Spreading speeds as slowest wave speeds for cooperative systems

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Abstract

It is well known that in many scalar models for the spread of a fitter phenotype or species into the territory of a less fit one, the asymptotic spreading speed can be characterized as the lowest speed of a suitable family of traveling waves of the model. Despite a general belief that multispecies (vector) models have the same property, we are unaware of any proof to support this belief. The present work establishes this result for a class of multispecies model of a kind studied by R. Lui [9] and generalized by the authors [12, 8]. Lui showed the existence of a single spreading speed c^* for all species. In the systems in [12, 8], which include related continuous-time models such as reaction-diffusion systems [12, 8], as well as some standard competition models, it sometimes happens that different species spread at different rates, so that there are a slowest speed c^* and a fastest speed c_f^*. It is shown here that, for a large class of such multispecies systems, the slowest spreading speed c^* is always characterized as the slowest speed of a class of traveling wave solutions.

1 Introduction.

It was shown by R. A. Fisher [3] that the scalar model

$$u_{,t} = du_{,xx} + ru(1-u)$$

for the spread of a more fit population into the territory of a less fit one has traveling wave solutions of all speeds $c \geq 2\sqrt{dr}$. Here the spatial density of the fitter of two alleles at a single gene locus is given by $\rho u(x,t)$, where the total allelic density ρ is assumed to be kept at a fixed constant value. Fisher conjectured that the slowest wave speed $c^* = 2\sqrt{dr}$ is also the spreading speed with which the region $\{x : u \sim 1\}$ where the fitter allele dominates takes over the set $\{x : u(x,0) = 0\}$ where the fitter allele is initially absent. This conjecture was proved by Kolmogorov, Petrowski, and Piscounov [7]. Similar results on the spreading speed as the slowest speed of a family of traveling waves have been shown for a more general class of reaction-diffusion models which includes Fisher's quadratic model as a special case [1, 2]. The dynamics of population spread and traveling waves can be extended beyond reaction-diffusion models to more general formulations. For example, a large class of scalar discrete-time, and possibly discrete-space, recursions of the form

$$u_{n+1} = Q[u_n], \quad n = 0, 1, 2, ... \tag{1.1}$$

was analyzed in [14]. For a subclass of these models, the spreading speed can be characterized as the slowest speed of a traveling wave. Such a result is useful, as it is often easier to calculate the slowest wave speed than to find the spreading speed. The latter is the quantity of biological interest when locally introduced populations are spreading into a new environment. Lui [9] extended the proof of the existence of a spreading speed to a multispecies version of (1.1)

$$\mathbf{u}_{n+1} = Q[\mathbf{u}_n], \quad n = 0, 1, 2, ... \tag{1.2}$$

Here the function $\mathbf{u}_n(x)$ is vector-valued, and its components can represent the population densities at time n of interacting species or age classes. Such a formulation can be applied to reaction-diffusion systems of the form

$$\begin{aligned} &[u_i]_{,t} = d_i[u_i]_{,xx} - e_i[u_i]_{,x} + f_i(\mathbf{u}), \quad i = 1, 2, ..., k, \\ &\mathbf{u}(0, x) = \mathbf{u}_0(x) \end{aligned} \tag{1.3}$$

by letting Q be the so-called time-one map which takes the initial values $\mathbf{u}_0(x)$ into the value $\mathbf{u}(x, 1)$ at $t = 1$ of the solution $\mathbf{u}(x, t)$ of (1.3). The operator Q in (1.2) may, however, correspond to a more general class of models. For example, Q may be a nonlinear integral operator, or (1.2) may be an explicit finite difference equation. For the recursion (1.2), Lui [10] showed how to define the spreading speed of a class of cooperative problems in population ecology and epidemic theory. His hypotheses, however, allowed only for a single nontrivial homogeneous equilibrium. Even though two-species competitive interactions can be transformed to cooperative systems by a change of variables, the assumption of a single nontrivial equilibrium prevents Lui's spreading speed result from being extended to situations involving competitive interactions between species. These systems may have several nontrivial boundary equilibria, which correspond to the absence of one or more of the species [12]. A weakening of Lui's hypotheses to include such nontrivial boundary equilibria introduces a new possibility—different species may have different spreading speeds [12, 8]. This can happen, for example, when there are two coupled species, at least one of which exhibits a "strong Allee effect" (bistable dynamics). Such situations, with the possibility of multiple spreading speeds, are characterized as follows: there is a slowest speed c^* with the property that no species spreads more slowly than c^*, and at least one species spreads at no faster speed, and there is a fastest speed c_f^* such that no species spreads at a speed greater than c_f^*, and at least one species spreads at no slower speed.[1]

The main result of the present work is the fact that the slowest spreading speed c^* can always be characterized as the slowest speed of a family of traveling waves. This is done for the discrete-time model (1.2) in Section 3. Section 4 shows how to extend this result to continuous-time models such as (1.3). Example 4.1 shows that the fastest speed can actually be larger than the slowest speed, so that components travel at different speeds. Section 5 is a summary of our results. In order to facilitate the flow of ideas, we have put the more intricate proofs into the Appendix, which is Section 6.

The existence of a family of monotone waves of all speeds above a minimal speed is known for some special cooperative monostable systems of reaction-diffusion equations. (See, e.g., Section 3.4.2 of [11], [6], or [5].) In these cases, our results show that the minimal wave speed is equal to the spreading speed.

[1] It was stated in our paper [12] that the fastest speed is the number c_+^*, which will be given by the formula (2.11). However, as stated near the end of Section 2, the proof of the statement that at least one species spreads at a speed no slower than c_+^* is incomplete, and we have had to resort here to showing how to define the possibly slower fastest speed c_f^* directly.

2 Hypotheses and spreading speeds.

We begin with some notation. We shall use boldface Roman symbols like $\mathbf{u}(x)$ to denote k-vector valued functions of the single variable x, and boldface Greek letters to stand for k-vectors, which may be thought of as constant vector-valued functions. Here k is the number of species. We shall usually think of $\mathbf{u}(x)$ as a function of x and the component number. Thus, for example, $\mathbf{u}(x) \geq \mathbf{v}(x)$ means that $u_i(x) \geq v_i(x)$ for all i and x, $\max\{\mathbf{u}(x), \mathbf{v}(x)\}$ means the vector-valued function whose ith component at x is $\max\{u_i(x), v_i(x)\}$, and $\limsup_{n\to\infty} \mathbf{u}^{(n)}(x)$ is the function whose ith component at x is $\limsup_{n\to\infty} u_i^{(n)}(x)$. We shall, however, use the usual symbol $\mathbf{u} >> \mathbf{v}$ 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. If $\boldsymbol{\beta} >> \mathbf{0}$ is a constant k-vector, we define the set of functions

$$\mathcal{C}_{\boldsymbol{\beta}} := \{\mathbf{u}(x) : \mathbf{u}(x) \text{ continuous and } \mathbf{0} \leq \mathbf{u}(x) \leq \boldsymbol{\beta}\}.$$

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 (1.2), then $\mathbf{u}_n = \mathbf{w}$ for all $n \geq \ell$. We shall study the evolution of the solution $\mathbf{u}_n$ of the recursion (1.2) from a $\mathbf{u}_0$ near an unstable constant equilibrium $\boldsymbol{\Theta}$ toward a stable equilibrium $\boldsymbol{\beta} >> \boldsymbol{\Theta}$. By making the change of dependent variable $\hat{\mathbf{u}}_n = \mathbf{u}_n - \boldsymbol{\Theta}$ if necessary, we shall assume that the unstable equilibrium $\boldsymbol{\Theta}$ from which the system moves away is the origin $\mathbf{0}$. We define the translation operator

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

for any real number y. Finally we shall use the convention that in an expression of the form $Q[\mathbf{u}(x, r, s, \cdots)](q(y, r, s, \cdots))$, x is a dummy variable. That is, this expression is the result of applying the operator Q to the function of x which is obtained by thinking of the other variables as fixed parameters, and evaluating the resulting function at the point $q(y, r, s, \cdots)$, which may depend on a new independent variable y and the parameters. We shall make the following assumptions about the operator Q in the recursion (1.2).

Hypotheses 2.1.

i. *The operator Q is order preserving in the sense that if $\mathbf{u}$ and $\mathbf{v}$ are any two functions in $\mathcal{C}_{\boldsymbol{\beta}}$ with $\mathbf{v} \geq \mathbf{u}$, then $Q[\mathbf{v}] \geq Q[\mathbf{u}]$. It follows that if only u_i is increased, then for any $j \neq i$ the specific growth rate $(\{Q[\mathbf{u}]\}_j - u_j)/u_j$ of the jth species is not decreased. While an increase in u_i may lower the specific growth rate of the ith species, this reduction is not so profound that the population density of the next generation is decreased. In biological terms, the dynamics are cooperative and there is no overcompensation.*

ii. $Q[\mathbf{0}] = \mathbf{0}$*, there is a constant vector $\boldsymbol{\beta} >> \mathbf{0}$ such that $Q[\boldsymbol{\beta}] = \boldsymbol{\beta}$, and if $\mathbf{u}_0$ is any constant vector with $\mathbf{u}_0 >> \mathbf{0}$, then the constant vectors $\mathbf{u}_n$ obtained from the recursion (1.2) converge to $\boldsymbol{\beta}$ as n approaches infinity. This hypothesis, together with (i) imply that Q takes $\mathcal{C}_{\boldsymbol{\beta}}$ into* *itself, and that the equilibrium* $\boldsymbol{\beta}$ *attracts all initial functions in* $\mathcal{C}_{\boldsymbol{\beta}}$ *with uniformly positive components. In biological terms,* $\boldsymbol{\beta}$ *is a globally stable coexistence equilibrium. There may also be other equilibria lying between* $\boldsymbol{\beta}$ *and the extinction equilibrium* $\mathbf{0}$*, in each of which at least one of the species is extinct.*

iii. Q *is translation invariant; i.e.,* $Q[T_y[\mathbf{v}]] = T_y[Q[\mathbf{v}]]$ *for all* y*. In biological terms this means that the habitat is homogeneous, so that the growth and migration properties are independent of location.*

iv. *If the sequence* $\mathbf{v}_n(x)$ *in* $\mathcal{C}_{\boldsymbol{\beta}}$ *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. This means that for any fixed* y*,* $|Q[\mathbf{v}](y) - Q[\mathbf{u}](y)|$ *is arbitrarily small, provided* $|\mathbf{v}(x) - \mathbf{u}(x)|$ *is sufficiently small on a sufficiently long interval centered at* y*. This and the following hypothesis are typically satisfied for biologically reasonable models.*

v. *Every sequence* $\mathbf{v}_n(x)$ *in* $\mathcal{C}_{\boldsymbol{\beta}}$ *has a subsequence* $\mathbf{v}_{n_\ell}$ *such that* $Q[\mathbf{v}_{n_\ell}]$ *converges uniformly on every bounded set.*

The first four of these hypotheses constitute a proper subset of Hypotheses 2.1 of [12]. In order to permit the modeling of a prevailing wind, a chemotactic gradient, or gravitation, we have dropped the hypothesis in [12] that Q is reflection invariant. Reflection invariance would, for instance, require the advection coefficients e_i in the reaction-diffusion model (1.3) to be zero. Because we shall not discuss the approximation of the spreading speeds by those of linear operators which was treated in [12] and [8], we have also dropped all assumptions about the linearization of Q. We have, however, assumed the global stability of $\boldsymbol{\beta}$, which is a consequence of the hypotheses of [12]. Hypothesis v is not required in [12], but it will be used in establishing the existence of waves. Our principal tool is the following:

Lemma 2.1. (Comparison Lemma.) *Let* R *be an order preserving operator. If* $\mathbf{u}_n$ *and* $\mathbf{v}_n$ *satisfy the inequalities* $\mathbf{u}_{n+1} \le R[\mathbf{u}_n]$ *and* $\mathbf{v}_{n+1} \ge R[\mathbf{v}_n]$ *for all* n*, and if* $\mathbf{u}_0 \le \mathbf{v}_0$*, then* $\mathbf{u}_n \le \mathbf{v}_n$ *for all* n*.*

Proof. The proof is by induction. If $\mathbf{u}_n \le \mathbf{v}_n$, then $\mathbf{u}_{n+1} \le R[\mathbf{u}_n] \le R[\mathbf{v}_n] \le \mathbf{v}_{n+1}$.

As in [12], we shall define two spreading speeds c^* and c_f^* for the recursion (1.2). The slowest speed c^* coincides with the speed of the same name in [12], but the fastest speed c_f^* may be less than the speed c_+^* of [12], and we shall show that c_f^* is the true fastest spreading speed. We begin by choosing a continuous vector-valued function $\boldsymbol{\phi}(x)$ with the properties

$$\begin{array}{l} \text{i. } \boldsymbol{\phi}(x) \text{ is nonincreasing in } x; \\ \text{ii. } \boldsymbol{\phi}(x) = \mathbf{0} \text{ for all } x \ge 0; \\ \text{iii. } \mathbf{0} << \boldsymbol{\phi}(-\infty) << \boldsymbol{\beta}. \end{array} \tag{2.1}$$

In order to define the slowest speed, we let $\mathbf{a}_0(c; s) = \boldsymbol{\phi}(s)$, and define the sequence $\mathbf{a}_n(c; s)$ by the recursion

$$\mathbf{a}_{n+1}(c; s) = \max\{\boldsymbol{\phi}(s), Q[\mathbf{a}_n(c; x)](s + c)\}. \tag{2.2}$$

The operator which takes $\mathbf{a}_n$ into the function on the right is again order preserving. By definition, $\mathbf{a}_1 \geq \boldsymbol{\phi} = \mathbf{a}_0$, and an induction argument shows that for all n, $\mathbf{a}_n \leq \mathbf{a}_{n+1} \leq \boldsymbol{\beta}$, and $\mathbf{a}_n(c; s)$ is non-increasing in c and s. Thus the sequence $\mathbf{a}_n$ converges to a limit function $\mathbf{a}(c; s)$ which is again nonincreasing in c and s and bounded by $\boldsymbol{\beta}$. An argument of Lui [9] shows that the vectors $\mathbf{a}(c; \pm\infty)$ are equilibria of Q. The first four of the Hypotheses 2.1 imply that $\mathbf{a}(c; -\infty) = \boldsymbol{\beta}$. It is easily seen that when c is sufficiently negative, $\mathbf{a}(c; s) \equiv \boldsymbol{\beta}$, or equivalently that $\mathbf{a}(c, \infty) = \boldsymbol{\beta}$. The function $\mathbf{a}(c; x)$ depends on the choice of the initial function $\boldsymbol{\phi}$. If we start with a different function $\hat{\boldsymbol{\phi}}$ with the properties (2.1), we obtain a different sequence $\hat{\mathbf{a}}_n(c; x)$ and a different limit function $\hat{\mathbf{a}}(c; x)$. Hypothesis 2.1.ii shows that $\lim_{n\to\infty} \mathbf{a}_n(c; -\infty) = \boldsymbol{\beta} >> \hat{\boldsymbol{\phi}}(-\infty)$. Hence, one can find an integer N and a translation τ such that $\mathbf{a}_N(c; x - \tau) \geq \hat{\boldsymbol{\phi}}(x) = \hat{\mathbf{a}}_0(c; x)$. The Comparison Lemma then shows that $\mathbf{a}(c; x - \tau) \geq \hat{\mathbf{a}}(c; x)$. In particular, we see that $\mathbf{a}(c; \infty) \geq \hat{\mathbf{a}}(c; \infty)$. By exchanging the roles of $\boldsymbol{\phi}$ and $\hat{\boldsymbol{\phi}}$ we also obtain the inequality $\hat{\mathbf{a}}(c; \infty) \geq \mathbf{a}(c; \infty)$. We conclude that $\hat{\mathbf{a}}(c; \infty) = \mathbf{a}(c; \infty)$, so that

$$\text{the vector } \mathbf{a}(c; \infty) \text{ is independent of the initial function } \boldsymbol{\phi}. \tag{2.3}$$

We define the slowest spreading speed $c^* \leq \infty$ by the equation

$$c^* = \sup\{c : \mathbf{a}(c; \infty) = \boldsymbol{\beta}\}. \tag{2.4}$$

This name is justified by the following Theorem, whose proof will be given in the Appendix.

Theorem 2.1. *There is an index j for which the following statement is true: Suppose that the initial function $\mathbf{u}_0(x)$ is $\mathbf{0}$ for all sufficiently large x, and that there are positive constants $0 < \rho \leq \sigma < 1$ such that $\mathbf{0} \leq \mathbf{u}_0 \leq \sigma\boldsymbol{\beta}$ for all x and $\mathbf{u}_0 \geq \rho\boldsymbol{\beta}$ for all sufficiently negative x. Then for any positive ϵ the solution $\mathbf{u}_n$ of the recursion (1.2) has the properties*

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

and

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

That is, the jth component spreads at a speed no higher than c^*, and no component spreads at a lower speed.

In order to define the fastest speed c_f^*, we choose a $\boldsymbol{\phi}$ with the properties (2.1), and let $\mathbf{b}_n(x)$ be the solution of the recursion (1.2) with $\mathbf{b}_0(x) = \boldsymbol{\phi}(x)$. We define the function

$$\mathbf{B}(c; x) = \limsup_{n\to\infty} \mathbf{b}_n(x + nc).$$

Because Q is order-preserving and translation invariant, Q applied to a monotone function is again monotone. Thus each $\mathbf{b}_n(x + nc)$ is nonincreasing in x and c, and hence the same is true of $\mathbf{B}(c; x)$. As in the case of the function $\mathbf{a}(c; x)$ we can show that $\mathbf{B}(c; \infty)$ is independent of the choice of the initial function $\boldsymbol{\phi}$ as long as $\boldsymbol{\phi}$ has the properties (2.1). We define the fastest spreading speed c_f^* by the formula

$$c_f^* := \sup\{c : \mathbf{B}(c; \infty) \neq \mathbf{0}\}. \tag{2.7}$$

The name fastest speed is justified by the following Theorem, whose proof will be given in the Appendix.

Theorem 2.2. *There is an index i for which the following statement is true: Suppose that the initial function $\mathbf{u}_0(x)$ is $\mathbf{0}$ for all sufficiently large x, and that there are positive constants $0 < \rho \leq \sigma < 1$ such that $\mathbf{0} \leq \mathbf{u}_0 \leq \sigma\boldsymbol{\beta}$ for all x and $\mathbf{u}_0 \geq \rho\boldsymbol{\beta}$ for all sufficiently negative x. Then for any positive ϵ the solution $\mathbf{u}_n$ of the recursion (1.2) has the properties*

$$\limsup_{n\to\infty} \left[\inf_{x \leq n(c_f^* - \epsilon)} \{\mathbf{u}_n\}_i(x) \right] > 0. \tag{2.8}$$

and

$$\lim_{n\to\infty} \left[\sup_{x \geq n(c_f^* + \epsilon)} \mathbf{u}_n(x) \right] = \mathbf{0}, \tag{2.9}$$

That is, the ith component spreads at a speed no less than c_f^*, and no component spreads at a higher speed.

We see from (2.6) and (2.9) that

$$c_f^* \geq c^*. \tag{2.10}$$

If $c_f^* = c^*$, all components of $\mathbf{u}_n$ spread at the same rate, and we say that the recursion (1.2) has the **single speed** c^*.

Remark. Equations (2.11) and (2.12) of [12] can be considered as a two-sided version of Theorem 2.1 of the present paper. That is, they deal with an initial function $\mathbf{u}_0(x)$ which vanishes outside a bounded set. Equations (2.10) and (2.13) of [12] are two-sided versions of the above Theorem 2.2 but with the speed c_f^* replaced by the quantity

$$c_+^* =: \sup\{c : \mathbf{a}(c; \infty) \neq 0\}. \tag{2.11}$$

The Comparison Lemma shows that $\mathbf{b}_n(x+nc) \leq \mathbf{a}(c;x)$, so that $\mathbf{B}(c;x) \leq \mathbf{a}(c;x)$. Therefore

$$c^* \leq c_f^* \leq c_+^*, \tag{2.12}$$

so that the property (2.9) implies the corresponding property of c_+^*. However, the proof in [12] of the property (2.8) with c_f^* replaced by c_+^* is incomplete, and we have been unable to complete it. It may well be true that $c_f^* < c_+^*$, in which case (2.9) shows that the inequality (2.8) with c_f^* replaced by c_+^* cannot be valid. However, we do not have an example to show that this phenomenon actually occurs.

3 The characterization of c^* as the slowest speed of a class of traveling waves.

In this section, we show that the slowest spreading speed c^* can be characterized as the slowest speed of a class of traveling waves. A traveling wave of speed c is a solution of the recursion (1.2) which has the form $\mathbf{u}_n(x) = \mathbf{W}(x-nc)$ with $\mathbf{W}(s)$ a function in $\mathcal{C}_{\boldsymbol{\beta}}$. That is, the solution at time $n+1$ is simply the translate by c of its value at n. Our basic result is the following.

Theorem 3.1. *Suppose that Q satisfies the Hypotheses 2.1. If $c \geq c^*$, there is a nonincreasing traveling wave solution $\mathbf{W}(x-nc)$ of speed c with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty)$ an equilibrium other than $\boldsymbol{\beta}$.*

If there is a traveling wave $\mathbf{W}(x-nc)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ such that for at least one component i

$$\liminf_{x\to\infty} W_i(x) = 0, \tag{3.1}$$

then $c \geq c^*$. If this property is valid for all components of $\mathbf{W}$, then $c \geq c_+^* \geq c_f^*$.

If there are no constant equilibria other than $\mathbf{0}$ and $\boldsymbol{\beta}$ in $\mathcal{C}_{\boldsymbol{\beta}}$, then $c_+^* = c_f^* = c^*$, so that the recursion (1.2) has a single spreading speed.

Proof. We begin with the proof of the first statement. We choose a fixed vector-valued initial function $\boldsymbol{\phi}(s)$ with the properties (2.1). For each positive number κ we define the sequence $\mathbf{a}_n(c,\kappa;s)$ by the recursion

$$\begin{aligned} &\mathbf{a}_n(c,\kappa;s) = \max\{\kappa\boldsymbol{\phi}(s), Q[\mathbf{a}_n(c,\kappa;x)](s+c)]\}, \\ &\mathbf{a}_0(c,k;s) = \kappa\boldsymbol{\phi}(s). \end{aligned} \tag{3.2}$$

As shown in Section 2, $\mathbf{a}_n(c,\kappa;s)$ is nonincreasing in c and s and nondecreasing in n. As $n\to\infty$, $\mathbf{a}_n(c,\kappa;s)$ converges to a limit function $\mathbf{a}(c,\kappa;s)$, which is nonincreasing in c and s. It is not difficult to see that $\mathbf{a}$ is lower semicontinuous in c, so that when $c \geq c^*$, $\mathbf{a}(c,\kappa,\infty)$ is a constant equilibrium $\boldsymbol{\nu}$ other than $\boldsymbol{\beta}$. By the property (2.3), $\boldsymbol{\nu}$ is independent of κ.

Because of Hypothesis 2.1.v, there is a sequence n_j such that $Q[\mathbf{a}_{n_j}(c,\kappa;x+c)](y)$ converges uniformly for y on bounded sets. Since $\mathbf{a}_n$ is nondecreasing in n and Q is order preserving, the whole sequence $Q[\mathbf{a}_n(c,\kappa;x+c)](y)$ converges uniformly on bounded sets. It follows from (3.2) that the sequence $\mathbf{a}_n(c,\kappa;y)$ converges to a function $\mathbf{a}(c,\kappa;y)$ uniformly for y in any bounded set. Hence $\mathbf{a}(c,\kappa;y)$ is a continuous function of y, and by Hypothesis 2.1.iv we can take limits in (3.2) to see that

$$\mathbf{a}(c,\kappa;s) = \max\{\kappa\boldsymbol{\phi}(s), Q[\mathbf{a}(c,\kappa;x)](s+c)\}. \tag{3.3}$$

We use $|\cdot|$ to denote the Euclidean norm. Since $\boldsymbol{\beta}$ is the only equilibrium in the interior of $\mathcal{C}_{\boldsymbol{\beta}}$, we can choose $\eta > 0$ so small that there is no constant equilibrium other than $\boldsymbol{\beta}$ in the set $\{\mathbf{u} \in \mathcal{C}_{\boldsymbol{\beta}} : |\boldsymbol{\beta} - \mathbf{u}| \le \eta\}$. Since the continuous function $|\boldsymbol{\beta} - \mathbf{a}(c,\kappa;s)|$ increases from $\mathbf{0}$ to $|\boldsymbol{\beta} - \boldsymbol{\nu}| > \eta$, the intermediate value theorem shows that there exists $\ell(\kappa)$ so that

$$|\boldsymbol{\beta} - \mathbf{a}(c,\kappa;\ell(\kappa))| = \eta. \tag{3.4}$$

Because of the equation (3.3) and Hypothesis 2.1.v, there is a sequence $\kappa_i \to 0$ such that $\mathbf{a}(c,\kappa_i;x+\ell(\kappa_i))$ converges uniformly for x on bounded sets to a function $\mathbf{W}(x)$. Therefore we may take limits in (3.3) with $\kappa = \kappa_i$ and $s = y + \ell(\kappa_i) - (n+1)c$ and use the translation invariance of Q to find that

$$\mathbf{W}(y-(n+1)c) = Q[\mathbf{W}(x-nc)](y). \tag{3.5}$$

Therefore $\mathbf{u}_n(x) = \mathbf{W}(x-nc)$ is a traveling wave solution of the recursion $\mathbf{u}_{n+1} = Q[\mathbf{u}_n]$ with

$$|\boldsymbol{\beta} - \mathbf{W}(0)| = \eta. \tag{3.6}$$

Letting y approach $\pm\infty$ in (3.5) shows that $\mathbf{W}(\pm\infty)$ are equilibria. Because $|\boldsymbol{\beta} - \mathbf{W}(x)|$ is nondecreasing, the definition of η shows that $\mathbf{W}(-\infty) = \boldsymbol{\beta}$, while $\mathbf{W}(+\infty) \neq \boldsymbol{\beta}$. Thus $\mathbf{W}$ has the properties in the first statement of the Theorem.

To prove the second statement, suppose there is a wave $\mathbf{W}(x-nc)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$. Choose a function $\boldsymbol{\phi}(s)$ with the properties (2.1) such that $\boldsymbol{\phi}(x) \le \mathbf{W}(x)$. Define the sequence $\mathbf{a}_n$ and its limit $\mathbf{a}$ by means of (2.2) with $\mathbf{a}_0(c;x) = \boldsymbol{\phi}(x)$. Induction shows that $\mathbf{a}_n(c;x) \le \mathbf{W}(x)$, which implies that $\mathbf{a}(c;x) \le \mathbf{W}(x)$, and therefore that $\mathbf{a}(c;\infty) \le \liminf_{x\to\infty} \mathbf{W}(x)$. Hence by definition, $c \ge c^*$ if (3.1) holds for at least one component, and $c \ge c_+^* \ge c_f^*$ if (3.1) is valid for all components.

Finally we note that if the only constant equilibrium other that $\boldsymbol{\beta}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ is $\mathbf{0}$, then the first statement shows that there is a traveling wave $\mathbf{W}(x-nc^*)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty) = \mathbf{0}$. The second statement now shows that $c^* \ge c_+^* \ge c_f^* \ge c^*$, which establishes the last statement. Thus Theorem 3.1 is proved.

EXAMPLE 3.1. Consider the discrete-time model

$$\begin{aligned} p_{n+1}(y) &= \int_{-\infty}^{\infty} \frac{(1+\rho_1)p_n(x)}{1+\rho_1[p_n(x)+\alpha_1 q_n(x)]} k_1(y-x)dx, \\ q_{n+1}(y) &= \int_{-\infty}^{\infty} \frac{(1+\rho_2)q_n(x)}{1+\rho_2[q_n(x)+\alpha_2 p_n(x)]} k_2(y-x)dx. \end{aligned} \tag{3.7}$$

for the growth and spread of two species whose population densities at time n and point x are $p_n(x)$ and $q_n(x)$. The model states that the species grow and compete according to Beverton-Holt (or Verhulst) dynamics, and then migrate with the migration kernels k_i. That is, $k_i(x)dx$ is the probability that the ith species moves by a distance between x and $x + dx$ during one unit of time. Each k_i is thus a probability density. Because we wish to consider such phenomena as prevailing winds, we do not require these kernels to be symmetric. The parameters α_i and ρ_i are all positive. It is easily verified that the system (3.7) has the unpopulated equilibrium (0,0) and the two monoculture equilibria (1,0) and (0,1). We shall consider the invasion of the state (0,1) by the first species. We assume that

$$0 < \alpha_1 < 1,$$

so that, for p near zero and q near 1, the growth rate of the first species is positive. That is, the state (0,1) is **invadable**. Then there is a coexistence equilibrium (p_+, q_+), where

$$p_+ = \frac{1-\alpha_1}{1-\alpha_1\alpha_2}, \; q_+ = \frac{1-\alpha_2}{1-\alpha_1\alpha_2} \tag{3.8}$$

if and only if $0 < \alpha_2 < 1$. We shall discuss the transition from the monoculture state $(0, 1)$ to the target state

$$(p^*, q^*) = \begin{cases} (p_+, q_+) & \text{if } 0 < \alpha_2 < 1 \\ (1, 0) & \text{if } \alpha_2 \geq 1. \end{cases}$$

The change of variables $u_n(x) = p_n(x)$, $v_n(x) = 1 - q_n(x)$ converts the competitive system (3.7) into the cooperative system

$$\begin{aligned} u_{n+1}(y) &= \int_{-\infty}^{\infty} \frac{(1+\rho_1)u_n(x)}{1+\rho_1[\alpha_1 + u_n(x) - \alpha_1 v_n(x)]} k_1(y-x)dx, \\ v_{n+1}(y) &= \int_{-\infty}^{\infty} \frac{\alpha_2\rho_2 u_n(x) + v_n(x)}{1+\rho_2[1 - v_n(x) + \alpha_2 u_n(x)]} k_2(y-x)dx. \end{aligned} \tag{3.9}$$

We shall assume the continuity condition

$$\lim_{\eta\to 0} \int_{-\infty}^{\infty} |k_i(x+\eta) - k_i(x)|dx = 0 \text{ for } i = 1, 2, \tag{3.10}$$

which implies that the family of function $Q[\mathbf{u}]$ with $\mathbf{u}$ in $\mathcal{C}_{\boldsymbol{\beta}}$ is equicontinuous. Then Ascoli's theorem implies Hypothesis 2.1.v. It is easily verified that the system (3.9) satisfies the Hypotheses 2.1 with

$$\boldsymbol{\beta} = (p^*, 1 - q^*).$$

The corresponding spreading speeds c^* and c_f^* give the speeds at which changes in p and q spread to the right into a population which is initially in the monoculture state (0,1) for all sufficiently large x. We observe that in addition to the equilibria $\mathbf{0}$ and $\boldsymbol{\beta}$, the system (3.9) has the equilibrium (0,1), which corresponds to the extinction state $p = q = 0$. This equilibrium lies in $\mathcal{C}_{\boldsymbol{\beta}}$ if and only if $\alpha_2 \geq 1$.

Theorem 3.1 shows that the slowest speed c^* of this transition can be characterized as the smallest value of c for which there is a monotone traveling wave $\mathbf{W}(x - nc))$ of the system (3.9) with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty)$ equal to either (0,0) or (0,1). If $\alpha_2 < 1$, then (0,1) is not in $\mathcal{C}_{\boldsymbol{\beta}}$, and hence $\mathbf{W}(\infty) = (0,0)$ and $c^*_+ = c^*_f = c^*$, so that there is a single spreading speed.

4 Traveling waves for continuous-time systems.

We shall extend the statement of Theorem 3.1 to well-posed continuous-time problems such as the reaction-diffusion system

$$\begin{aligned} &\mathbf{u}_{,t} = D\mathbf{u}_{,xx} - E\mathbf{u}_{,x} + \mathbf{f}(\mathbf{u}) \\ &\mathbf{u}(0,x) = \mathbf{u}_0(x). \end{aligned} \tag{4.1}$$

Here

$$D := \text{diagonal}(d_1, \cdots, d_k)$$

and

$$E := \text{diagonal}(e_1, \cdots, e_k)$$

are constant diagonal matrices. The mobilities d_i are positive, but the advections e_i may have any signs. For such a system there is a family of time-t maps Q_t, which are defined by the fact that $Q_t[\mathbf{u}_0](x) := \mathbf{u}(x,t)$. That is, Q_t takes the initial values of $\mathbf{u}$ to the values of $\mathbf{u}$ at time t. For obvious reasons, this family forms a semigroup in the sense that

$$Q_{t_1}[Q_{t_2}[\mathbf{v}]] = Q_{t_1+t_2}[\mathbf{v}] \tag{4.2}$$

for all positive t_1 and t_2, and

$$\lim_{t \searrow 0} Q_t[\mathbf{v}] = \mathbf{v}. \tag{4.3}$$

A traveling wave of a continuous-time recursion $\mathbf{u}(x, t_1+t_2) = Q_{t_2}[\mathbf{u}(\cdot, t_1)](x)$ is defined to be a solution which does not change its shape in time. That is, $\mathbf{W}(x - ct)$ is a continuous-time traveling wave of speed c if and only if

$$Q_t[\mathbf{W}](x) = \mathbf{W}(x - ct) \tag{4.4}$$

for all positive t. We can use Theorem 3.1 to obtain the existence of traveling waves for continuous-time systems.

Theorem 4.1. *Suppose that Q_t is a family of operators on the set $\mathcal{C}_{\boldsymbol{\beta}}$ with the properties (4.2) and (4.3) such that each Q_t with $t > 0$ satisfies the Hypotheses 2.1. Let c^* be the slowest spreading speed of the recursion (1.2)* *with Q replaced by Q_1. Then for every $c \geq c^*$ there is a traveling wave $\mathbf{W}(x-ct)$ which is nonincreasing in x and for which $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ while $\mathbf{W}(\infty)$ is an equilibrium other than $\boldsymbol{\beta}$.*

If there is a traveling wave $\mathbf{W}(x-ct)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ such that for at least one component i

$$\liminf_{x\to\infty} W_i(x) = 0,$$

then $c \geq c^*$. If this property is valid for all components of $\mathbf{W}$, then $c \geq c_+^* \geq c_f^*$.

If there is a positive t_0 such that the recursion (1.2) with Q replaced by Q_{t_0} has no constant equilibria other than $\mathbf{0}$ and $\boldsymbol{\beta}$ in $\mathcal{C}_{\boldsymbol{\beta}}$, then $c_+^*[Q_t] = c_f^*[Q_t] = c^*[Q_t] = tc^*[Q_1]$ for all $t > 0$, so that the recursion has a single spreading speed.

The proof will be found in the Appendix.

It is, of course, useful to know when this Theorem can be applied to the reaction-diffusion system (4.1). We have the following result.

Theorem 4.2. *Suppose that the system (4.1) has the following properties:*

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 is no constant $\boldsymbol{\nu}$ other than $\mathbf{0}$ and $\boldsymbol{\beta}$ such that $\mathbf{f}(\boldsymbol{\nu}) = \mathbf{0}$ and $\mathbf{0} << \boldsymbol{\nu} \leq \boldsymbol{\beta}$.*

ii. *The system (4.1) is cooperative; i.e., each $f_i(\boldsymbol{\alpha})$ 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 diagonal matrices D and E are constant.*

iv. $\mathbf{f}(\boldsymbol{\alpha})$ *is continuous and has uniformly bounded piecewise continuous first partial derivatives for $\mathbf{0} \leq \boldsymbol{\alpha} \leq \boldsymbol{\beta}$, and it is differentiable at $\mathbf{0}$. The Jacobian matrix $\mathbf{f}'(\mathbf{0})$, whose off-diagonal entries are nonnegative, has a positive eigenvalue whose eigenvector has positive components.*

v. *The mobilities d_i, which are the diagonal and only nonzero entries of D, are all positive.*

Then for every $c \geq c^*$ the system (4.1) has a nonincreasing traveling wave solution $\mathbf{W}(x-ct)$ of speed c with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty)$ a zero of $\mathbf{f}$ other than $\boldsymbol{\beta}$.

If there is a traveling wave $\mathbf{W}(x-ct)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ such that for at least one component i

$$\liminf_{x\to\infty} W_i(x) = 0,$$

then $c \geq c^*$. If this property is valid for all components of $\mathbf{W}$, then $c \geq c_+^* \geq c_f^*$.

If the only zeros of $\mathbf{f}(\mathbf{u})$ in $\mathcal{C}_{\boldsymbol{\beta}}$ are $\mathbf{0}$ and $\boldsymbol{\beta}$, then $c_+^* = c_f^* = c^*$, so that the system (4.1) has a single spreading speed.

Proof. The first four of the Hypotheses 2.1 for the time-t map Q_t follow as in Section 4 of [12]. Condition (v) implies that the system is uniformly parabolic, so that for each $t > 0$ the functions $Q_t[\mathbf{v}]$ with $\mathbf{v} \in \mathcal{C}_{\boldsymbol{\beta}}$ form an equicontinuous family. Hypothesis 2.1.v then follows from Ascoli's theorem. Thus we can apply Theorem 4.1. It is easily verified that $\mathbf{W}(x - ct)$ has sufficient differentiability to permit it to be substituted in the differential equation. The equation $Q_t[\mathbf{W}](x) = \mathbf{W}(x - ct)$ thus implies that $\mathbf{u}(x, t) = \mathbf{W}(x - ct)$ solves the system (4.1) with the initial condition $\mathbf{u}(x, 0) = \mathbf{W}(x)$. This proves the existence of waves for all $c \geq c^*$. The remaining statements follow from the corresponding statements of Theorem 4.1. Thus Theorem 4.2 is established.

EXAMPLE 4.1. Consider the cooperative two-species Lotka-Volterra model

$$\begin{aligned} u_t &= d_1 u_{xx} + r_1 u(1 - u + a_1 v) \\ v_t &= d_2 v_{xx} + r_2 v(1 - v + a_2 u). \end{aligned} \tag{4.5}$$

We assume that all parameters are positive constants, and that

$$a_1 a_2 < 1.$$

Then there are four equilibria: The extinction state (0,0), the two monoculture states (1,0) and (0,1), and the coexistence equilibrium (u^*, v^*) where

$$u^* = (1 + a_1)/(1 - a_1 a_2),\ v^* = (1 + a_2)/(1 - a_1 a_2).$$

It is easily verified that the system (4.5) satisfies the hypotheses of Theorem 4.2 with $\boldsymbol{\beta} = (u^*, v^*)$.

We consider the simultaneous invasion of the extinction state (0,0) by the two species. Because $v \geq 0$, the Comparison Lemma shows that u cannot spread more slowly than it would if v were replaced by 0 in the first equation of (4.5). The resulting equation is Fisher's equation, and we conclude that

$$c_f^* \geq 2\sqrt{d_1 r_1}. \tag{4.6}$$

Similarly we see that because $u \leq u^*$, v cannot spread more rapidly than it would if u were replaced by u^* in the second equation of (4.5). Since the resulting equation is turned into Fisher's equation by the change of variable $w = v/v^*$, we conclude that

$$c^* \leq 2\sqrt{d_2 r_2 v^*}. \tag{4.7}$$

Thus if the parameters have the property that

$$d_1 r_1 > d_2 r_2 v^*, \tag{4.8}$$

then we must have

$$c_f^* > c^*.$$

Then for any c such that $c^* \leq c < c_f^*$, the traveling wave of speed c given by Theorem 4.1 must have the property that $\mathbf{W}(\infty)$ is an equilibrium whose u-coordinate is positive, because u spreads more quickly than c. Thus $\mathbf{W}(\infty) = (1,0)$. To obtain such a wave, we make the change of variable $\hat{u} = u - 1$, so that in the new coordinates

$$\begin{aligned}\hat{u}_t &= d_1 \hat{u}_{xx} + r_1(\hat{u}+1)(-\hat{u} + a_1 v) \\ v_t &= d_2 v_{xx} + r_2 v(1 + a_2 - v + a_2 \hat{u}).\end{aligned} \tag{4.9}$$

This system satisfies the hypotheses of Theorem 4.2 with $\hat{\boldsymbol{\beta}} = (u^* - 1, v^*)$. Moreover, there are no nonnegative constant equilibria other than $\mathbf{0}$ and $\hat{\boldsymbol{\beta}}$ in $\mathcal{C}_{\hat{\boldsymbol{\beta}}}$. Thus it has a single spreading speed $\hat{c}^*$, and there is a traveling wave $\hat{\mathbf{W}}(x-ct)$ with $\hat{\mathbf{W}}(\infty) = \hat{\boldsymbol{\beta}}$ and $\hat{\mathbf{W}}(\infty) = \mathbf{0}$ if and only if $c \geq \hat{c}^*$. Because we have such a wave for $c = c^*$, we conclude that $c^* \geq \hat{c}^*$. On the other hand, we observe that the function $(\hat{W}_1(x - \hat{c}^* t) + 1, \hat{W}_2(x - \hat{c}^* t))$ is a traveling wave of the system (4.5), which implies that $\hat{c}^* \geq c^*$. Thus we find that $c^* = \hat{c}^*$. We have shown that if $c_f^* > c^*$ and the u-component spreads more quickly than the v-component, the slowest speed c^* of the problem (4.5) can be obtained as the single spreading speed $\hat{c}^*$ of the system (4.9). Symmetry shows that when $c_f^* > c^*$ and the v-component spreads more quickly, then c^* can be obtained as the single spreading speed for the invasion of the state (0,1). A sufficient condition for this is given by interchanging the indices 1 and 2 and replacing v^* by u^* in (4.8).

There are also parameter values for which the problem (4.5) has a single speed. Suppose, for instance, that

$$d_2 = d_1, \;\; r_2 = r_1, \;\; \text{and } a_2 = a_1 < 1.$$

If $u(x,0) = v(x,0)$, the equations show that $u(x,t) = v(x,t)$, and hence that

$$u_t = d_1 u_{xx} + r_1 u[1 - (1 - a_1)u],$$

Since this equation is turmed into Fisher's equation by the substitution $w = (1 - a_1)u$, we see that u and v spread at the speed $2\sqrt{d_1 r_1}$. Since any initial values can be bounded below by the initial data with both components equal to $\min\{u(x,0), v(x,0)\}$ and above by the initial data with both components equal to $\max\{u(x,0), v(x,0)\}$, the comparison lemma shows that u and v always spread at this rate. That is $c_f^* = c^* = 2\sqrt{d_1 r_1}$. When $c \geq 2\sqrt{d_1 r_1}$ the Fisher equation has a traveling wave $w(x - ct)$, and we observe that $\mathbf{W}(x - ct) := ((1 - a_i)^{-1} w(x - ct), (1 - a_i)^{-1} w(x - ct))$ is a traveling wave of our system. Note that $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty) = \mathbf{0}$.

For other parameter values for which $c_f^* = c^*$, Theorem 4.2 shows that for $c \geq c^*$ there is a monotone wave $\mathbf{W}(x - ct)$ with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$, but we do not know which of the values (0,0), (1,0), or (0,1) $\mathbf{W}(\infty)$ has.

EXAMPLE 4.2. Consider the Lotka-Volterra competition model

$$\begin{aligned}p_{,t} &= d_1 p_{,xx} - e_1 p_{,x} + r_1 p(1 - p - a_1 q), \\ q_{,t} &= d_2 q_{,xx} - e_2 q_{,x} + r_2 q(1 - q - a_2 p),\end{aligned} \tag{4.10}$$

where d_i, r_i, and a_i are positive constants, and the advections e_i are constants. This system always has the two monoculture equilibria (0,1) and (1,0) and the unpopulated equilibrium (0,0). We shall assume that $0 < a_1 < 1$ so that the monoculture state (0, 1) is invadable. Then there is also a coexistence equilibrium

$$(p_+, q_+) := \left(\frac{1 - a_1}{1 - a_1 a_2}, \frac{1 - a_2}{1 - a_1 a_2} \right),$$

if and only if $a_2 < 1$. We define the target state

$$(p^*, q^*) = \begin{cases} (p_+, q_+) & \text{if } 0 < a_2 < 1 \\ (1, 0) & \text{if } a_2 \geq 1. \end{cases}$$

The change of variables $u = p$, $v = 1 - q$ converts the competition system (4.10) into the system

$$\begin{aligned} u_{,t} &= d_1 u_{,xx} - e_1 u_{,x} + r_1 u(1 - a_1 - u + a_1 v), \\ v_{,t} &= d_2 v_{,xx} - e_2 v_{,x} + r_2 (1 - v)(a_2 u - v), \end{aligned} \tag{4.11}$$

which is cooperative in the biologically realistic range $u \geq 0$, $0 \leq v \leq 1$. It is easily verified that this system satisfies the conditions of Theorem 4.2 with $\boldsymbol{\beta} = (p^*, 1 - q^*)$. We observe that in addition to the equilibria $\mathbf{0}$ and $\boldsymbol{\beta}$ this system has an equilibrium at (0,1), and that this equilibrium is in $\mathcal{C}_{\boldsymbol{\beta}}$ if and only if $a_2 \geq 1$.

The spreading speeds c^* and c_f^* of (4.11) give the speeds at which the components of a solution of (4.10) which is initially equal to the monoculture (0,1) for all sufficiently large x spread toward the target state (p^*, q^*). Theorem 4.2 characterizes the slowest speed c^* as the smallest value of c for which there is a monotone traveling wave of (4.11) with $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty)$ equal to either $(0,0)$ or (0,1). When $a_2 < 1$, (0,1) is not in $\mathcal{C}_{\boldsymbol{\beta}}$, so that $\mathbf{W}(\infty) = (0, 0)$ and $c_+^* = c_f^* = c^*$. That is, there is a single spreading speed.

5 Summary.

This paper focuses on extending to a large class of cooperative multi-species models a piece of folklore which is well known for many scalar models. Namely, the asymptotic speed at which a new and more fit species invades the territory of an established set of species can be characterized as the lowest speed of a suitable family of traveling waves of the model. (A traveling wave is a solution of the equation which has the same shape at each time but which is translated by its speed c per unit time.) Because the population changes of different species in a multi-species model may spread at different speeds, this extension is a rather challenging problem. Theorem 3.1 establishes the desired result for the slowest spreading speed c^* of a discrete-time model. Theorems 4.1 and 4.2 show that the same result is true for continuous-time models, and, in particular, for reaction-diffusion models.

Earlier works have analyzed the population spreading speed for cooperative population models under particular restrictions on the dynamics [9, 10], or under the assumption of symmetric dispersal [12, 8]. We have shown that such restrictions and assumptions can be relaxed to allow for more general dynamics and asymmetric dispersal.

While the basic results involve cooperative dynamics, a simple change of variables sometimes translates the biologically prevalent case of competition into cooperation. Thus we are able to consider traveling wave solutions for competitive dynamics in two-species discrete-time (perhaps integrodifference) models (Section 3) and continuous-time (perhaps partial differential equation) models (Section 4). While our hypotheses permit the system to have a weak Allee effect, they do exclude a strong Allee effect for the system as a whole.

6 Appendix

Proof of Theorem 2.1. Because $\mathbf{u}_0$ vanishes for large x and is bounded away from $\boldsymbol{\beta}$, we can choose a function $\boldsymbol{\phi}(x)$ with the properties (2.1) and a number η such that $\mathbf{u}_0(x) \le \boldsymbol{\phi}(x-\eta)$. By noting that the right-hand side of the recursion (2.2) is bounded below by $Q[\mathbf{a}_n](s+c)$ and using the Comparison Lemma, we find that $\mathbf{u}_n(x) \le \mathbf{a}_n(c; x-\eta-nc)$. Since $\mathbf{a}_n$ is nonincreasing in x, we see that

$$\sup_{x \ge n(c+\frac{1}{2}\epsilon)} \mathbf{u}_n(x) \le \mathbf{a}_n(c; \tfrac{1}{2}n\epsilon - \eta) \le \mathbf{a}(c; \tfrac{1}{2}n\epsilon - \eta).$$

Thus,

$$\limsup_{n\to\infty} \left[\sup_{x \ge n(c+\frac{1}{2}\epsilon)} \mathbf{u}_n(x) \right] \le \mathbf{a}(c; \infty).$$

If we let $c = c^* + \frac{1}{2}\epsilon$, the right-hand side is a constant equilibrium other than $\boldsymbol{\beta}$. Therefore it has at least one zero component, and we find (2.5) for this component.

In order to derive (2.6), we temporarily assume that Q has the additional properties

a. If $\boldsymbol{\alpha}$ is a constant vector with $0 \le \boldsymbol{\alpha} << \boldsymbol{\beta}$, then $Q[\boldsymbol{\alpha}] << \boldsymbol{\beta}$.

b. There is a number γ with the property that if $\mathbf{u}(x) = \mathbf{0}$ for $x \ge \eta$, then $Q[\mathbf{u}](x) = \mathbf{0}$ for $x \ge \eta + \gamma$.

Choose a function $\boldsymbol{\phi}$ with the properties (2.1) and with $\boldsymbol{\phi}(x) \le \mathbf{u}_0(x)$, and let $c < c^*$. By the definition of c^*, $\mathbf{a}_n(c; 0)$ increases to $\boldsymbol{\beta}$. Therefore there is an index N such that $\mathbf{a}_N(c; 0) >> \boldsymbol{\phi}(-\infty)$. Since both $\mathbf{a}_N$ and $\boldsymbol{\phi}$ are nonincreasing and $\boldsymbol{\phi}$ vanishes for $x \ge 0$, it follows that $\mathbf{a}_N(c; x) >> \boldsymbol{\phi}(x)$. Let $\mathbf{b}_n$ be the solution of the recursion

$$\mathbf{b}_{n+1}(x) = Q[\mathbf{b}_n](x)$$

with $\mathbf{b}_0(x) = \boldsymbol{\phi}(x)$. Since $\boldsymbol{\phi} \le \mathbf{u}_0$, the Comparison Lemma shows that $\mathbf{u}_n(x) \ge \mathbf{b}_n(x)$ for all n. We see from Hypothesis 2.1.ii that $\mathbf{b}_n(-\infty)$ converges to $\boldsymbol{\beta}$. Moreover, by the above Property (a), $\mathbf{a}_N(c;-\infty) << \boldsymbol{\beta}$. Thus we can find an $M \ge N$ such that $\mathbf{b}_M(-\infty) >> \mathbf{a}_N(-\infty)$. Since Property (b) implies that $\mathbf{a}_N(c;x)$ vanishes for $x \ge N(\gamma + c)$, there is a number τ such that

$$\mathbf{b}_M(x) \ge \mathbf{a}_N(c; x+\tau).$$

Since $\mathbf{a}_n$ is nondecreasing in n, $\mathbf{a}_n(c;x) >> \boldsymbol{\phi}(x)$ for $n \ge N$, so that the maximum in the recursion (2.2) must be equal to $Q[\mathbf{a}_n](x+c)$. Therefore, $\mathbf{b}_n(x+nc)$ and $\mathbf{a}_n(c;x+\tau)$ satisfy the same recursion for $n \ge N$. The Comparison Lemma then shows that $\mathbf{b}_n(x+nc) \ge \mathbf{a}_{n+N-M}(c;x+\tau)$ when $n \ge M-N$. Therefore

$$\mathbf{u}_n(x+nc) \ge \mathbf{b}_n(x+nc) \ge \mathbf{a}_{n+N-M}(c;x+\tau).$$

Since $\mathbf{a}_n$ is nonincreasing, we find that if we take $c = c^* - \epsilon$,

$$\sup_{x \le n(c^*-\epsilon)} \{\boldsymbol{\beta} - \mathbf{u}_n(x)\} \le \{\boldsymbol{\beta} - \mathbf{a}_{n+N-M}(c^* - \epsilon; \tau)\}.$$

By the definition of c^*, the right-hand side approaches zero as n goes to infinity, and this yields (2.6). We have thus proved (2.6) under the additional assumption that Q has the above properties (a) and (b). If this is not the case, the following construction produces an operator $\hat{Q}$ which approximates Q from below, and has these properties. Define a "cutoff function" $\zeta(s)$ as a smooth scalar function with the properties

i. $\zeta(s)$ is nonnegative and nonincreasing for $s \ge 0$;

ii. $\zeta(s) = 0$ for $s \ge 1$;

iii. $\zeta(s) = 1$ for $0 \le s \le \frac{1}{2}$.

Choose two positive parameters α and δ, and define

$$\hat{Q}[\mathbf{v}](y) := \min\{Q[\zeta(|y-x|/\alpha)\mathbf{v}(x)](y), (1-\delta)Q[\zeta(|y-x|/\alpha)\mathbf{v}(x)](y) + \delta\mathbf{v}(y)\}.$$

It is easily seen that $\hat{Q}$ has the properties (a) and (b) and satisfies the Hypotheses 2.1, $\hat{Q}[\mathbf{v}] \le Q[\mathbf{v}]$. Moreover, $\hat{Q}[\mathbf{v}]$ approaches $Q[\mathbf{v}]$ as δ goes to zero and α approaches infinity. As in the proof of Lemma 5.1 of [15], applying the above proof to $\hat{Q}$ and taking these limits yields (2.6), and this finishes the proof of Theorem 2.1.

Proof of Theorem 2.2. To prove (2.8), we choose a $\boldsymbol{\phi}$ which has the properties (2.1) and satisfies the inequality $\boldsymbol{\phi} \le \mathbf{u}_0$. By the Comparison Lemma we have $\mathbf{u}_n(x) \ge \mathbf{b}_n(x)$. Since $\mathbf{b}_n$ is nonincreasing in x,

$$\inf_{x \le n(c_f^* - \epsilon)} \mathbf{u}_n(x) \ge \mathbf{b}_n(n(c_f^* - \epsilon)).$$

Then

$$\limsup_{n\to\infty}\left[\inf_{x\le n(c_f^*-\epsilon)}\mathbf{u}_n(x)\right]\ge\mathbf{B}(c_f^*-\epsilon;0)\ge\mathbf{B}(c_f^*-\epsilon;\infty). \tag{6.1}$$

By definition, the right-hand side is not $\mathbf{0}$. Hence some component, say the ith component, is positive, and we obtain (2.8). To prove (2.9), we choose a function $\boldsymbol{\phi}$ with the properties (2.1) and the additional property that $\boldsymbol{\phi}(x-\eta)\ge\mathbf{u}_0(x)$ for some η. By the Comparison Lemma $\mathbf{u}_n(x)\le\mathbf{b}_n(x-\eta)$. Since $\mathbf{b}_n$ is nonincreasing, we find that

$$\sup_{x\ge n(c_f^*+\epsilon)}\mathbf{u}_n(x)\le\mathbf{b}_n(n(c_f^*+\tfrac{1}{2}\epsilon)+\tfrac{1}{2}n\epsilon-\eta)\le\mathbf{b}_n(n(c_f^*+\tfrac{1}{2}\epsilon)+\tau)$$

for any τ, provided n is sufficiently large. Thus

$$\limsup_{n\to\infty}\left[\sup_{x\ge n(c_f^*+\epsilon)}\mathbf{u}_n(x)\right]\le\mathbf{B}(c_f^*+\tfrac{1}{2}\epsilon;\tau)$$

with τ arbitrary. We let τ go to infinity to see that

$$\limsup_{n\to\infty}\left[\sup_{x\ge n(c_f^*+\epsilon)}\mathbf{u}_n(x)\right]\le\mathbf{B}(c_f^*+\tfrac{1}{2}\epsilon;\infty)=\mathbf{0}. \tag{6.2}$$

Since $\mathbf{u}_n\ge\mathbf{0}$, this proves the statement (2.9). Thus Theorem 2.2 is proved.

Proof of Theorem 4.1. The equation(4.4) shows that for any fixed positive t, a continuous-time traveling wave $\mathbf{W}(x-ct)$ is a traveling wave of speed ct of the recursion (1.2) with Q replaced by Q_t. Therefore the second and third statements of the Theorem follow immediately from the corresponding statements of Theorem 3.1.

To prove the existence of the traveling wave when $c\ge c^*$, we first note that $\{Q_{p/q}\}^q=Q_p=\{Q_1\}^p$ when p and q are positive integers, where $\{Q_t\}^\ell$ denotes the ℓth iterate of the operator Q_t. It then follows from Theorem 2.1 that the slowest spreading speed $c_{p/q}$ of the operator $Q_{p/q}$ is just $(p/q)c^*$, where c^* is the slowest spreading speed of Q_1. The proof of Theorem 3.1 then shows that for each $c\ge c^*$ and for each rational t there is a nonincreasing traveling wave $\mathbf{W}_t(x-nct)$ of the operator Q_t which satisfies the equation

$$|\boldsymbol{\beta}-\mathbf{W}_t(0)|=\eta, \tag{6.3}$$

where η is so small that $\boldsymbol{\beta}$ is the only constant equilibrium which satisfies the condition $0\le|\boldsymbol{\beta}-\mathbf{W}_t(0)|\le\eta$. We see from Hypotheses 2.1.v and 2.1.iv that there is a sequence $r_i\to\infty$ such that $\mathbf{W}_{2^{-r_i}}(x)$ converges uniformly on bounded sets to a function $\mathbf{W}(x)$ which is again nonincreasing and satisfies the normalization (6.3). Since $\mathbf{W}_{2^{-r_i}}$ is a traveling wave for all Q_t for which t is a multiple of 2^{-r_i}, $Q_t[\mathbf{W}](x)=\mathbf{W}(x-ct)$ for every t which is a fraction whose denominator is a power of 2. Let t be an arbitrary positive number, and m any positive integer. Then one can write

$$t=k_m2^{-m}-r_m$$

where k_m is a positive integer and $0 \le r_m < 2^{-m}$. Then by (4.2) and the above observation

$$Q_t[\mathbf{W}](x) - \mathbf{W}(x-ct) = \{Q_t[\mathbf{W}] - Q_{r_m}[Q_t[\mathbf{W}]]\} \\ + \{\mathbf{W}(x - c(t+r_m)) - \mathbf{W}(x-ct)\}.$$

We let m approach infinity, so that r_m goes to zero. The property (4.3) shows that the first term on the right approaches zero, and the continuity of $\mathbf{W}$ shows that the second term also goes to zero. Therefore

$$Q_t[\mathbf{W}](x) = \mathbf{W}(x-ct),$$

so that $\mathbf{W}$ is a nonincreasing continuous-time traveling wave of speed c. Because $\mathbf{W}$ is nonincreasing and satisfies the condition (6.3), we conclude as before that $\mathbf{W}(-\infty) = \boldsymbol{\beta}$ and $\mathbf{W}(\infty)$ is an equilibrium other than $\boldsymbol{\beta}$. Thus Theorem 4.1 is proved.

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