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# RECENT PROGRESS ON REACTION-DIFFUSION SYSTEMS AND VISCOSITY SOLUTIONS

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#### PREFACE

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This volume grew out from the "International Conference on Reaction-Diffusion Systems and Viscosity Solutions" held at Providence University, Taiwan, during January 3–6, 2007. It consists mostly of selected articles representing the recent progress of some important areas of nonlinear partial differential equations. Some of the articles are research papers by participants of the conference, but most are invited survey papers by leading experts in the field, not necessarily participant of the conference. We hope that in the form of a collected volume, the themes of the conference are further developed, and more researchers can benefit from it. In particular, we hope that the book is useful for researchers and postgraduate students who want to learn about or follow some of the current research work in nonlinear partial differential equations.

The topics included here reflect the themes of the above-mentioned conference and the research interests of the editors, and therefore are naturally biased and incomplete. Nevertheless, they cover a wide range of partial differential equations, from regularity of viscosity solutions, to symmetry properties of positive solutions of parabolic equations, to nonlinear Schrödinger equations, to mention but a few. A complete list can be found from the content pages.

We thank Providence University for the financial support of the conference and of the publication of this volume; without doubt many researchers and postgraduate students will benefit from this generous support, for many years to come. We also thank the authors for their efforts to make this volume a valuable reference book. Finally we extend our thanks to the editors at World Scientific Publishing for their help and patience.

Yihong Du (University of New England, Australia) Hitoshi Ishii (Waseda University, Japan) Wei-Yueh Lin (Providence University, Taiwan)

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# SPATIAL DYNAMICS OF SOME EVOLUTION SYSTEMS IN BIOLOGY

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We first give a brief review on traveling waves, spreading speeds, and global stability for monotone evolution systems with monostable and bistable nonlinearities. Then we outline our recently developed theory and methods for general monotone semiflows and certain non-monotone systems, and their applications to some biological models.

Keywords and phrases: Spreading speeds, traveling waves, global stability, monotone semiflows, biological systems.

AMS Subject Classification: 35B40, 35K57, 35R10, 37C65, 37L60, 92B05, 92D25.

#### 1. Introduction

The study of traveling waves and spreading speeds for evolution equations with spatial structure has a history which is at least 70 years long. A solution u(t,x) of an evolutionary system is said to be a traveling wave solution if u(t,x) = U(x-ct) for some function U. Usually, U is called the wave profile, and c is called the wave speed. If, in addition, two limits  $U(\pm \infty)$  exist, this solution is also called a traveling wavefront. Monostable and bistable nonlinearities frequently appear in spatially homogeneous systems. In the following, we briefly review these two typical cases.

Fisher (1937) [38] considered the following equation

$$u_t = u_{xx} + u(1-u), x \in \mathbb{R}, t \ge 0.$$
 (1.1)

He showed that the wave solution u(t,x) = U(x-ct) exists if and only if  $|c| \geq c_{min} = 2$ , and conjectured that  $c_{min}$  is the asymptotic speed of propagation of the advantageous gene.

Kolmogoroff, Petrowsky and Piscounoff (1937) [66] established the same result with u(1-u) replaced by a function f(u) having the same qualitative properties, and proved that the solution u(t,x) with u(0,x) = H(-x) converges to the monotone (decreasing) traveling wave with speed  $c_{min}$  in profile.

Aronson and Weinberger (1975, 1978) [5, 6] studied a class of reaction-diffusion equations, and confirmed Fisher's conjecture. More precisely, they proved the following result.

**Theorem A.** Let u(t,x) be a nonzero solution of (1.1) with u(0,x) having compact support. Then the following two statements are valid:

- $\lim_{t\to\infty,|x|\geq ct}u(t,x)=0,\,\forall c>2;$
- (ii)  $\lim_{t\to\infty,|x|\leq ct}u(t,x)=1,\,\forall c\in(0,2).$

Let u(t,x) satisfy the properties (i) and (ii) above. For any given  $\rho \in (0,1)$ , let  $x_+^{\rho}(t)$  and  $x_-^{\rho}(t)$  be the most right and left points with  $u(t,x_{\pm}^{\rho}(t))=\rho$ , respectively. We can easily show that

$$\lim_{t \to \infty} \frac{x_{\pm}^{\rho}(t)}{t} = \pm 2$$

uniformly for  $\rho$  in any compact interval contained in (0,1). Thus, it is natural to call this  $c^* = 2$  as the asymptotic speed of spread (in short, spreading speed).

Since these fundamental works there have been extensive investigations on traveling waves, spreading speeds, convergence, uniqueness, minimal wave speeds, and stability for various evolution equations. It is impossible to include all the related papers in our references. The below is a partial list for the study of monostable waves and spreading speeds.

Autonomous reaction-diffusion equations: [47], [114, 115], [136], [107, 108], [35], [18], [65], [14], [138], [39], [139], [97], [94], [105], [129], [158], [46], [72], [154], [141], [71], [155], [87], and references therein.

Density-dependent reaction-diffusion equations: [110–113], [89–91], and 88].

Discrete-time systems  $u_{n+1} = Q[u_n]$ : [142, 143], [77–80], [67], [145], [75], [62], and [52].

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Integral and integrodifferential equations: [7], [19], [4], [27], [29], [117, 118], [28], [130–132], [101–104], [133], [95], [20], [81], and [148].

Time-delayed reaction-diffusion equations: [116], [150], [82], [2, 3], [42], [133], [53], [109], [34], [140], [159], [44], [83], [100], [147] and references therein.

Lattice equations: [57, 162], [149], [24, 25], [146], [85], [23], [45], [156], [87], and references therein.

Periodic and almost periodic evolution equations: [121], [74], and [60, 61]

Heterogeneous environment models: [62–64, 125], [152], [58], [15–17], [144], [123], [45], and references therein.

Fife and Mcleod (1977, 1981) [36, 37] proved the existence, uniqueness and asymptotic stability of monotone traveling waves of the following scalar reaction-diffusion equation with bistable nonlinearity:

$$u_t = u_{xx} + u(1-u)(u-a), \ x \in \mathbb{R}, \ t \ge 0,$$
 (1.2)

where  $a \in (0, 1)$ .

Chen (1997) [22] further extended this result to nonlocal evolution equations, and developed a squeezing technique for the global exponential stability.

**Theorem B.** Equation (1.2) admits a unique (up to translation) monotone traveling wave solution  $\varphi(x-ct)$ , and there exists a positive constant  $\mu>0$  such that for every bounded and uniformly continuous initial function  $\psi(\cdot)$  on  $\mathbb R$  with the property that

$$\limsup_{\xi \to -\infty} \psi(\xi) < a < \liminf_{\xi \to \infty} \psi(\xi),$$

the corresponding solution  $u(x,t,\psi)$  satisfies

$$\|u(x,t,\psi)-\varphi(x-ct+s_{\psi})\|\leq C_{\psi}e^{-\mu t},\ \forall x\in\mathbb{R},\,t\geq0,$$

for some constant  $s_{\psi} \in \mathbb{R}$  and  $C_{\psi} > 0$ .

Ludwig et al. (1979) [76] presented the following spruce budworm population model with bistable nonlinearity:

$$\frac{\partial N}{\partial t} = D\Delta N + r_B N \left(1 - \frac{N}{K_B}\right) - \frac{BN^2}{A^2 + N^2}.$$

Here  $r_B$  is the linear birth rate of the budworm, and  $K_B$  is the carrying capacity, which is related to the density of foliage available on the trees. The

term  $\frac{BN^2}{A^2+N^2}$  with A,B>0 represents predation, generally by birds. Both the refuge equilibrium and the outbreak equilibrium are linearly stable. The below is a partial list for the study of bistable waves.

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Monotone reaction-diffusion systems: [151], [139], [96], [106], [99], [54], [153], [134, 135], [59].

Time-delayed reaction-diffusion equations: [116], [127], [84], and references therein.

Integro-differential equations: [13], [22], [9], and [10].

Periodic reaction-diffusion equations: [1], [8].

Almost periodic and nonautonomous reaction-diffusion equations: [119–121, 124], [21].

Lattice equations: [160, 161], [26], [92, 93], [11, 12], [122], [86].

There are also numerous investigations on traveling waves for other types of evolution equations in biology. Among these models are two-species competition type reaction-diffusion systems (see, e.g., [40], [49–51], [70], [43], [73]) and predator-prey type reaction-diffusion systems (see, e.g., [41], [30–32], [128], [55, 56]).

The purpose of this paper is to survey the theory and methods of spreading speeds and traveling waves for general monotone semiflows and certain non-monotone systems, and their applications to some evolution systems in biology, which were previously presented in papers with collaborators.

### 2. Monotone systems

A family of mappings  $\{\Phi_t\}_{t\geq 0}$  is said to be a semiflow on a metric space (M,d) provided that  $\Phi_0=I, \Phi_{t_1}\circ\Phi_{t_2}=\Phi_{t_1+t_2}$ , and  $\Phi_t(v)$  is continuous in  $(t,v)\in\mathbb{R}_+\times M$ . In this section, we discuss spreading speeds and traveling waves for order-preserving (monotone) maps and semiflows on ordered spaces of functions.

#### 2.1. Monostable case

Let  $\tau$  be a nonnegative real number and  $\mathcal{C}$  be the set of all bounded and continuous functions from  $[-\tau,0] \times \mathcal{H}$  to  $\mathbb{R}^k$ , where  $\mathcal{H} = \mathbb{R}$  or  $\mathbb{Z}$ . Clearly, any vector in  $\mathbb{R}^k$  and any element in the space  $\tilde{\mathcal{C}} := C([-\tau,0],\mathbb{R}^k)$  can be regarded as a function in  $\mathcal{C}$ . Let X be the space of all bounded and continuous functions from  $\mathcal{H}$  to  $\mathbb{R}^k$  equipped with the compact open topology.

For  $u=(u^1,\cdots,u^k), v=(v^1,\cdots,v^k)\in\mathcal{C}$ , we write  $u\geq v(u\gg v)$  provided  $u^i(\theta,x)\geq v^i(\theta,x)(u^i(\theta,x)>v^i(\theta,x)), \forall i=1,\cdots,k,\theta\in[-\tau,0], x\in$ 

 $r\gg 0, \text{ we define } \mathcal{C}_r:=\{u\in\mathcal{C}: r\geq u\geq 0\} \text{ and } \bar{\mathcal{C}_r}:=\{u\in\bar{\mathcal{C}}: r\geq u\geq 0\}.$ functions  $a,b\in \bar{\mathcal{C}},$  we can define  $a\geq (>,\gg)$  b similarly. For any  $r\in \bar{\mathcal{C}}$  with  $\mathcal{H}$ ; and u>v provided  $u\geq v$  but  $u\neq v$ . For any two vectors a,b in  $\mathbb{R}^k$  or two

define the translation operator  $T_y$  by  $T_y[u](\theta,x) = u(\theta,x-y)$ . For given  $\theta_0 \in [-\tau,0], x_0 \in \mathcal{H}$  and  $W \subset \mathcal{C}$ , we use the following Define the reflection operator  $\mathcal{R}$  by  $\mathcal{R}[u](\theta,x)=u(\theta,-x)$ . Given  $y\in\mathcal{H}$ 

$$W(\cdot,x_0):=\{\phi(\cdot,x_0)\in \bar{\mathcal{C}}:\, \phi\in W\},\,\,W(\theta_0,\cdot):=\{\phi(\theta_0,\cdot)\in X:\, \phi\in W\}.$$

 $W \subset \mathcal{C}$  is said to be T-invariant if  $T_yW = W$  for all  $y \in \mathcal{H}$ 

subset  $\mathcal{D}$  of  $\mathcal{C}$ , we define a function  $\phi_I \in C([-\tau,0] \times I, \mathbb{R}^k)$  by  $\phi_I(\theta,x) = \phi(\theta,x)$ . Moreover, for any Given a function  $\phi \in \mathcal{C}$  and a bounded interval  $I = [a, b] \subset \mathcal{H}$ , we define

$$\mathcal{D}_I := \{ \phi_I \in C([-\tau, 0] \times I, \mathbb{R}^k) : \phi \in \mathcal{D} \}.$$

introduce the following assumptions on Q: Let  $\beta \in \overline{C}$  with  $\beta \gg 0$  and  $Q = (Q_1, \dots, Q_k) : C_{\beta} \to C_{\beta}$ . We first

- $(\mathrm{A1}) \ \ Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]], \ T_y[Q[u]] = Q[T_y[u]], \ \forall u \in \mathcal{C}_\beta, \ y \in \mathcal{H}$
- (A2)  $\,Q:\,\mathcal{C}_{eta} o\mathcal{C}_{eta}\,$  is continuous with respect to the compact open topology
- (A3) One of the following two properties holds:
- (a) There is a number  $l \in [0,1)$  such that for any  $A \subset \mathcal{C}_{\beta}$  and  $x \in \mathcal{H}$ ,  $\alpha(\{Q[u](\cdot,x):\,u\in A\})\leq l\alpha(\{u(\cdot,x):\,u\in A\}),$  where  $\alpha$  is the Kuratowski measure of noncompactness on the Banach space  $\bar{\mathcal{C}}$ .
- **E** The set  $Q[C_{\beta}](0,\cdot)$  is precompact in X, and there is a positive number  $\varsigma \le \tau$  such that  $Q[u](\theta,x) = u(\theta+\varsigma,x)$  for  $-\tau \le \theta \le -\varsigma$ . and the operator

$$S[u](\theta,x) := \left\{ \begin{aligned} u(0,x), & -\tau \leq \theta < -\varsigma \\ Q[u](\theta,x), & -\varsigma \leq \theta \leq 0, \end{aligned} \right.$$

invariant set  $D \subset C_{\beta}$  with  $D(0,\cdot)$  precompact in X. has the property that  $S[D](\cdot,0)$  is precompact in  $\overline{\mathcal{C}}$  for any T-

- (A4)  $Q: \mathcal{C}_{\beta} \to \mathcal{C}_{\beta}$  is monotone (order-preserving) in the sense that  $Q[u] \geq$ Q[v] whenever  $u \geq v$  in  $C_{\beta}$ .
- (A5)  $Q: \bar{\mathcal{C}}_{\beta} \to \bar{\mathcal{C}}_{\beta}$  admits exactly two fixed points 0 and  $\beta$ , and for any positive number  $\epsilon$ , there is  $\alpha \in \bar{\mathcal{C}}_{\beta}$  with  $\|\alpha\| < \epsilon$  such that  $Q[\alpha] \gg \alpha$ .

It is easy to see that the hypotheses (A3)(a) holds if  $\{Q[u](\cdot,x): u\in C_{\beta}, x\in \mathcal{H}\}$  is a precompact subset of  $\bar{C}$ .

the following statements are valid: Suppose that  $Q = Q_1$  satisfies all hypotheses (A1)-(A5), and  $Q_t$  satisfies  $\{Q_t\}_{t\geq 0}$  be a semiflow on  $C_{\beta}$  with  $Q_t[0]=0, Q_t[\beta]=\beta$  for all  $t\geq 0$ . (A1) for any t > 0. Let  $c^*$  be the asymptotic speed of spread of  $Q_1$ . Then Theorem 2.1. ([75, Theorem 2.17] and [74, Remark 2.1]) Let

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- (i) For any  $c > c^*$ , if  $v \in C_\beta$  with  $0 \le v \ll \beta$ , and  $v(\cdot, x) = 0$  for xfor  $\theta \in [-\tau, 0]$ . outside a bounded interval, then  $\lim_{t\to\infty,|x|\geq ct}Q_t[v](\theta,x)=0 \ \textit{uniformly}$
- (ii) For any  $c < c^*$  and  $\sigma \in \bar{\mathcal{C}}_\beta$  with  $\sigma \gg 0$ , there is a positive number  $r_{\sigma}$  such that if  $v \in \mathcal{C}_{eta}$  and  $v(\cdot,x) \gg \sigma$  for x on an interval of length addition,  $Q_1$  is subhomogeneous, then  $r_{\sigma}$  can be chosen to be indepen- $2r_{\sigma}$ , then  $\lim_{t\to\infty,|x|\leq ct}Q_t[v](\theta,x)=\beta(\theta)$  uniformly for  $\theta\in[-\tau,0]$ . If, in dent of  $\sigma \gg 0$ .

To estimate the spreading speed  $c^*$ , we can use the following linear operators approach. Let  $M: \mathcal{C} \to \mathcal{C}$  be a linear operator. Assume that

- (M1) M is continuous with respect to the compact open topology
- (M2) M is a positive operator, that is,  $M[v] \ge 0$  whenever v > 0.
- (M3)M satisfies (A3) with  $C_{\beta}$  replaced by any uniformly bounded subset
- $M[\mathcal{R}[u]] = \mathcal{R}[M[u]], T_{\mathcal{V}}[M[u]] = M[T_{\mathcal{V}}[u]], \forall u \in \mathcal{C}, y \in \mathcal{H}.$
- (M5) For some  $\Delta \in (0, +\infty]$ , M can be extended to a linear operator on the linear space  $\tilde{\mathcal{C}}$  of all function  $v \in C([-\tau,0] \times \mathcal{H},\mathbb{R}^k)$  having the

$$v(\theta,x) = v_1(\theta,x)e^{\mu_1x} + v_2(\theta,x)e^{\mu_2x}, v_1, v_2 \in \mathcal{C}, \mu_1, \mu_2 \in (-\Delta, \Delta),$$

such that if  $v_n, v \in \tilde{\mathcal{C}}$  and  $v_n(\theta, x) \to v(\theta, x)$  uniformly on any bounded set, then  $M[v_n](\theta, x) \to M[v](\theta, x)$  uniformly on any

(M6) For any  $\mu \in [0, \Delta)$ , the linear operator  $B_{\mu} : \overline{\mathcal{C}} \to \overline{\mathcal{C}}$ , defined by

$$B_{\mu}[\alpha](\theta) = M[\alpha e^{-\mu x}](\theta, 0), \forall \theta \in [-\tau, 0],$$

is positive, and there is  $n_0$  such that  $B^{n_0}_{\mu}$  is a compact and strongly positive linear operator on  $\bar{\mathcal{C}}$ .

(M7) The principal eigenvalue  $\lambda(\mu)$  of  $B_{\mu}$  satisfies that  $\lambda(0) >$ 

ing (A1)-(A5), and c\* be its spreading speed. Assume that there is a linear **Theorem 2.2.** ([75, Theorem 3.10]) Let Q be an operator on  $C_{\beta}$  satisfy-

operator M satisfying (M1)–(M7) such that  $\Phi(\mu) := \frac{1}{\mu} \ln \lambda(\mu)$  assumes its minimum value at some  $\mu^* \in (0, \Delta)$ . Then the following statements are

- (1) If  $Q[u] \leq M[u]$  for all  $u \in C_{\beta}$ , then  $c^* \leq \inf_{\mu \in (0,\Delta)} \Phi(\mu)$ . (2) If there is some  $\eta \in \overline{C}$  with  $\eta \gg 0$  such that  $Q[u] \geq M[u]$  for any  $u \in \mathcal{C}_{\eta}$ , then  $c^* \ge \inf_{\mu \in (0,\Delta)} \Phi(\mu)$ .

3.10] with  $\inf_{\mu>0} \Phi(\mu)$  replaced by  $\inf_{\mu\in(0,\Delta)} \Phi(\mu)$  is still valid, provided that (M5) holds for all  $\mu_1,\mu_2\in(-\Delta,\Delta)$  and  $\Phi(\mu)$  assumes its minimum value at  $\mu^* \in (0, \Delta)$ .  $\Delta \in (0, +\infty)$ , the proof of [75, Theorem 3.10] implies that [75, Theorem Note that  $\Delta = +\infty$  is assumed in [75, Theorem 3.10]. In the case where

to 0 if  $W(\cdot, -\infty) = \beta$  and  $W(\cdot, +\infty) = 0$ .  $\mathbb{R} \to \mathbb{R}^k$  and  $Q_t[W](\theta,x) = W(\theta,x-ct)$ , and that  $W(\theta,x-ct)$  connects  $\beta$ We say that  $W(\theta, x - ct)$  is a traveling wave of  $\{Q_t\}_{t\geq 0}$  if  $W: [-\tau, 0] \times$ 

speed  $c \ge c^*$ , we need to strengthen the hypothesis (A3) into the following In order to obtain the existence of the traveling wave with the wave

- (A6) One of the following two conditions holds:
- (a) For any number r > 0, there exists  $l = l(r) \in [0,1)$  such that of noncompactness on the Banach space  $C([-\tau, 0] \times I, \mathbb{R}^k)$ . have  $\alpha((Q[\mathcal{D}])_I) \leq l\alpha(\mathcal{D}_I)$ , where  $\alpha$  is the Kuratowski measure for any  $\mathcal{D} \subset \mathcal{C}_{\beta}$  and any interval I = [a, b] of the length r, we
- The set  $Q[C_{\beta}](0,\cdot)$  is precompact in X, and there is a positive number  $\varsigma \le \tau$  such that  $Q[u](\theta, x) = u(\theta + \varsigma, x)$  for  $-\tau \le \theta \le -\varsigma$ ,

$$S[u](\theta,x) := \begin{cases} u(0,x), -\tau \leq \theta < -\varsigma \\ Q[u](\theta,x), -\varsigma \leq \theta \leq 0, \end{cases}$$

has the property that S[D] is precompact in  $C_{\beta}$  for any Tinvariant set  $D \subset \mathcal{C}_{\beta}$  with  $D(0,\cdot)$  precompact in X.

then the hypothesis (A3) on Q implies the hypothesis (A6). in  $\mathcal{C}_{\beta}$  with respect to the compact open topology. Moreover, if  $\mathcal{H}$  is discrete It is easy to see that the hypotheses (A6)(a) holds if  $Q[C_{\beta}]$  is precompact

are valid: be the asymptotic speed of spread of  $Q_1$ . Then the following two statements Assume that for any t>0,  $Q_t$  satisfies hypotheses (A1)-(A5) and let  $c^*$ Theorem 2.3. ([75, Theorems 4.1 and 4.2] and [74, Remark 2.3])

- (i) For any  $0 < c < c^*$ ,  $\{Q_t\}_{t \ge 0}$  has no traveling wave  $W(\theta, x ct)$  con-
- (ii) If, in addition,  $Q_t$  satisfies (A6) for any t > 0, then for any  $c \ge c^*$  $W(\theta,s)$  is continuous and nonincreasing in  $s \in \mathbb{R}$ .  $\{Q_t\}_{t\geq 0}$  has a traveling wave  $W(\theta,x-ct)$  connecting  $\beta$  to 0 such that

in [79] in the case where the linear operators have compact supports. spreading speed results for a system of discrete-time recursions were given recent paper [72] for cooperative reaction-diffusion systems. Further, the approach to continuous-time models has been prescribed explicitly in the may be either continuous or discrete was established in [143]. The time map eling waves for a scalar discrete-time recursion model on a habitat which and Lewis [72]. More precisely, the existence of spreading speeds and travvated by the earlier works of Weinberger [143], Lui [79] and Li, Weinberger We should point out that Theorems 2.1,2.2 and 2.3 were highly moti-

tem, one can show that its solution map  $Q_t$  satisfies A(6)(a) for  $t > \tau$ , and A(6)(b) with  $\varsigma = t$  for  $t \in (0, \tau]$ , under appropriate assumptions. Note that for a time-delayed reaction-diffusion equation or lattice sys-

val  $[-\tau,0]$  is replaced with a compact metric space and that the hypotheses Remark 2.1. Theorems 2.1 and 2.3 are still valid provided that the inter-(A3) and (A6) are replaced with (A3)(a) and (A6)(a), respectively.

extend this theory to almost periodic and general nonautonomous systems developed to monotone periodic semiflows in [74]. It should be interesting to The theory of spreading speeds and traveling waves has been further

result. For the scalar reaction-diffusion equation wave fronts of minimal speed, in short minimal fronts, there is no general Regarding the global asymptotic stability with phase shift of traveling

$$u_t = u_{xx} + f(u), \quad (x,t) \in \mathbb{R} \times (0,\infty), \tag{2.1}$$

solutions and a squeezing technique under the following assumptions: this problem was addressed in [87] via the method of upper and lower

- (F1)  $f \in C^1([0,1],\mathbb{R}), \ f(0) = f(1) = 0, \ f'(1) < 0, \text{ and } f(u) > 0, \forall u \in \mathbb{R}$
- (F2) There exist two constants L>0 and  $\nu>0$  such that  $|f'(u_1) |f'(u_2)| \le L|u_1 - u_2|^{\nu}, \, \forall (u_1, u_2) \in [0, 1]^2.$

(U,c) be a traveling wave of (2.1) such that Theorem 2.4. ([87, Theorem A']) Assume that (F1) and (F2) hold. Let

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 $(P_c)$   $\lim_{x\to-\infty}\frac{U'(x)}{U(x)}=\Lambda_2>\Lambda_1$ , where  $\Lambda_1$  and  $\Lambda_2$  are two roots of  $c\lambda=\lambda^2+f'(0)$ .

Then U(x+ct) is globally exponentially stable with phase shift in the sense that for any  $\alpha \in (\Lambda_1/\Lambda_2, 1)$ , there exists a constant  $\gamma > 0$  such that for any initial data  $\varphi \in C(\mathbb{R}, [0, 1])$  with

$$\liminf_{x\to +\infty} \varphi(x)>0, \ \ and \ \limsup_{x\to -\infty} \varphi(x)e^{-\alpha\Lambda_2x}<+\infty,$$

the solution  $u(x,t,\varphi)$  of (2.1) with  $u(\cdot,0,\varphi)=\varphi$  satisfies

$$\left|\frac{u(x,t,\varphi)-U(x+ct+\xi_0)}{U^{\alpha}(x+ct+\xi_0)}\right| \leq Me^{-\gamma t}, \ \forall t \geq 0, \ x \in \mathbb{R},$$

for some  $M = M(\varphi) > 0$  and  $\xi_0 = \xi_0(\varphi) \in \mathbb{R}$ .

Note that  $U(x+c_{\min}t)$  of (2.1) with  $c_{\min}>2\sqrt{f'(0)}$  satisfies  $(P_c)$  with  $c=c_{\min}$ , and hence, it is globally exponentially stable. Further, Theorem A' is a nontrivial improvement of [108, Theorem 1] since it does not assume the condition that f'(0)>0.

#### .2. Bistable case

For cooperative reaction-diffusion systems with positive diffusion coefficients, and scalar nonlocal evolution equations, the existence, uniqueness and global asymptotic stability of bistable waves are well-known. However, there is no general result on the existence of bistable waves for monotone semiflows. The methods include the phase space analysis, shooting method, perturbation method, etc. In general, it is more difficult to obtain the existence of bistable waves than monostable waves.

The squeezing technique can be used effectively to prove the global asymptotic stability of bistable waves for scalar evolution equations (and their lattice versions). Recently, Tsai [135] also applied this technique to a class of monotone reaction-diffusion systems.

A dynamical systems approach was developed in [153, 157] to prove the global attractivity (and hence uniqueness) of bistable waves for monotone systems. For simplicity, we let  $\varphi(x-ct)$  be a monotone traveling wave of the reaction-diffusion equation

$$u_t(x,t) = du_{xx}(x,t) + f(u(x,t)).$$
 (2.2)

By the moving coordinate z = x - ct, we transform (2.2) into

$$u_t(z,t) = cu_z(z,t) + du_{zz}(z,t) + f(u(z,t)). \tag{2.3}$$

Then  $\varphi(z)$  is an equilibrium solution of equation (2.3). Let  $u(z,t,\psi)$  be the solution of (2.3) with  $u(\cdot,0,\psi)=\psi$ .

Clearly, the solution  $U(x,t,\psi)$  of (2.2) with initial value  $\psi$  is given by  $U(x,t,\psi)=u(x-ct,t,\psi)$ . Thus, the comparison principle holds for (2.2) and hence for (2.3). Note that (2.3) generates a monotone semiflow  $\{Q_t\}_{t\geq 0}$  on the Banach space  $BUC(\mathbb{R},\mathbb{R})$  of all bounded and uniformly continuous functions from  $\mathbb{R}$  to  $\mathbb{R}$  with the usual supreme norm, that is,

$$Q_t(\phi) = u(\cdot, t, \phi), \ t \ge 0, \ \phi \in BUC(\mathbb{R}, \mathbb{R}),$$

but  $\{Q_t\}_{t\geq 0}$  is not strongly monotone.

For any interval  $[a,b] \subset \mathbb{R}$ , the ordered arc

$$L := \{ \varphi(\cdot + s) : s \in [a, b] \}$$

consists of equilibria of (2.3). It then suffices to study the convergence of an orbit of (2.3) to some equilibrium in L. For this purpose, one can use the following convergence result for monotone semiflows.

**Theorem 2.5.** ([157, Theorem 2.2.4]) Let U be a closed convex subset of an ordered Banach space X, and  $\Phi(t): U \to U$  be a monotone semiflow. Assume that there exists a monotone homeomorphism h from [0,1] onto a subset of U such that

- (1) For each  $s \in [0,1]$ , h(s) is a stable equilibrium for  $\Phi(t): U \to U$ ;
- (2) Each orbit of  $\Phi(t)$  in  $[h(0), h(1)]_X$  is precompact;
- (3) If  $h(s_0) <_{\mathcal{X}} \omega(\phi)$  for some  $s_0 \in [0,1)$  and  $\phi \in [h(0),h(1)]_{\mathcal{X}}$ , then there exists  $s_1 \in (s_0,1)$  such that  $h(s_1) \leq_{\mathcal{X}} \omega(\phi)$ .

Then for any precompact orbit  $\gamma^+(\phi_0)$  of  $\Phi(t)$  in U with  $\omega(\phi_0) \cap [h(0), h(1)]_{\mathcal{X}} \neq \emptyset$ , there exists  $s^* \in [0, 1]$  such that  $\omega(\phi_0) = h(s^*)$ .

This approach was used to prove the global attractivity of traveling waves for scalar periodic reaction-diffusion equations in [157, Theorem 10.2.1] and for a class of reaction-diffusion systems in [153, Theorem 3.1]. To obtain the exponential stability of bistable waves for monotone systems, one needs to do spectral analysis (see, e.g., [153, Theorem 4.1]). In the rest of this subsection, we present the recent results obtained in [59].

Let D > 0. Consider a reaction-diffusion system

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u, v),$$

$$\frac{\partial v}{\partial t} = G(u, v).$$
(2.4)

Assume that

- (H1) There exist three points  $E_-=(0,0), E_0=(a_1,b_1)$  and  $E_+=(a_2,b_2)$  with  $0< a_1< a_2$  and  $0< b_1< b_2$  such that
- (1)  $F, G \in C^1(\mathbb{R}^2_+, \mathbb{R}), F_v(u, v) \ge 0, G_u(u, v) \ge 0$  and  $G_v(u, v) < 0$  on  $\mathbb{R}^2_+$ , and  $G_u(0, 0) > 0$ .
- (2)  $E_-$ ,  $E_0$  and  $E_+$  are only zeros of f(u,v):=(F(u,v),G(u,v)) in the order interval  $[E_-,E_+]$ .
- (3) All eigenvalues of the Jacobian matrices  $Df(E_{-})$  and  $Df(E_{+})$  have negative real parts, and  $Df(E_{0})$  has an eigenvalue with positive real part and another with negative real part.
- (4)  $F_v(u,v) > 0$  for  $(u,v) \in [0,a_2] \times [0,b_2]$ .

By the assumption (H1), it follows that the spatially homogeneous system

$$\frac{du}{dt} = F(u, v),$$

$$\frac{dv}{dt} = G(u, v)$$
(2.5)

has only three equilibria  $E_-$ ,  $E_0$  and  $E_+$  in  $[E_-, E_+]$ ,  $E_-$  and  $E_+$  are stable,  $E_0$  is a saddle. By a shooting method, we obtain the following result on the existence of bistable waves of (2.4) connecting  $E_-$  and  $E_+$ .

**Theorem 2.6.** ([59, Theorem 2.1]) Let (H1) hold. Then system (2.4) has a monotone increasing traveling wave solution (U(x+ct), V(x+ct)) connecting  $E_-$  to  $E_+$  for some real number c such that the wave speed c has the same sign as the integral  $\int_0^{a_2} F(U, V^*(U)) dU$ , where  $V^*(U)$  satisfies  $G(U, V^*(U)) = 0$ .

To obtain the global attractivity of bistable waves, we need the following additional conditions on F and G.

- (H2) F and G can be extended to the domain  $(-l,\infty)^2$  for some l>0 such that
- (1)  $F, G \in C^2((-l, \infty)^2, \mathbb{R}), F_u(u, v) < 0, F_v(u, v) > 0, G_u(u, v) \ge 0$ and  $G_v(u, v) < 0$  for  $(u, v) \in (-l, \infty)^2$ .
- (2) There exists L>0 such that for any  $l_2>L$ , there exists  $l_1>0$  such that  $F(l_1,l_2)<0$ .

Let  $\mathbb{X} = BUC(\mathbb{R}, \mathbb{R}^2)$  be the Banach space of all bounded and uniformly continuous functions from  $\mathbb{R}$  to  $\mathbb{R}^2$  with the usual supreme norm.

Let  $\mathbb{X}_{+}=\{(\psi_{1},\psi_{2})\in\mathbb{X}:\psi_{i}(x)\geq0,\forall x\in\mathbb{R},i=1,2\}$ . By the aforementioned dynamical systems approach as applied to system (2.4), we have the following result.

**Theorem 2.7.** ([59, Theorem 3.1]) Assume that (H1) and (H2) hold. Let  $\phi(x-ct)$  be a monotone traveling wave solution of system (2.4) and  $\Psi(t,x,\psi):=(u(t,x,\psi),v(t,x,\psi))$  be the solution of (2.4) with  $\Psi(0,\cdot,\psi)=\psi\in\mathbb{X}_+$ . Then for any  $\psi\in\mathbb{X}_+$  with

$$\limsup_{\xi \to -\infty} \psi(\xi) \ll E_0 \ll \liminf_{\xi \to \infty} \psi(\xi), \tag{2.6}$$

there exists  $s_{\psi} \in \mathbb{R}$  such that  $\lim_{t \to +\infty} \|\Psi(t, x, \psi) - \phi(x - ct + s_{\psi})\|_{\mathbb{R}^2} = 0$  uniformly for  $x \in \mathbb{R}$ . Moreover, any traveling wave solution of system (2.4) connection  $E_-$  and  $E_+$  is a translate of  $\phi$ .

We remark that by the spectrum analysis as in [153, Section 4], one can obtain the local exponential stability with phase shift of the bistable wave  $\phi(x-ct)$  with  $c \neq 0$ . This, together with Theorem 2.7, implies the global exponential stability with phase shift of the bistable wave  $\phi(x-ct)$  with  $c \neq 0$  of (2.4).

### 3. A class of non-monotone systems

Many discrete- and continuous-time population models with spatial structure are not monotone. For example, scalar discrete-time integrodifference equations with non-monotone growth functions (see, e.g., [67]), and predator-prey type reaction-diffusion systems are among such models. The spreading speeds were obtained for some non-monotone continuous-time integral equations and time-delayed reaction-diffusion models in [131, 133], and a general result on the nonexistence of traveling waves was also given in [133, Theorem 3.5]. The existence of monostable traveling waves were established for several classes of non-monotone time-delayed reaction-diffusion equations in [34, 83, 100, 150]. As an illustration, below we present the main results obtained recently in [52].

Let  $\mathcal{C}$  be the space of all bounded and continuous functions from  $\mathbb{R}$  to  $\mathbb{R}$  equipped with the compact open topology. For a given number r > 0, let  $\mathcal{C}_r := \{\phi \in \mathcal{C} : 0 \le \phi(x) \le r, \, \forall x \in \mathbb{R} \}$ .

Let k(x) be a nonnegative Lebesgue measurable function on  $\mathbb{R}$ . We assume that the kernel k(x) has the following property:

(K)  $\int_{\mathbb{R}} k(y)dy = 1$ , k(-y) = k(y),  $\forall y \in \mathbb{R}$ , and  $\int_{\mathbb{R}} e^{-\alpha y} k(y)dy < \infty$ ,  $\forall \alpha \in$ 

 $[0,\Delta)$ , where  $\Delta>0$  is the abscissa of convergence and it may be

Consider a discrete-time integrodifference equation

$$u_{n+1}(x) = \int_{\mathbb{R}} h(u_n(y))k(x-y)dy, \ x \in \mathbb{R}, \ n \ge 0$$
 (3.1)

with  $u_0 \in \mathcal{C}$ . Assume that there exists  $\beta > 0$  such that

- (B1)  $h \in C([0,\beta],[0,\beta]), h(0) = 0, h'(0) > 1, h(\beta) = \beta$ , and there is  $L_0 > 0$
- such that  $|h(u_1) h(u_2)| \le L_0|u_1 u_2|$ ,  $\forall u_1, u_2 \in [0, \beta]$ . (B2)  $u < h(u) \le h'(0)u$ ,  $\forall u \in (0, \beta)$ , and h(u) is nondecreasing in  $u \in (0, \beta)$ .

satisfies (3.1), and U(x+cn) connects 0 to  $\beta$  if  $U(-\infty)=0$  and  $U(+\infty)=\beta$ . wave solution of (3.1) with the wave speed c if  $u_n(x) = U(x+cn)$ ,  $\forall n \geq 0$ , Let U(x) be a continuous function on  $\mathbb{R}$ . We say U(x+cn) is a traveling

$$= \inf_{\mu \in (0,\Delta)} \frac{\ln\left(h'(0)\int_{\mathbb{R}} e^{-\mu y} k(y) dy\right)}{\mu}.$$
 (3.2)

 $c_h^*$  is not only the spreading speed but also the minimal wave speed of monotone traveling waves for system (3.1). The following result is essentially due to Weinberger [143], and shows that

following statements are valid: Theorem 3.1. ([52, Theorem 2.1]) Let (B1) and (B2) hold. Then the

- (i) For any  $u_0 \in C_\beta$  with compact support, the solution of (3.1) satisfies  $\lim_{n \to \infty, |x| \ge cn} u_n(x) = 0, \forall c > c_h^*.$
- $\Xi$ For any  $u_0 \in C_{\beta} \setminus \{0\}$ , the solution of (3.1) satisfies  $\lim_{n \to \infty, |x| \le c_n} u_n(x) =$  $\beta, \forall c \in (0, c_h^*).$
- (iii) For any  $c \geq c_h^*$ , (3.1) has a traveling wave U(x+cn) connecting 0 to  $\beta$  such that U(x) is nondecreasing in x, and for any  $c \in (0, c_h^*)$ , (3.1)has no traveling wave U(x+cn) connecting 0 to  $\beta$ .

Now we consider the discrete-time integrodifference equation

$$u_{n+1}(x) = \int_{\mathbb{R}} f(u_n(y))k(x-y)dy, \quad x \in \mathbb{R}, n \ge 0$$
 (3.3)

with  $u_0 \in \mathcal{C}$ . Assume that there exists b > 0 such that

- (D1)  $f \in C([0,b], [0,b]), f(0) = 0, f'(0) > 1$ , and there is L > 0 such that  $|f(u_1) - f(u_2)| \le L|u_1 - u_2|, \forall u_1, u_2 \in [0, b].$
- (D2)  $f(u) \le f'(0)u$ ,  $\forall u \in [0, b]$ , and there is  $u^* \in (0, b]$  such that  $f(u^*) = u^*$ , f(u) > u,  $\forall u \in (0, u^*)$ , and 0 < f(u) < u,  $\forall u \in (u^*, b]$ .

ology: logistic type function  $f(u) = ru(1 - \frac{u}{K}), r > 0, K > 0$ ; the Ricker Holt type function  $f(u) = \frac{pu}{q+u^m}$ , m > 0, and p > q > 0. type function  $f(u) = que^{-pu}$ , q > 1, p > 0; and the generalized Beverton Three types of growth functions are commonly used in population bi-

$$f^+(u) = \max_{0 \le v \le u} f(v), \quad f^-(u) = \min_{u \le v \le b} f(v), \quad \forall u \in [0, b].$$

It then follows that

$$f^{-}(u) \le f(u) \le f^{+}(u), \forall u \in [0, b],$$

 $0 < u^* \le u^* \le u^*_+ \le b.$ that  $f^{\pm}(u) = f(u), \forall u \in [0, \delta_0]$ . Let  $u_{\pm}^*$  be such that  $f^{\pm}(u_{\pm}^*) = u_{\pm}^*$ . Then the Lipschitz constant L, on [0,b], and that there exists  $\delta_0 \in (0,b]$  such that both  $f^+$  and  $f^-$  are nondecreasing and Lipschitz continuous, with

to impose one of the following two additional conditions on f. To obtain the upward convergence as stated in Theorem  $3.1(\mathrm{ii}),$  we need

- (C1)  $u^* = b$  and f(u) is nondecreasing in  $u \in [b \epsilon_0, b]$  for some  $\epsilon_0 \in (0, b)$
- (C2)  $\frac{f(u)}{u}$  is strictly decreasing for  $u \in (0, b]$ , and f(u) has the property  $w \le f(v)$ , we have v = w. (P) that for any  $v, w \in (0, b]$  satisfying  $v \leq u^* \leq w, v \geq f(w)$  and

tions is sufficient for the property (P) in condition (C2) to hold: It follows from [52, Lemma 2.1] that either of the following two condi-

- (P1) uf(u) is strictly increasing for  $u \in (0, b]$ .
- (P2) f(u) is nonincreasing for  $u \in [u^*, b]$ , and  $\frac{f^2(u)}{u}$  is strictly decreasing for  $u \in (0, u^*]$ .

ods, the Schauder fixed point theorem, and the limiting arguments. The following two results were proved in [52] via the comparison meth-

defined as in (3.2) with h = f. Then the following statements are valid: **Theorem 3.2.** ([52, Theorem 2.2]) Let (D1) and (D2) hold and  $c_t^*$  be

(i) For any  $u_0 \in C_{u_1^*}$  with compact support, the solution of (3.3) satisfies  $\lim_{n\to\infty,|x|\geq cn}u_n(x)=0,\,\forall c>c_f^*.$ 

(ii) For any  $u_0 \in C_{u_+^*} \setminus \{0\}$ , the solution of (3.3) satisfies

$$u_-^* \leq \liminf_{n \to \infty, |x| \leq cn} u_n(x) \leq \limsup_{n \to \infty, |x| \leq cn} u_n(x) \leq u_+^*, \, \forall c \in (0, c_f^*).$$

(iii) If, in addition, either (C1) or (C2) holds, then for any  $u_0 \in C_{u_{+}^*} \setminus \{0\}$ , the solution of (3.3) satisfies  $\lim_{n \to \infty, |x| \le n} u_n(x) = u^*, \forall c \in (0, c_f^*).$ 

on continuous-time integral equations. proof were highly motivated by [131, Lemma 3.10] and [133, Theorem 2.5] We should point out that Theorem 3.2 (iii) in the case of (C2) and its

**Remark 3.1.** Theorem 3.2 with  $\int_{\mathbb{R}}$  replaced by  $\int_{\mathbb{R}^m}$  is still valid under the assumption that  $\int_{\mathbb{R}^m} k(y)dy = 1$ , k(x) = k(y),  $\forall x, y \in \mathbb{R}^m$  with |x| = |y|.

Note that if f''(0) exists, then  $f(u) \ge f'(0)u - au^2$ ,  $\forall u \in [0, \delta]$ , for appropriate a > 0 and  $\delta > 0$ . To obtain the existence of traveling waves, we impose the following weaker condition on f.

(D3) There exist real numbers  $\delta^* \in (0, \delta_0], \ \sigma > 1$  and a > 0 such that  $f(u) \geq f'(0)u - au^{\sigma}, \ \forall u \in [0, \delta^*].$ 

the following statements are valid: Theorem 3.3. ([52, THEOREMS 3.1 AND 3.2]) Let (D1)-(D3) hold. Then

- (i) For any  $c \in (0, c_f^*)$ , (3.3) has no traveling wave U(x+cn) with  $U \in$  $C_{u_+^*}\setminus\{0\}$  and  $U(-\infty)=0$ .
- (ii) For any  $c > c_f^*$ , (3.3) has a traveling wave U(x+cn) such that  $U \in$  $C_{u_+^*}\setminus\{0\}, U(-\infty)=0$  and

$$u_-^* \leq \liminf_{\xi \to +\infty} U(\xi) \leq \limsup_{\xi \to +\infty} U(\xi) \leq u_+^*.$$

If, in addition, either (C1) or (C2) holds, then  $U(+\infty) = u^*$ . (iii) (3.3) has a traveling wave  $U(x + c_f^*n)$  such that  $U \in \mathcal{C}_{u_+^*} \setminus \{0, u^*\}$  and

$$u_{-}^{\star} \leq \liminf_{\xi \to +\infty} U(\xi) \leq \limsup_{\xi \to +\infty} U(\xi) \leq u_{+}^{\star}.$$

If, in addition, either (C1) or (C2) holds, then  $U(+\infty) = u^*$ 

equation population models. eling waves for this class of non-monotone discrete-time integrodifference linearly determinate and coincides with the minimal wave speed of trav-In view of Theorems 3.2 and 3.3, we see that the spreading speed is

## 4. Applications to biological systems

since it describes the speed at which the geographic range of the population section, we choose five biological models to illustrate the applicability of expands, see, e.g., [48, 68, 69, 98, 126, 137] and references therein. In this The invasion speed is a fundamental characteristic of biological invasions. the theory and methods mentioned in the previous sections

### 4.1. A model with a quiescent stage

Hadeler and Lewis (2002) [46] presented and discussed briefly the following

$$\partial_t u_1 = D\Delta u_1 + f(u_1) - \gamma_1 u_1 + \gamma_2 u_2, 
\partial_t u_2 = \gamma_1 u_1 - \gamma_2 u_2,$$
(4.1)

and nonmobile states, and only the migrants reproduce. Such behavior is which describes a population where the individuals move between mobile up and reappear subject to rainfall. Assume that typical for invertebrates living in small ponds in arid climates which dry

(E1) 
$$f \in C^1(\mathbb{R}_+, \mathbb{R})$$
,  $f(0) = 0$ ,  $f'(0) > 0$ ,  $\left(\frac{f(v)}{v}\right)' < 0$  for  $v > 0$ , and there exists  $H > 0$  such that  $f(v) \le 0$  for all  $v \ge H$ .

Then (4.1) has a unique positive constant solution  $u^*$ 

$$\lambda(\mu) = \frac{1}{2} \left[ D\mu^2 + f'(0) - \gamma_1 - \gamma_2 \right]$$
  
+ 
$$\frac{1}{2} \sqrt{(D\mu^2 + f'(0) - \gamma_1 - \gamma_2)^2 + 4\gamma_2(D\mu^2 + f'(0))}.$$

By the theory of spreading speeds and monostable traveling waves for monorespect to the compact open topology, but they satisfy assumption (A6)(a). tone systems, we then have the following result. Note that the solution maps associated with (4.1) are not compact with

 $\phi \in \mathbb{X}_{u^*} = C(\mathbb{R}, [0, u^*])$ . Then the following statements are valid: and let  $c^* = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu}$ . Let  $u(t,x,\phi)$  be the solution of (4.1) with  $u(0,\cdot,\phi) =$ Theorem 4.1. ([155, Theorems 2.1 and 2.2]) Assume that (E1) holds

(i) For any  $c > c^*$ , if  $\phi \in \mathbb{X}_{u^*}$  with  $0 \le \phi \ll u^*$ , and  $\phi(x) = 0$  for xoutside a bounded interval, then  $\lim_{t\to\infty,|x|\geq\alpha}u(t,x,\phi)=0$ ;

- (ii) For any  $c \in (0, c^*)$ , if  $\phi \in \mathbb{X}_{u^*}$  and  $\phi \neq 0$ , then  $\lim_{t \to \infty, |x| \leq ct} u(t, x, \phi) = u^*$ .
- (iii)  $c^*$  is the minimal wave speed for monotone traveling waves of (4.1) connecting 0 and  $u^*$ .

By Theorems 2.6 and 2.7, it is easy to see the following result on the bistable wave is valid.

Theorem 4.2. ([59, Example 3]) Assume that

(E2) There exists l>0 such that  $f\in C^2(-l,\infty)$  and  $f'(u_1)-\gamma_1<0$  for  $u_1\in (-l,\infty)$ , and  $f(u_1)$  has only three zeros  $0< a_1< a_2$  on the interval  $[0,a_2]$  with f'(0)<0,  $f'(a_1)>0$  and  $f'(a_2)<0$ .

Then system (4.1) admits a bistable traveling wave, which is globally attractive with phase shift and unique up to translation.

## 4.2. A nonlocal lattice differential system

Weng, Huang and Wu (2003) [146] derived a mature population growth model

$$\frac{dw_{j}(t)}{dt} = D[w_{j+1}(t) + w_{j-1}(t) - 2w_{j}(t)] - dw_{j}(t) 
+ \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta_{\alpha}(j-k)b(w_{k}(t-r)),$$
(4.2)

where t > 0,  $j \in Z$ ,

$$\beta_{\alpha}(l) = 2e^{-\nu} \int_{0}^{\pi} \cos(l\omega) e^{\nu \cos \omega} d\omega,$$

 $r\geq 0,\, D,d,\mu$  and  $\nu=2\alpha$  are all positive real numbers. Assume that

- (E3)  $b \in C(\mathbb{R}_+, \mathbb{R}_+), b(0) = 0, b'(0) > d/\mu, b(w) \le b'(0)w$  for  $w \in \mathbb{R}_+$ .
- (E4)  $b(\cdot)$  is strictly increasing on [0,K] for some K>0, and  $\mu b(w)=dw$  has a unique solution  $w^+\in(0,K]$ .

The authors of [146] also proved the existence of spreading speed  $c^*$  and the existence of traveling waves with wave speed  $c > c^*$  in the case where the time delay r is small. The following result gives a complete description of spatial dynamics of (4.2).

Defin

$$f(c,\chi) := c\chi - [D(e^{-\chi} + e^{\chi}) - (d+2D)] - \mu b'(0)e^{(\cosh\chi - 1)\nu - c\chi r}.$$

Let  $(c^*, \chi^*)$  be the positive solution to the following system

$$f(c,\chi) = 0$$
,  $\frac{\partial f}{\partial \chi}(c,\chi) = 0$ .

**Theorem 4.3.** ([75, THEOREMS 5.3 AND 5.4]) Assume that (E3) and (E4) hold. Let w(t) be a solution of (4.2) with  $0 \le w_i(t) < w^+$  for any  $t \in [-r, 0], i \in \mathbb{Z}$ . Then the following statements are valid:

- (i) If  $w_i(t) = 0$  for  $t \in [-r, 0]$  and i outside a bounded interval, then  $\lim_{t \to \infty, |i| \ge ct} w_i(t) = 0$  for any  $c > c^*$ .
- (ii) If  $w(t) \neq 0$  for  $t \in [-r, 0]$ , then  $\lim_{t \to \infty, |t| \leq ct} w_i(t) = w^+$  for any  $c < c^*$ .
- (iii) For any  $c \geq c^*$ , (4.2) has a traveling wave solution  $w_i(t) = U(i-ct)$  such that U(s) is continuous and nonincreasing in  $s \in \mathbb{R}$ , and  $U(-\infty) = w^+$  and  $U(+\infty) = 0$ . Moreover, for any  $c < c^*$ , (4.2) has no traveling wave U(i-ct) connecting  $w^+$  to 0.

## 4.3. A multi-type SIS epidemic model

Rass and Radcliffe (2003) [104] presented the following spatial epidemic model

$$egin{aligned} rac{\partial y_i(x,t)}{\partial t} &= (1-y_i(x,t)) \sum_{j=1}^n \sigma_j \lambda_{ij} \int_{\mathbb{R}} y_j(x-u,t) \ & \cdot p_{ij}(u) du - \mu_i y_i(x,t), \ 1 \leq i \leq n. \end{aligned}$$

Here  $y_i(x,t)$  is the proportion of individuals for the ith population at position x who were infectious at time t,  $\mu_i \geq 0$  is the combined death, emigration and recovery rate for infectious individuals,  $\sigma_i \geq 0$  is the population size of the ith population,  $\lambda_{ij} \geq 0$  is the infection rate of a type i susceptible by a type j infectious individual, and  $p_{ij}(u)$  is the corresponding contact distribution.

Let  $\Lambda:=(\sigma_j\lambda_{ij})_{n\times n}$ , and  $\Gamma=(\mathrm{diag}(\mu))^{-1}\Lambda$  in the case where  $\mu=(\mu_1,\cdots,\mu_n)\gg 0$ . Define

$$\rho(\Gamma) := \max\{|\lambda| : \det (\lambda I - \Gamma) = 0\}$$

Assume that

(E5) Either  $\mu_i = 0$  for some i, or  $\mu \gg 0$  and  $\rho(\Gamma) > 1$ .

It was proved in [104] that the spatially homogeneous system associated

$$\frac{dy_i(t)}{dt} = (1 - y_i(t)) \sum_{j=1}^n \sigma_j \lambda_{ij} y_j(t) - \mu_i y_i(t), \quad 1 \leq i \leq n,$$

admits a unique equilibrium  $y^*\gg 0$ , which is globally asymptotically stable in  $[0,1]^n\setminus\{0\}$ .

The open problem on the asymptotic speed of propagation of infection and traveling waves for model (4.3) was solved by Weng and Zhao (2006)

Define a matrix  $A(\alpha) = (A_{ij}(\alpha))_{n \times n}$ , where

$$A_{ij}(\alpha) = \begin{cases} \sigma_j \lambda_{ij} \left( \int_{\mathbb{R}} e^{\alpha u} p_{ij}(u) du \right) - \mu_i, i = j, \\ \\ \sigma_j \lambda_{ij} \left( \int_{\mathbb{R}} e^{\alpha u} p_{ij}(u) du \right), \quad i \neq j. \end{cases}$$

speed for monotone traveling waves of (4.3). functions having compact supports. Moreover,  $c^st$  is also the minimal wave  $\inf_{\alpha>0} \frac{\lambda(\alpha)}{\alpha}$ . Then  $c^*$  is the spreading speed for solutions of (4.3) with initial (E5) holds. Let  $\lambda(\alpha)$  be the principal eigenvalue of  $A(\alpha)$ , and define  $c^* :=$ Theorem 4.4. ([148, Theorems 3.1-3.2 and 4.1-4.2]) Assume that

By using the general theory of spreading speeds and traveling waves; Zhang and Zhao (2008) [156] studied the spatially discrete version of (4.3):

$$\frac{\partial y_m(x,t)}{\partial t} = (1 - y_m(x,t)) \sum_{n=1}^{\tau} \sigma_n \lambda_{mn} \int_{\mathbb{R}} y_n(x-u,t) p_{mn}(u) du - \mu_m y_m(x,t),$$

 $0, \forall k \in Z, \, 1 \leq m, n \leq r.$ where  $j \in Z$ ,  $1 \le m \le r$ ,  $\sum_{k=-\infty}^{\infty} p_{mn}(k) = 1$ , and  $p_{mn}(k) = p_{mn}(-k) \ge r$ 

## 4.4. A vector disease model with spatial spread

Ruan and Xiao (2004) [109] presented a diffusive and time-delayed integro

$$\frac{\partial u}{\partial t}(t,x) = d\Delta u(t,x) - au(t,x) + b[1 - u(t,x)]$$
$$\cdot \int_{-\infty}^{t} \int_{\Omega} F(t,s,x,y)u(s,y)dyds. \tag{4.4}$$

measurable in its variables  $x, y \in \Omega$ . kernel, which is positive, continuous in its variables  $t \in \mathbb{R}, s \in \mathbb{R}_+$  and Bore host, b is the host-vector contact rate, and F(t, s, x, y) is the convolution  $\Delta$  is the Laplacian operator, a is the cure/recovery rate of the infected point x, x is in a spatial habitat  $\Omega \subset \mathbb{R}^n (n \leq 3), d$  is the diffusion constant Here u(t,x) is normalized spatial density of infectious host at time t and at

two equilibria 0 and 1 - a/b with the wave speed c = c(r) close to  $c_0$ . for any  $r \in [0, r_0]$ , the model system admits a traveling wave connecting for any  $c_0 \ge 2\sqrt{b-a}$ , there exists a small number  $r_0 = r_0(c_0) > 0$  such that being the Dirac  $\delta$ -function and  $G(t) = \frac{t}{r^2}e^{-t/r}$ , it was showed in [109] that In the case where  $\Omega = \mathbb{R}$  and  $F(t, s, x, y) = \delta(x - y)G(t - s)$  with  $\delta(x)$ 

minimal wave speed of monotone traveling waves for the model (4.4) with [159] established the existence of the spreading speed of the disease and the approximations method, and the limiting arguments, Zhao and Xiao (2006) F(t, s, x, y) = F(t - s, x - y), that is, By the theory of spreading speeds and traveling waves, the finite delay

$$\frac{\partial u}{\partial t}(t,x) = d\Delta u(t,x) - au(t,x) + b[1 - u(t,x)]$$
$$\cdot \int_{-\infty}^{t} \int_{-\infty}^{\infty} F(t-s,x-y)u(s,y)dyds. \tag{4.5}$$

We assume that

(E6) 
$$b>a>0,$$
  $F(s,x)=F(s,-x),$  and  $\int_0^\infty\int_{-\infty}^\infty F(s,y)dyds=1.$  (E7)  $\int_0^\infty\int_{-\infty}^\infty F(s,y)e^{\lambda(y-cs)}dyds<\infty$  for all  $c\geq 0$  and  $\lambda\geq 0.$ 

E7) 
$$\int_0^\infty \int_{-\infty}^\infty F(s,y)e^{\lambda(y-cs)}dyds < \infty$$
 for all  $c \ge 0$  and  $\lambda \ge 0$ .

equation with finite time delay  $\tau$ : Let  $\tau > 0$  be a parameter. Consider the following reaction-diffusion

$$\frac{\partial u}{\partial t}(t,x) = d\Delta u(t,x) - au(t,x) + b[1 - u(t,x)]$$
$$\int_0^\tau \int_{-\infty}^\infty F(s,x-y)u(t-s,y)dyds. \tag{4.6}$$

spreading speed  $c_{\tau}^{*}$ , which is also the minimal wave speed for monotone traveling waves of (4.6) By the theory in Section 3, we can shown that system (4.6) admits a

For  $c \ge 0$  and  $\lambda \ge 0$ , define

$$P(c,\lambda) = d\lambda^2 - c\lambda - a + b \int_0^\infty \int_{-\infty}^\infty F(s,y)e^{\lambda(y-cs)}dyds.$$

It follows that there exists a unique positive solution  $(c^*, \lambda^*)$  to the system

$$P(c, \lambda) = 0,$$
  $\frac{\partial P}{\partial \lambda}(c, \lambda) = 0.$ 

By the comparison method and the results for integral equations in [133] we can further prove that  $\lim_{\tau \to \infty} c_{\tau}^* = c^*$ .

**Theorem 4.5.** ([159, Theorems 2.1 and 3.1]) Assume that (E6) and (E7) hold and let  $c^*$  be defined as above. Then  $c^*$  is the spreading speed for solutions of (4.5) with initial functions having compact supports. Moreover,  $c^*$  is also the minimal wave speed for monotone traveling waves of (4.5).

The finite delay approximations approach was also used in [33] to study the spreading speed and traveling waves for a nonlocal and time-delayed reaction-diffusion population model with age structure.

## 4.5. A nonlocal and periodic model with dispersal

Consider a periodic integro-differential equation

$$\frac{\partial u(t,x)}{\partial t} = F(t,u(t,x)) + a(t) \int_{\mathbb{R}} k(x-y)u(t,y)dy, \tag{4.7}$$

where u(t,x) is the spatial density of a population at the point  $x \in \mathbb{R}$  at time  $t \geq 0$ , F(t,u(t,x)) is the reaction function which governs the population dynamics such as birth and death, and other removal terms such as emigration of individuals at the point  $x \in \mathbb{R}$  at time  $t \geq 0$ ,  $a(t) \geq 0$  is the rate at which an individual leaves its current location at time  $t \geq 0$ , k(x,y) is the dispersal kernel that describes the probability that an individual moves from point y to point x. Moreover, two continuous functions F and a are  $\omega$ -periodic in t for some  $\omega > 0$ , and  $a(t) \not\equiv 0$ .

For simplicity, we neglect the birth and death of the population during the dispersal process and assume that k(x, y) depends only on the distance between x and y, and then write it as k(x - y). Assume that

- (E8) F(t,u) = ug(t,u) with  $g \in C(\mathbb{R}^2_+, \mathbb{R})$  and  $g_u(t,u) < 0$ ,  $\forall (t,u) \in \mathbb{R}^2_+$ ,  $\int_0^\omega (g(t,0) + a(t))dt > 0$ , and there exist  $\hat{u} > 0$  and L > 0 such that  $g(t,\hat{u}) + a(t) \le 0$ ,  $\forall t \ge 0$ , and  $|F(t,u_1) F(t,u_2)| \le L|u_1 u_2|$ ,  $\forall t \ge 0$ ,  $u_1, u_2 \in W := [0,\hat{u}]$ .
- (E9)  $k(y) \ge 0$ , k(-y) = k(y),  $\int_{\mathbb{R}} k(y)dy = 1$ , and the integral  $\int_{\mathbb{R}} k(y)e^{\alpha y}dy$  converges for all  $\alpha \in [0, \Delta)$ , where  $\Delta > 0$  is the abscissa of convergence and it may be infinity.

It is easy to show that the spatially homogeneous system

$$\frac{du(t)}{dt} = F(t, u(t)) + a(t)u(t) \tag{4.8}$$

has a positive  $\omega$ -periodic solution  $u^*(t)$ , which is globally asymptotically stable in  $[0, \hat{u}] \setminus \{0\}$ .

)efine

$$A(\alpha,t) := g(t,0) + a(t) \int_{\mathbb{R}} k(y)e^{\alpha y} dy$$

and

$$\Phi(lpha) := rac{\int_0^\omega A(lpha,s)ds}{lpha}, \quad orall lpha \in (0,\Delta).$$

**Theorem 4.6.** ([60, Theorem 3.1]) Assume that (E8) and (E9) hold and let  $c^* = \frac{\inf_{0 \le \alpha \le \Delta} \Phi(\alpha)}{\omega}$ . Let  $u(t, x, \varphi)$  be the solution of (4.7) with  $u(0, \cdot, \varphi) = \varphi \in \mathcal{C}_{\mathbf{u}^*(0)} := C(\mathbb{R}, [0, u^*(0)])$ . Then the following statements are valid:

- (i) For any  $c > c^*$ , if  $\varphi \in C_{u^*(0)}$  with  $\varphi(x) = 0$  for x outside a bounded interval, then  $\lim_{t\to\infty,|x|\geq ct} u(t,x,\varphi) = 0$ .
- (ii) For any  $0 < c < c^*$ , there is a positive number r such that if  $\varphi \in C_{u^*(0)}$  with  $\varphi(x) > 0$  for x on an interval of length 2r, then  $\lim_{t\to\infty,|x|\leq ct} (u(t,x,\varphi)-u^*(t))=0$ .
- (iii) In the case where a(t) > 0,  $\forall t \in \mathbb{R}$ , for any  $c \in (0, c^*)$ , if  $\varphi \in \mathcal{C}_{u^*(0)}$  with  $\varphi \not\equiv 0$ , then  $\lim_{t \to \infty, |x| \le ct} (u(t, x; \varphi) u^*(t)) = 0$ .

Recall that u(t,x)=U(t,x+ct) is an  $\omega$ -periodic traveling wave of (4.7) connecting 0 to  $u^*(t)$  if it is a solution of (4.7),  $U(t,\xi)$  is  $\omega$ -periodic in t, and  $U(t,-\infty)=0$  and  $U(t,\infty)=u^*(t)$  uniformly for  $t\in[0,\omega]$ .

**Theorem 4.7.** ([60, Theorem 4.1]) Assume that (E8) and (E9) hold. Let  $c^*$  be as defined in Theorem 4.6. Then for any  $c \in (0, c^*)$ , system (4.7) admits no  $\omega$ -periodic traveling wave solution  $\phi(t, x + ct)$  connecting 0 and  $u^*(t)$ .

It is reasonable to expect that (4.7) has periodic traveling waves with the wave speed  $c \ge c^*$ , that is, the above  $c^*$  is also the minimal wave speed for the monotone periodic traveling waves. Note that we can not use the afore-mentioned general theory to obtain the existence of periodic traveling waves since the solution maps associated with (4.7) are not compact with respect to the compact open topology. However, we have an affirmative

upper and lower solutions answer to this problem in the autonomous case of (4.7) by the method of

(E8)' F(0) = 0, F''(0) exists, F'(0) + a > 0 and there is  $u^* > 0$  such that  $u^*$  is the unique positive zero of the function F(u) + au in  $[0, u^*]$ , Fis Lipschitz continuous on  $W:=[0,u^*]$  with the Lipschitz constant L>0, and that  $F(u)\leq F'(0)u$  for all  $u\in [0,u^*].$ 

 $u^*$  such that  $\phi(s)$  is continuous and nondecreasing in  $s \in \mathbb{R}$ . for any  $c \geq c^*$ , system (4.7) has a traveling wave  $\phi(x+ct)$  connecting 0 to assume that (E8)' and (E9) Hold. Let  $c^*$  be defined in Theorem 4.6. Then Theorem 4.8. ([60, Theorem 4.2]) Let F(t,u) = F(u), a(t) = a, and

odic semiflows was also used in [61] to analyse a non-local periodic reactiondiffusion model with stage-structure. The theory of spreading speeds and traveling waves for monotone peri-

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