Analysis of linear determinacy for spread in cooperative models

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Abstract

The discrete-time recursion system $\mathbf{u}_{n+1} = Q[\mathbf{u}_n]$ with $\mathbf{u}_n(x)$ a vector of population distributions of species and Q an operator which models the growth, interaction, and migration of the species is considered. Previously known results are extended so that one can treat the local invasion of an equilibrium of cooperating species by a new species or mutant. It is found that, in general, the resulting change in the equilibrium density of each species spreads at its own asymptotic speed, with the speed of the invader the slowest of the speeds. Conditions on Q are given which insure that all species spread at the same asymptotic speed, and that this speed agrees with the more easily calculated speed of a linearized problem for the invader alone. If this is true we say that the recursion has a single speed and is linearly determinate. The conditions are such that they can be verified for a class of reaction-diffusion models.

1 Introduction.

Most models for the growth, spread, and interaction of several spatially distributed species can be written in the form of a discrete-time recursion

$$\mathbf{u}_{n+1} = Q[\mathbf{u}_n], \quad n = 0, 1, 2, ... \tag{1.1}$$

where the vector-valued function $\mathbf{u}_n(x) = (u_n^1(x), u_n^2(x), ..., u_n^k(x))$ represents the population densities of the populations of k species or classes at the point x at the time $n\tau$, with τ a fixed generation time. We shall be concerned with the spatio-temporal behavior of the invasion by one species of an unstable spatially uniform state $\boldsymbol{\theta}$ from which this species is absent, and the subsequent convergence of the $\mathbf{u}_n$ to a stable spatially uniform state $\boldsymbol{\beta}$.

Our basic assumption is that the operator Q is order-preserving, which means that increasing all the components of $\mathbf{u}$ increases all the components of $Q[\mathbf{u}]$. While this implies that all the species cooperate, certain models of competition can be reduced to this form. The more usual reaction-diffusion models of species interaction can be put into the form of the recursion (1.1) by defining $Q[\mathbf{v}]$ to be the solution at some fixed time τ of the system with initial values $\mathbf{v}$.

It was shown in Weinberger [21] that many of the properties of a scalar reaction-diffusion equation are also valid for a large class of single-species recursions. In particular, if Q is order-preserving and invariant under translation and direction reversal, then, under some natural conditions on Q, there is a spreading speed c^* with the properties that for any positive ϵ,

$$\lim_{n\to\infty}[\max|\mathbf{u}_n(x)-\boldsymbol{\theta}|:\{x:|x|\ge n[c^*+\epsilon]\}]=0 \tag{1.2}$$

for any initial function $\mathbf{u}_0(x)$ which lies between $\boldsymbol{\theta}$ and $\boldsymbol{\beta}$ and which coincides with $\boldsymbol{\theta}$ outside a bounded set, and that

$$\lim_{n\to\infty}[\max\{|\boldsymbol{\beta}-\mathbf{u}_n(x)|:\{x:|x|\le n[c^*-\epsilon]\}]=0, \tag{1.3}$$

for any initial function $\mathbf{u}_0(x)$ which lies above $\boldsymbol{\theta}$ plus some positive constant on a sufficiently long interval. Equation (1.2) states that if an observer were to move to the right or left at a fixed speed greater than c^*, the local population density would eventually look like $\boldsymbol{\theta}$. Equation (1.3) states that if an observer were to move to the right or left at a fixed speed less than c^*, the local population density would eventually look like $\boldsymbol{\beta}$. That is, the population spreads at roughly the speed c^*.

Moreover, it was shown that c^* is bounded below by the spreading speed $\bar{c}$ of the recursion in which Q is replaced by a truncation of its linearization M at $\boldsymbol{\theta}$:

$$c^*\ge\bar{c}. \tag{1.4}$$

It was further shown that if Q has the additional property that

$$Q[\mathbf{u}]-\boldsymbol{\theta}\le M[\mathbf{u}-\boldsymbol{\theta}], \tag{1.5}$$

and if for each positive ϵ there is a $\delta>0$ such that $Q[\mathbf{u}]-\theta\ge(\mathbf{1}-\delta)(\mathbf{M}[\mathbf{u}]-\theta)$ when $\mathbf{0}\le\mathbf{u}\le\epsilon$, then

$$c^*=\bar{c}. \tag{1.6}$$

These results extended earlier results for reaction-diffusion models [2]

Most models of interest in population ecology involve the interaction of multiple species. It was shown by Lui [13] that all the above results can be extended to a cooperative multi-species system which satisfies certain additional conditions. These include the requirements that (i) the linearization M of Q is irreducible; and (ii) there are no other constant equilibria of the recursion (1.1) in the closed parallelepiped with vertices $\boldsymbol{\theta}$ and $\boldsymbol{\beta}$. Lui gave applications of these results to models of epidemics and of population genetics [14]. Neubert and Caswell [16] have recently applied the results to a model of the interaction of stages of a single species.

Virtually all models for the interaction of separate species have the property that a species which is everywhere absent cannot appear spontaneously.

That is, $u_k = 0$ implies that the kth component of $Q[\mathbf{u}]$ is zero, regardless of the values of the other components of $\mathbf{u}$. It follows that the partial derivatives of the kth component of $Q[\mathbf{u}]$ with respect to all but the kth component of $\mathbf{u}$ vanish when $u_k = 0$. Therefore, the linearization of the operator Q about a state in which one of the species is absent is reducible. (The same argument can be extended to the case in which the invader has several stages but no spontaneous generation.)

While purely cooperative systems are rare in ecology, it is well known that the change of variables $u = p,\ v = 1 - q$ turns the classical Lotka-Volterra competition system

$$\begin{aligned} p_{,t} &= d_1 \nabla^2 p + r_1 p(1 - p - a_1 q) \\ q_{,t} &= d_2 \nabla^2 q + r_2 q(1 - q - a_2 p) \end{aligned} \tag{1.7}$$

into a cooperative system. This trick is equivalent to the fact that the system (1.7) is order preserving with respect to the partial ordering whose positive cone is the fourth quadrant [9]. If one wishes to study an invasion by the first species of the equilibrium state $p = 0,\ q = 1$ and the motion toward the new equilibrium (1,0), one notes that the extinction equilibrium (0,0) lies on the closed rectangle determined by these two equilibria. Thus both of Lui's additional conditions are violated in this case. Moreover, Lui's criterion (1.5) would require the restriction of the function $q(1 - q - a_2 p)$ to the line $p = 0$ to lie above its tangent line at $q = 1$. This is clearly violated at $q = 0$.

The purpose of the present paper is to extend Lui's results in such a way that they can be applied to invasion processes of certain models for cooperation or competition among multiple species, including the model (1.7).

The system (1.1) is said to be **linearly determinate** when the property (1.6) is valid. A statement of belief that under certain conditions a system is linearly determinate is called a **linear conjecture**. See, e.g., van den Bosch, Metz and Diekmann [20] or Mollison [15].

Linear determinacy is heuristically justified by the fact that if $\mathbf{u}_0 = \boldsymbol{\theta}$ outside a bounded set, then $\mathbf{u}_n$ is near $\boldsymbol{\theta}$ for large $|x|$. Therefore, the behavior for large $|x|$ and n might be expected to be governed by the recursion obtained by replacing Q by its linearization around $\boldsymbol{\theta}$. However, this reasoning depends on an interchange of the limits as $|x|$ and n approach infinity, and hence does not always apply. In fact, Hadeler and Rothe [5] showed that the spreading speed of the scalar reaction-diffusion equation

$$u_{,t} = u_{,xx} + u(1 - u)(1 + \nu u) \tag{1.8}$$

is given by the formula

$$c^* = \begin{cases} 2 & \text{for } -1 \le \nu \le 2 \\ \sqrt{\nu/2} + \sqrt{2/\nu} & \text{for } \nu \ge 2, \end{cases} \tag{1.9}$$

while the linearized speed $\bar{c}$ is always 2. Thus linear determinacy is violated for $\nu > 2$, so that it is not always true. Moreover, the inequality (1.5) is only satisfied for $\nu \le 1$, while linear determinacy is valid for $\nu \le 2$. Thus this condition is sufficient but not necessary for the linear determinacy to hold. Okubo, et al. [18] applied the above reasoning to the Lotka Volterra model (1.7) for the invasion of gray squirrels into an existing red squirrel population. Analysis and simulation by Hosono [7] showed that linear determinacy is sometimes but not always right for the model (1.7).

Because $\bar{c}$ is usually much easier to calculate than c^*, it is important to know conditions which are sufficient for the validity of linear determinacy. We shall obtain such a condition which is less stringent than (1.5) and which can be applied to ecological invasion problems.

The problem is formulated in Section 2. Lemma 2.2 and Example 2.1 show that the presence of an extra constant equilibrium in the rectangular parallelepiped determined by $\boldsymbol{\theta}$ and $\boldsymbol{\beta}$ can produce a new phenomenon. Namely, different components of the solution may spread at different speeds, so that there is no single spreading speed, but only a slowest speed c^* and a fastest speed c_+^*. Lemma 2.3 extends Lui's formula for the speed $\bar{c}$ of the truncated linearized recursion to formulas for the slowest speed $\bar{c}$ and the fastest speed $\bar{c}_+$. **Linear determinacy** is now defined to mean that $c^* = \bar{c}$ and $c_+^* = \bar{c}_+$.

Our basic results are stated and proved in Section 3. The main result is Theorem 3.1, which gives a sufficient condition for the recursion (1.1) to be linearly determinate and have a single speed. This condition is weaker than (1.5), and can be satisfied even when there is an extra equilibrium in the parallelepiped with corners at $\boldsymbol{\theta}$ and $\boldsymbol{\beta}$. Theorems 3.2 and 3.3 give less stringent sufficient conditions for the recursion to have a single spreading speed $c^* = c_+^*$, which may differ from $\bar{c}$.

Theorem 4.1 in Section 4 shows how to transfer any spreading result on recursions of the form (1.1) to an analogous result for a reaction-diffusion system. We then transfer the theorems of Section 3 to this case. Example 4.3 presents a reaction-diffusion model for the invasion by a competitor of a stable mono-culture in which the extinction of the original species spreads more rapidly than the population of the invader. Theorem 4.4 shows that this phenomenon does not occur in the Lotka-Volterra model (1.7), and that every invasion is successful in this model.

There are several reasons for studying the discrete-time model (1.1) rather than just reaction-diffusion models. As we shall point out in Section 5, the derivation of reaction-diffusion models, particularly for relatively small populations, is rather shaky. Secondly, a discrete-time model permits one to treat time-periodic variations such as annual reproduction and dispersal. Thirdly, we note that simulation of a continuous-time model is done by discretizing the time as well as space, so that one is really dealing with a recursion of the form (1.1). As this paper shows, the study of discrete-time recursions also provides a powerful tool for studying reaction-diffusion systems.

We shall show in a companion paper [11] that the results obtained here can be applied directly both to the Lotka-Volterra model (1.7) and to the corresponding discrete time model

$$\begin{aligned} p_{n+1}(x) &= \int_{-\infty}^{\infty} \frac{(1+\rho_1)p_n(x-y)}{1+\rho_1(p_n(x-y)+\alpha_1 q_n(x-y))} k_1(y,dy), \\ q_{n+1}(x) &= \int_{-\infty}^{\infty} \frac{(1+\rho_2)q_n(x-y)}{1+\rho_2(q_n(x-y)+\alpha_2 p_n(x-y))} k_2(y,dy). \end{aligned} \tag{1.10}$$

Here $k_1(y,dy)$ and $k_2(y,dy)$ are probability measures referred to as dispersal kernels which model migration of the two species after they have grown and competed locally. (The fact that the k_i may be measures permits one to treat spatially discrete migration models.) The change of variables $u_n = p_n,\ v_n = 1-q_n$ converts this system to a cooperative system, to which Theorem 3.1 can be applied. Theorem 3.4 shows that this model always has a single spreading speed, and that every invasion is successful in this model.

Both [21] and [13] obtained the above-cited results in the more general setting of a multidimensional habitat, and without the assumption of rotational symmetry. This is done by choosing any unit vector $\boldsymbol{\xi}$ and restricting the recursion (1.1) to sequences $\mathbf{u}_n$ which only depend on the single variable $\mathbf{x}\cdot\boldsymbol{\xi}$ to obtain a one-dimensional recursion, for which one defines a spreading speed $c^*(\boldsymbol{\xi})$. One then obtains results analogous to (1.2) and (1.3) where the interval $|x| \geq n(c^*+\epsilon)$ is replaced by the set $\{\mathbf{x} : \mathbf{x}\cdot\boldsymbol{\xi} \geq n[c^*(\boldsymbol{\xi})+\epsilon]$ for some unit vector $\boldsymbol{\xi}\}$ and the interval $|x| \leq n(c^*-\epsilon)$ is replaced by the set $\{\mathbf{x} : \mathbf{x}\cdot\boldsymbol{\xi} \leq n[c^*(\boldsymbol{\xi})-\epsilon]$ for all unit vectors $\boldsymbol{\xi}\}$, respectively. Since exactly the same procedure works in our more general case, we shall not carry it out here.

It has been noticed since the pioneering work of Fisher [4] and Kolmogorov, Petrowski, and Piscounov [8] that spreading speeds can often be characterized as slowest speeds of travelling waves. It will be shown in another work [12] that, under some restrictions on Q, both the slowest spreading speed c^* and the fastest spreading speed c_+^* of the components can be characterized in this fashion.

2 Hypotheses and spreading speeds.

We begin with some notation. The **habitat** $\mathcal{H}$ will denote either the real line (the continuous habitat) or the subset of the real line which consists of all integral multiples of a positive mesh size h (a discrete habitat). We shall use boldface Roman symbols like $\mathbf{u}(x)$ to denote k-vector valued functions of the single variable x in $\mathcal{H}$, and boldface Greek letters to stand for k-vectors, which may be thought of as constant vector-valued functions. We think of k as the number of species (or stages) in the recursion (1.1). We define $\mathbf{u} \geq \mathbf{v}$ to mean that $u_i(x) \geq v_i(x)$ for all i and x, and $\mathbf{u} >> \mathbf{v}$ to mean that $u_i(x) > v_i(x)$ for all i and x. We use the notation $\mathbf{0}$ for the constant vector all of whose components are 0.

The operator Q in the recursion (1.1) takes the set $\mathcal{C}$ of all continuous vector valued functions on $\mathcal{H}$ with nonnegative components into itself. A function $\mathbf{w}(x)$ is said to be an **equilibrium** of Q if $Q[\mathbf{w}] = \mathbf{w}$, so that if $\mathbf{u}_\ell = \mathbf{w}$ in the recursion (1.1), then $\mathbf{u}_n = \mathbf{w}$ for all $n \geq \ell$.

By introducing the new variable $\hat{\mathbf{u}} = \mathbf{u} - \boldsymbol{\theta}$ if necessary, we shall assume that the unstable equilibrium $\boldsymbol{\theta}$ from which the system moves away is the origin. In particular, $Q[\mathbf{0}] = \mathbf{0}$. We define the maximum norm

$$||\mathbf{u}(x)|| := \sup_x |\mathbf{u}(x)|.$$

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 $||Q[\mathbf{u}] - M[\mathbf{u}]|| \leq \epsilon ||\mathbf{u}||$. The most important property of M is that for every bounded $\mathbf{u} \geq \mathbf{0}$

$$M[\mathbf{u}] = \lim_{\rho \searrow 0} [(1/\rho) Q[\rho \mathbf{u}]]. \tag{2.1}$$

The operator Q is said to be **order-preserving** if $\mathbf{u} \geq \mathbf{v}$ implies that $Q[\mathbf{u}] \geq Q[\mathbf{v}]$. This means that an increase in any species is beneficial to all species. A recursion (1.1) in which Q has this property is said to be **cooperative**.

We define the translation and reflection operators

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

The habitat is said to be **homogeneous** if the growth and migration properties are the same at all points, and **isotropic** if the migration properties are the same in both directions. These properties are equivalent to the statements that the operator 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 $\mathbf{v}$.

It is easily seen that if Q has these properties, then so does M. In particular, it follows that M has the representation

$$(M[\mathbf{v}](x))_i = \sum_{j=1}^{k} \int_{-\infty}^{\infty} \mathbf{v}_j(x-y) m_{ij}(y, dy), \tag{2.2}$$

where each m_{ij} is a bounded symmetric nonnegative measure. (We permit measures rather than just densities in order to include discrete-space migration models.) It is useful to introduce the $k \times k$ matrix of two-sided Laplace transforms

$$B_\mu = \left(\int_{-\infty}^{\infty} e^{\mu y} m_{ij}(y, dy) \right). \tag{2.3}$$

Note that $B_\mu \boldsymbol{\alpha} = M[\boldsymbol{\alpha} e^{-\mu x}]\big|_{x=0}$ for every constant vector $\boldsymbol{\alpha}$. For the sake of simplicity, we shall assume that the entries of B_μ are finite for all μ.

A matrix is said to be **reducible** if the coordinates can be split into two nonempty disjoint subsets with the property that the (ij) element of the matrix vanishes whenever i is in the first set and j is in the second. This is equivalent to saying that the matrix can be put into lower block triangular form by reordering the coordinates so that the coordinates in the first set come before those of the second. If this cannot be done, the matrix is said to be **irreducible**. Because the m_{ij} are nonnegative, the entries of B_μ are nonnegative, and the ij entry of B_μ is 0 if and only if m_{ij} is identically zero, so that the ij entry of B_0 is also 0. Thus either all the B_μ are irreducible or they are all reducible.

By reordering the coordinates, one can put any matrix into a block lower triangular form, the so-called **Frobenius form**, in which all the diagonal blocks are irreducible. (See, e.g.[6].) (An irreducible matrix consists of the single diagonal block which is the matrix itself.) We shall suppose that this reordering has been done for B_0. Because all the B_μ have the same zero entries, it follows that all the matrices B_μ are in Frobenius form. A theorem of Frobenius states that any nonzero irreducible matrix with nonnegative entries has a unique positive eigenvalue, called the **principal eigenvalue**, with a corresponding **principal eigenvector** with strictly positive coordinates. Moreover, the absolute values of all the other eigenvalues are no larger than the principal eigenvalue.

Let $\lambda_\sigma(\mu)$ denote the principal eigenvalue of the σth diagonal block from the top of B_μ. These are, of course, eigenvalues of B_μ.

For any $\boldsymbol{\alpha} >> \mathbf{0}$ we define

$$\mathcal{C}_{\boldsymbol{\alpha}} := \{\mathbf{u}(x) : \mathbf{0} \leq \mathbf{u} \leq \boldsymbol{\alpha}\}.$$

We shall make the following assumptions, which are a proper subset of a variant of those used by Lui [13] .

Hypotheses 2.1

i. *$Q[\mathbf{0}] = \mathbf{0}$, and there is a constant vector $\boldsymbol{\beta} >> \mathbf{0}$ such that $Q[\boldsymbol{\beta}] = \boldsymbol{\beta}$, which is minimal in the sense there is no constant $\boldsymbol{\nu} \neq \boldsymbol{\beta}$ such that $Q[\boldsymbol{\nu}] = \boldsymbol{\nu}$ and $\mathbf{0} << \boldsymbol{\nu} \leq \boldsymbol{\beta}$; i.e., $\mathbf{0}$ and $\boldsymbol{\beta}$ are equilibria, and there is no constant all-species coexistence equilibrium below $\boldsymbol{\beta}$.*

ii. *Q is order-preserving on nonnegative functions, so that if $\mathbf{u} \geq \mathbf{v} \geq \mathbf{0}$, then $Q[\mathbf{u}] \geq Q[\mathbf{v}] \geq \mathbf{0}$; i.e., an increase in any species is beneficial (or at least not detrimental) to all species.*

iii. *Q is translation and reflection invariant so that $Q[T_y[\mathbf{v}]] = T_y[Q[\mathbf{v}]]$ for all y, and $Q[R[\mathbf{v}]] = R[Q[\mathbf{v}]]$; i.e., the environment is homogeneous and isotropic.*

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. In other words, the values of $Q[\mathbf{v}](x)$ are almost independent of those values of $\mathbf{v}(y)$ with y outside a sufficiently long interval centered at x.*

v. a. *The matrix B_μ defined by (2.3) has finite entries for all μ and is in Frobenius form. The principal eigenvalue of its σth diagonal block is $\lambda_\sigma(\mu)$.*

b. $\lambda_1(0) > 1$, *so that the equilibrium* $\mathbf{0}$ *is invadable; i.e., the populations which correspond to the first block grow when all populations are sufficiently small;*

c. $\lambda_1(0) > \lambda_\sigma(0)$ *for every* $\sigma > 1$*; i.e, at the time of the invasion, the growth rate of the invader is greater than that of the invadees. (Note that if the invaded equilibrium is stable,* $\lambda_\sigma(0) \leq 1$ *for* $\sigma \neq 1$*, so that this follows from* **b**.*)*

d. B_0 *has at least one nonzero entry to the left of each of its diagonal blocks other than the uppermost one; i.e, when the populations are very small, an increase in population of the first species increases the populations of all the other species in a finite number of time steps.*

vi. *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* κ *there is a constant vector* $\boldsymbol{\omega} >> 0$ *such that*

$$Q[\mathbf{v}] \geq M^{(\kappa)}[\mathbf{v}] \qquad \text{when } \mathbf{0} \leq \mathbf{v} \leq \boldsymbol{\omega}; \tag{2.4}$$

i.e., in a neighborhood of the zero equilibrium, one can bound the nonlinear operator below by a sequence of linear operators. (Lemma 4.1 will show that these conditions are automatically satisfied by a reaction-diffusion system. For most other biological models, they are satisfied with $M^{(\kappa)} = (1-\kappa^{-1})M$*.)*

b. *For every* $\mu > 0$ *the matrices* $B_\mu^{(\kappa)}$ *defined by* $B_\mu^{(\kappa)}\boldsymbol{\alpha} := M^{(\kappa)}[e^{-\mu x}\boldsymbol{\alpha}]\big|_{x=0}$ *converge to* B_μ *as* $\kappa\to\infty$*. This is true for a reaction-diffusion system and also when* $M^{(\kappa)} = (1-\kappa^{-1})M$*.*

Remarks. 1. As we remarked in the Introduction, when a new species invades an equilibrium of other species, the row of the matrix B_0 which corresponds to the new species has zero off-diagonal elements. Hence in the Frobenius form the invading species appears first, and the first diagonal block is 1×1. If there were a second invading species, there would be another row with only a diagonal element, and this is excluded by the Hypothesis v.d. Thus in most invasion problems, the first diagonal block is 1×1. If, as in the work of Neubert and Caswell [16], the population of the invader is subdivided into cooperating stages, the upper left block will consist of the populations of these stages.

2. We observe that Hypotheses (i) and (ii) show that $\mathcal{C}_{\boldsymbol{\beta}}$ is an invariant set for Q. That is, if $\mathbf{u}_0$ is in $\mathcal{C}_{\boldsymbol{\beta}}$, then the same is true of all the $\mathbf{u}_n$ generated by the recursion (1.1).

3. It is easily verified that Parts (c)and (d) of Hypothesis 2.1.v are equivalent to the existence of an eigenvector $\boldsymbol{\zeta}(0) >> \mathbf{0}$ of B_0 corresponding to the principal eigenvalue $\lambda_1(0)$.

We recall one of the results of Lui which uses one of his extra conditions.

Proposition 2.1 *If the Hypotheses 2.1 are satisfied and if, in addition, the only constant equilibria on $\mathcal{C}_{\boldsymbol{\beta}}$ are $\mathbf{0}$ and $\boldsymbol{\beta}$, then there is a spreading speed c^* with the properties that for every positive ϵ*

i. if $\mathbf{u}_0$ vanishes outside a bounded interval and $\mathbf{0} \leq \mathbf{u}_0 << \boldsymbol{\beta}$, then

$$\lim_{n\to\infty}\left[\sup_{|x|\geq n[c^*+\epsilon]} |\mathbf{u}_n(x)|\right] = 0; \tag{2.5}$$

and

ii. for any constant vector $\boldsymbol{\omega} >> \mathbf{0}$, there is a positive number $R_{\boldsymbol{\omega}}$ with the property that if $\mathbf{u}_0 \geq \boldsymbol{\omega}$ on an interval of length $2R_{\boldsymbol{\omega}}$, then

$$\lim_{n\to\infty}\left[\sup_{|x|\leq n[c^*-\epsilon]} |\boldsymbol{\beta} - \mathbf{u}_n(x)|\right] = 0. \tag{2.6}$$

This is a special case of Theorems 3.1 and 3.2 of Lui [13]. In order to see what may happen when the additional condition of this Proposition is not satisfied, we give a brief sketch of the proof. Choose a fixed vector-valued initial function $\mathbf{a}_0(x)$ all of whose components are non-increasing in x and vanish for $x \geq 0$, and such that $\mathbf{0} << \mathbf{a}_0(-\infty) << \boldsymbol{\beta}$. Define the sequence $\mathbf{a}_n(c;x)$ by the recursion

$$\mathbf{a}_{n+1}(c;x) = \max\{\mathbf{a}_0(x), T_{-c}[Q[\mathbf{a}_n(c;\cdot)]]\}. \tag{2.7}$$

The operator on the right is again order preserving. By definition, $\mathbf{a}_1 \geq \mathbf{a}_0$, and an induction argument shows that for all n, $\mathbf{a}_n \leq \mathbf{a}_{n+1} \leq \boldsymbol{\beta}$, and $\mathbf{a}_n(c;x)$ is non-increasing in c and x. Thus the sequence $\mathbf{a}_n$ increases to a limit function $\mathbf{a}(c;x)$ which is again nondecreasing in c and x and bounded by $\boldsymbol{\beta}$.

Lui also showed that the vectors $\mathbf{a}(c;\pm\infty)$ are equilibria[1] of Q. Parts i, ii, v.a, and vi of Hypothesis 2.1 imply that $\mathbf{a}(c;-\infty)=\boldsymbol{\beta}$. It can be shown that $\mathbf{a}(c;\infty)=\boldsymbol{\beta}$ when c is sufficiently negative. Lui defined

$$c^* := \sup\{c : \mathbf{a}(c;\infty)=\boldsymbol{\beta}\}, \tag{2.8}$$

and showed that this $c^* \leq \infty$ does not depend on the choice of $\mathbf{a}_0$.

The monotonicity shows that $\mathbf{a}(c;\infty)=\boldsymbol{\beta}$ for $c<c^*$. When $c^*>\epsilon>0$, Lui showed how to combine translates of $\mathbf{a}(c^*-\epsilon;x)$ and $\mathbf{a}(c^*-\epsilon;-x)$ to produce a nonnegative vector-valued function $\mathbf{s}_0(x)$ whose components are strictly below those of $\boldsymbol{\beta}$, which vanishes outside a bounded interval, and such that the sequence $\mathbf{s}_n(x)$ obtained by solving the recursion (1.1) with this initial function has the property that the maximum of $|\boldsymbol{\beta}-\mathbf{s}_n(x)|$ on the interval $|x|\leq n(c^*-\epsilon)$ converges to zero as n goes to infinity. It follows from parts (ii), (v.b), and (vi) of Hypotheses 2.1 that if $\mathbf{u}_0=\boldsymbol{\omega}>>0$, then the constants $\mathbf{u}_n$ converge to $\boldsymbol{\beta}$. By part (iv) of Hypotheses 2.1 there are an integer N and a positive $R_{\boldsymbol{\omega}}$ such that if $\mathbf{u}_0\geq\boldsymbol{\omega}$ for $|x|\leq R_{\boldsymbol{\omega}}$, then $\mathbf{u}_N\geq\mathbf{s}_0$, so that (2.6) is valid. By translating if necessary, one obtains the same result if $\mathbf{u}_0\geq\boldsymbol{\omega}$ on any interval of length $2R_{\boldsymbol{\omega}}$. (Of course, when $c^*\leq 0$, the property (2.6) is meaningless.)

Suppose that c^* is finite. Since, by the extra hypothesis of the Proposition, the only other equilibrium in $\mathcal{C}_{\boldsymbol{\beta}}$ is $\mathbf{0}$, we conclude that $\mathbf{a}(c;\infty)=\mathbf{0}$ for $c>c^*$. A semi-continuity argument then shows that the equality is still true at $c=c^*$, so that $\mathbf{a}(c;\infty)=\mathbf{0}$ for $c\geq c^*$. For any initial function $\mathbf{0}\leq\mathbf{u}_0<<\boldsymbol{\beta}$, which vanishes outside a bounded interval, let T_α be a translation which takes this interval into a subset of the negative x-axis, and choose an admissible function $\mathbf{a}_0$ such that $\mathbf{a}_0\geq T_\alpha[\mathbf{u}_0]$. Then $\mathbf{u}_0(x)\leq\mathbf{a}_0(c^*;x+\alpha)$, and therefore

$$\mathbf{u}_1(x)\leq Q[T_{-\alpha}[\mathbf{a}_0(c^*;\cdot)]]=T_{-\alpha+c^*}[T_{-c^*}[Q\mathbf{a}_0]]\leq T_{-\alpha+c^*}[\mathbf{a}_1(c^*;x)].$$

By induction we see that

$$\mathbf{u}_n(x)\leq\mathbf{a}_n(c^*,x-nc^*+\alpha)\leq\mathbf{a}(c^*,x-nc^*+\alpha).$$

[1]There is an easily fixed gap in the proof of Lemma 2.6 of [13]. The inequality $\mathbf{a}(c;\infty)\leq Q[\mathbf{a}(c;\infty)]$ is proved under the assumption that $Q[a(c;s)]$ is defined, but the limit function $\mathbf{a}$ may not be continuous. However, because $\mathbf{a}(\mathbf{c};\mathbf{s})$ is nonincreasing and bounded, one can construct a continuous piecewise linear function $\tilde{\mathbf{a}}\geq\mathbf{a}$ with the same limits at $\pm\infty$. It easily follows that $\mathbf{a}(s)\leq Q[\tilde{\mathbf{a}}(x+s+c)](0)$ for $s\geq 0$, and the desired inequality follows by letting s approach infinity.

Thus when $x \geq n(c^* + \epsilon)$, we have

$$\mathbf{u}_n(x) \leq \mathbf{a}(c^*, n\epsilon + \alpha),$$

which approaches zero as n goes to infinity. Since $\mathbf{u}_n(-x)$ also satisfies the recursion, we obtain the same result for $\mathbf{u}_n(-x)$, and this gives (2.5). Thus the Proposition is established.

We now examine what happens when the extra assumption that $\mathbf{0}$ and $\boldsymbol{\beta}$ are the only equilibria in $\mathcal{C}_{\boldsymbol{\beta}}$ is dropped. One can still define the function $\mathbf{a}(c; x)$ as above, and follow Lui in defining c^* by (2.8). The only difference is that $\mathbf{a}(c^*; \infty)$ may be an equilibrium $\boldsymbol{\nu}$ other than $\mathbf{0}$. The property (2.6) of a solution of (1.1) which becomes sufficiently large on a sufficiently large interval is proved as before. It is natural to define a second speed

$$c_+^* := \sup\{c : \mathbf{a}(c, \infty) \neq \mathbf{0}\}. \tag{2.9}$$

If $c_+^* = c^*$, we shall say that the recursion (1.1) has a **single speed**.

We can extend Proposition 2.1 to the case where extra equilibria are present. We define the projection operator P_σ by saying that $P_\sigma[\mathbf{v}]$ has the same coordinates as $\mathbf{v}$ in the directions corresponding to the σth diagonal block of B_0, and zero components in the other directions. We first state a simple algebraic fact, which will be proved in the Appendix.

Lemma 2.1 *Let the Hypotheses 2.1 be satisfied. Then for every constant equilibrium $\boldsymbol{\nu}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ other than $\boldsymbol{\beta}$, $P_1[\boldsymbol{\nu}] = \mathbf{0}$.*

This fact helps prove the following extension of Proposition 2.1.

Lemma 2.2 *Let $\mathbf{u}_n$ be a solution of the recursion (1.1). Then for any positive ϵ*

i. if $\mathbf{0} \leq \mathbf{u}_0 << \boldsymbol{\beta}$ and $\mathbf{u}_0 = \mathbf{0}$ outside a bounded interval, then

$$\lim_{n\to\infty} [\sup_{|x| \geq n[c_+^* + \epsilon]} |\mathbf{u}_n(x)|] = 0, \tag{2.10}$$

and

$$\lim_{n\to\infty} [\sup_{|x| \geq n[c^* + \epsilon]} |P_1[\mathbf{u}_n(x)]|] = 0; \tag{2.11}$$

ii. for any constant vector $\boldsymbol{\omega} >> \mathbf{0}$, there is a positive number $R_{\boldsymbol{\omega}}$ with the property that if $\mathbf{u}_0 \geq \boldsymbol{\omega}$ on an interval of length $2R_{\boldsymbol{\omega}}$, then

$$\lim_{n\to\infty} [\sup_{|x|\leq n[c^*-\epsilon]} \{|\boldsymbol{\beta} - \mathbf{u}_n(x)|\}] = 0, \tag{2.12}$$

and there is a $\sigma > 1$ such that when $c < c_+^*$, all the components of $\mathbf{a}(c;\infty)$ in the directions corresponding to the σth block of B_0 are positive, and

$$\liminf_{n\to\infty} [\inf_{|x|\leq n[c_+^*-\epsilon]} P_\sigma[\mathbf{u}_n(x)] \geq P_\sigma[\mathbf{a}(c_+^* - \tfrac{1}{2}\epsilon, \infty)]. \tag{2.13}$$

Proof. The equation (2.10) is obtained by applying the proof used to establish the property (2.5) in Proposition 2.1. Because $P_1[\mathbf{a}(c^*;\infty)] = \mathbf{0}$ by Lemma 2.1, the same proof applied to $P_1[\mathbf{u}_n]$ yields (2.11). The proof of (2.6) in Proposition 2.1 gives the property (2.12).

The definition (2.9) of c_+^* shows that for $c < c_+^*$, $\mathbf{a}(c;\infty)$ is nonzero and nonincreasing in c. Therefore there is at least one σ such that all the components of the equilibrium $\mathbf{a}(c;\infty)$ are positive for all $c < c_+^*$. The proof of Lemma 2.1 shows that if $\mathbf{u}_0$ is uniformly positive on a sufficiently large set, then for $|x| \leq n(c_+^* - \epsilon)$, $\mathbf{u}_n(x)$ becomes larger than $\mathbf{a}(c_+^* - \frac{1}{2}\epsilon;\infty)$, and (2.13) follows. Thus the Lemma is established.

Remark. The properties (2.10) and (2.12) show that no component of $\mathbf{u}_n$ can spread more rapidly than c_+^* or more slowly than c^*. The properties (2.11) and (2.12) state that the first component (the invader) spreads at the slowest speed c^*. (2.13) shows that there is at least one component which spreads at the maximal speed c_+^*. Thus if $c_+^* > c^*$, there is no single spreading speed. If $c_+^* = c^*$, the equations (2.10) and (2.12) show that their common value is the spreading speed of all components of $\mathbf{u}_n$.

EXAMPLE 2.1 Consider the operator

$$Q[(u,v)] := \begin{pmatrix} \int_{-\infty}^{\infty} (4\pi d_1)^{-1/2} e^{-(x-y)^2/(4d_1)} \\ \quad u(y)[1 + r_1(1 - 2\min\{u(y),1\} + \min\{v(y),1\})]dy \\ \int_{-\infty}^{\infty} (4\pi d_2)^{-1/2} e^{-(x-y)^2/(4d_2)} \\ \quad [v(y) + r_2 \max\{1 - v(y), 0\}(u(y) + v(y))]dy \end{pmatrix} \tag{2.14}$$

with d_1 and d_2 positive, and

$$0 < r_2 < r_1 < 1/3. \tag{2.15}$$

It is easily verified that the Hypotheses 2.1 with $\boldsymbol{\beta} = (1,1)$ are satisfied. The points $\mathbf{0}$, $\boldsymbol{\beta}$, and $(0,1)$ are all equilibria, so that Lui's additional hypothesis in Proposition 2.1 is violated. The first component Q_1 of the operator Q is bounded above by setting $v \equiv 1$:

$$\begin{aligned}(Q[(u,v)])_1 &\leq \tilde{Q}_1[u] \\ &:= \int_{-\infty}^{\infty} (4\pi d_1)^{-1/2} e^{-(x-y)^2/(4d_1)} u(y)[1 + r_1(1 - 2\min\{u(y), 1\} + 1]dy.\end{aligned}$$

The second component Q_2 is bounded below by setting $u \equiv 0$:

$$\begin{aligned}(Q[(u,v)])_2 &\geq \tilde{Q}_2[v] \\ &:= \int_{-\infty}^{\infty} (4\pi d_2)^{-1/2} e^{-(x-y)^2/(4d_2)} [v(y) + r_2 \max\{1 - v(y), 0\}(0 + v(y))]dy.\end{aligned}$$

Thus if $\mathbf{u}_n = (u_n, v_n)$ satisfies the recursion $\mathbf{u}_{n+1} = Q[\mathbf{u}_n]$ with $\mathbf{u}_0(x) = \mathbf{0}$ for large $|x|$, and if u_0 is nonnegative and uniformly less than 1, then u_n can be bounded above by the solution $\tilde{u}_n$ of the recursion $\tilde{u}_{n+1} = \tilde{Q}_1[\tilde{u}_n]$ with $\tilde{u}_0 = u_0$. The results on scalar recursions in [21] show that $\tilde{u}_n$ spreads with the speed $2\sqrt{d_1 \ln(1 + 2r_1)}$. Therefore,

$$\lim_{n\to\infty} [\sup\{u_n(x) : |x| \geq n(2\sqrt{d_1 \ln(1 + 2r_1)} + \epsilon)\}] = 0.$$

By definition, $c^* \leq 2\sqrt{d_1 \ln(1 + 2r_1)}$. A similar argument shows that v_n is bounded below by $\tilde{v}_n$, which spreads with the speed $2\sqrt{d_2 \ln(1 + r_2)}$. Hence,

$$\lim_{n\to\infty} [\sup\{1 - v_n(x) : |x| \leq n(2\sqrt{d_2 \ln(1 + r_2)} - \epsilon)\}] = 0,$$

so that $c_+^* \geq 2\sqrt{d_2 \ln(1 + r_2)}$. Thus if

$$d_2 \ln(1 + r_2) > d_1 \ln(1 + 2r_1), \tag{2.16}$$

then the second component spreads at a speed c_+^* greater than the speed c^* of the first component. Therefore there is no single spreading speed for this problem (Figure 1a).

In order to discuss linear determinacy, we need to talk about the spreading speeds of a recursion in which the operator Q is a truncated linear operator. Let $\tilde{L}$ be a bounded linear order-preserving translation and reflection invariant operator on $\mathcal{C}$, for which there is a constant vector $\boldsymbol{\omega} >> \mathbf{0}$ such that $\tilde{L}[\boldsymbol{\omega}] >> \boldsymbol{\omega}$. We consider the truncated linear recursion

$$\mathbf{u}_{n+1} = \min\{\tilde{L}[\mathbf{u}_n], \boldsymbol{\omega}\} \tag{2.17}$$

We suppose that for every μ the matrix $\tilde{B}_\mu$ defined by the fact that

$$\tilde{L}[e^{-\mu x}\boldsymbol{\alpha}]|_{x=0} = \tilde{B}_\mu \boldsymbol{\alpha}$$

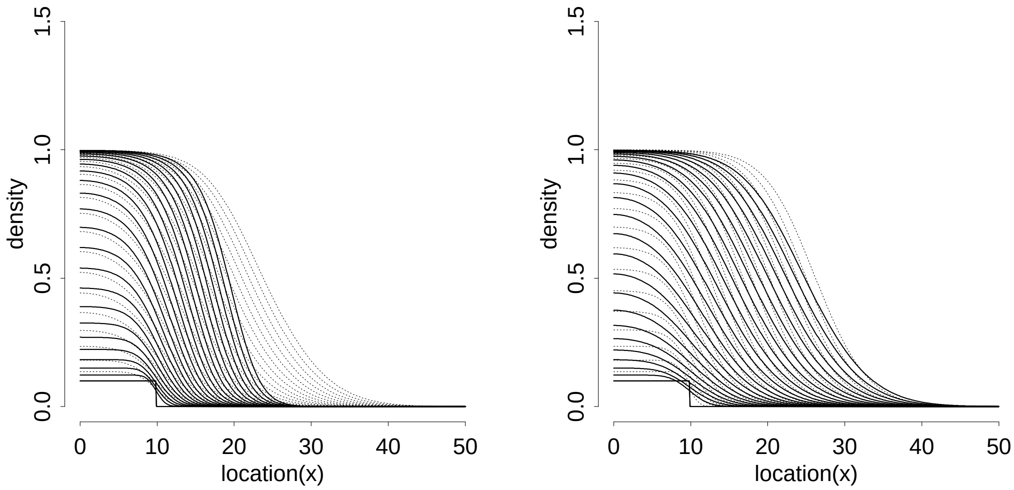

Figure 1: Numerical simulation of model (2.14) with with $r_1 = 0.25$, $r_2 = .02$, so that (2.15) is satisfied. The discrete time model (1.1) where Q is given by (2.14) ($\mathbf{u} = (u, v)$) was simulated numerically on a domain $-50 \leq x \leq 50$ with initial data $u = v = 0.1$ on $-10 \leq x \leq 10$ and $u = v = 0$ elsewhere. The solution is shown on the right half of the domain for times $n = 0$ to $n = 25$. Solid lines indicate u and dotted lines indicate v. (a) $d_1 = 0.5$, $d_2 = 2$ so that (2.16) is satisfied. Note that, as predicted in Example 2.1, the spreading speed of v is greater than that of u. (b) $d_1 = 2$, $d_2 = 0.5$ so that (2.16) is violated and (3.21) is satisfied. Note that there is a single spreading speed, as will be predicted by Example 3.3.

for every constant vector $\boldsymbol{\alpha}$ has finite nonnegative entries. We suppose the coordinates have been ordered so that these matrices are in Frobenius form. Let $\tilde{\lambda}_\sigma(\mu)$ denote the principal eigenvalue of the σth diagonal block of $\tilde{B}_\mu$, and define the numbers

$$\tilde{c}_\sigma := \inf_{\mu>0}\{\mu^{-1}\ln\tilde{\lambda}_\sigma(\mu)\}. \tag{2.18}$$

Note that $\tilde{c}_\sigma = -\infty$ when $\lambda_\sigma(0) < 1$. The following Lemma gives explicit expressions for the two speeds of the recursion (2.17).

Lemma 2.3 *Suppose that the truncated linear operator* $\min\{\tilde{L}[\mathbf{u}], \boldsymbol{\omega}\}$ *satisfies the Hypotheses 2.1 with* $\boldsymbol{\beta} = \boldsymbol{\omega}$*. Then the slowest spreading speed* $\tilde{c}$ *of the recursion (2.17) is* $\tilde{c}_1$*, and its fastest spreading speed* $\tilde{c}_+$ *is the largest of the numbers* $\tilde{c}_\sigma$*.*

The proof is straightforward, and will be presented in the Appendix.

Linear determinacy concerns the particular case when $\tilde{L}$ is the linearization M of Q at $\mathbf{0}$. By Lemma 2.3 the two speeds for the truncation of this operator are the slower speed

$$\bar{c} := \inf_{\mu>0}[\mu^{-1}\ln\lambda_1(\mu)]. \tag{2.19}$$

and the faster speed

$$\bar{c}_+ := \max_\sigma[\inf_{\mu>0}[\mu^{-1}\ln\lambda_\sigma(\mu)]]. \tag{2.20}$$

We shall say that the recursion (1.1) is **linearly determinate** if $c_+^* = \bar{c}_+$ and $c^* = \bar{c}$.

3 Sufficient conditions for linear determinacy and single speed.

We first generalize Lui's result that $\bar{c}$ is a lower bound for c^*.

Lemma 3.1 *If Q satisfies the Hypotheses 2.1, then*

$$c^* \geq \bar{c}, \tag{3.1}$$

and

$$c_+^* \geq \bar{c}_+. \tag{3.2}$$

Proof. Let ℓ_σ be the dimension of the σth diagonal block of B_0. For any ℓ_σ-vector-valued function $\mathbf{w}(x)$, we define the k-vector valued function $\tilde{\mathbf{w}}$ by saying that its components corresponding to the σth block of B_0 are those of $\mathbf{w}$, and its remaining components are zero. We now define the auxiliary operator

$$
\begin{aligned}
Q_\sigma[\mathbf{w}] \;:=\; & \text{the } \ell_\sigma\text{-vector whose entries are those coordinates of } Q[\tilde{\mathbf{w}}] \\
& \text{which correspond to the } \sigma\text{th block.}
\end{aligned}
$$

The linearization of Q_σ at $\mathbf{0}$ is the σth diagonal block of B_0. Because this matrix is irreducible, Lui's work shows that Q_σ has the single speed c_σ, and that

$$c_\sigma \geq \inf_{\mu>0}[\mu^{-1}\ln \lambda_\sigma(\mu)] = \bar{c}_\sigma. \tag{3.3}$$

(In proving this result, Lui used the special case $M^{(\kappa)} := [1-(1/\kappa)]M$ of the Hypothesis 2.1.vi. His proof is easily extended to one which only uses Hypothesis 2.1.vi. As Lemma 4.1 will show, our hypothesis has the advantage that it is automatically satisfied by the time 1 map of a reaction-diffusion model.)

Because $Q[P_\sigma[\mathbf{v}]] \leq Q[\mathbf{v}]$, the components of $Q[\mathbf{v}]$ corresponding to the σth block are bounded below by those of Q_σ applied to the corresponding components of $\mathbf{v}$. It follows that if $\mathbf{u}_n$ satisfies (1.1), then $P_\sigma \mathbf{u}_n$ spreads at a speed which is at least $\bar{c}_\sigma$. This together with Lemma 2.3 proves the inequalities (3.1) and (3.2), so the Lemma is proved.

Remarks: 1. It was shown by Lui that $\ln \lambda_1(\mu)$ is a convex function of μ. The reflection invariance of Q implies that $\lambda_1(\mu)$ is even in μ. Hence the minimum value of $\ln \lambda_1(\mu)$ occurs at $\mu = 0$. Since $\lambda_1(0) > 1$ by Hypothesis 2.1.v.b, we conclude that $\mu^{-1}\ln \lambda_1(\mu) > 0$. It follows from (2.19) that $\bar{c} \geq 0$, so that $c^* \geq 0$. In fact, a strengthening of Lui's proof of the convexity of $\ln \lambda_1(\mu)$ shows that if the support of at least one of the measures m_{ij} in the first block of the representation (2.2) of M contains at least one point other than the origin, then $\bar{c} > 0$ so that $c^* > 0$.

2. The inequality (3.2) implies that if the linearized problem does not have a single speed so that $\bar{c}_+ > \bar{c}$, then either the recursion (1.1) does not have a single speed or it is not linearly determinate.

Our main result gives a simple condition under which (1.1) has a single speed and is linearly determinate. We note that the matrices B_μ all have the same positive elements. In particular, B_μ again satisfies the Hypothesis 2.1.v.d. It follows as in Remark 3 after Hypotheses 2.1 that if for some μ, $\lambda_1(\mu) > \lambda_\sigma(\mu)$ for all $\sigma > 1$, then B_μ has an eigenvector $\boldsymbol{\zeta}(\mu) >> \mathbf{0}$ corresponding to the principal eigenvalue $\lambda_1(\mu)$.

Theorem 3.1 (Main result) *Suppose that Q satisfies the Hypotheses 2.1. Let the infimum in (2.19) be attained at $\bar{\mu} \in (0, \infty]$. Assume that either*

a. $\bar{\mu}$ is finite,

$$\lambda_1(\bar{\mu}) > \lambda_\sigma(\bar{\mu}) \text{ for all } \sigma > 1, \tag{3.4}$$

(i.e., for any initial distribution of the form $\mathbf{u}_0 = e^{-\bar{\mu}x}\boldsymbol{\alpha}$ all components of the solution of the linearized recursion $\mathbf{u}_{n+1} = M[\mathbf{u}_n]$ grow at the asymptotic rate $(\lambda_1(\bar{\mu}))^n e^{-\bar{\mu}x}$) and

$$Q[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})] \le M[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})]; \tag{3.5}$$

(i.e., while Q may have an Allee effect so that (1.5) is not satisfied for all $\mathbf{u}$, it does not display this effect for the particular function $e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})$.)

or

b. there is a sequence $\mu_\nu \nearrow \bar{\mu}$ such that for each ν

$$\lambda_1(\mu_\nu) > \lambda_\sigma(\mu_\nu) \text{ for all } \sigma > 1 \tag{3.6}$$

and

$$Q[e^{-\mu_\nu x}\boldsymbol{\zeta}(\mu_\nu)] \le M[e^{-\mu_\nu x}\boldsymbol{\zeta}(\mu_\nu)]. \tag{3.7}$$

Then

$$c_+^* = c^* = \bar{c} = \bar{c}_+,$$

so that (1.1) has a single speed and is linearly determinate.

Proof. Suppose condition (a) is valid. By definition

$$M[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})] = \lambda_1(\bar{\mu})e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu}) = e^{-\bar{\mu}(x-\bar{c})}\boldsymbol{\zeta}(\bar{\mu}).$$

The hypothesis (3.5) can therefore be written in the form

$$Q[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})] \le e^{-\bar{\mu}(x-\bar{c})}\boldsymbol{\zeta}(\bar{\mu}). \tag{3.8}$$

Let $\mathbf{0} \leq \mathbf{u}_0(x) << \boldsymbol{\beta}$ and let $\mathbf{u}_0 = \mathbf{0}$ for all sufficiently large x. The inequality $\boldsymbol{\zeta}(\bar{\mu}) >> 0$ shows that there is a ρ such that $\mathbf{u}_0 \leq e^{-\bar{\mu}x+\rho}\boldsymbol{\zeta}(\bar{\mu})$. Because Q is translation invariant, (3.8) shows that the sequence of functions $\mathbf{v}_n = e^{-\bar{\mu}(s-n\bar{c})+\rho}\boldsymbol{\zeta}(\bar{\mu})$ satisfies the recursive inequalities $Q[\mathbf{v}_n] \leq \mathbf{v}_{n+1}$. We note that if $\mathbf{u}_n \leq \mathbf{v}_n$, then $\mathbf{u}_{n+1} = Q[\mathbf{u}_n] \leq Q[\mathbf{v}_n] \leq \mathbf{v}_{n+1}$. Since $\mathbf{u}_0 \leq \mathbf{v}_0$, induction shows that $\mathbf{u}_n \leq \mathbf{v}_n$ for all n. Thus for any positive ϵ

$$\sup\{\mathbf{u}_n(x) : x \geq n(\bar{c}+\epsilon)\} \leq e^{-n\bar{\mu}\epsilon+\rho}\boldsymbol{\zeta}(\bar{\mu}). \tag{3.9}$$

This, together with the same inequality for $\mathbf{u}(-x)$, immediately implies the property (2.5). Therefore

$$\bar{c}+\epsilon \geq c_+^*. \tag{3.10}$$

Since ϵ is arbitrary, this inequality and (3.1) show that $\bar{c} \leq c^* \leq c_+^* \leq \bar{c}$, so that $c_+^* = c^* = \bar{c}$. (3.4) shows that $\bar{c}_\sigma < \bar{c}_1$ for all $\sigma > 1$, so that $\bar{c}_+ = \bar{c}$.

If condition (b) holds, the above argument gives the inequality (3.8) with $\bar{\mu}$ replaced by μ_ν and $\bar{c}$ replaced by $\ln\lambda_1(\mu_\nu)/\mu_\nu$. Thus

$$c_+^* \leq \ln\lambda_1(\mu_\nu)/\mu_\nu. \tag{3.11}$$

By definition, the limit of the right-hand side as $\nu\to\infty$ is $\bar{c}$. As above, $\bar{c}_+ = \bar{c}$. Thus we again have the inequalities $\bar{c} \leq c^* \leq c_+^* \leq \bar{c}$ which imply that $c_+^* = c^* = \bar{c}$. As above, $\bar{c}_+ = \bar{c}$, and the Theorem is established.

Remark: *Because c^* only depends on the behavior of $Q[\mathbf{u}]$ on functions which satisfy the inequalities $\mathbf{0} \leq \mathbf{u} \leq \boldsymbol{\beta}$, we may replace Q by the smallest translation invariant order preserving operator which agrees with Q on this set. We define the function $\min\{\mathbf{u}, \boldsymbol{\beta}\}$ by saying that its ith component at x is $\min\{u_i(x), \beta_i\}$. Then the condition (3.5) can be replaced by*

$$Q[\min\{e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu}), \boldsymbol{\beta}\}] \leq M[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})]. \tag{3.12}$$

This condition is useful if Q is undefined for functions which are not bounded by $\boldsymbol{\beta}$. In principle, the criterion (3.12) is less stringent than (3.5), but it may be harder to verify.

EXAMPLE 3.1 As in Example 2.1, we look at the system (2.14) with the conditions (2.15) on the parameters. An easy calculation shows that

$$B_\mu = \begin{pmatrix} e^{d_1\mu^2}(1+r_1) & 0 \\ e^{d_2\mu^2}r_2 & e^{d_2\mu^2}(1+r_2) \end{pmatrix}. \tag{3.13}$$

This matrix is already in block diagonal form with 1×1 blocks, and $\lambda_1(\mu) = e^{d_1\mu^2}(1+r_1)$. Thus $\mu^{-1}\ln\lambda_1(\mu) = d_1\mu + \mu^{-1}\ln(1+r_1)$ and we find that that

$$\bar{\mu} = \sqrt{[\ln(1+r_1)]/d_1} \tag{3.14}$$

and

$$\bar{c} = 2\sqrt{d_1\ln(1+r_1)}. \tag{3.15}$$

The Hypotheses 2.1 are satisfied. The condition (3.4) is

$$(1+r_1)^2 > (1+r_1)^{(d_2/d_1)}(1+r_2).$$

A sufficient condition for (3.5) is

$$\begin{aligned} &p[1+r_1(1+\min\{q,1\}-2\min\{p,1\})] \le (1+r_1)p \\ &q + r_2\max\{1-q,0\}(p+q) \le q + r_2(p+q) \end{aligned}$$

when $(p,q) = e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})$. The second inequality is satisfied for any nonnegative (p,q). The first inequality is satisfied when either $q \le 2p$ or $p \ge 1/2$. Thus the condition is valid when $\zeta_2(\bar{\mu}) \le 2\zeta_1(\bar{\mu})$. We see from (3.14) and the form (3.13) of B_μ that $\boldsymbol{\zeta}(\bar{\mu})$ is proportional to

$$\left((1+r_1)^2 - (1+r_1)^{d_2/d_1}(1+r_2), (1+r_1)^{d_2/d_1}r_2\right).$$

Therefore (3.5) is satisfied when

$$(1+r_1)^{2-(d_2/d_1)} \ge 1 + (3/2)r_2. \tag{3.16}$$

Since this condition is stronger than the above form of condition (3.4), the inequality (3.16) implies both conditions of Theorem 3.1. That is, when this inequality is valid, $c_+^* = c^* = \bar{c}_+ = \bar{c} = 2\sqrt{d_1\ln(1+r_1)}$.

Theorem 3.1 gives conditions which are so strong that not only is $c_+^* = c^*$ so that there is a single spreading speed, but also linear determinacy is valid. It is useful to have a weaker set of conditions which still implies that $c_+^* = c^*$. Such conditions will require the following additional Hypothesis.

Hypotheses 3.1 *The operator Q has one of the two properties*

a. the family of functions $Q[\mathbf{v}]$ with $\mathbf{v}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ is equicontinuous; or

b. if the nondecreasing sequence $\mathbf{v}_n$ in $\mathcal{C}_{\boldsymbol{\beta}}$ converges to $\mathbf{v}$, then $Q[\mathbf{v}]$ is defined, and $Q[\mathbf{v}_n]$ converges to $Q[\mathbf{v}]$.

Remark. This Hypothesis is always satisfied when $\mathcal{H}$ is discrete.

To obtain sufficient conditions for having a single speed, we shall make use of the following lemma.

Lemma 3.2 *Suppose that Q satisfies the Hypotheses 2.1 and 3.1. Let $\boldsymbol{\nu} \in \mathcal{C}_{\boldsymbol{\beta}}$ be a constant equilibrium other than $\mathbf{0}$ or $\boldsymbol{\beta}$. If there exists an operator $Q^{(\boldsymbol{\nu})}$ which satisfies Hypotheses 2.1 and has the additional properties*

i. $Q^{(\boldsymbol{\nu})}[\mathbf{u}] \geq Q[\mathbf{u}]$ for all $\mathbf{u}$ in $\mathcal{C}_{\boldsymbol{\beta}}$*;*

ii. $Q^{(\boldsymbol{\nu})}[\mathbf{u}] = Q[\mathbf{u}]$ when $\mathbf{u} \geq \boldsymbol{\nu}$*;*

iii. the recursion (1.1) with Q replaced by $Q^{(\boldsymbol{\nu})}$ has a single speed $c_{\boldsymbol{\nu}}$.

Then $\mathbf{a}(c^*; \infty)$ cannot be equal to $\boldsymbol{\nu}$.

Proof. Suppose for the sake of contradiction that $\mathbf{a}(c^*; \infty) = \boldsymbol{\nu}$. By (i) the $\mathbf{a}_n^{(\boldsymbol{\nu})}$ defined by (2.7) with Q replaced by $Q^{(\boldsymbol{\nu})}$ and with $\mathbf{a}_0^{(\boldsymbol{\nu})} = \mathbf{a}_0$ are at least as large as the $\mathbf{a}_n$, and hence

$$c_+^* \leq c_{\boldsymbol{\nu}}.$$

If the Hypothesis 3.1.b is valid, we can take limits of both sides of the defining equation (2.7) to see that $\mathbf{a}(c^*; x)$ satisfies the equation

$$\mathbf{a} = \max\{\mathbf{a}_0, T_{-c^*}[Q[\mathbf{a}]]\}. \tag{3.17}$$

If, instead, the Hypothesis 3.1.a holds, it is easily seen that $\mathbf{a}(c^*; x)$ is continuous. Then Dini's theorem shows that the $\mathbf{a}_n$ converge to $\mathbf{a}$ uniformly on bounded sets, and (3.17) follows from (2.7) and Hypothesis 2.1.iv

Since $\mathbf{a}(c^*, x)$ is non-increasing in x and has the value $\boldsymbol{\nu}$ at infinity, we conclude that $\mathbf{a} \geq \boldsymbol{\nu}$. Then (ii) shows that $Q^{(\boldsymbol{\nu})}[\mathbf{a}] = Q[\mathbf{a}]$, so that $\mathbf{a}(c^*; x) = \max\{\mathbf{a}_0(x), T_{-c^*}[Q^{(\boldsymbol{\nu})}[\mathbf{a}]](x)\}$. We see from the recursion for $\mathbf{a}^{(\boldsymbol{\nu})}$ and the order-preserving property of $Q^{(\boldsymbol{\nu})}$ that if $\mathbf{a}_n^{(\boldsymbol{\nu})}(c^*; x) \leq \mathbf{a}(c^*; x)$, then

$$\mathbf{a}_{n+1}^{(\boldsymbol{\nu})} \leq \max\{\mathbf{a}_0, T_{-c^*}[Q^{(\boldsymbol{\nu})}[\mathbf{a}]]\} = \mathbf{a}.$$

Since $\mathbf{a}_0^{(\boldsymbol{\nu})} = \mathbf{a}_0 \leq \mathbf{a}$, induction shows that all the $\mathbf{a}_n^{(\boldsymbol{\nu})}$, and hence also $\mathbf{a}^{(\boldsymbol{\nu})}(c^*; x)$, are bounded by $\mathbf{a}(c^*; x)$. Therefore $\mathbf{a}^{(\boldsymbol{\nu})}(c^*; \infty) \leq \boldsymbol{\nu}$, and hence $c_{\boldsymbol{\nu}} \leq c^*$. Thus we have the inequalities $c_{\boldsymbol{\nu}} \leq c^* \leq c_+^* \leq c_{\boldsymbol{\nu}}$. This shows that

$c_+^* = c^*$, which implies that $\mathbf{a}(c^*;\infty) = \mathbf{0}$. This contradicts the assumption that $\mathbf{a}(c^*;\infty) = \boldsymbol{\nu}$, and hence proves Lemma 3.2.

Since Theorem 3.1 gives a sufficient condition for a recursion to have a single speed, combining it with Lemma 3.2 immediately gives a sufficient condition for $c_+^* = c^*$. We recall that $P_1[\boldsymbol{\alpha}]$ is the projection of the vector $\boldsymbol{\alpha}$ which replaces those components which do not correspond to the upper left block of the matrix B_0 by zeros.

Theorem 3.2 *Suppose that Hypotheses 2.1 and 3.1 are satisfied and that for every constant solution $\boldsymbol{\nu}$ of $Q[\boldsymbol{\nu}] = \boldsymbol{\nu}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ other than $\mathbf{0}$ and $\boldsymbol{\beta}$ the operator*

$$Q^{(\boldsymbol{\nu})}[\mathbf{v}] := P_1 Q[\max\{\mathbf{v}, \boldsymbol{\nu}\}] + (I - P_1)Q[\mathbf{v}]$$

satisfies the conditions of Theorem 3.1. Then $c_+^* = c^*$ so that the recursion (1.1) has a single speed.

Proof. Theorem 3.1 shows that $Q^{(\boldsymbol{\nu})}$ has a single speed, so that it satisfies the conditions of Lemma 3.2. Therefore $\mathbf{a}(c^*;\infty)$ cannot be any equilibrium other than $\mathbf{0}$. Therefore $c_+^* = c^*$, and the Theorem is proved.

EXAMPLE 3.2 As in Examples 2.1 and 3.1, we consider the recursion for the operator (2.14) with the conditions (2.15). There is an extra equilibrium at $\boldsymbol{\nu} = (0, 1)$. The matrix $B_\mu^{(\boldsymbol{\nu})}$ of the operator

$$Q^{(\boldsymbol{\nu})}[(u,v)] = \begin{pmatrix} \int_{-\infty}^{\infty} (4\pi d_1)^{-1/2} e^{-(x-y)^2/(4d_1)} u(y)[1 + r_1(1 - 2\min\{u(y), 1\} + 1)]dy \\ \int_{-\infty}^{\infty} (4\pi d_2)^{-1/2} e^{-(x-y)^2/(4d_2)} [v(y) + r_2 \max\{1 - v(y), 0\}(u(y) + v(y))]dy \end{pmatrix} \tag{3.18}$$

is

$$B_\mu^{(\boldsymbol{\nu})} = \begin{pmatrix} e^{d_1\mu^2}(1 + 2r_1) & 0 \\ e^{d_2\mu^2} r_2 & e^{d_2\mu^2}(1 + r_2) \end{pmatrix}.$$

The requirement that $Q^{(\boldsymbol{\nu})}$ satisfy the conditions of Theorem 3.1 again reduces to $\zeta_2 \leq 2\zeta_1$, where now $\boldsymbol{\zeta}$ is the principal eigenvector of $B_\mu^{(\boldsymbol{\nu})}$ at $\mu^* = \sqrt{d_1^{-1} \ln(1 + 2r_1)}$. This condition can be written as

$$(1 + 2r_1)^{2 - (d_2/d_1)} \geq 1 + r_2. \tag{3.19}$$

This is less stringent than the condition (3.16). Of course, this condition also implies less. Namely it implies the property $c_+^* = c^*$ but not linear determinacy.

Note that because $2-(d_2/d_1) \le d_1/d_2$, the condition (3.19) is not satisfied when $d_2 \ln(1+r_2) > d_1 \ln(1+2r_1)$, which was shown in Example 2.1 to lead to a violation of the property $c_+^* = c^*$.

The following alternative to Theorem 3.1 can also be used to prove the single-speed linear determinacy in some cases.

Lemma 3.3 *Suppose that Q satisfies the Hypotheses (2.1) and (3.1), and that there is an order preserving translation and reflection invariant linear operator $\tilde{L}$ which satisfies the conditions of Lemma 2.3 and has the additional properties*

i. $Q[\mathbf{u}] \le \tilde{L}[\mathbf{u}]$ for all $\mathbf{u}$ in $\mathcal{C}_{\boldsymbol{\beta}}$.

ii. $P_1[\tilde{L}[\mathbf{u}]] = P_1[M[\mathbf{u}]]$ where M is the linearization of Q at $\mathbf{0}$ and P_1 is the orthogonal projection onto the coordinates corresponding to its upper left diagonal block.

iii. $\tilde{c}_1 \ge \tilde{c}_\sigma$ for all σ, where $\tilde{c}_\sigma$ is defined by (2.18).

Then $c_+^* = c^* = \bar{c} = \bar{c}_+$, so that the recursion (1.1) has a single speed and is linearly determinate.

Proof. By Lemma 2.3 and (iii), the truncated operator $\min\{\tilde{L}[\mathbf{u}], \alpha\tilde{\boldsymbol{\zeta}}(0)i\}$ where $\alpha\tilde{\boldsymbol{\zeta}}(0) \ge \boldsymbol{\beta}$ has the single speed $\tilde{c}_1$. By (ii), this value is the same as $\bar{c}$. Since (i) implies that $M[u] \le \tilde{L}[u]$, we have $\bar{c}_+ \le \tilde{c}_1 = \bar{c} \le \bar{c}_+$, so that $\bar{c}_+ = \bar{c}$. Also by (i), $c_+^* \le \tilde{c}_1 = \bar{c} \le c^*$, so that $c_+^* = c^* = \bar{c} = \bar{c}_+$. This proves the Lemma.

The conditions (i) and (ii) of this lemma imply that the components of $Q[\mathbf{a}]$ which correspond to the first block of B_0 are independent of the remaining components of $\mathbf{a}$, which is rarely true of a biological model. However, combining Lemma 3.3 with Lemma 3.2 yields another sufficient condition for the existence of a single speed.

Theorem 3.3 *Suppose that Q satisfies the Hypotheses 2.1 and 3.1, and that for each constant equilibrium $\boldsymbol{\nu}$ in $\boldsymbol{\beta}$ other than $\mathbf{0}$ or $\boldsymbol{\beta}$ the operator $Q^{(\boldsymbol{\nu})}[\mathbf{u}] = P_1Q[\max\{\mathbf{u}, \boldsymbol{\nu}\}] + (I - P_1)Q[\mathbf{u}]$ satisfies the conditions of Lemma 3.3.*

Then the recursion (1.1) has a single speed.

EXAMPLE 3.3 The system (2.14) in Examples 2.1, 3.1 and 3.2 has the extra equilibrium $\boldsymbol{\nu} = (0,1)$. The operator $Q^{(\boldsymbol{\nu})}$ is given by replacing v_n by 1 in the first equation. It certainly satisfies the Hypotheses 2.1 and 3.1. The conditions (i) and (ii) of Lemma 3.3 are satisfied for this operator when

$$\tilde{L}[(u,v)] := \begin{pmatrix} \int_{-\infty}^{\infty} (4\pi d_1)^{-1/2} e^{-(x-y)^2/(4d_1)} (1+2r_1) u(y) dy \\ \int_{-\infty}^{\infty} (4\pi d_2)^{-1/2} e^{-(x-y)^2/(4d_2)} [r_2 u(y) + (1+r_2) v(y)] dy \end{pmatrix}. \tag{3.20}$$

We easily see that $\tilde{c}_1 = 2\sqrt{d_1 \ln(1+2r_1)}$, while $\tilde{c}_2 = 2\sqrt{d_2 \ln(1+r_2)}$. Thus condition (iii) is satisfied so that $c_+^* = c^*$ when

$$d_2 \ln(1+r_2) \le d_1 \ln(1+2r_1). \tag{3.21}$$

Thus Theorem 3.3 shows that this inequality implies the existence of a single speed.

This inequality just says that (2.16) is violated. Thus for this particular system we have obtained the precise parameter set where there is a single spreading speed.

We can use Theorem 3.3 to show that the model (1.10) for the invasion of an equilibrium population of the second species by a competing species always has a single speed. In fact, we find a simple condition on the migration kernel which produces a hair-trigger effect, in the sense that every invasion is successful. We assume that $\alpha_1 < 1$, so that the original equilibrium is invadable.

Theorem 3.4 *Let $0 < \alpha_1 < 1$ and let all the other parameters in the system (1.10) be positive. Then the cooperative system*

$$\begin{aligned} u_{n+1}(x) &= \int_{-\infty}^{\infty} \frac{(1+\rho_1) u_n(x-y)}{1+\rho_1(\alpha_1 + u_n(x-y) - \alpha_1 v_n(x-y))} k_1(y, dy) \\ v_{n+1}(x) &= \int_{-\infty}^{\infty} \frac{v_n(x-y) + \rho_2 \alpha_2 u_n(x-y)}{1+\rho_2(1 - v_n(x-y) + \alpha_2 u_n(x-y))} k_2(y, dy), \end{aligned} \tag{3.22}$$

which is obtained by making the substitution $u_n = p_n$, $v_n = 1 - q_n$ in the model (1.10), has a single speed c^*.

Moreover, if either the habitat $\mathcal{H}$ is the real line and there is an open interval on which the measure k_1 has a positive density or $\mathcal{H}$ is discrete and every number in $\mathcal{H}$ can be written as a sum of finitely many numbers to which k_1 assigns positive weights (with repetitions allowed), then there is a *hairtrigger effect in the sense that the property (2.6) holds as long as* $\mathbf{u}_0$ *is not identically zero.*

Proof. The dominated convergence theorem for measurable spaces [19] implies Hypothesis 3.1.b.

The equilibria of the system (3.22) are (0,0), (1,1), (0,1), and $((1-\alpha_1)/(1-\alpha_1\alpha_2), \alpha_2(1-\alpha_1)/(1-\alpha_1\alpha_2))$. When $\alpha_2 < 1$, the latter point is strictly between (0,0) and (1,1). Therefore it is the point $\boldsymbol{\beta}$, and there is no extra equilibrium in $\mathcal{C}_{\boldsymbol{\beta}}$. Thus the result follows from Proposition 2.1.

If $\alpha_2 = 1$, the fourth equilibrium coincides with the third, while if $\alpha_2 > 1$, the q-coordinate of the fourth equilibrium is negative so that it no longer relevant. In these cases, $\boldsymbol{\beta} = (1,1)$ and the equilibrium $\boldsymbol{\nu} = (0,1)$ lies in $\mathcal{C}_{\boldsymbol{\beta}}$. The operator $Q^{(\boldsymbol{\nu})}$ is obtained by replacing v_n by 1 in the right-hand side of the first equation (3.22). We note that for (u,v) in $\mathcal{C}_{\boldsymbol{\beta}}$ the numerators of the two fractions in (3.22) are nonnegative and the denominators are at least equal to 1. Therefore the linear operator

$$\tilde{L}[(u,v)] := \begin{pmatrix} \int_{-\infty}^{\infty}(1+\rho_1)u_n(x-y)k_1(y,dy) \\ \int_{-\infty}^{\infty}[v_n(x-y)+\rho_2\alpha_2 u_n(x-y)]k_2(y,dy) \end{pmatrix} \tag{3.23}$$

has the property (i) of Lemma 3.3 with Q replaced by $Q^{(\boldsymbol{\nu})}$. It is easily verified that it also has the property (ii).

To verify property (iii), we note that because $k_1(y,dy)$ is reflection invariant, $\tilde{\lambda}_1(\mu) = (1+\rho_1)\int_{-\infty}^{\infty} \cosh \mu y\ k_1(y,dy) > 1$, so that $\tilde{c}_1 \geq 0$. On the other hand, $\tilde{\lambda}_2(\mu) = \int_{-\infty}^{\infty} \cosh \mu y\ k_2(y,dy)$. This function is even and has the value 1 at 0. Therefore $\mu^{-1}\ln \tilde{\lambda}_2(\mu)$ has the limit 0 as μ approaches 0. It follows that $\tilde{c}_2 = 0 \leq \tilde{c}_1$. Thus property (iii) of Theorem 3.3 is also satisfied, and the equation $c_+^* = c^*$ is established.

To prove the hairtrigger effect, we note that for $0 \leq u \leq (1-\alpha_1)/2$ and $0 \leq v \leq 1$, the operator Q determined by the right-hand sides of (3.22) satisfies

$$Q[(u,v)] \geq \begin{pmatrix} \min\{(1-\alpha_1)/2, \dfrac{1+\rho_1}{1+\rho_1(1+\alpha_1)/2}\int_{-\infty}^{\infty} u(x-y)k_1(y,dy)\} \\ \\ \dfrac{\rho_2\alpha_2}{1+\rho_2[1+\alpha_2(1-\alpha_1)/2]}\int_{-\infty}^{\infty} u(x-y)k_2(y,dy) \end{pmatrix}. \tag{3.24}$$

If the kernel k_1 satisfies the additional properties in the last paragraph of the statement of the Theorem, then Theorem 6.5 of [21] applied to the first equation shows that if $\mathbf{u}_0$ is positive somewhere, the solution of the recursion (1.1) with Q replaced by the right-hand side of (3.24) converges to $((1-\alpha_1)/2, \rho_2\alpha_2(1-\alpha_1)/[2+2\rho_2+\rho_2\alpha_2(1-\alpha_1)])$, and the convergence is uniform on every bounded interval. Since this solution is a lower bound for the solution of (3.22) with the same initial values, we see that for sufficiently large n, (u_n, v_n) lies above a fixed constant vector on an arbitrarily large set, so that the last statement of Theorem 3.4 follows from Lemma 2.2.

EXAMPLE 3.4. To see the importance of the extra condition for the hairtrigger effect, choose the measures $k_1 = k_2$ with

$$\int_{-\infty}^{\infty} \phi(y)k_i(y, dy) := \tau h^{-2}[\phi(h) + \phi(-h)] + (1 - 2\tau h^{-2})\phi(0),$$

and $r_i = \tau s_i$, where $h > 0$ and $0 < 2\tau h^{-2} < 1$. Then the system (3.22) is a somewhat unusual finite-difference approximation with time step τ and space step h to a reaction diffusion system. The first statement of Theorem 3.4 is valid. If $\mathcal{H}$ is the set of integral multiples of h, the additional condition is also satisfied, so that there is a hairtrigger effect. If, on the other hand, $\mathcal{H}$ contains all the multiples of $h/2$, the extra condition is violated. In fact, we see that if u_0 vanishes at all the odd multiples of $h/2$, then u_n has the same property for all n, which shows that there is no hairtrigger effect.

4 Applications to reaction-diffusion systems

In this section, we shall show how to apply the results of the previous sections to a weakly coupled reaction-diffusion system of the form

$$\begin{aligned} &[u_i]_{,t} = d_i[u_i]_{,xx} + f_i(\mathbf{u}), \quad i = 1, 2, ..., k, \\ &\mathbf{u}(t, x) = \mathbf{u}_0(x), \end{aligned} \tag{4.1}$$

where each d_i is a nonnegative constant, and $\mathbf{f} = (f_1, f_2, ..., f_k)$ is independent of x and t. This model can be put into the form (1.1) by letting Q be its time τ map. That is, $Q_\tau[\mathbf{u}_0]$ is defined to be the value $\mathbf{u}(x, \tau)$ of the solution of this initial value problem at time τ. The sequence of functions $\mathbf{u}_n(x) := \mathbf{u}(x, n\tau)$ clearly satisfies the recursion (1.1) with Q replaced by Q_τ.

The following theorem shows that the spreading speed of the time 1 map of a weakly coupled parabolic system also gives the spreading speed for solutions of the system itself. Note that this theorem is valid without the assumption that the system is cooperative. It is, of course, only useful if the existence of a single spreading speed can be established.

Theorem 4.1 *Suppose that* $\mathbf{f}(\mathbf{0}) = \mathbf{0}$, $\mathbf{f}(\boldsymbol{\beta}) = \mathbf{0}$, $\boldsymbol{\beta} >> \mathbf{0}$, *and* $\mathbf{f}(\boldsymbol{\alpha})$ *is continuous on the set* $\mathbf{0} \le \boldsymbol{\alpha} \le \boldsymbol{\beta}$. *Let* Q_τ *be the time* τ *map of the weakly coupled, possibly degenerate, parabolic system (4.1) with constant coefficients. Suppose that the set* $\mathcal{C}_{\boldsymbol{\beta}} = \{\mathbf{u}(x) : \mathbf{0} \le \mathbf{u} \le \boldsymbol{\beta}\}$ *is an invariant set of (4.1) in the sense that any solution which starts in* $\mathcal{C}_{\boldsymbol{\beta}}$ *remains there. Also suppose that for each* τ *the recursion (1.1) with* $Q = Q_\tau$ *has a single speed* c^*_τ *with the properties (2.6) and(2.5). If* c^* *is defined to be* c^*_1, *then* $c^*_\tau = \tau c^*$, *and for any initial function* $\mathbf{u}_0(x)$ *in* $\mathcal{C}_{\boldsymbol{\beta}}$ *which vanishes outside a bounded set the solution of (4.1) has the properties that for each positive* ϵ

$$\lim_{t\to\infty}\left[\max_{|x|\ge t(c^*+\epsilon)} |\mathbf{u}(x)|\right] = 0, \tag{4.2}$$

and for any strictly positive constant vector $\boldsymbol{\omega}$ *there is a positive* $R_{\boldsymbol{\omega}}$ *with the property that if* $\mathbf{u}_0 \ge \boldsymbol{\omega}$ *on an interval of length* $2R_{\boldsymbol{\omega}}$, *then*

$$\lim_{t\to\infty}\left[\max_{|x|\le t(c^*-\epsilon)} |\boldsymbol{\beta} - \mathbf{u}(x)|\right] = 0. \tag{4.3}$$

The proof of this Theorem is given in the Appendix.

Remark. If the time one map Q_1 has the speeds $c^*_+ > c^*$, a similar proof gives the analogs of formulas (2.10) to (2.13).

We wish to show how Theorem 3.1 can be applied to the special case where Q is the time 1 map of the reaction diffusion model (4.1). For this purpose, we need hypotheses on $\mathbf{f}$ which imply that Q satisfies the Hypotheses 2.1. Note that a constant equilibrium $\boldsymbol{\nu}$ is now a vector such that $\mathbf{f}(\boldsymbol{\nu}) = \mathbf{0}$.

We observe that if a square matrix A is irreducible and has nonnegative off-diagonal elements, then there is a constant α such that $A + \alpha I$ is irreducible and has nonnegative entries. Hence this matrix has a positive principal eigenvalue δ with a positive eigenvector. We shall call the eigenvalue $\delta - \alpha$ of A, which has the same positive eigenvector, the principal eigenvalue of A. .

Hypotheses 4.1

i. $\mathbf{f}(\mathbf{0}) = \mathbf{0}$, *and there is a* $\boldsymbol{\beta} >> \mathbf{0}$ *such that* $\mathbf{f}(\boldsymbol{\beta}) = \mathbf{0}$ *which is minimal in the sense there are no* $\boldsymbol{\nu}$ *other than* $\mathbf{0}$ *and* $\boldsymbol{\beta}$ *such that* $f(\boldsymbol{\nu}) = \mathbf{0}$ *and* $\mathbf{0} << \boldsymbol{\nu} \le \boldsymbol{\beta}$.

ii. *The system (4.1) is cooperative; i.e.,* $f_i(\boldsymbol{\alpha})$ *is nondecreasing in all components of* $\boldsymbol{\alpha}$ *with the possible exception of the ith one.*

iii. $\mathbf{f}$ *does not depend explicitly on either x or t, and the coefficients d_i are constant and nonnegative.*

iv. $\mathbf{f}(\boldsymbol{\alpha})$ *is continuous and piecewise continuously differentiable in $\boldsymbol{\alpha}$ for $\mathbf{0} \leq \boldsymbol{\alpha} \leq \boldsymbol{\beta}$ 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.*

It is obvious from elementary properties of parabolic systems that the first four Hypotheses 4.1 imply the corresponding Hypotheses 2.1. It is easily seen that the linearization M at $\mathbf{0}$ of the time 1 map Q_1 is the time 1 map of the linearized system

$$v_{i,t} = d_i v_{i,xx} + (\mathbf{f}'(\mathbf{0})\mathbf{v})_i \tag{4.4}$$

Separation of variables shows that if the initial data are of the form $e^{-\mu x}\boldsymbol{\alpha}$, then the solution of this system has the form $e^{-\mu x}\boldsymbol{\eta}(t)$, where the vector-valued function $\boldsymbol{\eta}$ is the solution of the system of ordinary differential equations with constant coefficients

$$\boldsymbol{\eta}_{,t} = C_\mu \boldsymbol{\eta} \tag{4.5}$$

with $\boldsymbol{\eta}(0) = \boldsymbol{\alpha}$. The coefficient matrix is given by

$$C_\mu = \operatorname{diag}\left(d_i \mu^2\right) + \mathbf{f}'(\mathbf{0}), \tag{4.6}$$

where $\mathbf{f}'(\mathbf{0})$ is the Jacobian matrix with entries $f_{i,u_j}(\mathbf{0})$. The off-diagonal entries of C_μ are nonnegative because the system is cooperative.

By definition, the matrix B_μ for the time 1 map M of (4.5) is given by the formula

$$B_\mu = \exp\left[C_\mu\right]. \tag{4.7}$$

It is easily seen that $\lambda_\sigma(\mu) = e^{\gamma_\sigma(\mu)}$ where γ_σ is the principal eigenvalue of the σth diagonal block of the matrix C_μ defined by (4.6). Thus Hypothesis 4.1.v implies Hypothesis 2.1.v

The following Lemma, whose proof appears in the Appendix, states that Hypothesis 2.1.vi is automatically satisfied by the time 1 map of the system (4.1).

Lemma 4.1 *If* $\mathbf{f}$ *satisfies the Hypotheses 4.1, then there exists a family* $M^{(\kappa)}$ *of linear maps which satisfies the Hypothesis 2.1.vi.*

The following theorem is thus an immediate corollary of Theorem 3.1. Because $\lambda_1(\mu) = e^{\gamma_1(\mu)}$, the formula (2.19) for $\bar{c}$ becomes

$$\bar{c} := \inf_{\mu>0}[\gamma_1(\mu)/\mu].$$

(There is an analogous formula for $\bar{c}_+$.) Let $\bar{\mu} \in (0, \infty]$ again denote the value of μ at which this infimum is attained, and let $\boldsymbol{\zeta}(\mu)$ be the eigenvector of B_μ which corresponds to the eigenvalue $\lambda_1(\mu)$.

Theorem 4.2 *Suppose that* $\mathbf{f}$ *satisfies the Hypotheses 4.1. Assume that either*

(a) $\bar{\mu}$ *is finite,*

$$\gamma_1(\bar{\mu}) > \gamma_\sigma(\bar{\mu}) \text{ for all } \sigma > 1, \tag{4.8}$$

and

$$\mathbf{f}(\rho\boldsymbol{\zeta}(\bar{\mu})) \leq \rho\mathbf{f}'(0)\boldsymbol{\zeta}(\bar{\mu}) \tag{4.9}$$

for all positive ρ*;*

or

(b) There is a sequence $\mu_\nu \nearrow \bar{\mu}$ *such that for each* ν *the inequalities (4.8) and (4.9) with* $\bar{\mu}$ *replaced by* μ_ν *are valid.*

Then $c_+^* = c^* = \bar{c} = \bar{c}_+$*, so that the problem (4.1) has a single speed and is linearly determinate.*

Proof. The inequality (4.9) implies that $e^{\gamma_1(\bar{\mu})t-\mu x}\boldsymbol{\zeta}(\bar{\mu})$ is a supersolution of (4.1). The comparison principle for parabolic systems then implies that $Q_1[e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})] \leq e^{\gamma_1(\bar{\mu})}e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})$, and the result follows from Theorem 3.1.

Remark: Just as the condition (3.5) can be replaced by the condition (3.12) which depends only on the behavior of Q in $\mathcal{C}_{\boldsymbol{\beta}}$, the condition (4.9) can be replaced by the condition

$$\mathbf{f}(\min\{\rho\boldsymbol{\zeta}(\bar{\mu}), \boldsymbol{\beta}\}) \leq \rho\{\mathbf{f}'(\mathbf{0})\boldsymbol{\zeta}(\bar{\mu})\}, \tag{4.10}$$

which depends only on the values of $\mathbf{f}$ in $\mathcal{C}_{\boldsymbol{\beta}}$. This inequality implies that $\mathbf{w} := \min\{e^{-\bar{\mu}(x-\bar{c}t)}\boldsymbol{\zeta}(\bar{\mu}), \boldsymbol{\beta}\}$ is a supersolution. Note that when $\rho\zeta_i(\bar{\mu}) \leq$

β_i, the monotonicity of f_i shows that (4.9) implies the ith component of this condition. On the other hand, when $\rho\zeta_i(\bar{\mu}) \geq \beta_i$, the monotonicity of f_i implies that $f_i(\min\{\rho\boldsymbol{\zeta}(\bar{\mu}), \boldsymbol{\beta}\}) \leq \mathbf{0}$, so that the ith component of the inequality (4.10) is automatically satisfied. Thus the condition (4.10) is more easily satisfied than (4.9).

EXAMPLE 4.1 The competition system

$$\begin{aligned} p_{,t} &= p_{,xx} + p(4 - 4p - q) \\ q_{,t} &= d_2 q_{,xx} + q[(1-q)(4q-3) - 8p] \end{aligned} \tag{4.11}$$

is transformed into the cooperative system

$$\begin{aligned} u_{,t} &= u_{,xx} + u(3 - 4u + v) \\ v_{,t} &= d_2 v_{,xx} + (1-v)[v(4v-1) + 8u]. \end{aligned} \tag{4.12}$$

by the change of variables $u = p,\ v = 1 - q$. An easy calculation shows that

$$C_\mu = \begin{pmatrix} \mu^2 + 3 & 0 \\ 8 & d_2\mu^2 - 1 \end{pmatrix} \tag{4.13}$$

The Hypotheses 4.1 are clearly satisfied. We find that $\bar{\mu} = \sqrt{3}$, $\bar{c} = 2\sqrt{3}$, and the conditions (4.8) and (4.10) are satisfied when

$$d_2 \leq 2/3. \tag{4.14}$$

Thus $c_+^* = c^* = 2\sqrt{3}$ whenever $d_2 \leq 2/3$.

We recall that P_1 is the orthogonal projection to the coordinates which correspond to the first block of $C_0 = \mathbf{f}'(\mathbf{0})$. By applying Lemma 3.1 to the operator $Q^{(\boldsymbol{\nu})}$ which is the time one map of the equations obtained by replacing $\mathbf{f}(\mathbf{u})$ by $P_1\mathbf{f}(\max\{\mathbf{u}, \boldsymbol{\nu}\} + (I - P_1)\mathbf{f}(\mathbf{u})$ and using Theorem 4.2, we obtain the following analog of Theorem 3.2.

Theorem 4.3 *Suppose that the Hypotheses 4.2 are satisfied. If every zero $\boldsymbol{\nu}$ of $\mathbf{f}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ other than $\mathbf{0}$ or $\boldsymbol{\beta}$ has the property that the system obtained from (4.1) by replacing the argument $\mathbf{u}$ of $\mathbf{f}$ in the equations which correspond to the upper left block of B_0 by $\max\{\mathbf{u}, \boldsymbol{\nu}\}$ satisfies the conditions of Theorem 4.2, then $c_+^* = c^*$, so that the system (4.1) has a single speed.*

EXAMPLE 4.2 As in Example 4.1, we consider the cooperative system (4.12), which comes from (4.11) by the usual change of variables. The system now has four equilibrium states: (0,0), which corresponds to the pre-invasion state $p = 0,\ q = 1$; (0,1), which corresponds to the extinction state $p = q = 0$; (1,1), which corresponds to $p = 1,\ q = 0$, so that the invader has driven the invaded species to extinction; and (0,1/4). Thus $\boldsymbol{\beta} = (1,1)$, and there are two extra equilibria (0,1) and (0,1/4) in $\mathcal{C}_{\boldsymbol{\beta}}$. In order to apply Theorem 4.3 we need to check for what values of d_2 the two operators $Q^{(\boldsymbol{\nu})}$ satisfy the conditions (4.8) and (4.10) of Theorem 4.2. The operator $Q^{(0,1)}$ is the time-one map of the system which is obtained from (4.12) by replacing v by 1 in the first equation. The calculations which gave the condition (4.14) now give the condition $d_2 \le 1$.

The operator $Q^{(0,1/4)}$ is the time-one map of the system obtained from (4.12) by replacing v by $\max\{v, 1/4\}$ in the first equation. This leads to the criterion $d_2 \le 10/13$. The conditions of Theorem 4.3 are thus satisfied when

$$d_2 \le 10/13. \tag{4.15}$$

This condition, which is less stringent than (4.14), implies that $c_+^* = c^*$, so that the system (4.11) has a single speed.

We can also apply Lemma 3.2 to $Q^{(\boldsymbol{\nu})}$ to obtain the following analog of Theorem 3.3.

Lemma 4.2 *Suppose that for each zero $\boldsymbol{\nu}$ of $\mathbf{f}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ other than $\mathbf{0}$ or $\boldsymbol{\beta}$ there is a constant matrix $E^{(\boldsymbol{\nu})}$ with the properties*

i. $E^{(\boldsymbol{\nu})} \ge P_1\mathbf{f}'(\boldsymbol{\nu}) + (I - P_1)\mathbf{f}'(\mathbf{0})$ *componentwise;*

ii. $P_1 E^{(\boldsymbol{\nu})} = P_1\mathbf{f}'(\boldsymbol{\nu})$*;*

iii. The spreading speeds $\tilde{c}_\sigma^{(\boldsymbol{\nu})}$ of the time one map $\tilde{L}$ of the system (4.1) with $\mathbf{f}$ replaced by $E^{(\boldsymbol{\nu})}$ have the property that their maximum is $\tilde{c}_1^{(\boldsymbol{\nu})}$.

Then the system (4.1) has a single speed.

Proof. By Lemma 2.3 $\tilde{c}_+^{(\boldsymbol{\nu})} = \tilde{c}^{(\boldsymbol{\nu})} = \tilde{c}_1^{(\boldsymbol{\nu})}$. By (i) and (ii), $c_+^* \le \tilde{c}_{\boldsymbol{\nu}} = \bar{c} \le c^* \le c_+^*$, which proves the Theorem.

The first component of the function $P_1\mathbf{f}(\max\{(u,v),(0,1/4)\}) + (I - P - 1)\mathbf{f}(u,v)$ in the definition of $Q^{(0,1/4)}$ in Example 4.2 is $u(3-4u+\max\{v,1/4\})$, which is strictly increasing in v when $u \ne 0$ and $v \ge 1/4$. Hence there is no matrix $E^{(0,1/4)}$ with the properties (i) and (ii) of Lemma 4.2. We can, however, obtain information about the Lotka-Volterra system (4.11) by applying this lemma. As in Theorem 3.4, we also obtain a hair-trigger effect here.

Theorem 4.4 *If all the parameters are nonnegative,* $r_1(1-a_1) > 0$*, and* $r_2 a_2 > 0$*, then the cooperative system*

$$\begin{aligned} u_{,t} &= d_1 u_{,xx} + r_1 u(1 - a_1 - u + a_1 v) \\ v_{,t} &= d_2 v_{,xx} + r_2(1-v)(a_2 u - v), \end{aligned} \tag{4.16}$$

which is obtained from the Lotka-Volterra competition model (1.7) by introducing the new variables $u = p$*,* $v = 1 - q$*, has a single speed* c^**.*

If, in addition, $d_1 > 0$*, there is a hairtrigger effect in the sense that the property (4.2) is valid as long as* $u_0 = u(0, x)$ *is not identically zero.*

Proof. We must only find a matrix $E^{(\boldsymbol{\nu})}$ which satisfies the conditions (i)–(iii) of lemma 4.2.

The system (4.16) has the equilibria (0,0), (0,1), (1,1), and $((1-a_1)/(1-a_1a_2), a_2(1-a_1)/(1-a_1a_2))$. If $a_2 < 1$, the last equilibrium lies in the interior of the biologically interesting region $\mathcal{C}_{(1,1)}$. In this case, $\boldsymbol{\beta}$ is this last equilibrium, and there is no extra equilibrium in $\mathcal{C}_{\boldsymbol{\beta}}$. Thus $c_+^* = c^*$ by Proposition 2.1.

If $a_2 = 1$, the last equilibrium is just (1,1), while if $a_2 > 1$ it is outside $\mathcal{C}_{(1,1)}$. Thus if $a_2 \geq 1$, we have $\boldsymbol{\beta} = (1,1)$, and $\boldsymbol{\nu} = (0,1)$ lies in $\mathcal{C}_{\boldsymbol{\beta}}$. It is easily seen that for (u,v) in $\mathcal{C}_{\boldsymbol{\beta}}$ the inequalities $r_1 u(1-u) \leq r_1 u$ and $r_2(1-v)(a_2u - v) \leq r_2 a_2 u$ for the function $P_1\mathbf{f}(\max\{(u,v),(0,1)\}) + (I - P_1)\mathbf{f}(u,v)$ are valid. Moreover, the right-hand side of the first inequality is the linearization of the left-hand side at (0,0). Therefore the matrix

$$E^{(\boldsymbol{\nu})} = \begin{pmatrix} r_1 & 0 \\ r_2 a_2 & 0 \end{pmatrix} \tag{4.17}$$

satisfies the first two conditions of Lemma 4.2.

To verify the Hypothesis (iii), we observe that $\tilde{c}_1 = 2\sqrt{d_1 r_1}$, while $\tilde{c}_2 = 0$. Thus $\tilde{c}_2 = 0 \leq \tilde{c}_1$, and the statement $c_+^* = c^*$ follows from Lemma 4.2.

If $d_1 > 0$, we note that since $v \geq 0$, the solution u of (4.16) is bounded below by the solution $\hat{u}$ of the Fisher equation

$$\hat{u}_{,t} = d_1 \hat{u}_{,xx} + r_1 \hat{u}(1 - a_1 - \hat{u})$$

with the same initial conditions. Since $\hat{u}$ converges to $1-a_1$ uniformly on any bounded interval as $t\to\infty$, we find that for any interval $-s \le x \le s$ there is a t_s such $u \ge (1-a_1)/2$ for $|x| \le s$ and $t \ge t_s$. Then for $t \ge t_s$ the solution v of (4.16) on $[-s, s]$ is bounded below by the solution $\hat{v}$ of the Fisher equation

$$\hat{v}_{,t} = d_2\hat{v}_{,xx} + r_2[a_2(1-a_1)(1-\hat{v})/2 - \hat{v}]$$

which is zero at $t = t_0$ and on the boundaries $x = \pm s$. $\hat{v}$ approaches the function

$$\frac{a_2(1-a_1)}{2+a_2(1-a_1)}\left\{1 - \frac{\cosh\sqrt{r_2[2+a_2(1-a_1)]/2}x}{\cosh\sqrt{r_2[2+a_2(1-a_1)]/2}s}\right\}$$

uniformly in x. Because $\cosh z$ is a convex function, we find that $\cosh(z/2) < [1+\cosh z]/2$ for $z > 0$. Therefore the term in braces is bounded below by $[1-\operatorname{sech}\sqrt{r_2[2+a_2(1-a_1)]/2}s]/2$ for $|x| \le s/2$. Thus the limit function is bounded below by $a_2(1-a_1)/\{4[2+a_2(1-a_1)]\}$ for $-s/2 \le x \le s/2$, when s is sufficiently large. For such s there is a value $\hat{t}_s$ of t such that $u(x,\hat{t}) \ge (1-a_1)/2$ and $v(x,\hat{t}) \ge a_2(1-a_1)/\{8[2+a_2(1-a_1)]\}$ for $-s/2 \le x \le s/2$. Since s is arbitrarily large, the last statement of Theorem 4.4 follows from Theorem 4.1 with the initial time $\hat{t}$.

The following example shows that for large values of d_2, the model (4.11) for the invasion of the stable mono-culture (0,1) by a competing species does not have a single speed.

EXAMPLE 4.3 As in Examples 4.1 and 4.2, we consider the system (4.12). An upper bound for the spreading speed of the first component is obtained by replacing v by 1 in the first equation. The result is a Fisher equation, for which linear determinacy is known to be valid, so that its spreading speed is 4. Thus

$$c^* \le 4. \tag{4.18}$$

In order to obtain a lower bound for the spreading speed c_+^* of v, we note that the right-hand side of the second equation of (4.12) is reduced by replacing u by 0. Thus if w is a solution of

$$w_{,t} = d_2 w_{,xx} + (1-w)w(4w-1) \tag{4.19}$$

and $v \ge w$ at some time, then $v \ge w$ for all larger times. It was shown in Theorems 3.3 and 4.5 of Aronson and Weinberger [1] that this equations displays a threshold effect. That is, if $w(x,0)$ is uniformly below $1/4$, the solution tends to 0. On the other hand, the fact that $\int_0^{1/2} w(1-w)(4w-1)dw > 0$ implies that if $w(x,0) \geq 1/2$ on a sufficiently long interval, the solution approaches 1 uniformly on every bounded set. In the second case, there is a unique number C such that there exists a traveling wave solution $W(x-nC)$ of speed C, and this speed is also the spreading speed. By generalizing the ideas of Hadeler and Rothe [5], Lewis and Kareiva [10] gave a formula for C which shows that $C = \sqrt{d_2/2}$.

Choose any $c < \sqrt{d_2/2}$, and define the sequence $\mathbf{a}_n$ by the recursion (2.7) with Q the time 1 map of the system (4.12). Since $\mathbf{a}(c,-\infty) = (1,1)$, we can find an n_0 so large that $\mathbf{a}_{n_0}(c;-\infty) >> (1/2,1/2)$. If we set $w(x,n_0)$ equal to the second component of $\mathbf{a}_{n_0}(c;x)$, we see that it is above $1/2$ on an infinitely long interval. By the above comparison, the second component of $\mathbf{a}_n(c;x)$ lies above $w(x+(n-n_0)c,n)$ for $n \geq n_0$. Since $c < \sqrt{d_2/2}$, this lower bound approaches 1 uniformly on bounded sets. We conclude that $\mathbf{a}(c;\infty) \neq 0$, so that $c_+^* \geq c$. Because c is any number below $\sqrt{d_2/2}$, we conclude that

$$c_+^* \geq \sqrt{d_2/2}.$$

This inequality combined with (4.18) shows that if

$$d_2 > 32, \tag{4.20}$$

then $c_+^* > c^*$, so that there is no single spreading speed.

Figure 2 plots approximations to the speeds $\bar{c}$, c^*, and c_+^* obtained from numerical simulations of (4.11) as functions d_2. As predicted by (4.14), the system has a single speed and is linearly determinate when $d_2 \leq 2/3$. In fact, this seems to hold for $d_2 \leq 4$. As predicted by (4.15), (4.11) has a single speed $c_+^* = c^*$ when $d_2 \leq 10/13$ but this equality seems to be true for $d_2 \leq 8$. As predicted by (4.18), $c_+^* > c^*$ for $d_2 > 32$, but this also seems to happen for $d_2 \geq 16$. Thus all our bounds are sufficient but not necessary.

5 Discussion.

We have shown how to extend the results of Lui [13] in such a way that they can be applied to ecological invasion processes. This has involved not only the elimination of Lui's assumptions of irreducibility and nonexistence of extra equilibria, but also the weakening of his condition (1.5) in such a way that it can hold in the case of invasion by a competitor. This weakening

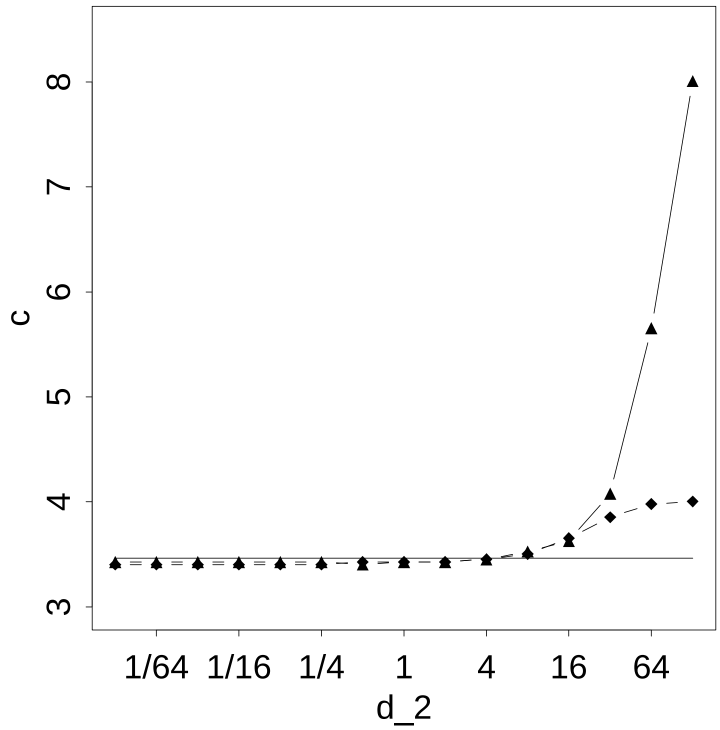

Figure 2: Numerical calculation of wave speeds for the reaction diffusion equation (4.11). The parameter d_2 varies on a log scale. The solid line shows $\bar{c} = 2\sqrt{3}$, diamonds show numerically calculated values for c^* and triangles show numerically calculated values c_+^*. The numerical solution method uses the method of lines and Gear's method with 1000 spatial grid points.

can be understood intuitively by applying the (not always correct) heuristic argument that near the head of the spreading population the solution of the recursion (1.1) should look like the most rapidly spreading solution of the linearization of this recursion. That is, it should behave roughly like $e^{-\bar{\mu}x}\boldsymbol{\zeta}(\bar{\mu})$. Thus it makes sense that Theorem 3.1 only requires the inequality (1.5) to hold for this function. Note that the replacement of (1.5) by (3.12) improves Lui's result on single speed and linear determinacy when his extra conditions are satisfied.

As Examples 2.1 and 4.3 show, the existence of an extra equilibrium on the parallelepiped with corners at $\mathbf{0}$ and $\boldsymbol{\beta}$ can make different components spread at different speeds. In Example 4.3 the mono-culture $v = 1$ is a stable equilibrium as long as the invader is absent. We have shown that if the mobility d_2 of the original species is sufficiently large, then the extinction of the first species spreads at a greater speed than the growth of the invading species. Thus an observer who is far from the original point of invasion will see the extinction of the first species long before the invading species which caused the extinction appears. The origin of this apparently paradoxical behavior is the fact that when $p \equiv 0$, the stable state $q \equiv 1$ can be driven to extinction by a sufficiently large die-off on a sufficiently long bounded interval.

Theorem 4.4 shows that such a phenomenon never occurs in the Lotka-Volterra model. Thus a small change in the details of the model can influence the asymptotic behavior profoundly.

The trick of converting a competition model to a cooperative system by a change of dependent variables can be generalized to more than two species, provided the species can be broken into two "teams" such that each species cooperates with the species of the same team and competes with those of the other team. In particular, one can treat the invasion of an equilibrium of cooperating species by an invader which competes with all these species.

Since "fat" migration tails occur in some models, it of interest to weaken the condition in Hypothesis 2.1.v.a, which requires that the entries of B_μ are finite for all μ. If, instead, we only assume that the entries of B_μ are finite for $|\mu| < \alpha$ for some positive α, we define B_μ for all μ by replacing any integral in (2.3) which diverges by $+\infty$. If the entries of the σth diagonal block of B_μ are all finite for $\mu < \hat{\mu}_\sigma$ but not for $\mu > \hat{m}_\sigma$, then $\lambda_\sigma(\mu)$ is finite for $\mu < \hat{\mu}_\sigma$ and $+\infty$ for $\mu > \hat{\mu}_\sigma$, and its logarithm is still convex. Thus the infimum in the definition (2.18) of $\bar{c}_1$ is taken on at a point $\bar{\mu}$ of the interval $(0, \hat{\mu}_\sigma]$ where λ_1 is finite. The eigenvector $\boldsymbol{\zeta}(\bar{\mu})$, which is required for the conditions of Theorem 3.1 is not defined unless all entries of $B_{\bar{\mu}}$ are finite. If we interpret the conditions to include this finiteness assumption, the proof of Theorem 3.1 goes through without change. Since our other results are based on Theorem 3.1, they remain true when Hypothesis 2.1.v.a is weakened to require the entries of B_μ to be finite only on some interval of which 0 is an interior point.

We have defined the concept of linear determinacy as $c^* = \bar{c}$ and $c_+^* = \bar{c}_+$. A stronger definition would be that each species spreads at a speed which is equal to that of the same species under the recursion with Q replaced by a truncation of the linear operator M. It is easily seen that for this truncated linear recursion the spreading speed of the species in the σth block is the largest of the numbers $\bar{c}_\tau$ among those $\tau \leq \sigma$ with the the property that some power of the matrix B_0 has a positive ij entry with i in the τth block and j in the σth block.

Although our analysis includes the assumption of reflection symmetry in the operator Q, the results can be extended to cover the case with no reflection symmetry. In this case, we define the rightward spreading speeds $c^*(+1)$ and $c^*_+(+1)$ by the formulas (2.8) and (2.9) with the function $\mathbf{a}$ defined as before. If R is the reflection operator $R[\mathbf{u}](x) := \mathbf{u}(-x)$, then the leftward speeds $c^*(-1)$ and $c^*_+(-1)$ are defined by replacing the operator Q by RQR in the definition (2.7) of the sequence $\mathbf{a}_n$. When there are single speeds in both directions, the properties (2.5) and (2.6) are replaced by

$$\lim_{n\to\infty}\left[\sup_{x\geq n(c^*(+1)+\epsilon)}|\mathbf{u}(x)|\right] = \lim_{n\to\infty}\left[\sup_{x\leq -n(c^*(-1)+\epsilon)}|\mathbf{u}(x)|\right] = 0 \tag{5.1}$$

and

$$\lim_{n\to\infty}\left[\sup_{-n(c^*(-1)-\epsilon)\leq x\leq n(c^*(-1)-\epsilon)}|\boldsymbol{\beta} - \mathbf{u}(x)|\right] = 0. \tag{5.2}$$

The obvious adjustments in (2.10) to (2.13) are made if $c^*_+(+1) > c^*(+1)$ or $c^*_+(-1) > c^*(-1)$. In two or more dimensions one can define spreading speeds $c^*(\boldsymbol{\xi})$ and $c^*_+(\boldsymbol{\xi})$ in the direction of any unit vector by essentially the same formulas. (See [21], [13], [22]). One can then define the concepts of having a single speed in the direction $\boldsymbol{\xi}$ or of being linearly determinate in the direction $\boldsymbol{\xi}$

As promised in the introduction, we shall say a few words about the advantage of a discrete-time model (1.1) over a reaction-diffusion model. The derivation of a reaction-diffusion equation from a stochastic model assumes that the system is in statistical equilibrium at every instant, while the purpose of the model is to treat non-equilibrium situations. This inherent contradiction manifests itself by requiring the possibility of arbitrarily far migration in arbitrarily small time. Another manifestation of this contradiction is the fact that the derivation of a reaction-diffusion model as a limit of a family of stochastic models with a small parameter, as in Durrett and Neuhauser [3], requires the migration rate to become very large, which may or may not be biologically reasonable. It was shown by Neuhauser [17] that under a different assumption the limit is an integro-differential equation model.

Discrete-time models, on the other hand, permit one to wait until some kind of statistical equilibrium is established before measuring the input-output function. Our results show that the spreading properties of reaction-diffusion systems are shared by a more general class of discrete-time recursions. Thus the fact that one gets qualitatively correct spreading properties does not, in itself, justify the use of reaction-diffusion models.

6 Acknowledgments

We thank the two referees for helpful suggestions for improving this paper.

7 Appendix

In this Appendix we shall present proofs of Lemmas 2.1 and 2.3, Theorem 4.1, and Lemma 4.1, in that order.

Proof of Lemma 2.1. By Hypothesis 2.1.i, any constant equilibrium $\boldsymbol{\nu}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ other than $\boldsymbol{\beta}$ must have at least one zero component. The order preserving property shows that if $\mathbf{0} \leq \mathbf{v} \leq \boldsymbol{\nu}$, then $\mathbf{0} \leq Q[\mathbf{v}] \leq \boldsymbol{\nu}$. That is, $\mathcal{C}_{\boldsymbol{\nu}}$ is an invariant set of Q. It follows that if $\nu_i = 0$, then $(B_0[\boldsymbol{\nu}])_i = 0$. This property shows that if $\nu_i = 0$ and $\nu_j \neq 0$, then the ij entry of B_0 must be zero. If $\nu_i = 0$ for some but not all of the coordinates i of the σth block of B_0, then writing the coordinates i with $\nu_i = 0$ before the others would put B_σ into a lower block triangular form, which would contradict the fact that it is irreducible. Thus the components of an equilibrium $\boldsymbol{\nu}$ corresponding to any diagonal block are either all zero or all nonzero. Suppose that the components of $\boldsymbol{\nu}$ which correspond to the σth diagonal block vanish. If $\sigma > 1$, the Hypothesis 2.1.v.d shows that there are nonzero elements to the left of the σth diagonal block. That is, unless $\sigma = 1$, there is an earlier diagonal block on whose coordinates $\boldsymbol{\nu}$ also vanishes. We conclude that the coordinates of $\boldsymbol{\nu}$ corresponding to the first (upper left) diagonal block of B_0 are 0, which is the statement of the Lemma.

Proof of Lemma 2.3. Because the equations corresponding to the upper left block $\tilde{B}_0$ depend only on the components in these directions and because $\tilde{B}_0$ is irreducible, the results of Lui [13] show that the components of $\mathbf{u}_n$ which correspond to this first block spread at exactly the speed $\tilde{c}_1$. Therefore the slowest spreading speed must be $\tilde{c}_1$.

Let $\tilde{\boldsymbol{\zeta}}_\sigma(\mu) >> \mathbf{0}$ be an eigenvector of the σth diagonal block of $\tilde{B}_\mu$ corresponding to its principal eigenvalue $\tilde{\lambda}_\sigma(\mu)$. Let $\tilde{\mu}_\sigma \in (0, \infty]$ denote the value of μ at which the infimum in (2.18) is attained. Let $\tilde{P}_\sigma$ denote the coordinate projection to the coordinates corresponding to the σth diagonal block of B_0.

Because of the Frobenius form, $\tilde{P}_\sigma[\tilde{L}[\mathbf{v}]]$ only depends on the $\tilde{P}_\tau[\mathbf{v}]$ with $\tau \le \sigma$. Assume for the moment that the $\tilde{\mu}_\sigma$ are all finite, and that the numbers $\tilde{\lambda}_\tau(\tilde{\mu}_\sigma)$ are distinct for all $\tau \ge \sigma$. In order to construct a supersolution of the recursion (2.17), we note that for any positive ρ_1 the function

$$\mathbf{w}_1(x,n) := \rho_1 e^{-\tilde{\mu}_1(x-n\tilde{c}_1)}\tilde{\boldsymbol{\zeta}}_1(\tilde{\mu}_1) \tag{7.1}$$

is positive and satisfies the inequality

$$\mathbf{w}_1(x,n+1) \ge \tilde{P}_1[\tilde{L}[\mathbf{w}_1(x,n)]]. \tag{7.2}$$

(Here we think of $\mathbf{w}_1$ as the k-vector-valued function obtained by defining the undefined coordinates to be 0.)

We next construct a vector $\mathbf{w}_2(x,n)$ corresponding to the components of the second diagonal block such that

$$\mathbf{w}_2(x,n+1) \ge \tilde{P}_2[\tilde{L}[\mathbf{w}_1(x,n) + \mathbf{w}_2(x,n)]]. \tag{7.3}$$

We observe that $\tilde{P}_2[\tilde{L}[\mathbf{w}_1]]$ is $e^{-\tilde{\mu}_1(x-n\tilde{c}_1)}$ times a nonnegative constant vector. Since $\tilde{\boldsymbol{\zeta}}_2(\tilde{\mu}_1) >> \boldsymbol{\theta}$, there is a positive η_{21} such that this constant vector is bounded above by $\eta_{21}\boldsymbol{\zeta}_2(\tilde{\mu}_1)$. It is easily verified that for any positive ρ_2 the vector

$$\mathbf{w}_2 := \max\{\rho_2 e^{-\tilde{\mu}_2(x-n\tilde{c}_2)}\tilde{\boldsymbol{\zeta}}_2(\tilde{\mu}_2) + \eta_{21}[\tilde{\lambda}_1(\tilde{\mu}_1) - \tilde{\lambda}_2(\tilde{\mu}_1)]^{-1}e^{-\tilde{\mu}_1(x-n\tilde{c}_1)}\tilde{\boldsymbol{\zeta}}_2(\tilde{\mu}_1), 0\} \tag{7.4}$$

satisfies the inequality (7.3).

Since $\mathbf{w}_2$ is bounded above by a linear combination of two exponentials, we can use the same method to find a function of the form

$$\begin{aligned}\mathbf{w}_3 = \max\{&\rho_3 e^{-\tilde{\mu}_3(x-n\tilde{c}_3)}\tilde{\boldsymbol{\zeta}}_3(\tilde{\mu}_3) + \eta_{31}[\tilde{\lambda}_1(\tilde{\mu}_1) - \tilde{\lambda}_3(\tilde{\mu}_1)]^{-1}e^{-\tilde{\mu}_1(x-n\tilde{c}_1)}\tilde{\boldsymbol{\zeta}}_3(\tilde{\mu}_1)\\ &+\eta_{32}[\tilde{\lambda}_2(\tilde{\mu}_2) - \tilde{\lambda}_3(\tilde{\mu}_2)]^{-1}e^{-\tilde{\mu}_2(x-n\tilde{c}_2)}\tilde{\boldsymbol{\zeta}}_3(\tilde{\mu}_2), 0\}\end{aligned} \tag{7.5}$$

which satisfies the inequality

$$\mathbf{w}_3(x,n+1) \ge \tilde{P}_3[\tilde{L}[\mathbf{w}_1(\cdot,n) + \mathbf{w}_2(\cdot,n) + \mathbf{w}_3(\cdot,n)]]. \tag{7.6}$$

We inductively define $\mathbf{w}_\sigma$ for all σ in this way, and define

$$\mathbf{w} = \sum_\sigma \mathbf{w}_\sigma$$

to be the k-vector such that $\tilde{P}_\sigma[\mathbf{w}] = \mathbf{w}_\sigma$ for all σ. By construction,

$$\mathbf{w}(x, n+1) \geq \tilde{L}[\mathbf{w}(x, n)]. \tag{7.7}$$

If $\mathbf{u}_0$ is bounded and vanishes outside a bounded set, we can choose ρ_1 so large that $\tilde{P}_1[\mathbf{u}_0] \leq \mathbf{w}_1(x, n)$, then choose ρ_2 so large that $\tilde{P}_2[\mathbf{u}_0] \leq \mathbf{w}_2(x, n)$, and so forth until $\mathbf{u}_0 \leq \mathbf{w}(x, 0)$. Since $\mathbf{u}_{n+1} \leq \tilde{L}[\mathbf{u}_n]$, we find that $\mathbf{u}_n(x) \leq \mathbf{w}(x, n)$ for all n. Since $\mathbf{w}$ is bounded above by a linear combination of the exponentials $e^{-\tilde{\mu}_\sigma(x - n\tilde{c}_\sigma)}$, no component of $\mathbf{u}_n$ can spread at a speed greater than the largest of the $\tilde{c}_\sigma$. On the other hand, by looking at the comparison problem with the initial value $\tilde{P}_\sigma[\mathbf{u}_0]$, we see that the components corresponding to the σth block spread at at least the speed $\tilde{c}_\sigma$. We conclude that the fastest spreading speed is the largest of the $\tilde{c}_\sigma$.

We have established the Lemma under some additional hypotheses. We see from the the second term on the right of formula (7.4) that something goes wrong when $\tilde{\lambda}_2(\tilde{\mu}_1) = \tilde{\lambda}_1(\tilde{\mu}_1)$. This term is $e^{-\tilde{\mu}_1 x}$ times a particular solution of the recursion

$$\alpha_{n+1} = \tilde{\lambda}_2(\tilde{\mu}_1)\alpha_n + \eta_{21}\tilde{\lambda}_1(\tilde{\mu}_1)^n. \tag{7.8}$$

When $\tilde{\lambda}_2(\tilde{\mu}_1) = \tilde{\lambda}_1(\tilde{\mu}_1)$, this recursion has the solution $\alpha_n = \eta_{21} n \tilde{\lambda}_1(\tilde{\mu}_1)^n$, so that the singular factor must simply be replaced by n. In this way, we see that if coincidences occur, one obtains formulas for the $\mathbf{w}_\sigma$ in which the coefficients $\eta_{\sigma\tau}$ may be replaced by polynomials in n. This leaves the asymptotic speeds unchanged, so that the proof is still valid.

Finally, we observe that if one or more of the $\tilde{\mu}_\sigma$ is infinite, we can replace the infinite ones by very large values. This increases the spreading speeds by arbitrarily small amounts, and the argument can be carried through as before. Thus the Lemma is established.

Proof of Theorem 4.1. Because $\mathcal{C}_{\boldsymbol{\beta}}$ is closed and bounded and $\mathbf{f}$ is continuous, there is a number ρ such that $|\mathbf{f}(\mathbf{u})| \leq \rho$ for $\mathbf{u} \in \mathcal{C}_{\boldsymbol{\beta}}$. As before, let $\boldsymbol{\zeta}(0)$ be a positive principal eigenvector of B_0. Choose any positive numbers ϵ and δ, and an integer ℓ so large that

$$\rho/\ell \leq (\delta/4)|\boldsymbol{\zeta}(0)|. \tag{7.9}$$

The properties (2.5) and (2.6) applied to the time 1 map Q_1 and the time $1/\ell$ map $Q_{1/\ell}$ of the system (4.1) show that $c^*_{1/\ell} = c^*_1/\ell := c^*/\ell$. Property (2.5) for $Q_{1/\ell}$ with ϵ replaced by $\epsilon/2$ shows that there exists a number N_δ such that

$$\mathbf{u}(x, n/\ell) \le (\delta/2)\boldsymbol{\zeta}(0) \qquad \text{when } |x| \ge n(c^*/\ell + \epsilon/2) \text{ and } n \ge N_\delta. \tag{7.10}$$

Because $|\mathbf{f}(\mathbf{u})| \le \rho$,

$$u_{i,t} - d_i u_{i,xx} \le \rho$$

for all i. Standard results for the heat equation show that if $\mathbf{u}(x, n/\ell) \le (\delta/2)\boldsymbol{\zeta}(0)$ for $|x| \le R$ and $\mathbf{u}(x, n/\ell) \le \boldsymbol{\beta}$ for all x then

$$u_i(0,t) \le [t-n/\ell]\rho + (\delta/2)\zeta_i(0) + |\boldsymbol{\beta}|(2\pi d_i[t-n/\ell])^{-1/2} e^{-R^2/(4d_i[t-n/\ell])}. \tag{7.11}$$

We choose $R = R_\delta$ so large that the last term on the right is also bounded by $(\delta/4)\zeta_i(0)$ when $0 \le [t - n/\ell] \le 1/\ell$. Thus we find that the inequality (7.9) implies that

$$\mathbf{u}(x,t) \le \delta\boldsymbol{\zeta}(0) \text{ when } |x| \ge t(c^* + \epsilon/2) + R_\delta,\ n/\ell \le t \le (n+1)/\ell, \text{ and } n \ge N_\delta. \tag{7.12}$$

We note that if $t \ge \max\{N_\delta/\ell, 2R_\delta/\epsilon\}$, the inequality for $|x|$ is implied by the inequality $|x| \ge t(c^* + \epsilon)$. Thus we have shown that

$$\overline{\lim_{t\to\infty}} \left[\max_{|x| \le t(c^*+\epsilon)} |\mathbf{u}(x,t)| \right] \le \delta |\boldsymbol{\zeta}(0)|.$$

Since δ is arbitrary, this is exactly the statement (4.2). The statement (4.3) is proved by applying the same method to the function $\boldsymbol{\beta} - \mathbf{u}$, and the Theorem is proved.

We remark that if $c^*_+ > c^*$, the same proof gives the analog of Lemma 2.2.

Proof of Lemma 4.1. Choose $\rho \ge 0$ such that the diagonal elements of the matrix $\mathbf{f}'(\mathbf{0}) + \rho I$ are strictly positive. Hypothesis 4.1.ii shows that all the entries of this matrix are nonnegative. For any $\kappa > 1$ we define $M^{(\kappa)}[\mathbf{v}]$ to be the time one map of the linear system

$$\begin{aligned} &\mathbf{w}_{,t} = (\mathrm{diag}(d_i))\mathbf{w}_{,xx} + (1-\kappa^{-1})\mathbf{f}'(\mathbf{0})\mathbf{w} - \kappa^{-1}\rho\mathbf{w} \\ &\mathbf{w}(x,0) = \mathbf{v}(x). \end{aligned} \tag{7.13}$$

That is, $M^{(\kappa)}[\mathbf{v}](x) := \mathbf{w}(x,1)$.

It is easily seen that when $\mathbf{v} = e^{-\mu x}\boldsymbol{\alpha}$, the solution has the separated form $\mathbf{w} = e^{-\mu x}\boldsymbol{\eta}(t)$, where $\boldsymbol{\eta}' = [\mu^2 \mathrm{diag}(d_i) + (1-\kappa^{-1})\mathbf{f}'(\mathbf{0})]\boldsymbol{\eta} - \kappa^{-1}\rho\boldsymbol{\eta}$. Thus

$$B^{(\kappa)}_\mu = e^{-\kappa^{-1}\rho} e^{\mu^2 \mathrm{diag}(d_i) + (1-\kappa^{-1})\mathbf{f}'(\mathbf{0})},$$

and a standard result on ordinary differential equations show that this matrix converges to the matrix B_μ, which is obtained by replacing κ^{-1} by 0, as κ approaches infinity. This is Property b of Hypothesis 2.1.vi.

In order to establish Property a, we define for each i the projection

$$\{\pi_i[\boldsymbol{\alpha}]\}_j = \begin{cases} \alpha_j \text{ if } \{\mathbf{f}'(\mathbf{0}) + \rho I\}_{ij} > 0 \\ 0 \text{ if } \{\mathbf{f}'(\mathbf{0}) + \rho I\}_{ij} = 0. \end{cases}$$

Note that by the definition of ρ, $\{\pi_i[\boldsymbol{\alpha}]\}_i = \alpha_i$, and that $\pi_i[\boldsymbol{\alpha}] \leq \boldsymbol{\alpha}$ when $\boldsymbol{\alpha} \geq 0$. Hypothesis 4.1.ii then shows that

$$f_i(\boldsymbol{\alpha}) \geq f_i(\pi_i[\boldsymbol{\alpha}]). \tag{7.14}$$

Moreover,

$$\pi_i[\boldsymbol{\alpha}] \cdot \nabla f_i(\mathbf{0}) = (\mathbf{f}'(\mathbf{0})\mathbf{a})_i \tag{7.15}$$

for all $\boldsymbol{\alpha}$.

Let σ be a positive lower bound for all the positive entries of the matrix $\mathbf{f}'(\mathbf{0}) + \rho I$. By the triangle inequality

$$|\pi_i[\boldsymbol{\alpha}]| \leq \sum_{j=1}^{k} \{\pi_i[\boldsymbol{\alpha}]\}_j \leq \sigma^{-1}\{\pi_i[\boldsymbol{\alpha}] \cdot \nabla f_i(\mathbf{0}) + \rho\alpha_i\}. \tag{7.16}$$

for all $\boldsymbol{\alpha} \geq \mathbf{0}$.

Let $\boldsymbol{\zeta}(0) >> \mathbf{0}$ be the eigenvector of B_0 mentioned in Remark 3 after the Hypotheses 2.1. The differentiability of f_i shows that for any $\kappa \geq 1$ there is a positive number δ_κ such that if $\mathbf{0} \leq \boldsymbol{\alpha} \leq \delta_\kappa \boldsymbol{\zeta}(0)$, then for all i

$$\nabla f_i(\mathbf{0}) \cdot \pi_i[\boldsymbol{\alpha}] - f_i(\pi_i[\boldsymbol{\alpha}]) \leq (\sigma/\kappa)|\pi_i[\boldsymbol{\alpha}]|.$$

By inserting (7.14), (7.15), and (7.16) into this inequality, we find that

$$(1-\kappa^{-1})\mathbf{f}'(\mathbf{0})\boldsymbol{\alpha} - \kappa^{-1}\rho\boldsymbol{\alpha} \leq \mathbf{f}(\boldsymbol{\alpha}) \text{ when } \mathbf{0} \leq \boldsymbol{\alpha} \leq \delta_\kappa \boldsymbol{\zeta}(0). \tag{7.17}$$

We now observe that the solution of the system (7.13) with $\mathbf{v} = \boldsymbol{\zeta}(0)$ is $e^{[(1-\kappa^{-1})\gamma_1(0)-\kappa^{-1}\rho]t}\boldsymbol{\zeta}(0)$. Therefore, if

$$\mathbf{0} \leq \mathbf{v} \leq \delta_\kappa e^{-\gamma_1}\boldsymbol{\zeta}(0),$$

then $\mathbf{0} \leq \mathbf{w} \leq \delta_\kappa \boldsymbol{\zeta}(0)$ for $0 \leq t \leq 1$. Then (7.17) shows that $\mathbf{w}$ is a sub-solution of the system (4.1). Hence, a standard comparison theorem shows that $M^{(\kappa)}[\mathbf{v}] \leq Q[\mathbf{v}]$. This is the Property a of Hypothesis 2.1.vi with $\boldsymbol{\omega} = \delta_\kappa e^{-\gamma_1}\boldsymbol{\zeta}(0)$, and the Lemma is established.

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