

## SOME RECENT DEVELOPMENTS ON LINEAR DETERMINACY

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**ABSTRACT.** The process of invasion is fundamental to the study of the dynamics of ecological and epidemiological systems. Quantitatively, a crucial measure of species' invasiveness is given by the rate at which it spreads into new open environments. The so-called "linear determinacy" conjecture equates full nonlinear model spread rates with the spread rates computed from linearized systems with the linearization carried out around the leading edge of the invasion. A survey that accounts for recent developments in the identification of conditions under which linear determinacy gives the "right" answer, particularly in the context of non-compact and non-cooperative systems, is the thrust of this contribution. Novel results that extend some of the research linked to some the contributions covered in this survey are also discussed.

**1. Introduction.** The need for macroscopic descriptions that capture the dynamics and behavior of heterogeneous large ensembles of individuals subject to ecological forces like dispersal provides challenges and opportunities for mathematical and biological scientists – particularly at a time when agent-based or individually-based models of single and interacting populations are systematically used by social scientists like Epstein[11, 12] and epidemiologists like [13], Ferguson et al. [16, 17],

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Germann et al. [19], and Longini et al. [38]; a fertile area full of *computational and mathematical* challenges, some taken on impressively by Ioannis G. Kevrekidis and collaborators ([36, 37]). Over the past century, particular attention has been placed on the study of the role played by dispersal in shaping plant communities, understanding and quantifying biological invasions, carrying out systematic efforts to quantify and mitigate the spread of infectious disease, disentangling the dynamics of marine open-ocean and intertidal systems, and more. The work of pioneers like Aronson [3, 4], Fisher [15], Haderler [20, 21, 22], Kolmogorov [40], Levin [44], Okubo [45], Skellam [60], Slobodkin [35], Weinberger [73] and the extensions carried out subsequently by a cadre of *distinguished* mathematicians and theoreticians across the world have set not only the foundation of an important and fertile area of interdisciplinary research (ecology, epidemiology, mathematics, and evolutionary biology) but in the process it has inspired novel mathematical research, re-energized by unsolved questions coming from emerging fields that include urban ecology, sustainability and the co-evolving dynamics of socio-biological systems [8] [43] [64].

Early models (theoretical-empirical studies) for the dynamics of invasive species include the models of Fisher [15], Skellam [60] and others (for extensive review see the works of Hengeveld [26]; Andow et al. [1, 2]; Okubo [45], Okubo and Levin [56]). The mathematical analysis of these nonlinear systems, in particular, establishing the existence of traveling waves of partial differential equations and of the convergence of initial data to wave solutions has been a fruitful area of mathematical research for nearly a century. The traveling wave speed, interpreted biologically as the rate of spread of the introduced population, has successfully predicted spread rates of some introduced species, but has failed dramatically with others. Ingredients generally missing in these early models include: rare, long-distance dispersal events which cannot be captured by classical diffusion, age- and stage-structured population dynamics, interspecific interactions, and nonlinear stochastic effects. It is possible to include such ingredients in systems of coupled systems of integral-based equations, integro-difference (discrete-time, continuous space) equations. The study of integro-difference systems of nonlinear equations has often focused on the derivation of the speed of invasion, a result that makes explicit use of the *linear conjecture*, that is, it computes it from the appropriate linearization. The linear conjecture is believed to hold under some “restrictions” (no Allee effects etc) at low population densities. There are mathematical results of situations when the linear conjecture is not true. Hence, it is not surprising to see efforts to identify sufficient conditions guaranteeing the validity of the linear conjecture.

Haderler and Rothe [20] showed that linear determinacy can be violated in certain cases; the linear conjecture is not always true. Hosono [34] only showed numerically that the linear determinacy may not be true for the Lotka-Volterra competition model. W. Huang and M. Han [32] showed analytically the linear determinacy does not hold for some range of parameters. Thus the blind application of the formula in this case can fail to predict the spreading speed of the nonlinear competition system. The studies in Weinberger [73] and Lui [57] expanded the mathematical foundation for the theory of spreading speeds and traveling waves, through their analysis of traveling waves via the convergence of initial data to wave solutions, in the context of *cooperative* operators. Recently, Weinberger, Lewis and Li made additional contributions [71, 46, 50, 72]. The pervasiveness of overcompensation in biological systems implies that biological models are in general non-monotone. The

incorporation of biological forces tied in to overcompensation leads to models with not fully understood dynamics [41].

This survey reports recent developments about linear determinacy in the studies of biological invasion models, in particular, for noncompact and non-cooperative systems. These results will help identify conditions that guarantee the validity of the linear conjecture while increasing our understanding as to why the traveling wave speed can predict the speed of biological invasions. Results of this type provide detailed understanding of the process of invasion, including the spatial spread of disease while demanding that researchers develop new methods to predict the response of, for example, vegetation to climate change, or the spread of weed species through ecosystems, or the identification of effective spatial-explicit biocontrol pest-species control methods.

## 2. Minimum speeds for monotone systems.

**2.1. Single-species models.** Studies on population spread can be traced back to R. A. Fisher [15], who investigated the spatial spread of advantageous genes in a population. Fisher considered the model

$$u_t = du_{xx} + ru\left(1 - \frac{u}{K}\right), \quad (1)$$

where  $u(x, t)$  represents the population density at location  $x$  and time  $t$ ,  $r$  is the intrinsic rate of population increase,  $K$  is the environmental carrying capacity, and  $d$  is the diffusion coefficient. Fisher showed that (1) has a traveling wave solution of the form  $w(x - ct)$  if and only if  $c \geq c^*$  with  $c^* = 2\sqrt{dr}$ . Kolmogorov, Petrowski, and Piscounov [40] proved that the spreading speed for

$$u_t = du_{xx} + f(u) \quad (2)$$

is

$$c^* = 2\sqrt{f'(0)d} \quad (3)$$

if  $f(0) = f(1) = 0$ ,  $f(u) > 0$  for  $0 < u < 1$ ,  $f(u) \leq f'(0)u$  (also see Okubo and Levin [56]). Model (2) contains (1) as a special case. The spreading speed is the asymptotic rate at which a species initially concentrated in a finite region, will expand its spatial range. A traveling wave solution describes the propagation of a species as a wave with a fixed shape and a fixed speed. The spreading speeds and traveling wave solutions provide important insight into the spatial patterns and rates of invading species in space. The formulas for  $c^*$  given above indicate that the rate of spread is a linear function of time and that it can be predicted quantitatively as a function of measurable life history parameters.

However, it has been observed that *empirically* measured rates of dispersal when combined with Model (2) do not accurately predict the rates of range expansion in invasions (Hastings et al. [25]). The inability of the model to explain the data is usually justified or explained away as the kind of discrepancies generated by the inability of the model to capture the effect of rare long-distance dispersal events. Model (2) allows for diffusive movement, and in fact, it assumes that the distribution of dispersal distances is normal. Model (2) ignores the role of population structure, including age structure while assuming that reproduction and movement occur randomly over the lifetime of an individual, conditions, that of course, are rarely met by populations. In fact, there are a wide variety of measured distributions, peaking around their mode, with fatter tails than a normal distribution and the same variance.

Evidence that integro-difference equations can effectively model biological dispersal processes has been well documented ( see Kot [41], Hastings et al. [25] and references therein). For a single population composed of identical individuals, all distributed along an infinite one-dimensional habitat, the process of dispersal, using re-distribution kernels can be modeled by

$$u_{n+1} = Q[u_n] \quad (4)$$

where  $Q$  is an operator on a set of functions on a habitat with  $u_n$  representing the population density at time  $n$ . A very useful operator is

$$Q[u_n] = \int_{-\infty}^{\infty} k(x-y)g(u_n(y))dy \quad (5)$$

where the change of population density from  $u_n$  from  $n$  to  $n+1$  is reflected in two sub-processes: growth  $g$  and dispersal [via a kernel  $k(x-y)$ ]. It is assumed that the probability of moving from point  $y$  to point  $x$  depends only on the relative locations of the two points. Under a monotonicity (local dynamics) and additional assumptions, it is shown (e.g. Weinberger [3, 4], Weinberger and Zhao [77] ) that the spreading speed of (4) with  $Q$  given by (5) is

$$c^* = \min_{\mu > 0} \frac{1}{\mu} \ln(f'(0) \int_{-\infty}^{\infty} k(s)e^{\mu s} ds). \quad (6)$$

Diekmann [9] and Weinberger [73] showed that  $c^*$  given by (3) also represents the slowest speed of a class of traveling wave solutions.

There are a number of advantages that integro-difference equations have over reaction-diffusion equations. Integro-difference equations can handle an extremely wide variety of dispersal distributions and support traveling wave solutions similar to those arising from reaction-diffusion equations. Further more, integro-difference equations can also give rise to accelerating invasions ([68]).

$c^*$  given in (3) and (6) are determined by the intrinsic growth rate, a linearization parameter, and the diffusion coefficient or dispersal kernel. The right-hand sides of (3) and (6) also represent the spreading speed of the linearized system about zero. Consequently, the nonlinear model is linearly determinant, i.e., the spreading speed of the nonlinear system equals that of the linearized system. For some detailed discussions on linear determinacy, see, e.g., van den Bosch, Metz and Diekmann [59], Mollison [39], Liang and Zhao [54].

**2.2. Multi-species systems.** Most models of interest in population ecology involve the interactions of multiple species. The dynamics of multi-species can be described by the abstract recursion

$$\mathbf{u}_{n+1}(x) = Q[\mathbf{u}_n](x), \quad n = 0, 1, 2, \dots \quad (7)$$

Here  $\mathbf{u}_n(x) = (u^1(x), u^2(x), \dots, u^m(x))$ .  $Q$  is an operator which takes a set of bounded continuous nonnegative  $m$ -vector-valued functions of one variable into itself. We define  $\mathbf{u} \geq \mathbf{v}$  to mean that  $u_i(x) \geq v_i(x)$  for all  $i$  and  $x$ , and  $\mathbf{u} \gg \mathbf{v}$  to mean that  $u_i(x) > v_i(x)$  for all  $i$  and  $x$ . We use  $|\cdot|$  to denote the Euclidean norm. We use the notation  $\mathbf{0}$  for the constant vector all of whose components are 0. For any constant vector  $\boldsymbol{\alpha} \gg \mathbf{0}$  we define

$$\mathcal{C}_{\boldsymbol{\alpha}} := \{\mathbf{u} : \mathbf{u}(x) \text{ is continuous, and } \mathbf{0} \leq \mathbf{u}(x) \leq \boldsymbol{\alpha} \text{ for all } x\}.$$

The linear operator  $M$  is said to be the **linearization** (or Fréchet derivative) of  $Q$  at  $\mathbf{0}$  if for any  $\epsilon > 0$  there is a  $\delta > 0$  such that  $\|\mathbf{u}\| \leq \delta$  implies that  $\|Q[\mathbf{u}] - M[\mathbf{u}]\| \leq \epsilon\|\mathbf{u}\|$ .

We define the translation and reflection operators

$$T_y[\mathbf{v}](x) := \mathbf{v}(x - y), \quad R[\mathbf{v}](x) := \mathbf{v}(-x).$$

We assume that  $Q$  is translation invariant in the sense that  $Q[T_y[\mathbf{v}]] = T_y[Q[\mathbf{v}]]$  for all  $\mathbf{v}$  and  $y$  and reflection invariant in the sense that  $Q[R[\mathbf{v}]] = R[Q[\mathbf{v}]]$  for all  $\mathbf{v}$ .  $M$  has the representation

$$(M[\mathbf{v}](x))_i = \sum_{j=1}^k \int_{-\infty}^{\infty} \mathbf{v}_j(x - y) m_{ij}(dy), \tag{8}$$

where each  $m_{ij}$  is a symmetric nonnegative measure such that  $m_{ij}((-\infty, \infty))$  is finite. It is useful to introduce the  $m \times m$  matrix of two-sided Laplace transforms

$$B_\mu = \left( \int_{-\infty}^{\infty} e^{\mu y} m_{ij}(dy) \right).$$

Note that  $M[\boldsymbol{\alpha}e^{-\mu x}]|_{x=0} = B_\mu \boldsymbol{\alpha}$  for every constant vector  $\boldsymbol{\alpha}$ . For the sake of simplicity, we shall assume that the entries of  $B_\mu$  are finite for all  $\mu$ . By reordering the coordinates, one can put  $B_\mu$  into a block lower triangular form, the so-called Frobenius form with diagonal block matrices irreducible. Let  $\lambda_\sigma(\mu)$  denote the principal eigenvalue of the  $\sigma$ th diagonal block from the top of  $B_\mu$ . In what follows we use  $\boldsymbol{\xi}(\mu)$  to denote an eigenvector of  $B_\mu$  that corresponds to  $\lambda_1(\mu)$ . Define

$$\bar{c}_1 = \inf_{\mu > 0} \phi(\mu) \tag{9}$$

where  $\phi(\mu) := (1/\mu) \ln \lambda_1(\mu)$ . This represents a spreading speed of the linearized system for (7).

We assume that  $Q$  is cooperative, i.e.,  $Q[\mathbf{u}] \geq Q[\mathbf{v}]$  for  $\mathbf{u} \geq \mathbf{v} \geq \mathbf{0}$ . Lui [57] proved that if  $Q$  has only two equilibria, then (7) has a spreading speed  $c^*$ . He also showed that  $c^* = \bar{c}_1$  under the condition

$$Q[\mathbf{u}] \leq M[\mathbf{u}]$$

for  $\mathbf{u} \in \mathcal{C}_\beta$ . This condition guarantees (7) to be linearly determinat.

Weinberger, Lewis and Li considered (7) for the case where the system is allowed to have three or more equilibria [71, 46, 50, 72]. Their results show that, in general, recursion (7) has a fastest spreading speed  $c_f^*$  and a slowest spreading speed  $c^*$ , and  $c_f^* = c^*$  if there are only two equilibria.

**Hypotheses 2.1.**

- i.  $Q[\mathbf{0}] = \mathbf{0}$ , and there is a constant vector  $\boldsymbol{\beta} \gg \mathbf{0}$  such that  $Q[\boldsymbol{\beta}] = \boldsymbol{\beta}$ , which is minimal in the sense there is no  $\boldsymbol{\nu} \neq \boldsymbol{\beta}$  such that  $Q[\boldsymbol{\nu}] = \boldsymbol{\nu}$  and  $\mathbf{0} \ll \boldsymbol{\nu} \leq \boldsymbol{\beta}$ .
- ii.  $Q$  is order-preserving on nonnegative functions; i.e., if  $\mathbf{u} \geq \mathbf{v} \geq \mathbf{0}$ , then  $Q[\mathbf{u}] \geq Q[\mathbf{v}] \geq \mathbf{0}$ .
- iii.  $Q$  is translation invariant and reflection invariant; i.e.,  $Q[T_y[\mathbf{v}]] = T_y[Q[\mathbf{v}]]$  and  $Q[R_y[\mathbf{v}]] = R_y[Q[\mathbf{v}]]$  for all  $y$ .
- iv.  $Q$  is continuous in the topology of uniform convergence on bounded sets; i.e., if the uniformly bounded sequence  $\mathbf{v}_n(x)$  converges to  $\mathbf{v}(x)$ , uniformly on every bounded set, then  $Q[\mathbf{v}_n]$  converges to  $Q[\mathbf{v}]$ , uniformly on every bounded set.
- v.
  - a.  $\lambda_1(0) > 1$ ;
  - b.  $\lambda_1(0) > \lambda_\sigma(0)$  for every  $\sigma > 1$ ;

- c.  $B_0$  has at least one nonzero entry to the left of each of its diagonal blocks other than the uppermost one.
- vi. Let the infimum in (9) be attained at  $\bar{\mu} \in (0, \infty]$ . Either
  - (a)  $\bar{\mu}$  is finite,
 
$$\lambda_1(\bar{\mu}) > \lambda_\sigma(\bar{\mu}) \text{ for all } \sigma > 1,$$
 and
 
$$Q[e^{-\bar{\mu}x} \xi(\bar{\mu})] \leq M[e^{-\bar{\mu}x} \xi(\bar{\mu})];$$
 or
  - (b) there is a sequence  $\mu_\nu \nearrow \bar{\mu}$  such that for each  $\nu$ 

$$\lambda_1(\mu_\nu) > \lambda_\sigma(\mu_\nu) \text{ for all } \sigma > 1$$
 and
 
$$Q[e^{-\mu_\nu x} \zeta(\mu_\nu)] \leq M[e^{-\mu_\nu x} \zeta(\mu_\nu)].$$
- vii. There is a family  $M^{(\kappa)}$  of bounded linear order preserving operators on  $k$ -vector-valued functions with the properties that
  - a. for every sufficiently large positive integer  $\kappa$  there is a constant vector  $\omega \gg 0$  such that

$$Q[\mathbf{v}] \geq M^{(\kappa)}[\mathbf{v}] \quad \text{when } \mathbf{0} \leq \mathbf{v} \leq \omega.$$

- b. For every  $\mu > 0$  the matrices  $B_\mu^{(\kappa)}$  defined by  $B_\mu^{(\kappa)} \alpha := M^{(\kappa)}[e^{-\mu x} \alpha]_{x=0}$  converge to  $B_\mu$  as  $\kappa \rightarrow \infty$ .

Observe that under Hypotheses 2.1, if  $\lambda_1(\mu) > \lambda_\sigma(\mu)$  for  $\sigma \geq 2$ , then  $\xi(\mu) \gg \mathbf{0}$ .

**Theorem 2.1.** (Weinberger, Lewis and Li [71] [Lemma 2.2, Theorem 3.1]) Assume that Hypotheses 2.1 are satisfied. Then  $\bar{c}_1$  is the spreading speed of (7) in the following sense:

- (i) For any  $\mathbf{u}_0 \in \mathcal{C}_\beta$  with compact support and  $0 \leq u_0 \ll \beta$ , the solution  $\mathbf{u}_n(x)$  of (7) satisfies

$$\lim_{n \rightarrow \infty} \sup_{|x| \geq nc} \mathbf{u}_n(x) = \mathbf{0}, \text{ for } c > c^*$$

- (ii) For any strictly positive vector  $\omega \in \mathbb{R}^N$ , there is a positive  $R_\omega$  with the property that if  $\mathbf{u}_0 \in \mathcal{C}_\beta$  and  $\mathbf{u}_0 \geq \omega$  on an interval of length  $2R_\omega$ , then the solution  $\mathbf{u}_n(x)$  of (7) satisfies

$$\lim_{n \rightarrow \infty} \inf_{|x| \leq nc} \mathbf{u}_n(x) = \beta, \text{ for } 0 < c < c^*$$

This theorem shows that Hypotheses 2.1 are sufficient for (7) to be linearly determinant. It can be directly applied to multi-species integro-difference model (14).

We now consider multi-species reaction-diffusion systems

$$\frac{\partial \mathbf{u}}{\partial t} = D \frac{\partial^2 \mathbf{u}}{\partial x^2} + \mathbf{f}(\mathbf{u}), \tag{10}$$

where  $D = \text{diag}(d_1, \dots, d_m)$  with  $d_i \geq 0$  for all  $i$ , and  $\mathbf{f}(\mathbf{u}) = (f_1(\mathbf{u}), \dots, f_m(\mathbf{u}))$ . Under appropriate assumptions the linearization  $M$  at  $\mathbf{0}$  of the time 1 map  $Q_1$  for (10) can be explicitly found, and  $B_\mu$  associated with  $M$  is given by

$$B_\mu = \exp[C_\mu], \tag{11}$$

where

$$C_\mu = \text{diag}(d_i \mu^2) + \mathbf{f}'(\mathbf{0}).$$

It is easily seen that  $\lambda_\sigma(\mu) = e^{\gamma_\sigma(\mu)}$  where  $\gamma_\sigma$  is the principal eigenvalue of the  $\sigma$ th diagonal block of the matrix  $C_\mu$ .

**Hypotheses 2.2.**

- i.  $\mathbf{f}(\mathbf{0}) = \mathbf{0}$ , and there is a  $\beta \gg \mathbf{0}$  such that  $\mathbf{f}(\beta) = \mathbf{0}$  which is minimal in the sense that there are no  $\nu$  other than  $\mathbf{0}$  and  $\beta$  such that  $f(\nu) = \mathbf{0}$  and  $\mathbf{0} \ll \nu \leq \beta$ .
- ii. The system (10) is cooperative; i.e.,  $f_i(\alpha)$  is nondecreasing in all components of  $\alpha$  with the possible exception of the  $i$ th one.
- iii.  $\mathbf{f}$  does not depend explicitly on either  $x$  or  $t$ , and the coefficients  $d_i$  are constant and nonnegative.
- iv.  $\mathbf{f}(\alpha)$  is continuous, piecewise continuously differentiable in  $\alpha$  for  $\mathbf{0} \leq \alpha \leq \beta$  and differentiable at  $\mathbf{0}$ .
- v. The Jacobian matrix  $\mathbf{f}'(\mathbf{0})$  is in Frobenius form. The principal eigenvalue  $\gamma_1(0)$  of its upper left diagonal block is positive and strictly larger than the principal eigenvalues  $\gamma_\sigma(0)$  of its other diagonal blocks, and there is at least one nonzero entry to the left of each diagonal block other than the first one.
- vi. Either
  - (a)  $\bar{\mu}$  is finite,

$$\gamma_1(\bar{\mu}) > \gamma_\sigma(\bar{\mu}) \text{ for all } \sigma > 1,$$

and

$$\mathbf{f}(\rho\zeta(\bar{\mu})) \leq \rho\mathbf{f}'(0)\zeta(\bar{\mu})$$

for all positive  $\rho$ ;

or

- (b) There is a sequence  $\mu_\nu \nearrow \bar{\mu}$  such that for each  $\nu$  the inequalities (2.2) and (2.2) with  $\bar{\mu}$  replaced by  $\mu_\nu$  are valid.

Define

$$\bar{c}_1 := \inf_{\mu > 0} \gamma_1(\mu)/\mu. \tag{12}$$

**Theorem 2.2.** (Weinberger, Lewis and Li [71] [Theorem 4.2]) Assume that Hypotheses 2.2 are satisfied. Then  $\bar{c}_1$  given by (12) is the spreading speed of (10) in the following sense:

- (i) For any  $\mathbf{u}(0, x) \in \mathcal{C}_\beta$  with compact support and  $0 \leq u_0 \ll \beta$ , the solution  $\mathbf{u}(t, x)$  of (10) satisfies

$$\lim_{t \rightarrow \infty} \sup_{|x| \geq ct} \mathbf{u}(t, x) = \mathbf{0}, \text{ for } c > c^*$$

- (ii) For any strictly positive vector  $\omega \in \mathbb{R}^N$ , there is a positive  $R_\omega$  with the property that if  $\mathbf{u}(0, x) \in \mathcal{C}_\beta$  and  $\mathbf{u}(0, x) \geq \omega$  on an interval of length  $2R_\omega$ , then the solution  $\mathbf{u}(t, x)$  of (10) satisfies

$$\liminf_{t \rightarrow \infty} \inf_{|x| \leq ct} \mathbf{u}(t, x) = \beta, \text{ for } 0 < c < c^*$$

**2.3. Traveling wave solutions in noncompact systems.** The existence of traveling wave solutions for (7) with three or more equilibria were established in Li et al. [71] and Li and Zhang [49]. It was showed that the spreading speeds can be related to speeds of traveling wave solutions, and particularly  $c^*$  can be characterized as the slowest speed of a class of traveling wave solutions connecting  $\beta$  with an equilibrium other than  $\beta$ . The proofs given in these papers critically depend on

the assumption that  $Q$  is compact with respect to the topology of uniform convergence on bounded intervals. For the reaction-diffusion system (10), compactness is guaranteed by the assumption that  $d_i > 0$  for all  $i$ . However, there are many biological reaction-diffusion models where at least one diffusion coefficient is zero; see for example Lewis and Schmitz [47], Haderer and Lewis [23], and Capasso and Maddalena [7].

Li [48] proved the existence of traveling wave solutions for a system with advection terms that is more general than (10). His results show that if Hypotheses 2.2 are satisfied, then  $\bar{c}_1$  can be characterized as a slowest speed of class of traveling wave solutions.

**Theorem 2.3.** (Li [48]) [Theorem 5.1] *Assume that Hypotheses 2.2 are satisfied and  $d_i = 0$  for at least one  $i$ . Let  $\bar{c}_1$  be given by (12). Then for  $c > \bar{c}_1$ , system (10) has a monotone traveling wave solution  $\mathbf{w}(x - ct)$  connecting  $\mathbf{0}$  with  $\beta$ , and such a traveling wave solution does not exist if  $c < \bar{c}_1$ .*

In [48] an example is provided, which shows that system (10) with  $d_i = 0$  for some  $i$  can have no traveling wave solution with speed  $\bar{c}_1$  connecting  $\mathbf{0}$  with  $\beta$ .

We next consider the existence of traveling wave solutions for recursion (7) where  $Q$  is allowed to be non-compact.

vi'. Let the infimum in (9) be attained at  $\bar{\mu} \in (0, \infty]$ . For  $0 < \mu < \bar{\mu}$ ,  $\lambda_1(\bar{\mu}) > \lambda_\sigma(\mu)$  for all  $\sigma > 1$ , and

$$Q[e^{-\mu x} \xi(\mu)] \leq M[e^{-\mu x} \xi(\mu)].$$

This Hypothesis is stronger than Hypotheses 2.1. vi.

**Theorem 2.4.** *Assume that Hypotheses 2.1 are satisfied with Hypotheses 2.1. vi replaced by (vi'). Furthermore assume that*

- (a)  $Q[\mathbf{u}]$  is well defined for any nonincreasing function  $\mathbf{u}$  with  $\mathbf{0} \leq \mathbf{u} \leq \beta$ , and if the monotone sequence of nonincreasing functions  $\mathbf{u}_n(x)$  with  $\mathbf{0} \leq \mathbf{u}_n(x) \leq \beta$  converges to  $\mathbf{u}(x)$  point-wise, then  $Q[\mathbf{u}_n](x)$  converges to  $Q[\mathbf{u}](x)$  point-wise.
- (b) There exist  $\varepsilon > 0$ ,  $\delta > 0$ , and  $\sigma > 0$  such that for  $0 \leq |\mathbf{u}| < \varepsilon$

$$Q[\mathbf{u}] \geq M[\mathbf{u} - \delta|\mathbf{u}|^\sigma \mathbf{u}] - \delta|\mathbf{u}|^\sigma \mathbf{u}.$$

Then for  $c > \bar{c}_1$  with  $\bar{c}_1$  given by (9), system (7) has a monotone traveling wave solution  $\mathbf{w}(x - ct)$  connecting  $\mathbf{0}$  with  $\beta$ , and such a traveling wave solution does not exist if  $c < \bar{c}_1$ .

*Proof.* Let  $\phi(\mu) = (1/\mu) \ln \lambda_1(\mu)$ . The results from Lui [57] show that  $\ln \lambda_1(\mu)$  is convex, and  $\phi(\mu)$  has no local maximum at a positive number. We use  $\bar{\mu}$  to denote an extended positive real number at which the infimum in (9) is attained. Note that it is possible  $\bar{\mu} = \infty$ .  $\phi(\mu)$  is nonincreasing in the interval  $(0, \bar{\mu})$ . Choose  $c > \bar{c}_1$ . Let  $\mu_c$  denote the largest root of  $\lambda_1(\mu) = c$ , which is less than  $\bar{\mu}$ .

Define  $\mathbf{w}^+(x) = \min\{e^{-\mu_c x} \xi(\mu_c), \beta\}$ . The hypothesis (vi') and the fact that  $Q[\beta] = \beta$  show that

$$Q[\mathbf{w}^+](x) \leq \mathbf{w}^+(x - c).$$

Define

$$\mathbf{v}(x) = \max\{\epsilon[e^{-\mu_c x} \xi(\mu_c) - e^{-sx} \xi(s)], \mathbf{0}\}$$

where  $\epsilon$  is a small positive number and  $\mu_c < s < \min\{\bar{\mu}, (1 + \sigma)\mu_c\}$ . Choose  $\xi(\mu_c) \leq \xi(s)$  so that  $e^{-\mu_c x} \xi(\mu_c) - e^{-sx} \xi(s) < \mathbf{0}$  for  $x \leq 0$ . The definition of  $\mu_c$  shows that  $\phi(s) < c$ . Let  $\xi(\mu) = \max\{\xi_1(\mu), \dots, \xi_m(\mu)\}$ , and  $\eta = \max\{[I +$



$B_{(1+\sigma)\mu_c}[\xi(\mu_c)]_i/(\xi(s))_i$ . By using the assumption (b) and the fact that  $\epsilon[e^{-\mu_c x}\xi(\mu_c) - e^{-sx}\xi(s)] \leq \mathbf{v}(x) \leq \epsilon e^{-\mu_c x}\xi(\mu_c)$  we have that

$$\begin{aligned} & Q[\mathbf{v}](x) \\ & \geq M[\mathbf{v} - \delta|\mathbf{v}|^\sigma \mathbf{v}](x) - \delta|\mathbf{v}(x)|^\sigma \mathbf{v}(x) \\ & \geq \epsilon[B_{\mu_c}\xi(\mu_c)e^{-\mu_c x} - B_s\xi(s)e^{-sx}] - \epsilon^{1+\sigma}\delta\bar{\xi}(\mu_c)e^{-(1+\sigma)\mu_c x}[I + B_{(1+\sigma)\mu_c}]\xi(\mu_c) \\ & = \epsilon[e^{-\mu_c(x-c)}\xi(\mu_c) - e^{-s(x-c)}\xi(s)] \\ & \quad - \epsilon\delta e^{-s(x-c)}\xi(s)\{1 - e^{-(c-\phi(s))} - \epsilon^\sigma\bar{\xi}(\mu_c)\eta e^{(s-(1+\sigma)\mu_c)x-sc}\}. \end{aligned}$$

It follows that for any real number  $\rho$ , if  $\epsilon$  is sufficiently small,  $Q[\mathbf{v}](x) \geq \mathbf{v}(x - c)$  for  $x \geq \rho$ . Since  $\mathbf{v}(x) \leq 0$  for  $x \leq 0$ , we have that for sufficiently small  $\epsilon$ ,  $Q[\mathbf{v}](x) \geq \mathbf{v}(x - c)$  for all  $x$ .

Define  $Q_c$  by  $Q_c[\mathbf{u}](x) = Q[\mathbf{u}](x + c)$ . Define

$$\mathbf{u}_0 = \mathbf{w}^+(x), \quad \mathbf{u}_{n+1} = Q_c[\mathbf{u}_n]. \tag{13}$$

Induction shows that  $\mathbf{u}_n(x)$  is nonincreasing in  $x$  and  $\mathbf{w}^+(x) \geq \mathbf{u}_n(x) \geq \mathbf{u}_{n+1}(x) \geq \mathbf{v}(x)$ . Let  $\mathbf{w}(x) = \lim_{n \rightarrow \infty} \mathbf{u}_n(x)$ . Using the assumption (a) and taking a limit in (13), we have  $\mathbf{w}(x) = Q_c[\mathbf{w}](x)$ .  $\mathbf{w}(x - nc)$  is a traveling wave solution of (7). Since  $\mathbf{u}_n(x)$  is nonincreasing in  $x$ ,  $\mathbf{w}$  is nonincreasing in  $x$ . Since  $\mathbf{w} \leq \mathbf{w}^+$ ,  $\mathbf{w}(\infty) = \mathbf{0}$ . Since  $\mathbf{v}(x) \gg \mathbf{0}$ ,  $\mathbf{w}(-\infty) \gg \mathbf{0}$ . Consider the sequence  $\mathbf{w}(x - n)$ . Using the assumption (a) and take the limit  $n \rightarrow \infty$  in  $\mathbf{w}(x - n) = Q[\mathbf{w}(\cdot - n)](x)$ , we find  $\mathbf{w}(-\infty) = Q[\mathbf{w}(-\infty)]$  so that  $\mathbf{w}(-\infty) = \beta$ . The proof is complete.  $\square$

This proof makes use of the iteration method involving lower and upper solutions to establish the existence of traveling wave solutions. This method has proven to be useful in establishing traveling wave solutions for population models; see Weinberger [74], Wu and Zou [78], Volkov and Lui [63], and Fang and Zhao [14].

This Theorem can be directly applied to integro-difference system (14) where at least one  $k_i$  is the Dirac Delta function.

**3. Minimum speeds for non-monotone system.** The existence of traveling wave solutions of scalar integro-difference equations with nonmonotone growth functions was studied by Hsu, Zhao [30], Li, Lewis and Weinberger [51], K.R. Rios-Soto, C. Castillo-Chavez, M. Neubert, E.S. Titi, and A-A Yakubu [61]. Wang [67] and Wang and Castillo-Chavez [66] studied traveling waves in nonmonotone reaction-diffusion systems and integro-difference equations. We shall give a brief review on results in Wang [67], Wang and Castillo-Chavez [66] and Wang, Wang and Wu [70].

**3.1. Integro-difference systems.** In this section, we consider the system of integro-difference equations

$$\mathbf{u}_{n+1} = Q[F(\mathbf{u}_n)]; \tag{14}$$

where  $\mathbf{u}_n = (u_n^i) \in \mathcal{C}_{\beta^+}$ ,  $F(\mathbf{u}) = (f_i(\mathbf{u}))$ ;

$$Q[F(\mathbf{u})] = (Q^i[F(\mathbf{u})]);$$

$$Q^i[F(\mathbf{u})](x) = \int_{\mathbb{R}} k_i(x - y)f_i(\mathbf{u}(y))dy;$$

$\mathbf{u}_n(x)$  is the density of individuals at point  $x$  and time/generation  $n$ ;  $F(\mathbf{u})$  is the density-dependent fecundity (local growth rate); and  $k_i(x - y)$  (dispersal kernel)

models the dispersal of the  $i$ th species. As noted before,  $k_i(x - y)$  can be viewed as a probability kernel since  $\int_{-\infty}^{\infty} k_i(x)dx = 1$ .

We make use of prior results, as is typical in mathematics, whenever possible of established results for *cooperative* systems ([71]). The existence of two additional monotone functions  $\mathbf{f}^{\pm}$  with the properties that the first lies above  $\mathbf{f}$  and the second below  $\mathbf{f}$  is required by our method of proof. The use of this approach is motivated by prior work on non-monotone equations [62, 30, 51, 76, 65]. Specifically, we observe that  $\mathbf{f}^{\pm}$  can be “constructed” via piecewise functions made up of “monotone pieces” of  $\mathbf{f}$  and the incorporation of appropriate constants. If  $\mathbf{f}$  happens to be monotone, then naturally  $\mathbf{f}^{\pm} = \mathbf{f}$ . We now make the following hypotheses for (14).

- (H1) For  $i = 1, \dots, N$ ,  $k_i(\tau) \geq 0$  is integrable on  $\mathbb{R}$ ,  $k_i(\tau) = k_i(-\tau)$ ,  $\tau \in \mathbb{R}$ , and  $\int_{\mathbb{R}} k_i(\tau)d\tau = 1$ ,  $\int_{\mathbb{R}} k_i(\tau)e^{\lambda\tau} d\tau < +\infty$ , for all  $\lambda > 0$ .
- (H2) (i) Let  $0 \ll \beta^- = (\beta_i^-) \leq \beta = (\beta_i) \leq \beta^+ = (\beta_i^+)$ . Assume that  $F : [0, \beta^+] \rightarrow [0, \beta^+]$  is a continuous, twice piecewise continuous differentiable function, and that there exist continuous, twice piecewise continuous differentiable functions  $F^{\pm} = (f_i^{\pm}) : [0, \beta^+] \rightarrow [0, \beta^+]$  such that for  $\mathbf{u} \in [0, \beta^+]$ ,

$$F^-(\mathbf{u}) \leq F(\mathbf{u}) \leq F^+(\mathbf{u}).$$

- (ii)  $F(0) = 0, F(\beta) = \beta$  and there is no other positive equilibrium of  $Q[F]$  between 0 and  $\beta$  (that is, there is no constant  $\mathbf{v} \neq \beta$  such that  $F(\mathbf{v}) = \mathbf{v}, 0 \ll \mathbf{v} \leq \beta$ ).  $F^{\pm}(0) = 0, F^{\pm}(\beta^{\pm}) = \beta^{\pm}$  and there is no other positive equilibrium of  $Q[F^{\pm}]$  between 0 and  $\beta^{\pm}$ .  $F$  has a finite number of equilibria in  $[0, \beta^+]$ .
  - (iii)  $F^{\pm}$  are nondecreasing functions on  $[0, \beta^+]$  and  $F^{\pm}(\mathbf{u})$  and  $F(\mathbf{u})$  have the same Jacobian at 0.
- (H3) (i) Assume that  $B_{\mu}$  is in Frobenius form and that the principal eigenvalue,  $\lambda(\mu)$ , of the first diagonal block is strictly larger than the principal eigenvalues of other diagonal blocks. Further, let's assume that  $B_{\mu}$  has a positive eigenvector  $\nu_{\mu} = (\nu_{\mu}^i) \gg 0$  corresponding to  $\lambda(\mu)$  with the additional requirement that  $\lambda(0) > 1$ .
- (ii) For each  $\mu > 0$  and  $\alpha > 0$ , we let  $\mathbf{v}^{\pm} = (\mathbf{v}_i^{\pm}) = (\min\{\beta_i^{\pm}, \nu_{\mu}^i \alpha\})$ , and assume that

$$F^{\pm}(\mathbf{v}^{\pm}) \leq B_0 \mathbf{v}^{\pm}.$$

- (iii) For every sufficiently large positive integer  $k$ , there is a small constant vector  $\omega = (\omega^i) \gg 0$  such that

$$F^{\pm}(\mathbf{u}) \geq (1 - \frac{1}{k})B_0 \mathbf{u}, \quad \mathbf{u} \in [0, \omega],$$

The following theorem summarizes the main results in Wang and Castillo-Chavez [66].

**Theorem 3.1.** *Assume (H1) – (H3) hold, then (14) is linearly determinant and the following statements are valid:*

- (i) *For any  $\mathbf{u}_0 \in \mathcal{C}_{\beta}$  with compact support and  $0 \leq \mathbf{u}_0 \ll \beta$ , the solution  $\mathbf{u}_n$  of (14) satisfies*

$$\lim_{n \rightarrow \infty} \sup_{|x| \geq nc} \mathbf{u}_n(x) = 0, \text{ for } c > c^*.$$

(ii) For any strictly positive vector  $\omega \in \mathbb{R}^N$ , there is a positive  $R_\omega$  with the property that if  $\mathbf{u}_0 \in \mathcal{C}_\beta$  and  $\mathbf{u}_0 \geq \omega$  on an interval of length  $2R_\omega$ , then the solution  $\mathbf{u}_n(x)$  of (14) satisfies

$$\beta^- \leq \liminf_{n \rightarrow \infty} \inf_{|x| \leq nc} \mathbf{u}_n(x) \leq \beta^+, \text{ for } 0 < c < c^*.$$

(iii) For each  $c > c^*$  (14) admits a traveling wave solution  $\mathbf{u}(\xi - cn) = (u^i(\xi - cn))$  such that  $0 \ll \mathbf{u}(\xi) \leq \beta^+, \xi \in \mathbb{R}$ ,

$$\beta^- \leq \liminf_{\xi \rightarrow -\infty} u(\xi) \leq \limsup_{\xi \rightarrow -\infty} u(\xi) \leq \beta^+$$

$\lim_{\xi \rightarrow \infty} \mathbf{u}(\xi) = 0$  and

$$\lim_{\xi \rightarrow \infty} \mathbf{u}(\xi)e^{\Lambda_c \xi} = \nu_{\Lambda_c}. \tag{15}$$

If, in addition,  $F$  is non-decreasing on  $\mathcal{C}_\beta$ , then  $\mathbf{u}$  is non-increasing on  $\mathbb{R}$ .

(iv) For  $c = c^*$  (14) admits a non-constant traveling wave solution  $\mathbf{u}(\xi - cn) = (u^i(\xi - cn))$  such that  $0 \leq \mathbf{u}(\xi) \leq \beta^+, \xi \in \mathbb{R}$ .

(v) For  $0 < c < c^*$  (14) does not admit a traveling wave solution  $\mathbf{u}_n(\xi) = \mathbf{u}(\xi - cn)$  such that  $\mathbf{u} \in \mathcal{C}_{\beta^+}$  with  $\liminf_{\xi \rightarrow -\infty} \mathbf{u}(\xi) \gg 0$  and  $\mathbf{u}(+\infty) = 0$ .

As an application, Theorem 3.1 was applied to a spatial interference-competition model. Its non-spatial version is the following system proposed by Hassell and Comins:

$$\begin{aligned} X_{n+1}(x) &= X_n(x)e^{r_1 - X_n(x) - \sigma_1 Y_n(x)} \\ Y_{n+1}(x) &= Y_n(x)e^{r_2 - Y_n(x) - \sigma_2 X_n(x)} \end{aligned} \tag{16}$$

where  $r_1, r_2, \sigma_1, \sigma_2$  are all positive constants. The possibility that individuals in the above two populations may disperse to different sites is modeled with a redistribution kernel  $k_i(y)$ . Hence, a discrete-time model, where individuals interact locally according to model (16), can be naturally formulated via a system of coupled nonlinear integro-difference equations. Hence, we have that

$$\begin{aligned} X_{n+1}(x) &= \int_{\mathbb{R}} k_1(x - y)X_n(y)e^{r_1 - X_n(y) - \sigma_1 Y_n(y)} dy \\ Y_{n+1}(x) &= \int_{\mathbb{R}} k_2(x - y)Y_n(y)e^{r_2 - Y_n(y) - \sigma_2 X_n(y)} dy \end{aligned} \tag{17}$$

where the dispersal of the  $i$ -species is modeled by a redistribution kernel  $k_i, i = 1, 2$  that depends just on the signed distance  $x - y$ , connecting the ‘‘birth’’  $y$  location and the ‘‘settlement’’ location  $x$ . In other words,  $k_i(y)$  is a homogenous ‘‘probability’’ kernel that satisfies  $\int_{-\infty}^{\infty} k_i(y)dy = 1$ . Here we simply state the following result for (17). Its proof can be found in [66].

**Theorem 3.2** (Wang and Castillo-Chavez [66]). *Let  $0 < r_2 < 1 < r_1, 0 < \sigma_1 < 1 < \sigma_2, \sigma_1\sigma_2 < 1$ , and*

$$r_2 < \sigma_2 e^{r_1 - 1 - e^{r_1 - 1}}$$

and

$$\sigma_1 r_2 < e^{r_1 - 1 - e^{r_1 - 1}}.$$

Assume that  $k_1, k_2$  satisfy (H1) and  $\int_{\mathbb{R}} k_1(s)e^{\mu s} ds \geq \int_{\mathbb{R}} k_2(s)e^{\mu s} ds$  for  $\mu > 0$ . Then (17) is linear-determinant and the conclusions of Theorem 3.1 hold for (17).

The biological interpretation of the conditions in Theorem 3.2 in the context of this application are straightforward. For an invasion to be successful, the overall dispersal of the invader (X) is relatively larger than the overall dispersal of the out-competed resident (Y). Further competition favors the invader whenever  $\sigma_1$  is sufficiently small (invader less affected by competition) and  $\sigma_2$  is sufficiently large (a relatively fragile resident, that is, the resident is more susceptible to interference competition). Under these conditions, there are traveling wave solutions of (17) “loosely” connecting its two boundary states  $(0, r_2)$  and  $(r_1, 0)$ . Here the term “loosely” means the traveling waves may oscillate around the equilibria since they are not necessarily monotone. For specific  $k_i$ , the exact value of  $c^*$  can be computed and compared to experimental data as it has been done by Kot, Lewis, others and their collaborators

**3.2. Reaction-diffusion systems.** In this section we review two results on the linear determinacy for non-cooperative reaction-diffusion systems. We begin with a result in Wang [67] where it is assumed that there are two cooperative systems

$$\mathbf{u}_t = D\mathbf{u}_{xx} + \mathbf{f}^+(\mathbf{u}) \text{ for } x \in \mathbb{R}, t \geq 0 \quad (18)$$

$$\mathbf{u}_t = D\mathbf{u}_{xx} + \mathbf{f}^-(\mathbf{u}) \text{ for } x \in \mathbb{R}, t \geq 0 \quad (19)$$

such that  $\mathbf{f}$  lies between  $\mathbf{f}^+$  and  $\mathbf{f}^-$ . It is assumed in [67] that Hypotheses 2.2 hold for  $\mathbf{f}^+(\mathbf{u}), \mathbf{f}^-(\mathbf{u}), \mathbf{f}(\mathbf{u})$  except that  $\mathbf{f}$  may be non-cooperative, and that  $\mathbf{f}^+(\mathbf{u}), \mathbf{f}^-(\mathbf{u}), \mathbf{f}(\mathbf{u})$  have the same Jacobian at the origin. The result in [67] gives sufficient conditions that the reaction-diffusion system has a single speed which can be determined by its linearization, and established that the slowest spreading speed  $c^*$  can always be characterized as the slowest speed of a family of traveling waves. The results in [67] can be summarized as the followings

**Theorem 3.3** (Wang [67]). *Assume that  $\mathbf{f}$  lies between  $\mathbf{f}^+$  and  $\mathbf{f}^-$  and Hypotheses 2.2 hold for  $\mathbf{f}^+(\mathbf{u}), \mathbf{f}^-(\mathbf{u}), \mathbf{f}(\mathbf{u})$  except that  $\mathbf{f}$  may be non-cooperative, and that  $\mathbf{f}^+(\mathbf{u}), \mathbf{f}^-(\mathbf{u}), \mathbf{f}(\mathbf{u})$  have the same Jacobian at the origin (see [67] for more precious conditions). Then (10) is linearly determinant and the following statements are valid:*

- (i.) *For initial function  $\mathbf{u}_0(x, 0)$  with compact support, the solution  $\mathbf{u}(x, t)$  of (10) with the initial condition satisfies*

$$\lim_{t \rightarrow \infty} \sup_{|x| \geq tc} \mathbf{u}(x, t) = 0, \text{ for } c > c^*.$$

- (ii.) *For any vector  $\omega \in \mathbb{R}^N, \omega \gg 0$ , there is a positive  $R_\omega$  with the property that if an initial function  $u_0(x, 0)$  such that  $\mathbf{u}_0(x, 0) \geq \omega$  on an interval of length  $2R_\omega$ , then the solution  $\mathbf{u}(x, t)$  of (10) with the initial condition satisfies*

$$k^- \leq \liminf_{t \rightarrow \infty} \inf_{|x| \leq tc} \mathbf{u}(x, t) \leq k^+, \text{ for } 0 < c < c^*.$$

- (iii.) *For each  $c > c^*$  (10) admits a traveling wave solution  $\mathbf{u} = \mathbf{u}(x + ct)$  such that  $0 \ll \mathbf{u}(\xi) \leq k^+, \xi \in \mathbb{R}$ ,*

$$k^- \leq \liminf_{\xi \rightarrow \infty} \mathbf{u}(\xi) \leq \limsup_{\xi \rightarrow \infty} \mathbf{u}(\xi) \leq k^+$$

and

$$\lim_{\xi \rightarrow -\infty} \mathbf{u}(\xi) e^{-\Lambda_c \xi} = \nu_{\Lambda_c}. \quad (20)$$

where  $\nu_{\Lambda_c}$  are corresponding eigenvectors. If, in addition, (10) is cooperative then  $\mathbf{u}$  is nondecreasing on  $\mathbb{R}$ .

(iv.) For  $c = c^*$  (10) admits a nonconstant traveling wave solution  $\mathbf{u} = \mathbf{u}(x + ct)$  such that  $0 \leq \mathbf{u}(\xi) \leq k^+, \xi \in \mathbb{R}$ ,

$$k^- \leq \liminf_{\xi \rightarrow \infty} \mathbf{u}(\xi) \leq \limsup_{\xi \rightarrow \infty} \mathbf{u}(\xi) \leq k^+.$$

(v.) For  $0 < c < c^*$  (10) does not admit a traveling wave solution  $\mathbf{u} = \mathbf{u}(x + ct)$  with  $\liminf_{\xi \rightarrow \infty} \mathbf{u}(\xi) \gg 0$  and  $\mathbf{u}(-\infty) = 0$ .

In addition, the result in [67] is applied to a partially cooperative 2-species reaction-diffusion model, meaning that it is cooperative for small population densities but not for large ones. The model was studied in Weinberger, Kawasaki and Shigesada [76]

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1[-\alpha - \delta u_1 + r_1 u_2] \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + u_2 r_2 [1 - u_2 + h(u_1)] \end{aligned} \tag{21}$$

where  $d_1, \alpha, \delta, r_1, d_2, r_2$  are all positive parameters. This system describes the interaction between ungulates with linear density  $u_1(x, t)$  and grass with linear density  $u_2(x, t)$ . The function  $h(u_1)$  models the increase in the specific growth rate of the grass due to the presence of ungulates. When the density  $u_1$  is small the net effect of ungulates is increasingly beneficial, but as the density increases above a certain value, the benefits decrease with increasing  $u_1$ . By employing comparison methods [76] established spreading speeds for (21). We take the non-monotone Ricker function  $u_1 e^{-u_1}$  as  $h(u_1)$ , which is simpler than that of [76] and apply the abstract theorem in [67] to (21). The application of our general theorem allows us to characterize the spreading speed as the slowest speed of traveling wave solutions to (21) with assumptions that  $d_1 \geq d_2, r_1 > \alpha$  and others.

Therefore we now calculate the minimum speed of (21) from its largest eigenvalue of linearization at the initial equilibrium. Indeed, (21) has the two equilibria  $(0, 0), (0, 1)$  and the coexistence equilibrium. From biological perspective, we are interested in the traveling wave solutions in connecting  $(0, 1)$  and the coexistence equilibrium. Now a standard procedure can calculate that the Jacobian of (21) at  $(0, 1)$  is

$$\begin{pmatrix} r_1 - \alpha & 0 \\ r_2 & -r_2 \end{pmatrix}$$

Its largest eigenvalue is  $r_1 - \alpha$ . For  $\mu \geq 0$ , the largest eigenvalue of the matrix

$$\begin{pmatrix} d_1 \mu^2 + r_1 - \alpha & 0 \\ r_2 & d_2 \mu^2 - r_2 \end{pmatrix}$$

is  $d_1 \mu^2 + r_1 - \alpha$ . Therefore, the minimum wave speed  $c^*$  is the minimum of

$$\inf_{\mu > 0} \frac{d_1 \mu^2 + r_1 - \alpha}{\mu}$$

A standard calculation shows that  $c^* = 2\sqrt{d_1(r_1 - \alpha)}$ .

At the end of the paper, we shall examine the linear determinacy for a predator-prey system. The classical result by Dunbar [10] shows the simplest diffusive predator-prey system is linearly determinant from the perspective of traveling wave solutions. Related results may also be found in Huang [33], Huang, Lu and Ruan [31], Li and Wu [52], Lin, Wu and Weng [53]. Here we would like to review a recent result by Wang, Wang and Wu [70] on the minimum speed of a predator-prey

system, which is a simple deterministic susceptible-infected-removed (SIR) model for an infectious disease outbreak in a closed population consisting of susceptible individuals ( $S(t)$ ), infected individuals ( $I(t)$ ) and removed individuals ( $R(t)$ ). We assume that the recovered are removed and thus not involved in the contact and disease transmission. Hence, the diffusive SIR model with the standard incidence takes the following form

$$\partial_t S = d_1 \partial_{xx} S - \beta SI / (S + I), \quad (22)$$

$$\partial_t I = d_2 \partial_{xx} I + \beta SI / (S + I) - \gamma I, \quad (23)$$

$$\partial_t R = d_3 \partial_{xx} R + \gamma I. \quad (24)$$

where  $\beta$  is the transmission coefficient,  $\gamma$  is the recovery/remove rate, and  $d_1$ ,  $d_2$  and  $d_3$  are the diffusion rates of the susceptible, infective and removed individuals, respectively. The model is non-cooperative and captures the essential transmission dynamics and predicts infection propagation from the initial source of an outbreak. We refer to [5, 6] for the detailed epidemiological consideration of the corresponding ODE model. Relevant results can be found in Hosono and Ilyas [28], Hosono and Ilyas [29].

Because  $R$  does not appear in the system of equations for the susceptible individuals  $S$  and infected individuals  $I$ , we omit the  $R$  equation and study the following system with  $S$  and  $I$  only:

$$\partial_t S = d_1 \partial_{xx} S - \beta SI / (S + I), \quad (25)$$

$$\partial_t I = d_2 \partial_{xx} I + \beta SI / (S + I) - \gamma I. \quad (26)$$

We look for the non-trivial and non-negative traveling wave solutions ( $S(x+ct)$ ,  $I(x+ct)$ ) which satisfy the following boundary conditions at infinity:

$$S(-\infty) = S_{-\infty}, \quad S(\infty) < S_{-\infty}, \quad I(\pm\infty) = 0. \quad (27)$$

The ordinary differential system describing the traveling waves (or wave profiles) is given below:

$$cS' = d_1 S'' - \beta SI / (S + I), \quad (28)$$

$$cI' = d_2 I'' + \beta SI / (S + I) - \gamma I. \quad (29)$$

The main theorem in Wang, Wang and Wu [70] is as follows:

**Theorem 3.4.** *If the basic reproduction number  $R_0 := \beta/\gamma > 1$  and  $c > c^* := 2\sqrt{d_2(\beta - \gamma)}$ , then there exists a non-trivial and non-negative traveling wave solutions  $(S, I)$  such that the boundary conditions (27) are satisfied. Furthermore,  $S$  is monotonically decreasing,  $0 \leq I(x) \leq S(-\infty) - S(\infty)$  for all  $x \in \mathbb{R}$ , and*

$$\int_{-\infty}^{\infty} \gamma I(x) dx = \int_{-\infty}^{\infty} \frac{\beta S(x) I(x)}{S(x) + I(x)} dx = c[S(-\infty) - S(\infty)]. \quad (30)$$

*If  $R_0 = \beta/\gamma \leq 1$  or  $c < c^* := 2\sqrt{d_2(\beta - \gamma)}$ , then there exist no non-trivial and non-negative traveling wave solution  $(S, I)$  satisfying the boundary conditions (27).*

We note that the minimum wave speed  $c^* = 2\sqrt{d_2(\beta - \gamma)}$  for (22-23) can be obtained by its linearization at the initial state  $(S_{-\infty}, 0)$ . In fact, it is easy to calculate that the Jacobian of (22-23) at  $(S_{-\infty}, 0)$  is

$$\begin{pmatrix} 0 & -\beta \\ 0 & \beta - \gamma \end{pmatrix}$$

Its largest eigenvalue is  $\beta - \gamma$ . For  $\mu \geq 0$ , the largest eigenvalue of the matrix

$$\begin{pmatrix} d_1\mu^2 & -\beta \\ 0 & d_2\mu^2 + \beta - \gamma \end{pmatrix}$$

is  $d_2\mu^2 + \beta - \gamma$ . Therefore, the minimum wave speed  $c^*$  is the minimum of

$$\inf_{\mu > 0} \frac{d_2\mu^2 + \beta - \gamma}{\mu}$$

A standard calculation shows that  $c^* = 2\sqrt{d_2(\beta - \gamma)}$ . Thus (22-23) may be thought as linearly determinant from the perspective of traveling wave solutions.

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