Spreading speed and linear determinacy for two-species competition models

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Abstract

One crucial measure of a species' invasiveness is the rate at which it spreads into a competitor's environment. A heuristic spread rate formula for a spatially explicit, two-species competition model relies on 'linear determinacy' which equates spread rate in the full nonlinear model with spread rate in the system linearized about the leading edge of the invasion. However, linear determinacy is not always valid for two-species competition; it has been shown numerically that the formula only works for certain values of model parameters when the model is diffusive Lotka-Volterra competition [2]. This paper derives a set of sufficient conditions for linear determinacy in spatially explicit two-species competition models. These conditions can be interpreted as requiring sufficiently large dispersal of the invader relative to dispersal of the out-competed resident and sufficiently weak interactions between the resident and the invader. When these conditions are not satisfied, spread rate may exceed linearly determined predictions. The mathematical methods rely on the application of results established in a companion paper [11].

1 Introduction.

While agricultural scientists often try to sponsor beneficial invasions to control selected pest problems, they are also interested in stemming the invasion of introduced pests [1]. Some biocontrol agents, such as genetically engineered microbes in agriculture, require both an invasion for effective use, and containment for effective control [3]. Because invaders may have potentially lethal effects on native populations, preservation of a species may hinge upon preventing the invasion of a competitor. For example, there is a clear historical record of the gray squirrel *Sciurus carolinensis* out-competing and replacing the red squirrel in the United Kingdom [8]. One crucial measure of a species' invasiveness is the speed at which it spreads into a competitor's environment.

In this paper we will establish some sufficient conditions for the validity of a heuristic spreading speed formula used by Okubo and coworkers [8] to model the spread of grey squirrel into red squirrel populations. The formula equates the spreading speed c^* of the full nonlinear competition system with the spreading speed $\bar{c}$ of the system linearized about the leading edge of the wave. When $c^* = \bar{c}$ we say that the spreading speed is **linearly determined**. For general spatio-temporal models, the belief that a certain list of properties implies linear determinacy has been called the **linear conjecture**.

(See, e.g., van den Bosch and coworkers [9] or Mollison [7].) Our companion paper [11] gives sufficient conditions for linear determinacy in cooperative or competitive systems.

Numerical tests by Hosono [2] have shown that, in the case of Lotka-Volterra competition plus diffusion, c^* and $\bar{c}$ are equal only for some values of model parameters. Thus blind application of the formula can fail to predict the spreading speed of the nonlinear competition system. The present work will show how Theorem 3.1 of the companion paper [11] can be applied to obtain parameter ranges for which the spreading speed is linearly determined in two simple models of two-species competition.

In Section 2, Theorem 4.2 from our companion paper [11] is applied to the Lotka-Volterra competition model system

$$\begin{aligned} p_{,t} &= d_1 p_{,xx} + r_1 p(1 - p - a_1 q), \\ q_{,t} &= d_2 q_{,xx} + r_2 q(1 - q - a_2 p). \end{aligned} \tag{1.1}$$

to obtain parameter ranges for which the spreading speed is linearly determined. Here all parameters are positive, and the population densities p and q are required to be nonnegative.

Section 3 applies a result in [11] to obtain a parameter range on which the spreading speed is linearly determined for the discrete-time spatial spreading model:

$$\begin{aligned} p_{n+1}(x) &= \int_{R^1} \frac{(1+\rho_1)p_n(x-y)}{1+\rho_1(p_n(x-y)+\alpha_1 q_n(x-y))} k_1(y,dy), \\ q_{n+1}(x) &= \int_{R^1} \frac{(1+\rho_2)q_n(x-y)}{1+\rho_2(q_n(x-y)+\alpha_2 p_n(x-y))} k_2(y,dy). \end{aligned} \tag{1.2}$$

This model assumes that the life cycle consists of a time period in which the two species are sedentary and compete locally according to the Beverton-Holt dynamics, followed by a dispersal period during which both species migrate without interacting, growing, or dying. In equation (1.2), all parameters are positive; $p_n(x)$ and $q_n(x)$ denote the population densities of two species at time n and position x respectively; k_i represents the probability measures for the dispersals of two populations, with

$$\int_{R^1} k_i(y,dy) = 1, \quad i = 1, 2. \tag{1.3}$$

We assume that the kernels k_i have the symmetry property $k_i(-y,dy) = k_i(y,dy)$. This and the convolution forms of (1.2) reflect the facts that the dispersal is isotropic and that the space is homogeneous in the sense that the growth and dispersal properties are the same at each point.

It is well known that a simple change of variables can change two-species competition models into cooperative models. Lui [5, 6] obtained sufficient conditions for the linear determinacy of a certain class of cooperative multi-species models. However, analyses of the above continuous- and discrete-time models require a sharper set of conditions than Lui's. These conditions are given in our companion paper [11]. Thus, the present paper is an application of the theory developed in the companion paper [11] which is, in turn, an extension of work by Weinberger [10] and Lui [5, 6].

2 The Lotka-Volterra Competition Model.

We shall study the Lotka-Volterra two-species competition model (1.1). All parameters are nonnegative with r_1 and r_2 positive, and the population densities $p(x,t))$ and $q(x,t)$ are required to be nonnegative. This system has, in general, four constant equilibria: The unpopulated state $(0,0)$; the first-species monoculture state $(1,0)$; the second-species monoculture state $(0,1)$; and the coexistence state (p^*, q^*), where

$$p^* = \frac{1-a_1}{1-a_1a_2},\ q^* = \frac{1-a_2}{1-a_1a_2}. \tag{2.1}$$

The latter state is in the first quadrant if and only if $(1-a_1)(1-a_2) > 0$, and is otherwise irrelevant.

Standard stability analysis shows that the species 1 monoculture state (1,0) is unstable (invadable by the second species) if and only if $a_2 < 1$, that (0,1) is invadable if and only if $a_1 < 1$, and that the coexistence state (p^*, q^*) is stable when $a_1 < 1$ and $a_2 < 1$ and unstable when $a_1 > 1$ and $a_2 > 1$. Thus if $a_1 < 1$, we expect that a population which invades a second-species monoculture state $(0,1)$ will grow and that of the second species will diminish until the two populations reach either the coexistence state (p^*, q^*) $(a_2 < 1)$ or the first species monoculture state (1,0) $(a_2 \geq 1)$. A corresponding invasion of the state $(1,0)$ can occur if $a_2 < 1$. When $a_1 < 1 \leq a_2$, so that there is no coexistence equilibrium, we define $p^* = 1$ and $q^* = 0$, so that the invasion of the state (0,1) always produces a transition toward (p^*, q^*).

As is well known, the change of variables

$$u = p,\ v = 1 - q$$

converts the system (1.1) into the system

$$\begin{aligned} u_{,t} &= d_1 u_{,xx} + r_1 u(1 - a_1 - u + a_1 v), \\ v_{,t} &= d_2 v_{,xx} + r_2(1 - v)(a_2 u - v), \end{aligned} \tag{2.2}$$

which is cooperative in the biologically realistic range $0 \le u \le 1$, $0 \le v \le 1$. This change of variables maps the monoculture state (0,1) into the origin $(0,0)$, the extinction state $(0,0)$ into $(0,1)$ and the state (1,0) into (1,1). The target state (p^*, q^*) goes into the equilibrium (β_1, β_2) where $\beta_1 = p^*$ and $\beta_2 = 1 - q^*$. Note that if $a_2 < 1$, then $\beta_2 = a_2\beta_1 < a_2$, while $\beta_1 = \beta_2 = 1$ if $a_2 \ge 1$. Then (β_1, β_2) is the equilibrium state which is closest to $(0,0)$ in the sense there is no other constant equilibrium (ν_1, ν_2) which satisfies $0 < \nu_1 \le \beta_1$ and $0 < \nu_2 \le \beta_2$. The equilibrium $(0,0)$ is unstable, and (β_1, β_2) is stable. Note that if $a_1 < 1$ and $a_2 \ge 1$, there is an extra equilibrium $(0,1)$ for (2.2) which lies on the closed rectangle with vertices (0,0) and (β_1, β_2).

The companion paper [11] shows that there are two-species competition models in which the two species spread at different speeds. However, Theorem 4.4 of [11] shows that for the Lotka-Volterra model (1.1) both species spread at the same speed c^* and that if d_1 is positive, every invasion, no matter how small, succeeds. More specifically, the following Proposition is a paraphrase of Theorems 4.1 and 4.4 of [11].

Proposition 2.1 *If all the parameters are nonnegative, $d_1 > 0$, $r_1(1-a_1) > 0$, and $r_2 a_2 > 0$, then the cooperative system (2.2) which is obtained from the Lotka-Volterra competition model (1.1) by introducing the new variables $u = p$, $v = 1 - q$, has the single spreading speed c^* and the hairtrigger property, in the following sense: If $0 \le u(x,0) < \beta_1$, $0 \le v(x,0) < \beta_2$, $u(x,0)$ and $v(x,0)$ are zero outside a bounded set, and $u(x,0) \not\equiv 0$, then for every positive number ϵ*

$$\lim_{t\to\infty} \left[\sup_{|x| \ge (c^*+\epsilon)t} \{u(x,t)^2 + v(x,t)^2\} \right] = 0, \tag{2.3}$$

and

$$\lim_{t\to\infty} \left[\sup_{|x| \le (c^*-\epsilon)t} \{(\beta_1 - u(x,t))^2 + (\beta_2 - v(x,t))^2\} \right] = 0. \tag{2.4}$$

Because of the above change of variables, one can rewrite this proposition as a statement about the solution of the Lotka-Volterra system (1.1). Namely, if the parameters have the above properties, if $0 \le p(x,0) < p^*$, $q^* < q(x,0) \le$

1, $(p(x,0),q(x,0)) = (0,1)$ outside a bounded interval, and $p(x,0) \not\equiv 0$ so that an actual local invasion occurs, then

$$\lim_{t\to\infty}[\sup\{p^2(x,t)+(1-q(x,t))^2 : |x| \geq t[c^*+\epsilon]\}] = 0, \tag{2.5}$$

and

$$\lim_{t\to\infty}[\sup\{(p^*-p(x,t))^2+(q^*-q(x,t))^2 : |x| \leq t[c^*-\epsilon]\}] = 0. \tag{2.6}$$

In other words, if an observer were to move to the right or left at a fixed speed greater than c^*, the local population density (p,q) would eventually appear to approach $(0,1)$, and if an observer were to move to the right or left at a speed less than c^*, the local population density would eventually appear to approach (p^*,q^*).

The following theorem gives a parameter range under which the Lotka-Volterra competition system (1.1) has a linearly determined spreading speed
.

Theorem 2.1 *Suppose that all parameters of the Lotka-Volterra system (1.1) are nonnegative, that d_1, $r_1(1-a_1)$, and r_2a_2 are positive, and that the inequalities*

$$\begin{array}{l} \frac{d_2}{d_1} \leq 2 \\ \frac{a_2a_1-1}{1-a_1} \leq \frac{r_1}{r_2}\left(2-\frac{d_2}{d_1}\right) \end{array} \tag{2.7}$$

are satisfied. Then the spreading speed c^* with the properties (2.5) and (2.6) is equal to the speed $\bar{c} = 2\sqrt{d_1r_1(1-a_1)}$ of the linearization at $(0,1)$ of the model (1.1). That is, the system (1.1) is linearly determinate.

Proof. We again introduce the new variables $u = p$ and $v = 1-q$, which converts the competition system (1.1) into the cooperative system (2.2). The linearization of (2.2) about $u = v = 0$ is the system

$$\begin{array}{l} u_{,t} = d_1u_{,xx} + r_1(1-a_1)u, \\ v_{,t} = d_2v_{,xx} + r_2(a_2u-v). \end{array} \tag{2.8}$$

We shall prove Theorem 2.1 by using Theorem 4.2 in the companion paper [11]. The conditions of this theorem involve a matrix C_μ, defined to be the coefficient matrix for the vector of linear combinations of α_1 and α_2 obtained by substituting $u = \alpha_1e^{-\mu x}$, $v = \alpha_2e^{-\mu x}$ into the right-hand of (2.8) and setting $x = 0$:

$$C_\mu = \begin{pmatrix} d_1\mu^2 + r_1(1-a_1) & 0 \\ r_2a_2 & d_2\mu^2 - r_2 \end{pmatrix}.$$

The eigenvalues of this upper triangular matrix are the diagonal elements $\gamma_1(\mu) = d_1\mu^2 + r_1(1-a_1)$ and $\gamma_2(\mu) = d_2\mu^2 - r_2$. An eigenvector corresponding to $\gamma_1(\mu)$ is the vector $(\zeta_1(\mu), \zeta_2(\mu))$ where

$$\zeta_1(\mu) = \gamma_1(\mu) - \gamma_2(\mu), \quad \zeta_2(\mu) = r_2 a_2. \tag{2.9}$$

Because the first equation of (2.8) is just the heat equation with linear growth and because, once u is known, the second equation is an inhomogeneous version of an equation of the same form, one can solve the initial value problem for the linearized system explicitly. Well-known methods show that the function u spreads to infinity with the asymptotic speed

$$\bar{c} = \inf_{\mu>0}[\mu^{-1}\gamma_1(\mu)].$$

An exercise in calculus shows that this infimum is taken on when μ has the value

$$\bar{\mu} = \sqrt{r_1(1-a_1)/d_1}, \tag{2.10}$$

so that

$$\bar{c} = 2\sqrt{d_1 r_1(1-a_1)}. \tag{2.11}$$

The following Proposition is a specialization to the system (2.2) of Theorem 4.2 of the companion paper [11].

Proposition 2.2 *Suppose that the system (2.2) has the following properties:*

i. *(0,0) and (β_1, β_2) are equilibria with the β_i positive, and there is no other constant equilibrium (α_1, α_2) such that $0 < \alpha_1 \leq \beta_1$ and $0 < \alpha_2 \leq \beta_2$.*

ii. *The system is cooperative; that is, the growth term in the u-equation is nondecreasing in v and the growth term in the v-equation is nondecreasing in u.*

iii. *The equations in (2.2) have no explicit x or t dependence.*

iv. *The growth functions are continuous and piecewise continuously differentiable for $0 \leq u \leq \beta_1$ and $0 \leq v \leq \beta_2$.*

v. *The upper left element $\gamma_1(0)$ of the matrix C_0 is positive and greater than the lower right element $\gamma_2(0)$, and the (2,1) element of C_0 is positive.*

vi. *With $\bar{\mu}$ defined by (2.10), $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$.*

vii. *For every positive number ρ each of the right-hand sides of the system (2.2) evaluated at $u = \rho\zeta_1(\bar{\mu})$, $v = \rho\zeta_2(\bar{\mu})$ is no larger than the corresponding right-hand side of the linearization (2.8) evaluated at $(\rho\zeta_1(\bar{\mu}), \rho\zeta_2(\bar{\mu}))$.*

Then the spreading speed c^* of the cooperative system (2.2) is equal to $\bar{c}$, so that the system is linearly determinate.

It is easily verified that the system (2.2) satisfies the first five hypotheses of this Proposition when $r_1(1 - a_1) > 0$ and $r_2 a_2 > 0$. The hypothesis (vii) takes the form

$$\begin{aligned} r_1\zeta_1(\bar{\mu})[-\zeta_1(\bar{\mu}) + a_1\zeta_2(\bar{\mu})] \leq 0 \\ -r_2\zeta_2(\bar{\mu})[a_2\zeta_1(\bar{\mu}) - \zeta_2(\bar{\mu})] \leq 0. \end{aligned}$$

We see from the formula (2.9) for the ζ_ν that if (vi) is valid, then this condition is equivalent to

$$\gamma_1(\bar{\mu}) - \gamma_2(\bar{\mu}) \geq r_2 \max\{a_1 a_2, 1\}.$$

Because the right-hand side is positive, this condition implies the hypothesis (vi) as well as (vii). Because the γ_ν are just the diagonal elements of $C_{\bar{\mu}}$ and $\bar{\mu}$ is given by (2.10), this inequality is equivalent to the conditions (2.7). Thus we can apply Proposition 2.2. Since the system (2.2) is equivalent to the original system (1.1), this establishes Theorem 2.1.

We observe that the parameters r_i and d_i only enter the condition (2.7) as the ratios d_2/d_1 and r_2/r_1. This reflects the fact that a scaling of the x and t variables takes the system (1.1) with one set of parameters into a system with any other parameters as long as the values of d_2/d_1, r_2/r_1, a_1, and a_2 are the same, and that it multiplies c^* and $\bar{c}$ by the same constant. Therefore linear determinacy can only depend on these combinations of parameters.

3 A Discrete-time Competition Model.

In this section, we consider the discrete-time competition model (1.2). As in the Lotka-Volterra model, we shall assume that all parameters are nonnegative, and that $\rho_1(1 - \alpha_1)$ and $\rho_2\alpha_2$ are positive. The variables $p_n(x)$ and $q_n(x)$ can be thought of as functions on the real line. However, if the measures k_i consist of discrete masses at points which are all integral multiples of a positive number h, the domain of these functions can be thought of as the set $\mathcal{H}$ of these multiples. Then (1.2) is a discrete-time discrete-space or finite difference model, as is the case for all simulations.

Like the system (1.1), system (1.2) has four possible constant equilibria: The unpopulated state $(0,0)$, the first-species monoculture state $(1,0)$; the second-species monoculture state $(0,1)$; and the coexistence state (p^*, q^*), where

$$p^* = \frac{1-\alpha_1}{1-\alpha_1\alpha_2}, \; q^* = \frac{1-\alpha_2}{1-\alpha_1\alpha_2}. \tag{3.1}$$

The coexistence state lies in the first quadrant if and only if $(1-\alpha_1)(1-\alpha_2) > 0$, and is otherwise biologically irrelevant.

This model has the following behavior: the species 1 monoculture state (1,0) is invadable if and only if $\alpha_2 < 1$, (0,1) is invadable if and only if $\alpha_1 < 1$, and the coexistence state (p^*, q^*) is stable when $\alpha_1 < 1$ and $\alpha_2 < 1$, and unstable when $\alpha_1 > 1$ and $\alpha_2 > 1$. When $\alpha_1 < 1 \le \alpha_2$ so that there is no coexistence equilibrium, we shall define $p^* = 1$ and $q^* = 0$, so that the invasion of the state (0,1) always produces a transition toward (p^*, q^*).

The change of variables

$$u_n = p_n, \; v_n = 1 - q_n$$

converts the system (1.2) into the system

$$\begin{aligned} u_{n+1}(x) &= \int_{R^1} \frac{(1+\rho_1)u_n(x-y)}{1+\rho_1(\alpha_1 + u_n(x-y) - \alpha_1 v_n(x-y))} k_1(y, dy), \\ v_{n+1}(x) &= \int_{R^1} \frac{\alpha_2\rho_2 u_n(x-y) + v_n(x-y)}{1+\rho_2(1 - v_n(x-y) + \alpha_2 u_n(x-y))} k_2(y, dy), \end{aligned} \tag{3.2}$$

which is order preserving on the biologically significant range $0 \le u_n \le 0$, $0 \le v_n \le 1$. That is, increasing either u_n or v_n increases u_{n+1} and v_{n+1}. This change of variables takes the equilibrium (0,1) into $(0,0)$, the equilibrium $(0,0)$ into $(0,1)$, and the equilibrium (1,0) into (1,1). The target state (p^*, q^*) goes into the equilibrium (β_1, β_2) where $\beta_1 = p^*$ and $\beta_2 = 1-q^*$. Then (β_1, β_2) is the equilibrium state which is closest to $(0,0)$ in the sense that there is no constant equilibrium (ν_1, ν_2) with $0 < \nu_1 \le \beta_1$ and $0 < \nu_2 \le \beta_2$. $(0,0)$ is unstable, and (β_1, β_2) is stable. Note that if $\alpha_1 < 1$ and $\alpha_2 \ge 1$ so that $(\beta_1, \beta_2) = (1,1)$, there is an extra equilibrium $(0,1)$ for (3.2) which lies on the closed rectangle with vertices (0,0) and (β_1, β_2).

The following Proposition is a paraphrase of Theorems 3.1 and 3.4 of our companion paper [11].

Proposition 3.1 *Let all the parameters in the system (3.2) be nonnegative, and assume that the quantities $\rho_1(1-\alpha_1)$ and $\rho_2\alpha_2$ are positive. Assume,* *moreover, that either the habitat $\mathcal{H}$ is the real line and there is an open interval on which the measure k_1 has a continuous 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 a positive weight, with repetitions allowed.*

Then the cooperative system (3.2) which is obtained by making the substitution $u_n = p_n$, $v_n = 1 - q_n$ in the model (1.2), has a single speed c^* for both components, and there is a hairtrigger effect, so that the following property is valid: Suppose that $0 \le u_0 < \beta_1$, $0 \le v_0 < \beta_2$, u_0 and v_0 are zero outside a bounded interval, and $u_0 \not\equiv 0$. Then for every positive number ϵ

$$\lim_{n\to\infty}[\max\{(u_n(x))^2 + (v_n(x))^2 : |x| \ge n[c^* + \epsilon]\}] = 0, \tag{3.3}$$

and

$$\lim_{t\to\infty}[\max\{(\beta_1 - u_n(x))^2 + (\beta_2 - v_n(x))^2 : |x| \le n[c^* - \epsilon]\}] = 0. \tag{3.4}$$

By recalling the change of variables $u_n = p_n$, $v_n = 1 - q_n$, we conclude that if $0 \le p_0 < p^*$, $q^* < q_0 \le 1$, $(p_0, q_0) = (0, 1)$ outside a bounded interval, and $p_0 \not\equiv 0$ so that an invasion occurs, then

$$\lim_{n\to\infty}[\max\{(p_n(x))^2 + (1 - q_n(x))^2 : |x| \ge n[c^* + \epsilon]\}] = 0, \tag{3.5}$$

and

$$\lim_{t\to\infty}[\max\{(p^* - p_n(x))^2 + (q_n(x) - q^*)^2 : |x| \le n[c^* - \epsilon]\}] = 0. \tag{3.6}$$

The linearization of (3.2) about $u = v = 0$ is the system

$$\begin{aligned} u_{n+1}(x) &= \int_{R^1} \frac{(1+\rho_1)u_n(x-y)}{1+\rho_1\alpha_1} k_1(y, dy), \\ v_{n+1}(x) &= \int_{R^1} \frac{\alpha_2\rho_2 u_n(x-y) + v_n(x-y)}{1+\rho_2} k_2(y, dy). \end{aligned} \tag{3.7}$$

In order to calculate the spreading speed for the linearized system (3.7), we need the matrix B_μ, which is defined by setting $u = \alpha e^{-\mu x}$ and $v = \beta e^{-\mu x}$ on the right hand sides of (3.7), multiplying the result by $e^{\mu x}$, and writing the vector so obtained as a matrix product $B_\mu \begin{pmatrix} \alpha \\ \beta \end{pmatrix}$. We find that

$$B_\mu = \begin{pmatrix} \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu) & 0 \\ \frac{\alpha_2\rho_2}{1+\rho_2}\bar{k}_2(\mu) & \frac{1}{1+\rho_2}\bar{k}_2(\mu) \end{pmatrix}, \tag{3.8}$$

where each $\bar{k}_i(\mu)$ is the moment generating function

$$\bar{k}_i(\mu) = \int_{-\infty}^{\infty} e^{\mu y} k_i(y, dy), \quad i = 1, 2,$$

of the probability kernel k_i.

The eigenvalues of this matrix are the diagonal entries

$$\lambda_1(\mu) = \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu),$$

and

$$\lambda_2(\mu) = \frac{1}{1+\rho_2}\bar{k}_2(\mu).$$

It is easily shown (see Lemma 2.3 of [11]) that the spreading speed of the linearized problem (3.7) is

$$\bar{c} = \inf_{\mu>0}\{\mu^{-1}\ln[\bar{k}_1(\mu)(1+\rho_1)/(1+\alpha_1\rho_1)]\} \tag{3.9}$$

The following theorem provides sufficient conditions for linear determinacy for the invasion of the state (0,1) of the system (1.2).

Theorem 3.1 *Assume that the probability measures k_i in (1.2) are invariant under the reflection $x \to -x$, and that their moment generating functions $\bar{k}_i(\mu)$ are finite for all $\mu > 0$. Also suppose that the parameters and the measure k_1 satisfy the conditions of Proposition 3.1. Let $\bar{\mu}$ be the value of μ where the minimum in (3.9) is attained. Assume that either*
(a) $\bar{\mu}$ is finite, and

$$\frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\bar{\mu}) \geq \frac{1+\rho_2 \max\ \{\alpha_1\alpha_2, 1\}}{1+\rho_2}\bar{k}_2(\bar{\mu}); \tag{3.10}$$

or
(b) $\bar{\mu} = +\infty$ and there is a sequence $\mu_\sigma \to \infty$ such that for each σ

$$\frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu_\sigma) \geq \frac{1+\rho_2 \max\ \{\alpha_1\alpha_2, 1\}}{1+\rho_2}\bar{k}_2(\mu_\sigma). \tag{3.11}$$

Then the spreading speed c^* of the problem (1.2) is equal to the spreading speed of the linearized problem $\bar{c}$ given in (3.9).

Proof.

The eigenvalues of the matrix B_μ in (3.8) are the diagonal entries

$$\lambda_1(\mu) = \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu),$$

and

$$\lambda_2(\mu) = \frac{1}{1+\rho_2}\bar{k}_2(\mu).$$

An eigenvector of B_μ which corresponds to $\lambda_1(\mu)$ is $\boldsymbol{\zeta}(\mu) = (\zeta_1(\mu), \zeta_2(\mu))$ where

$$\zeta_1(\mu) = \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu) - \frac{1}{1+\rho_2}\bar{k}_2(\mu), \quad \zeta_2(\mu) = \frac{\alpha_2\rho_2}{1+\rho_2}\bar{k}_2(\mu). \tag{3.12}$$

We shall use the following proposition which is a specialization to the system (3.2) of Theorem 3.1 of the companion paper [11].

Proposition 3.2 *Suppose that the system (3.2) has the following properties:*

i. *(0,0) and (β_1, β_2) are equilibria with the β_i positive, and there is no other constant equilibrium (α_1, α_2) such that $0 < \alpha_1 \le \beta_1$ and $0 < \alpha_2 \le \beta_2$.*

ii. *The system is order-preserving; that is, the right-hand side of each equation is nondecreasing in both u_n and v_n.*

iii. *The equations in (3.2) have no explicit dependence on space and time.*

iv. *$k_i(y, dy)$ are nonnegative measures with $k_i((-\infty,\infty)) = 1$, and $k(-y, dy) = k_i(y, dy)$.*

v. *The eigenvalue $\lambda_1(0)$ of the matrix B_0 is greater than one and greater than the other eigenvalue $\lambda_2(0)$, and the (2,1) element of B_0 is positive.*

vi. *With $\bar{\mu}$ defined in the statement of Theorem 3.1, either*
(a) $\bar{\mu}$ is finite, $\lambda_1(\bar{\mu}) > \lambda_2(\bar{\mu})$, and each of the right-hand sides of the system (3.2) evaluated at $u = e^{-\bar{\mu}x}\zeta_1(\bar{\mu})$, $v = e^{-\bar{\mu}x}\zeta_2(\bar{\mu})$ is no larger than the corresponding right-hand side of the linearization (3.7) evaluated at the same u and v,
or
(b) $\bar{\mu} = \infty$, and there is a sequence $\{\mu_\sigma\}$ with $\mu_\sigma \to \infty$ as $\sigma \to \infty$ such that $\lambda_1(\mu_\sigma) > \lambda_2(\mu_\sigma)$, and each of the right-hand sides of the system (3.2) evaluated at $u = e^{-\mu_\sigma x}\zeta_1(\mu_\sigma)$, $v = e^{-\mu_\sigma x}\zeta_2(\mu_\sigma)$ is no larger than the corresponding right-hand side of the linearization (3.7) evaluated at the same u and v.

Then the transition from (0,0) to (β_1, β_2) has the spreading speed $\bar{c}$ in the sense that if $0 \le u_0(x) < \beta_1$, $0 \le v_0(x) < \beta_2$, $u_0(x) \not\equiv 0$, and $u_0(x) = v_0(x) = 0$ outside a bounded set, then for any positive ϵ

$$\lim_{n\to\infty}[\max\{(u_n(x))^2 + (v_n(x))^2 : |x| \ge n(\bar{c}+\epsilon)\}] = 0,$$

and

$$\lim_{n\to\infty}[\max\{(\beta_1 - u_n(x))^2 + (\beta_2 - v_n(x))^2 : |x| \le n(\bar{c}_1 - \epsilon)\}] = 0.$$

It is easily verified that the system (3.2) satisfies the first five hypotheses of this proposition. If $\bar{\mu}$ is finite and if the first part of (vi) is satisfied so that $\zeta_1(\bar{\mu})$ is positive, the second part of this hypothesis takes the form

$$\zeta_1(\bar{\mu}) - \alpha_1\zeta_2(\bar{\mu}) \ge 0,$$

$$\alpha_2\zeta_1(\bar{\mu}) - \zeta_2(\bar{\mu}) \ge 0.$$

These two inequalities can be put into the form

$$\zeta_1(\bar{\mu}) \ge \max(\alpha_1, 1/\alpha_2)\zeta_2(\bar{\mu}).$$

By (3.12), this is equivalent to (3.10). Since $\zeta_2(\bar{\mu}) > 0$, this inequality also implies the first part of (vi.a), and hence Proposition 3.2 shows that $c^* = \bar{c}$. A similar calculation shows that (3.11) implies the hypotheses (vi.b). Thus Theorem 3.1 is established.

In order to apply Theorem 3.1, one needs to know the moment generating functions of the migration kernels k_1 and k_2. Some kernels of possible interest are given in the following examples.

EXAMPLE 3.1. The moment generating function of the distribution with the Gaussian density kernel

$$k_g(x) = (\pi)^{-1/2}e^{-x^2} \tag{3.13}$$

is

$$\bar{k}_g(\mu) = e^{\mu^2/4}. \tag{3.14}$$

EXAMPLE 3.2. The moment generating function of the distribution with the 'rooftop' density kernel

$$k_r(x) = \max\{1 - |x|, 0\} \tag{3.15}$$

is

$$\bar{k}_r(\mu) = \frac{2(\cosh\mu - 1)}{\mu^2}. \tag{3.16}$$

EXAMPLE 3.3. The distribution

$$k_\sigma(x) = [1-\sigma^2]\delta(x) + \tfrac{1}{2}\sigma^2[\delta(x-1)+\delta(x+1)], \tag{3.17}$$

where δ is the Dirac delta distribution and $0 \le \sigma^2 \le 1$, describes a symmetric random walk on a one-dimensional lattice. Its variance is σ^2, and its moment generating function is

$$\bar{k}_\sigma(\mu) = 1 + \sigma^2[\cosh\mu - 1].$$

When the measures k_i both have form (3.17), the recursion (1.2) permits one to solve for the values of u_{n+1} and v_{n+1} at the integers in terms of the values of u_n and v_n at the integers. This recursion thus leads to a discrete space model in which $u_n(j)$ and $v_n(j)$ can be interpreted as the total population in the census tract (or deme) $j - 1/2 < x \le j + 1/2$. Since $Q[(u,v)](0)$ depends only on the values of u and v at three points, there is a good chance that one can obtain an accurate description of this function from a reasonable number of experiments. Moreover, the concept of local interactions between migrations becomes much more precise.

We note that if the probability measure $k(x, dx)$ has the moment distribution function $\bar{k}(\mu)$, then the dilated measure $k(h^{-1}x, h^{-1}dx)$ has the moment distribution $\bar{k}(\mu h)$. If $k(x, dx)$ has a density so that it takes the form $k(x, dx) = k(x)dx$, then $k(h^{-1}x, h^{-1}dx) = k(h^{-1}x)h^{-1}dx$, so that the new density is $h^{-1}k(h^{-1}x)$. With this fact each of the above instances leads to a one parameter family of examples. For example, the moment distribution of the Gaussian density $(\pi h^2)^{-1/2}e^{-x^2/h^2}$ is $e^{\mu^2h^2/4}$, while replacing $\delta(x \pm 1)$ by $\delta(x \pm h)$ in (3.17) gives the moment distribution $1 + \sigma^2[\cosh(\mu h) - 1]$.

The difficulty of finding the minimizer $\bar{\mu}$ for the problem (3.9) depends, of course, on the moment generating function of the kernel k_1. One is to find the point at which the function

$$\mu^{-1}[\ln \bar{k}_1(\mu) + \ln\{(1+\rho_1)/(1+\alpha_1\rho_1)\}] \tag{3.18}$$

attains its minimum. Because the function $\ln \bar{k}_1(\mu)$ is convex, one can easily show that the function in (3.18) is convex in the variable $1/\mu$. Therefore, if

$\bar{\mu}$ is finite, it is the unique solution of the equation

$$\mu \frac{\bar{k}_1'(\mu)}{\bar{k}_1(\mu)} - \ln[\bar{k}_1(\mu)] = \ln\{(1+\rho_1)/(1+\alpha_1\rho_1)\}, \tag{3.19}$$

whose left-hand side is increasing in μ. The parameter $\bar{\mu}$ can be found numerically with a root finder.

The case $\bar{\mu} = \infty$ is characterized by the fact that the left-hand side of (3.19) is less than the right-hand side for all positive μ. Because this cannot be established with a root finder, it is good to have the following criterion, which is derived on pages 386 and 387 of [10].

Proposition 3.3 *$\bar{\mu} = \infty$ if and only if the support of the measure k_1 lies on a finite interval $[-\alpha, \alpha]$ and $k_1(\{\alpha\}) \geq (1+\alpha_1\rho_1)/(1+\rho_1)$.*

We see from this Proposition that if k_σ, like the Gaussian kernel in Example 3.1 or the rooftop kernel in Example 3.2, has a density, then $\bar{\mu}$ is finite. If k_1 is the random walk measure (3.17) in Example 3.3, Proposition 3.2 shows that $\bar{\mu}$ is finite if and only if $\frac{1}{2}\sigma^2(1+\rho_1)/(1+a_1\rho_1) < 1$. In fact, for k_σ the function in (3.18) is $1 + \mu^{-1}\ln[\frac{1}{2}\sigma^2(1+\rho_1)/(1+\alpha_1\rho_1)] + \mu^{-1}\ln[1+2(\sigma^{-2}-1)e^{-\mu}+e^{-2\mu}]$. Thus if $\frac{1}{2}\sigma^2(1+\rho_1)/(1+\alpha_1\rho_1) \geq 1$, this function is always larger than its limit 1 at infinity so that $\bar{\mu}$ is infinite. If $\frac{1}{2}\sigma^2(1+\rho_1)/(1+\alpha_1\rho_1) < 1$, then the function is smaller than this limit for all sufficiently large μ, so that $\bar{\mu}$ is finite.

EXAMPLE 3.4. When k_1 is a Gaussian kernel $(2\pi\sigma_1^2)^{-1/2}e^{-x^2/(2\sigma_1^2)}$, then $\ln \bar{k}_1(\mu) = \sigma_1^2\mu^2/2$, so that it is easy to find the minimizer $\bar{\mu}$ and the minimum $\bar{c}$ of the function in (3.18). In fact,

$$\bar{\mu} = \sqrt{2\ln[(1+\rho_1)/(1+\alpha_1\rho_1)]}/\sigma_1, \tag{3.20}$$

and

$$\bar{c} = \sigma_1\sqrt{2\ln\frac{1+\rho_1}{1+\alpha_1\rho_1}}. \tag{3.21}$$

One can then use the above value of $\bar{\mu}$ in the condition (3.10).

If the k_i are Gaussian, so that $k_i(y, dy) = (4\pi d_i)^{-1/2}e^{-y^2/(4d_i)}dy$, and if the relation $r_1(1-a_1) = \ln[(1+\rho_1)/(1+\alpha_1\rho_1)]$ holds, we observe that the values of $\bar{\mu}$ and $\bar{c}$ of the models (1.1) and (1.2) coincide. If, in addition, the relation $r_2(a_1a_2 - 1) = \ln[(1+\alpha_1\alpha_2\rho_2)/(1+\rho_2)]$ is satisfied, then the condition (3.10) is equivalent to (2.7).

4 Discussion.

We have obtained some sufficient conditions which assure the linear determinacy of the Lotka-Volterra competition model with diffusion (see Theorem 2.1), and of a related discrete-time model (see Theorem 3.1). In the Lotka-Volterra competition model these conditions can be interpreted as requiring sufficiently large dispersal of the invader relative to dispersal of the out-competed resident ($d_1 \geq d_2/2$) and sufficiently weak interactions between the resident and the invader ($(a_2a_1-1)/(1-a_1)$ sufficiently small). As we have pointed out earlier, these Theorems give sufficient but not necessary conditions for the linearization to give the correct spreading speed. That is, there may be parameter values at which the inequalities in the Theorem are not satisfied, but for which the linearization still gives the correct wave speed.

Hosono[2] analyzed the Lotka-Volterra model (1.1) for the invasion of the state $(0,1)$ by species 1 in detail. He found that, for the case $d_2 = 0$, if $(a_1a_2-1)/(1-a_1) \leq 2r_1/r_2$, then $\bar{c}$ given in our Theorem 2.1 is the minimal wave speed. By this he means that, for $c < c^*$ there exists no traveling wave solution for (1.1), and for each $c \geq c^*$ there exists a traveling wave solution for system (1.1) (Theorem 2, [2]). We shall show elsewhere [4] that the spreading speed c^* can, indeed, be characterized as the slowest speed of a traveling wave. Note that the above inequality of Hosono is just the condition (2.7) when $d_2 = 0$. In [2], Hosono used Heaviside step initial data to compute the minimal wave speed. On the basis of some numerical experiments, Hosono (Conjecture 6, [2]) conjectured that when d_2/d_1 is sufficiently small, the spreading speed is always $\bar{c}$ when $a_1a_2 \leq 1$, while if $a_1a_2 > 1$, there is a critical number r_c such that $c^* = \bar{c}$ when $0 < r_2/r_1 < r_c$ but not when $r_2/r_1 > r_c$. Theorem 2.1 shows that the first part of this conjecture is correct when $d_2/d_1 \leq 2$, and that if $d_2/d_1 < 2$ and $a_1a_2 > 1$, then $c^* = \bar{c}$ when $r_2/r_2 \leq (2d_1-d_2)(1-a_1)/d_1(a_1a_2-1)$. Therefore Hosono's conjectured r_c must satisfy the inequality $r_c \geq (2d_1-d_2)(1-a_1)/d_1(a_1a_2-1)$. This is consistent with Hosono's computations.

We have not been able to prove the existence of Hosono's r_c. We can, however, prove that for any fixed values of the other parameters there is a critical value $1 \leq A_c(d_2/d_1, r_2/r_1, a_1) \leq \infty$ of a_2 with the property that the Lotka-Volterra system (1.1) is linearly determinate if and only if $a_2 \leq A_c(d_2/d_1, r_2/r_1, a_1)$. This statement follows from the observation that the solution of the system (2.2) with any initial conditions between 0 and 1 is nondecreasing in a_2, so that c^* is nondecreasing in a_2. Because $\bar{c}$ is independent of a_2, one sees that if the system is linearly determinate for one value of a_2, the same is true for all smaller values, which implies the existence of A_c. When $d_2/d_1 \leq 2$, the second inequality in (2.7) gives a lower bound for A_c as $\left[1 + (1-a_1)(2 - d_2/d_1) r_1/r_2\right]/a_1$.

The Lotka-Volterra competition model (1.1) has been applied to populations which occupy similar niches but differ slightly in competitive ability. Examples include red and grey squirrel populations in the United Kingdom [8], and genetically engineered (ice-minus) versus wild strain (ice-plus) bacteria *Pseudomonas syringae*, strains which differ by a single gene [3]. In both these studies, populations were taken to share the same growth rates ($r_1 = r_2$) and to have competition coefficients which differ slightly from unity: $a_1 = 1 - \epsilon$, $a_2 = 1 + \epsilon$, $0 < \epsilon < 1$, so that the second condition of (2.7) is automatically satisfied.

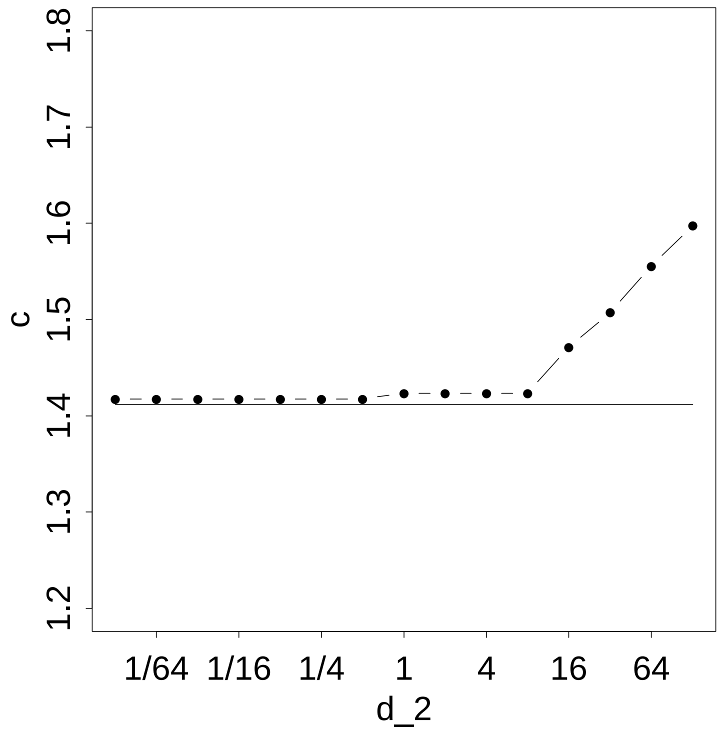

Figure 1: Numerical calculation of spreading speed for Lotka-Volterra competition model. Parameter values are $a_1 = 2/3$, a_2=4/3, $r_1 = r_2 = 1$ and $d_1 = 1$. The parameter d_2 varies on a log scale. The solid line shows $\bar{c} = \sqrt{2}$ and dots show numerically calculated values for c^*. The numerical solution method uses the method of lines and Gear's method with 4000 spatial grid points.

A numerical evaluation of the spreading speed for this situation ($r_1 = r_2$, $a_1 = 2/3,\ a_2 = 4/3$) is shown in Figure 1. Here the diffusion coefficient for the invader is fixed at $d_1 = 1$ and the diffusion coefficient for the retreating species d_2 is varied from 1/128 to 128. It appears that for values of d_2 up to 8 the computed spreading speed c^* is close to the speed $\bar{c}$ predicted by the linearization even though the sufficient condition (2.7) is violated when $d_2 > 2$. However, the two speeds differ for larger d_2. The spreading speed was calculated from the traveling wave profile for (1.1) which was obtained numerically (Figure 2).

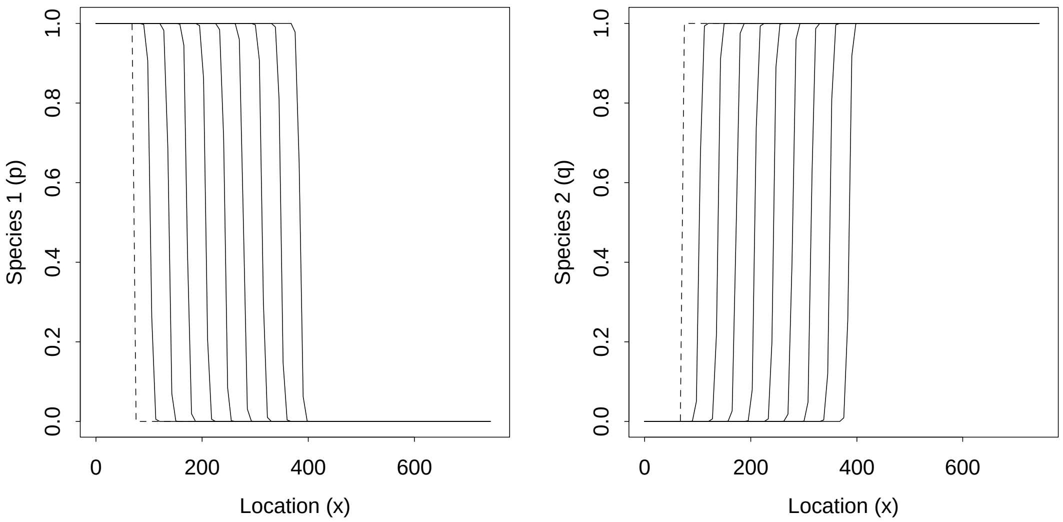

Figure 2: Numerical simulation of Lotka-Volterra competition model. Parameter values are $a_1 = 2/3$, a_2=4/3, $r_1 = r_2 = 1$ and $d_1 = d_2 = 1$. Dashed lines show initial conditions. Solutions are given every 25 time units, and are denoted by the solid curves.

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