line) and $u_2(x,t)$ (blue line) at $t = 100, 150$ defined by (2) with (28) and (29).

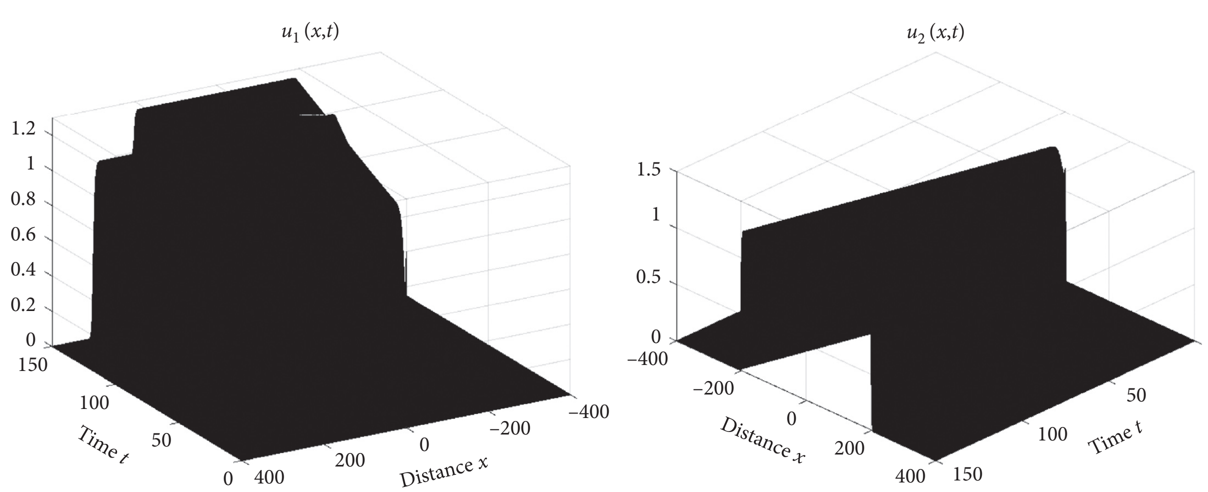

FIGURE 5: Simulation of $(u_1(x,t), u_2(x,t))$ defined by (2) with (32) and (33).

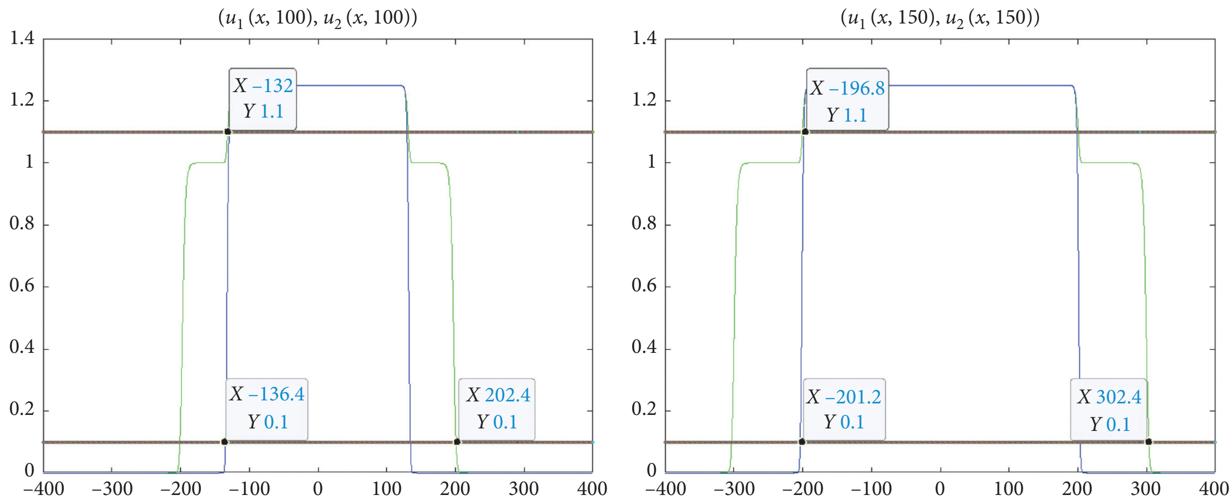

FIGURE 6: Spatial plots of $u_1(x,t)$ (green line) and $u_2(x,t)$ (blue line) at $t = 100, 150$ defined by (2) with (32) and (33).

some invadable steady state (unstable steady state), then it is possible that there are several different spreading speeds, which at least has been observed in (2) (see Li et al. [2] and Lin [3]). However, it remains open to present complete conclusion of spreading speed of (2), and it is a challenging question to further develop the propagation theory of monotone semiflows that are not subhomogeneous and irreducible.

For scalar equations with constant coefficients, the propagation dynamics has been widely explored. In particular, it has been observed a unique spreading speed in both monostable case and bistable case [4, 12] if the solutions could spread. When the coefficients depend on spatial or temporal variables, the propagation dynamics may be more complex [13]. In particular, different propagation terraces occur due to the different movement speeds of different level sets [14]. Although the propagation terraces do not occur in classical monostable or bistable scalar reaction-diffusion equations with constant coefficients, we can observe different terraces in (2). To further show different spreading speeds of different terraces is also an interesting question.

Data Availability

The data used to support the findings of the study are available from the corresponding author upon request.

Conflicts of Interest

The author declares that there are no conflicts of interest regarding the publication of this paper.

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