Anomalous spreading speeds of cooperative recursion systems

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Abstract

This work presents an example of a cooperative system of truncated linear recursions in which the interaction between species causes one of the species to have an anomalous spreading speed. By this we mean that this species spreads at a speed which is strictly greater than its spreading speed in isolation from the other species and the speeds at which all the other species actually spread. An ecological implication of this example is discussed in Section 5. Our example shows that the formula for the fastest spreading speed given in Lemma 2.3 of our paper [4] is incorrect. However, we find an extra hypothesis under which the formula for the faster spreading speed given in [4] is valid. We also show that the hypotheses of all but one of the theorems of [4] whose proofs rely on Lemma 2.3 imply this extra hypothesis, so that all but one of the theorems of [4] and all the examples given there are valid as they stand.

1 Introduction.

The authors' paper [4] presents sufficient conditions for a cooperative system of discrete-time recursions

$$\mathbf{u}_{n+1} = Q[\mathbf{u}_n] \tag{1.1}$$

to be linearly determinate. By this we mean that the spreading speeds are the same as those of the truncated linear recursion

$$\mathbf{u}_{n+1} = \min\{\boldsymbol{\omega}, \tilde{L}[\mathbf{u}_n]\}, \tag{1.2}$$

where $\boldsymbol{\omega}$ is a constant vector with positive entries, and $\tilde{L}$ is the linearization of the operator $Q[\mathbf{u}]$ about $\mathbf{u} = \mathbf{0}$.[1] Such a statement is, of course, only useful if the spreading speeds of a truncated linear recursion (1.2) can be found with relative ease.

It was shown in [4] that, under a few hypotheses, any recursion of the form (1.1), and, in particular, the recursion (1.2), has a slowest spreading speed c^* with the following property: If $\mathbf{u}_0 \leq \boldsymbol{\beta}$ where $\boldsymbol{\beta}$ is the smallest positive constant solution of the equilibrium equation $\boldsymbol{\beta} = Q[\boldsymbol{\beta}]$, and if $\mathbf{u}_0(x) = 0$ for all sufficiently large $|x|$, all components of $\mathbf{u}_n$ spread toward positive values at speeds which are at least c^*, and at least one component spreads at no higher speed. It was shown in [2] that there is also a fastest speed c_f^* with the properties that no component of $\mathbf{u}_n$ spreads at a speed higher than c_f^* and at least one component spreads no more slowly. [2]

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[1]The minimum of two vector-valued functions is that vector-valued function whose ith component at x is the smaller of the ith components of the two functions at x.

[2]The earlier paper [4] claimed a similar result, but with c_f^* replaced by a number c_+^*, which was defined in a different manner. It is easily seen that $c_+^* \geq c_f^*$, but, as pointed out in [2], the proof in [4] of the property that at least one component spreads at a speed no smaller than c_+^* turned out to be incomplete.

When the linear operator $\tilde{L}$ is irreducible, an earlier work of R. Lui [3] showed this result with $c^* = c^*_f$ for the recursion (1.2), and gave a simple formula for the common value. The existence of two distinct values c^* and c^*_f can only arise in the non-generic case when $\tilde{L}$ is reducible. In this case, the set of coordinates is broken into blocks. Lui's formula gives speeds $\tilde{c}_\rho$ with which the components of the ρth block would spread if all components except for one in this block were initially zero. It is natural to define the **individual speed** of a component (species) as the speed at which this component spreads when the initial values of all the other components are zero. It is not difficult to show that the speed at which a component of the system spreads is at least as large as its individual speed. Therefore, the maximum $c^{(\ell)}$ of the individual speeds is certainly a lower bound for the fastest spreading speed c^*_f of (1.2). Lemma 2.3 of [4] claims that $c^*_f = c^{(\ell)}$. This statement seems intuitively obvious. However, Angela Stevens and Frauke Albrecht have kindly pointed out a gap in the the proof of this Lemma.

Our exploration of this gap has led to the discovery of a new phenomenon. In Section 3 we shall give a counterexample in which all the hypotheses of [4] are satisfied, but for which $c^*_f > c^{(\ell)}$. This counter-intuitive fact seems to occur because spreading speeds are only asymptotic speeds. That is, a particular component $v_n(x)$ need not be zero ahead of its front, but may have a small positive tail. If v_n appears as a driving (in-migration) term in the recursion for another component w_n, the small value of v_n at a point x well beyond the front of either variable alone can lead to an appreciable value of $w_n(x)$. This phenomenon is interesting, because it is a property of a reaction-diffusion system which cannot occur for a hyperbolic system.

Section 2 presents the fundamental ideas and hypotheses. The counterexample which shows that c^*_f may be greater than $c^{(\ell)}$ is presented in Section 3. Section 4 contains positive results. Proposition 4.1 shows what actually follows from the proof which was supposed to establish lemma 2.3 in [4]. It produces a pair of bounds $c^{(\ell)} \le c^*_f \le c^{(u)}$ rather than a formula for c^*_f. Theorem 4.1 adds an Extra Hypothesis which forces the equality $c^{(u)} = c^{(\ell)}$, and thereby permits one to obtain the statement of Lemma 2.3 of [4]. We then show that almost all of results of [4] and all the results in its companion paper [1] follow by replacing Lemma 2.3 there by our Theorem 4.1, while the few remaining results of [4] can be justified by the addition of the Extra Hypothesis.

Section 5 gives an application of our counterexample to a reaction-diffusion model in population ecology. Section 6 summarizes our results. The Appendix present the proofs of the Propositions and the Theorem.

2 Hypotheses and Lemma 2.3 of [4]

We are dealing with vector-valued functions. We shall think of such a function as a function of both the space variable x and the component index. For example, $\mathbf{u} \ge \mathbf{v}$ means that at each x every component of $\mathbf{u}$ is at least as large as the corresponding component of $\mathbf{v}$. However, we shall use the usual notation $\mathbf{u} >> \mathbf{v}$ to mean that at every x each component of $\mathbf{u}(x)$ is strictly greater than the corresponding component of $\mathbf{v}(x)$. We shall deal with the class of truncated linear recursions (1.2) for which $\tilde{L}$ and $\boldsymbol{\omega}$ satisfy the following hypotheses:

Hypotheses 2.1.

i. *$\tilde{L}$ is a linear operator which takes the class of k-vector valued functions whose components are continuous and nonnegative and grow at most exponentially at $\pm\infty$ into the same class of functions. (In particular, $\tilde{L}$ is order-preserving, so that the recursion (1.2) is cooperative.)*

ii. *$\tilde{L}$ is translation invariant in the sense that $\tilde{L}[\mathbf{u}(\cdot+h)](x) = \tilde{L}[\mathbf{u}(\cdot)](x+h)$. That is, the habitat is homogeneous.*

iii. *If a sequence $\mathbf{u}_n$ converges to a bounded function $\mathbf{u}$, uniformly on each bounded interval, then $\tilde{L}[\mathbf{u}_n]$ converges to $\tilde{L}[\mathbf{u}]$ uniformly on each bounded interval.*

iv. *$\tilde{L}[\boldsymbol{\omega}] >> \boldsymbol{\omega} >> \mathbf{0}$. That is, $\mathbf{0}$ is an unstable equilibrium and $\boldsymbol{\omega}$ is a stable equilibrium of (1.2).*

The following Lemma shows that $\boldsymbol{\omega}$ is a global attractor in a very strong sense.

Lemma 2.1. *If all the components of $\mathbf{u}_0(x)$ are uniformly positive and $\mathbf{u}_n(x)$ is the solution of the recursion (1.2), then $\mathbf{u}_n \equiv \boldsymbol{\omega}$ for all sufficiently large n.*

Proof. The hypothesis (iv) above shows that there is a number $\mu > 1$ such that $\tilde{L}[\boldsymbol{\omega}] \geq \mu\boldsymbol{\omega}$. Because $\mathbf{u}_0$ is uniformly positive, there is an integer ℓ so large that $\mathbf{u}_0 \geq \mu^{-\ell}\boldsymbol{\omega}$. A simple induction argument shows that $\mathbf{u}_n \geq \mu^{n-\ell}\boldsymbol{\omega}$ for $n \leq \ell$. Since $\mathbf{u}_n \leq \boldsymbol{\omega}$, it follows that $\mathbf{u}_n \equiv \boldsymbol{\omega}$ for $n \geq \ell$, which proves the Lemma.

It follows from the Hypotheses (i) and (ii) above that for each nonnegative number μ there is a matrix B_μ with nonnegative entries such that

$$\tilde{L}[e^{-\mu x}\boldsymbol{\alpha}](y) = e^{-\mu y} B_\mu \boldsymbol{\alpha} \tag{2.1}$$

for all nonnegative constant vectors $\boldsymbol{\alpha}$.

The operator $\tilde{L}$ is said to be **reducible** if there is a nonempty subset s with nonempty complement of the set of components $\{1, 2 \cdots, k\}$ such that if all the components of the function $\mathbf{u}(x)$ with indices in s are zero, then the function $\tilde{L}[\mathbf{u}]$ has the same property. If this is not the case, then $\tilde{L}$ is said to be **irreducible**. It is easily seen that $\tilde{L}$ is irreducible if and only if its restriction to the constant vectors, which is defined by B_0, is irreducible.

Lui [3] has shown that if $\tilde{L}$ is irreducible, then the recursion (1.2) has a single speed c^* with which all the components of $\mathbf{u}_n$ spread. Lui also gave a formula for this spreading speed. If $\lambda(\mu)$ denotes the principal eigenvalue of B_μ, that is, the eigenvalue whose eigenvector has positive components, then

$$c^* = \inf_{\mu>0} \mu^{-1} \ln \lambda(\mu).$$

The case when $\tilde{L}$ is not irreducible has been studied in [4]. In this case, B_μ is a reducible matrix, and a theorem of Frobenius shows that after a permutation of the vector coordinates, the matrix is block lower triangular, with the diagonal blocks square and irreducible. That is,

$$B_\mu = \begin{pmatrix} \{B_\mu\}_{11} & 0 & \cdots & \cdots & \cdot & 0 \\ \{B_\mu\}_{21} & \{B_\mu\}_{22} & 0 & \cdot & \cdots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & 0 \\ \{B_\mu\}_{m1} & \cdot & \cdot & \cdot & \cdot & \{B_\mu\}_{mm} \end{pmatrix}, \tag{2.2}$$

where each diagonal block is square and irreducible. Because $\tilde{L}$ is order-preserving, all the entries of B_μ are nonnegative, and the zero entries of B_μ are the same for all μ. Therefore, a single permutation of coordinates puts all the matrices B_μ into the Frobenius form (2.2). We shall always assume that this permutation of coordinates has been made.

Each of the diagonal blocks $\{B_\mu\}_{\rho\rho}$ has a principal eigenvalue $\lambda_\rho(\mu)$, and one can define the numbers

$$\tilde{c}_\rho := \inf_{\mu>0} \mu^{-1} \ln \lambda_\rho(\mu). \tag{2.3}$$

It was shown in [4], and, under weaker hypotheses, in [2] that, in general, there are two spreading speeds: a slowest spreading speed c^* and a fastest spreading speed c_f^*. The slowest speed is characterized by the properties that for any solution of (1.2) for which $\mathbf{u}_0(x)$ is nondecreasing with $\mathbf{u}_0 = \mathbf{0}$ for all sufficiently large x and $\mathbf{0} << \mathbf{u}(-\infty) << \boldsymbol{\omega}$ and for any positive ϵ

$$\lim_{n\to\infty} \left\{ \sup_{x \le n(c^*-\epsilon)} [\boldsymbol{\omega} - \mathbf{u}_n(x)] \right\} = \mathbf{0},$$

while for some index i

$$\lim_{n\to\infty} \left\{ \sup_{x \ge n(c^*+\epsilon)} \{\mathbf{u}_n(x)\}_i \right\} = \mathbf{0}.$$

The fastest speed is similarly characterized by the fact that, under the same conditions,

$$\lim_{n\to\infty} \left\{ \sup_{x \ge n(c_f^*+\epsilon)} \mathbf{u}_n(x) \right\} = \mathbf{0}, \tag{2.4}$$

while for some index j

$$\limsup_{n\to\infty}\left\{\inf_{x\le n(c_f^*-\epsilon)}\{\mathbf{u}_n(x)\}_j\right\}>0. \tag{2.5}$$

By using Lemma 2.1, one easily checks that the Hypotheses 2.1 imply all the hypotheses of [2] with $\boldsymbol{\beta}=\boldsymbol{\omega}$, except for the last hypothesis. One sees from [2] that the latter is not used in proving the above spreading results, so that these results are valid for the truncated recursion (1.2).

Remarks.

1. One can easily verify that the spreading speeds c^* and c_f^* do not depend upon the truncation vector $\boldsymbol{\omega}$.
2. It is easily seen from the recursion (1.2) and the results of Lui [3] that if all components but the ith one of $\mathbf{u}_0(x)$ are identically zero, and if i belongs to the ρth block of the matrix (2.2) then $\{\mathbf{u}_n(x)\}_j\equiv 0$ when j is in a block $\sigma<\rho$, and all the components of the ρth block, including the ith component, spread at the speed $\tilde{c}_\rho$. Thus, every individual component speed is one of the $\tilde{c}_\rho$, so that $c^{(\ell)}$ is also the largest of these block speeds. That is,
$$c^{(\ell)}=\max_\rho \tilde{c}_\rho. \tag{2.6}$$

3 A counterexample.

We give a counterexample to show that the fastest spreading speed of a truncated linear recursion may be larger than $c^{(\ell)}$. Consider the recursion

$$\begin{pmatrix}u_{n+1}\\ v_{n+1}\\ w_{n+1}\end{pmatrix}=\min\left\{\begin{pmatrix}1\\1\\1\end{pmatrix},\tilde{L}\left[\begin{pmatrix}u_n\\ v_n\\ w_n\end{pmatrix}\right]\right\}, \tag{3.1}$$

where $\tilde{L}[(u_0,v_0,w_0)](x)$ is defined to be the value at time $t=1$ of the solution $(u(x,t),v(x,t),w(x,t))$ of the cooperative linear system

$$\begin{aligned}u_t&=(1/32)u_{xx}+16u\\ v_t&=v_{xx}+u+v\\ w_t&=(1/4)w_{xx}+v+12w\end{aligned} \tag{3.2}$$

with the initial conditions

$$u(x,0)=u_0(x),\ v(x,0)=v_0(x),\ w(x,0)=w_0(x).$$

The linearization of the recursion (3.1) is obtained by replacing the right-hand side by $\tilde{L}\left[\begin{pmatrix}u_n\\ v_n\\ w_n\end{pmatrix}\right]$. Because the coefficients of the system (3.2) are constant, we can write an explicit solution when the initial values are given by $e^{-\mu x}$ times a constant vector $\boldsymbol{\alpha}$. From this fact we find that

$$B_\mu = \begin{pmatrix} e^{(1/32)\mu^2+16} & 0 & 0 \\ \frac{e^{(1/32)\mu^2+16}-e^{\mu^2+1}}{(1/32)\mu^2+16-[\mu^2+1]} & e^{\mu^2+1} & 0 \\ \{B_\mu\}_{31} & \frac{e^{\mu^2+1}-e^{(1/4)\mu^2+12}}{\mu^2+1-[(1/4)\mu^2+12]} & e^{(1/4)\mu^2+12} \end{pmatrix}, \tag{3.3}$$

where

$$\begin{aligned}\{B_\mu\}_{31} &= \frac{e^{(1/32)\mu^2+16}}{\{(1/32)\mu^2+16-[\mu^2+1]\}\{(1/32)\mu^2+16-[(1/4)\mu^2+12]\}} \\ &+ \frac{e^{\mu^2+1}}{\{\mu^2+1-[(1/32)\mu^2+16]\}\{\mu^2+1-[(1/4)m^2+12]\}} \\ &+ \frac{e^{(1/4)\mu^2+12}}{\{(1/4)\mu^2+12-[(1/32)\mu^2+16]\}\{(1/4)\mu^2+12-[\mu^2+1]\}}.\end{aligned}$$

B_μ is in the Frobenius form (2.2) with 1×1 diagonal blocks. Thus

$$\lambda_1(\mu) = e^{(1/32)\mu^2+16},\ \lambda_2(\mu) = e^{\mu^2+1},\ \lambda_3(\mu) = e^{(1/4)\mu^2+12},$$

so that

$$\begin{aligned}\tilde{c}_1 &:= \inf_{\mu>0}\{\mu^{-1}\ln e^{(1/32)\mu^2+16}\} = \sqrt{2}, \\ \tilde{c}_2 &= 2, \\ \tilde{c}_3 &= 2\sqrt{3},\end{aligned}$$

and

$$c^{(\ell)} = 2\sqrt{3}. \tag{3.4}$$

Because $4 > 2\sqrt{3} = c^{(\ell)}$, the following Proposition shows that for this example the fastest spreading speed c_f^* is strictly greater than $c^{(\ell)}$.

Proposition 3.1. *The fastest spreading speed c_f^* of the recursion (3.1) satisfies the inequality*

$$c_f^* \geq 4 > c^{(\ell)}. \tag{3.5}$$

The proof of this Proposition will be presented in the Appendix.

Remarks.

1. Applying Theorem 4.1 in the next Section to the recursion for the u and v components alone shows that the u-component in this example has the asymptotic spreading speed $\tilde{c}_1 = \sqrt{2}$ and the v-component has the spreading speed $\tilde{c}_2 = 2$. These two components force the w-component to spread at a speed which is not only greater than the spreading speed of w in their absence, but also greater than the speeds at which these two components actually spread. This apparently paradoxical behavior is caused by the fact that although v is small ahead of the front which travels at speed 2, it is positive there.

2. In the recursion (3.1), $\lambda_1(0)$ is strictly larger than the other two eigenvalues at $\mu = 0$. This is Hypothesis 2.1.v.c of [4]. It is easily verified that the recursion (3.1) satisfies the remainder of the Hypotheses 2.1 of [4] as well. Therefore, Lemma 2.3 of [4] asserts that $c_f^* = c^{(\ell)}$, and the above Proposition shows that this is not correct.

3. The only reason we have included the first equation in the system (3.1) is to make the system satisfy the hypotheses of [4]. The proof is carried out with $u \equiv 0$. For this reason, the statement of Proposition 3.1 is also valid for the 2-component system obtained by eliminating the u-equation, and replacing u by 0 in the other two equations.

4 Results on the fastest spreading speed.

The counterexample of the preceding Section showed that, contrary to Lemma 2.3 of [4], the fastest spreading speed can be larger than the number $c^{(\ell)}$ defined by (2.6). A look at the proof of this Lemma on page 214 of [4] shows that the inequality (6.3) does not follow from the equation (6.4) unless it is known that $\tilde{\lambda}_1(\tilde{\mu}_1) \le \tilde{\lambda}_2(\tilde{\mu}_1)$. Similar problems arise with the other $\mathbf{w}_\rho$ in the proof. One can, however, adapt the ideas of the proof to obtain an upper bound for the fastest spreading speed. As will be shown in the Appendix, the following Proposition is valid.

Proposition 4.1. *The fastest spreading speed c_f^* of the recursion (1.2) satisfies the inequalities*

$$c^{(\ell)} \le c_f^* \le c^{(u)}, \tag{4.1}$$

where $c^{(\ell)}$ is defined by (2.6) and

$$c^{(u)} := \inf_{\mu_1 \ge \mu_2 \ge \cdots \ge \mu_m > 0} \left\{ \max_\rho \mu_\rho^{-1} \ln \lambda_\rho(\mu_\rho) \right\}. \tag{4.2}$$

Example. To compute the upper bound $c^{(u)}$ for the counterexample problem (3.2), we note that the eigenvalues λ_ρ are the diagonal elements of the the matrix B_μ in (3.3). We write $q_\rho(\mu) := \mu^{-1} \ln \lambda_\rho(\mu)$ for the functions which appear in the definition (4.2) of $c^{(u)}$. We observe that this definition is equivalent to the iterated form

$$c^{(u)} = \inf_{\mu_3} \left\{ \max \left\{ q_3(\mu_3), \left\{ \inf_{\mu_2 \ge \mu_3} \left\{ \max \left\{ q_2(\mu_2), \inf_{\mu_1 \ge \mu_2} q_1(\mu_1) \right\} \right\} \right\} \right\} \right\}. \tag{4.3}$$

In order to evaluate this quantity, we first observe that the function $q_1(\mu_1) := (1/32)\mu_1 + 16\mu^{-1}$ is decreasing to the left of its minimizer $\tilde{\mu}_1 = 16\sqrt{2}$ and increasing to the right of it. It is easily seen that $\inf_{\mu_1 \ge \mu_2} q_1(\mu_1)$ is obtained by replacing the decreasing part by the minimum value $\sqrt{2}$. That is,

$$\inf_{\mu_1 \ge \mu_2} q_1(\mu_1) = \begin{cases} \sqrt{2} \text{ for } \mu_2 \le 16\sqrt{2} \\ q_1(\mu_2) \text{ for } \mu_2 \ge 16\sqrt{2}. \end{cases}$$

A simple calculation shows that this function is less than $q_2(\mu_2) := \mu_2 + \mu_2^{-1}$ everywhere. Thus, the maximum of the two functions of μ_2 in (4.3) is q_2, and hence the infimum for $\mu_2 \geq \mu_3$ is given by

$$\inf_{\mu_2 \geq \mu_3} q_2(\mu_2) = \begin{cases} 2 \text{ for } \mu_3 \leq 1 \\ q_2(\mu_3) \text{ for } \mu_3 \geq 1. \end{cases}$$

Because $\tilde{\mu}_3 = 4\sqrt{3} > 1 = \tilde{\mu}_2$, there is a point $\tilde{\mu}_{23} = \sqrt{44/3}$ between $\tilde{\mu}_2$ and $\tilde{\mu}_3$ at which $q_3(\mu_3)$ and this function coincide. That is, $q_2(\tilde{\mu}_{23}) = q_3(\tilde{\mu}_{23})$. Moreover the maximum of the two functions is the decreasing function $q_3(\mu_3)$ to the left of $\tilde{\mu}_{23}$, and the increasing function $q_2(\mu_3)$ to the right. This shows that the infimum with respect to μ_3 in (4.3) is equal to the common value $q_2(\tilde{\mu}_{23}) = 47/\sqrt{132}$. We conclude that for the problem (3.2)

$$c^{(u)} = 47/\sqrt{132} \sim 4.091.$$

This upper bound is quite close to the lower bound 4 for c_f^* in Proposition 3.1. It is possible that $c_f^* = c^{(u)}$, but we do not know how to prove this.

Proposition 4.1 gives bounds but not a formula for c_f^*. It obviously does give a formula if one makes the extra assumption that $c^{(u)} = c^{(\ell)}$. This gives the following result.

Theorem 4.1. *The equation*

$$c_f^* = c^{(\ell)} \tag{4.4}$$

is satisfied if, in addition to the Hypotheses 2.1, the principal eigenvalues of B_μ *satisfy the*
Extra Hypothesis: *There exist numbers*

$$\hat{\mu}_1 \geq \hat{\mu}_2 \geq \cdots \tag{4.5}$$

on the extended interval $[0, \infty]$ *such that*

$$\hat{\mu}_\rho^{-1} \ln \lambda_\rho(\hat{\mu}_\rho) \leq c^{(\ell)} \textit{ for } \rho = 1, 2, \cdots. \tag{4.6}$$

(If μ_ρ *is 0 or* ∞*, the expression* $\hat{\mu}_\rho^{-1} \ln \lambda_\rho(\hat{\mu}_\rho)$ *is to be understood as a limit.)*

Remarks.

1. If there is an index ρ_0 with the property that

$$\lambda_\rho(\tilde{\mu}_{\rho_0}) \leq \lambda_{\rho_0}(\tilde{\mu}_{\rho_0}) \text{ for all } \rho,$$

the the Extra Hypothesis is satisfied with $\hat{\mu}_\rho = \tilde{\mu}_{\rho_0}$ for all ρ.

2. If there is a ρ_0 such that $c_{\rho_0} = c^{(\ell)}$, $\lambda_\rho(0) < 1$ for all $\rho > \rho_0$, and $\tilde{\mu}_\sigma \geq \tilde{\mu}_\rho$ for all $\sigma \leq \rho \leq \rho_0$, then the Extra Hypothesis is satisfied with $\hat{\mu}_\rho = \tilde{\mu}_\rho$.

3. The counterexample of Section 3 shows that the formula (4.4) is not, in general, valid when the Extra Hypothesis is not satisfied.

We need to assess the effect of the error in Lemma 2.3 of [4]. The proofs of Theorems 3.1, 3.2, 4.1, and 4.2 of [4] do not use Lemma 2.3, so that they are valid. On the other hand, Lemma 3.3 depends upon Lemma 2.3, so it can only be carried out by assuming the Extra Hypothesis. The same is then true of Theorem 3.3, which depends on Lemma 2.3. On the other hand, Remark 1 shows that the assumption on Theorem 3.1 of [4] implies the Extra Hypothesis, so that this theorem is established by replacing Lemma 2.3 of [4] by Theorem 4.1. The 2-species systems treated in Theorems 3.4 and 4.4 and in all the examples of [4] have the property that $\lambda_1(0) > 1 > \lambda_2(0)$, so that Remark 2 shows that the Extra hypothesis is valid in these cases. Therefore, Lemma 2.3 of [4] can be replaced by Theorem 4.1 of the present work to show that these results are valid. This makes all the examples in [4] and all the results of the companion paper [1] valid.

5 An ecological model with anomalous speed.

The counterexample in Section 3 can be used to obtain properties of some systems of ecological interest. Consider for instance, a two-allele, one-gene-locus model of a diploid species. We suppose that the three genotypes aa, aA, and AA occupy different niches. In particular, we assume that there is neither competition nor cooperation between different genotypes. We also assume that the gametes of the AA homozygotes do not pair with those of the other two genotypes. This means that the time evolutions of the population density $v(x,t)$ of the heterozygotes and $w(x,t)$ of the aa homozygotes do not depend on the density of the AA heterozygotes. As is usual in population models, we shall assume that a large proportion of the gametes produced by the heterozygotes find mates among the other gametes from the heterozygotes, and that the same is true of the gametes produced by the aa homozygotes. This means that when v and w are small, the growth rates due to gametes coming from the same genotype behave linearly in v and w, respectively. Because 1/4 of the matings of the gametes coming from the heterozygotes produce aa homozygotes, this also gives a term proportional to v in the growth rate of the homozygote. We assume that pairings between gametes produced by the heterozygotes and the aa homozygotes are rare when the populations are small, so that they produce growth terms proportional to v^2w^2. Then the following system can serve as a model for this situation.

$$\begin{aligned} v_t &= v_{xx} + v(1-2v) + v^2w^2 \\ w_t &= (1/4)w_{xx} + v + w(12-14w) + v^2w^2 \end{aligned} \tag{5.1}$$

This system has the globally stable coexistence equilibrium $v = w = 1$, and is cooperative on the invariant set $0 \le v \le 1$, $0 \le w \le 1$. On this set the right-hand side of (5.1) is bounded above by that of its linearization. It is easily verified that the proofs of Theorem 3.4, Theorem 3.5, and their Corollary in the paper [3] of Lui still show that the system (5.1) has the same spreading speeds as the truncated linear recursion (3.1), even though not all the hypotheses of [3] are satisfied. That is, the system (5.1) is linearly determinate.

Finally, we observe that the linearization of the system (5.1) is the system (3.2) with the first equation removed and u replaced by 0 in the other two equations. Thus Remark 3 after Proposition 3.1 shows that the homozygotes spread at a speed which is not only greater than the speed at which they spread in the absence of the heterozygotes, but also greater than the speed at which the heterozygotes, which trigger this faster speed, actually spread. As in the case of the truncated linear recursion, the explanation of this apparent paradox lies in the fact that $c^* = 2$ is only the asymptotic spreading speed of the heterozygotes. $v(x,t)$ has an exponential tail beyond the front, and this small density of heterozygotes is able to produce the anomalous speedup in the spreading of the homozygotes.

We observe that the two genotypes spread as what Fife and McLeod called a stacked front. That is, there is a front of speed c_f^* in which (v, w) rises to the monoculture equilibrium (0,12/14), which is followed by a slower front of speed c^* in which (v, w) rises to the coexistence equilibrium (1,1).

A slight variant of this example shows that one can obtain the anomalous speed without assuming the complete segregation of the AA homozygotes. If $z(x, t)$ denotes the density of these homozygotes, if interbreeding between these homozygotes and the heterozygotes occurs at the rate $0.1v^2z^2$ but there is no interbreeding between the two homozygote populations, we obtain a three-equation model of the form

$$\begin{aligned} v_t &= v_{xx} + v(1 - 2.1v) + v^2w^2 + .1v^2z^2 \\ w_t &= (1/4)w_{xx} + v + w(12 - 14w) + v^2w^2 \\ z_t &= 2z_{xx} + v + z(1 - 2.1z) + .1v^2z^2, \end{aligned} \tag{5.2}$$

which has the global attractor (1,1,1) and is linearly determinate. Because the last two equations of the linearized system

$$\begin{aligned} v_t &= v_{xx} + v \\ w_t &= (1/4)w_{xx} + v + 12w \\ z_t &= 2z_{xx} + v + z, \end{aligned}$$

are not coupled to each other, we can apply Remark 1 after Theorem 4.1 to the system which consists of the first and third equation to find that v spreads with speed 2 and z spreads with speed $2\sqrt{2}$. On the other hand, applying Remark 3 after Proposition 3.1 to the first two equations shows that w again spreads at an anomalous speed which is at least 4.

If the two homozygotes interbreed, one must add a growth term which is positive even when $v = 0$ to the right-hand side of the first equation. Because this term cannot be bounded by a function of v which vanishes when $v = 0$, we can no longer prove that a system of this form is linearly determinate. Thus, it is possible that all the genotypes spread at the faster speed, so that no anomaly occurs.

6 Discussion.

We have shown that there are both linear truncated and nonlinear cooperative recursions with anomalous spreading speeds. Such a system must have the property that its linearization is reducible. We observe that a reducible order-preserving linear operator $\tilde{L}$ lies on the boundary of the class of all irreducible order-preserving linear operators in the following sense: If M is any bounded irreducible order preserving linear operator, then for any positive ϵ, no matter how small, $\tilde{L} + \epsilon M$ is irreducible. On the other hand, $\tilde{L} - \epsilon M$ is not order-preserving, because the matrix which describes the action of this operator on constant vectors must have some negative entries to the right of the diagonal blocks of the Frobenius form (2.2) of B_0. By the result of Lui, the truncated recursion of $\tilde{L} + \epsilon M$ has a single spreading speed $c^*(\epsilon)$. It is easy to show that the limit of this speed as ϵ decreases to 0 is at least $c^{(u)}$. Thus if $\tilde{c}_1 < c^{(u)}$, then the spreading speed of the first component jumps downward at $\epsilon = 0$.

The existence of anomalous spreading speeds shows that Lemma 2.3 of [4] is incorrect as it stands. However, Theorem 4.1 shows that the statement of this Lemma becomes true when the Extra Hypothesis in this Theorem is added to the other hypotheses. We have also shown that one can obtain all but one of the theorems of [4] and all the results of [1] by replacing Lemma 2.3 of [4] with Theorem 4.1.

The examples of Section 5 show that anomalous spreading speeds are not simply mathematical curiosities of no biological significance. They can arise from models of two-allele, one-gene-locus diploid species with segregation of the homozygous classes. Here a small density of heterozygotes well ahead of the front produces a corresponding anomalous speedup in the spreading of one of the homozygotes. We anticipate that this kind of anomalous spreading speed phenomenon will be found in other similar reaction-diffusion models.

7 Appendix: Proofs.

Proof of Proposition 3.1. To prove the inequality (3.5), we need a lower bound for the solution of the recursion (3.1). To obtain such a bound, we take the particular initial values

$$\begin{aligned} &u_0(x) \equiv 0 \\ &v_0(x) = \begin{cases} 1/2 & \text{for } x \leq 0 \\ 0 & \text{for } x > 0 \end{cases} \\ &w_0(x) \equiv 0. \end{aligned}$$

The first equation of the system (3.2) shows that $u(x,t) \equiv 0$. By the maximum principle the second equation then shows that the solution v of the second equation of (3.2) is bounded below by the solution of the heat equation with the same initial values. That is,

$$v(x,t) \geq V(x,t) := (1/2)(4\pi t)^{-1/2} \int_{-\infty}^{0} e^{-(x-z)^2/(4t)} dz \tag{7.1}$$

for $t \leq 1$. Since V is bounded above by 1/2, its values at the integers n are not affected by truncation by 1, so that $V(x,n)$ is a subsolution of the recursion (3.1) as well.

Suppose now for the sake of contradiction that

$$c_f^* < 4. \tag{7.2}$$

Then we may choose two positive constants c_1 and c_2 such that

$$\max\{2\sqrt{3},\ c_f^*\} < c_1 < c_2 < 4. \tag{7.3}$$

By the definition of spreading speed, the first inequality shows that for any positive δ there is a number t_δ such that

$$v + w \leq \delta \text{ in } S_\delta, \tag{7.4}$$

where

$$S_\delta := \{(x,t) : x \geq c_1 t,\ t \geq t_\delta\}.$$

We choose $\delta < 1$, so that we can find the values $w_n(x)$ of the solution of the recursion by using the differential equation in S_δ without any truncation.

We choose a point (x,t) in S_δ, and integrate $w_\tau(y,\tau) - (1/4)w_{yy} - 12w$ times the fundamental solution $[\pi(t-\tau)]^{-1/2} e^{-(x-y)^2/[(t-\tau)]+12(t-\tau)}$ with respect to τ and y over the set $\{(y,\tau) : y \geq c_1\tau,\ t_\delta \leq \tau \leq t\}$. Integration by parts then shows that

$$w(x,t) = I_1(x,t) + I_2(x,t) + I_3(x,t), \tag{7.5}$$

where

$$I_1(x,t) := \int_{c_1 t_\delta}^{\infty} [\pi(t-t_\delta)]^{-1/2} e^{-(x-y)^2/[(t-t_\delta)]+12(t-t_\delta)} w(y,t_\delta) dy,$$

$$\begin{aligned} I_2(x,t) :=& \int_{t_\delta}^{t} [\pi(t-\tau)]^{-1/2} e^{-(x-c_1\tau)^2/[(t-\tau)]+12(t-\tau)} \{-c_1 w(c_1\tau,\tau) \\ &- (1/4)w_y(c_1\tau,\tau) + 2((x-c_1\tau)/(t-\tau))w(c_1\tau,\tau)\} d\tau, \end{aligned} \tag{7.6}$$

and

$$I_3(x,t) := \int_{t_\delta}^{t} \int_{c_1\tau}^{\infty} [\pi(t-\tau)]^{-1/2} e^{-(x-y)^2/[(t-\tau)]+12(t-\tau)} v(y,\tau) dy d\tau. \tag{7.7}$$

We shall find a lower bound for w by finding lower bounds for these three integrals. Because $w \geq 0$, we can immediately write

$$I_1 \geq 0. \tag{7.8}$$

Because the initial data are all nonincreasing, it follows from the translation invariance of the recursion (3.1) and the maximum principle that the functions u, v, and w are all nonincreasing in x for each t. In particular, we see that $w_y \leq 0$, so that the term involving w_y in the integral in (7.6) gives a nonnegative contribution to the integral. Because $x - c_1\tau \geq c_1(t-\tau) \geq 0$ and w is nonnegative, the same is true of the term which involves $(x - c_1\tau)$. Thus the only term of the integral for I_2 which may make a negative contribution is the one which involves $-c_1 w$. To bound this term below, we use the inequality (7.4) to find that

$$I_2(x,t) \geq -c_1\delta \int_{t_\delta}^{t} [\pi(t-\tau)]^{-1/2} e^{-(x-c_1\tau)^2/[(t-\tau)]+12(t-\tau)} d\tau. \tag{7.9}$$

It is easily seen that since $x \geq c_1 t$, the exponent in the integral is bounded above by

$$-(c_1^2 - 12)(t-\tau).$$

We make the change of variable of integration $\sigma = t - \tau$ to see that integral in the right-hand side of (7.9) can be bounded by a constant multiple of

$$\int_0^{t-t_\delta} \sigma^{-1/2} e^{-(c_1^2-12)\sigma} d\sigma.$$

Because $c_1^2 > (2\sqrt{3})^2 = 12$, we conclude that there is a positive constant K_2 such that

$$I_2(x,t) \geq -K_2. \tag{7.10}$$

By inserting the lower bound (7.1) into (7.7), see that for (x,t) in S_δ

$$\begin{aligned} I_3(x,t) \geq \int_{t_\delta}^{t} \int_{-\infty}^{0} \int_{c_1\tau}^{\infty} & (1/2)[\pi(t-\tau)]^{-1/2}[4\pi\tau]^{-1/2} \\ & e^{-(x-y)^2/[(t-\tau)]+12(t-\tau)-(y-z)^2/[4\tau]} dy dz d\tau. \end{aligned} \tag{7.11}$$

A little manipulation shows that because $z \leq 0$, the exponent in the integrand takes its maximum at the point $(\bar{y}, \bar{z}, \bar{\tau})$ where

$$\bar{y} = 4(x-2t)/3, \ \bar{z} = 0, \ \bar{\tau} = (x-2t)/6.$$

Because $2 < c_1 < 8$ we see that when $c_1 t \leq x < 8t$, $\bar{y} > c_1\bar{\tau}$ and $0 < \bar{\tau} < t$, so that this point is in the range of integration. At $(\bar{y}, \bar{z}, \bar{\tau})$ the exponent has the value $4(4t - x) \geq 4(4 - c_2)t$ when $x \leq c_2 t$. We recall that $c_2 < 4$ so that the coefficient of t is positive. By bounding the first and second derivatives of the exponent, we can find a neighborhood of $(\bar{y}, \bar{z}, \bar{\tau})$ of a volume which is bounded below by a negative power of t on which the value of the exponential on the right of (7.11) is at least $(1/2)e^{4(4-c_2)t}$, and we obtain a lower bound for I_3 by integrating only over this neighborhood. In this way we find positive constants α and K_3 such that

$$I_3(c_2 t, t) \geq K_3 t^{-\alpha} e^{4(4-c_2)t}.$$

By combining this inequality with the lower bounds (7.8) and (7.9) and using (7.5), we conclude that $w(c_2 t, t)$ approaches infinity as t goes to infinity. This clearly contradicts the inequality (7.4), which implies that $w(c_2 t, t) \leq \delta$. Since this contradiction followed directly from the assumption (7.2), we conclude that this assumption cannot be valid. That is, $c_f^* \geq 4$, which is the statement of the Proposition.

Proof of Proposition 4.1. We first note that by the result of Lui, the components of the ρth block must spread with at least the speed $\tilde{c}_\rho$. Therefore, $c_f^* \geq c^{(\ell)}$.

To prove the inequality $c_f^* \leq c^{(u)}$, we shall construct a supersolution of (1.2). The definition (4.2) of $c^{(u)}$ and the definition of an infimum show that for any positive δ there are finite positive numbers μ_ρ such that

$$\mu_1 \geq \mu_2 \geq \cdots$$

and

$$\mu_\rho^{-1} \ln \lambda_\rho(\mu_\rho) < c^{(u)} + \delta \text{ for all } \rho. \tag{7.12}$$

We now define the block lower triangular matrix $\hat{B}$ by the equation

$$\{\hat{B}\}_{\rho\sigma} := \{B_{\mu_\rho}\}_{\rho\sigma}.$$

That is, the ρth block row of $\hat{B}$ is equal to the ρth block row of B_{μ_ρ}. By (7.12), the spectral radius of $\{\hat{B}_\mu\}_{\rho\rho}$ is strictly less than $e^{\mu_\rho(c^{(u)}+\delta)}$. Because $\hat{B}$ is lower triangular, we can solve the system

$$\{\boldsymbol{\alpha}\}_\rho = e^{-\mu_\rho(c^{(u)}+\delta)}\{\hat{B}\boldsymbol{\alpha}\}_\rho + \{\boldsymbol{\omega}\}_\rho \tag{7.13}$$

for $\{\boldsymbol{\alpha}\}_1$, then for $\{\boldsymbol{\alpha}\}_2$, and so forth, by the method of successive approximation. We find that $\boldsymbol{\alpha} \geq \boldsymbol{\omega} >> 0$. We now define the function $\mathbf{w}$ by

$$\{\mathbf{w}(x)\}_\rho := \min\{\{\boldsymbol{\omega}\}_\rho, e^{-\mu_\rho x}\{\boldsymbol{\alpha}\}_\rho\}$$

Since $\boldsymbol{\alpha} \geq \boldsymbol{\omega}$, the components of $\mathbf{w}$ are exponential functions only for nonnegative values of x. Because the μ_ρ are nonincreasing in ρ, we see that the exponential factors $e^{-\mu_\rho x}$ are then nonincreasing in ρ. Since $\{\tilde{L}[\mathbf{w}]\}_\rho$ only depends on the components $\{\mathbf{w}\}_\sigma$ with $\sigma \leq \rho$, we see that

$$\begin{aligned}\{\tilde{L}[\mathbf{w}]\}_\rho \leq \{\tilde{L}[e^{-\mu_\rho x}\boldsymbol{\alpha}]\}_\rho &= e^{-\mu_\rho x}\{B_{\mu_\rho}\boldsymbol{\alpha}\}_\rho \\ &= e^{-\mu_\rho x}\{\hat{B}\boldsymbol{\alpha}\}_\rho.\end{aligned}$$

We see from (7.13) that

$$\{\hat{B}\boldsymbol{\alpha}\}_\rho \leq e^{\mu_\rho(c^{(u)}+\delta)}\{\boldsymbol{\alpha}\}_\rho.$$

Thus we have shown that

$$\{\tilde{L}[\mathbf{w}]\}_\rho \leq e^{-\mu_\rho(x-(c^{(u)}+\delta))}\{\boldsymbol{\alpha}\}_\rho.$$

Therefore

$$\{\min\{\boldsymbol{\omega}, \tilde{L}[\mathbf{w}]\}_\rho \leq \min\{\{\boldsymbol{\omega}\}_\rho, e^{-\mu_\rho(x-(c^{(u)}+\delta))}\{\boldsymbol{\alpha}\}_\rho\}$$
$$= \{\mathbf{w}(x-(c^{(u)}+\delta))\}_\rho.$$

We have shown that $\mathbf{w}(x - n(c^{(u)} + \delta))$ is a supersolution of the truncated recursion (1.2). We see from the fact that $\boldsymbol{\alpha} >> 0$ that if $\mathbf{u}_0(x)$ is any nonnegative function which is zero for all large x and is uniformly below $\boldsymbol{\omega}$, then there is a translation constant γ such that $\mathbf{u}_0 \leq \mathbf{w}(x-\gamma)$. Induction shows that if $\mathbf{u}_n$ satisfies the recursion (1.2), then $\mathbf{u}_n(x) \leq \mathbf{w}(x-\gamma-n(c^{(u)}+\delta))$. Since $\mathbf{w}(\infty) = \mathbf{0}$, this shows that c_f^* is bounded above by $c^{(u)}+\delta$. Because δ is any positive number, we have $c_f^* \leq c^{(u)}$, which proves Proposition 3.1. This inequality, together with the lower bound $c_f^* \geq c^{(\ell)}$, proves Theorem 4.1.

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