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ON THE UNIQUENESS AND STABILITY OF POSITIVE SOLUTIONS IN THE LOTKA-VOLTERRA COMPETITION MODEL WITH DIFFUSION

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1. Introduction. Much attention has been given recently to reaction-diffusion systems which model the competitive interaction of two or more organisms allowed to move freely throughout a bounded medium. A particular model which has been widely investigated (see [7] for references) is the following Lotka-Volterra system:

$$(1.1)\qquad \begin{aligned} u_t &= k_1\Delta u + u[a - bu - cv] \\ v_t &= k_2\Delta v + v[d - eu - fv]. \end{aligned}$$

The equations are assumed to be satisfied in a cylinder $\Omega \times (0, \infty)$, where Ω is an open, bounded smooth domain in $\mathbf{R}^N$, and are supplemented by linear boundary conditions on $\partial\Omega \times (0, \infty)$. The solutions to (1.1) represent population densities for the competing species. In general, the coefficient functions in (1.1) are assumed to be nonnegative and smooth on $\overline{\Omega} \times (0, \infty)$. They represent growth rates (a and d), self-regulation (b and f), and competitive interaction (c and e). The diffusion coefficients k_1 and k_2 are assumed positive.

Throughout this article, the coefficient functions shall be taken to be constant. In this case, if homogeneous Neumann boundary conditions are imposed on (1.1), substantial progress in understanding the model has been made. In fact, necessary and sufficient conditions have been given [5] for the existence of a globally attracting componentwise-positive steady-state (coexistence state). (Steady states which are identically zero in one component are referred to as extinction states.) However, if the Neumann boundary data are replaced by homogeneous Dirichlet boundary conditions, the level of understanding is somewhat less. Definitive, readily computable answers to the important questions of existence, uniqueness, and stability of steady-state solutions to (1.1) do not yet exist. Some progress has been made. In [8], Dancer gives a condition which is necessary and sufficient for existence in a number of cases. However, this condition is acknowledged in [8] to be "complicated and rather implicit." In the case of equal diffusion rates and equal growth rates in (1.1), Cosner and Lazer [7] have given conditions which guarantee the existence of a unique globally asymptotically stable coexistence state. Valuable perspective on the problem is provided by the observation by several workers (Blat and Brown [4], among them) that coexistence states arise as bifurcations from extinction states. This bifurcation occurs when the growth rates a and d vary while the other coefficients are held fixed.

In the present article we shall address the question of uniqueness and stability of component-wise positive steady state solutions to (1.1) in the case of unequal growth rates. We shall assume that k_1 and k_2 are both equal to 1. By normalizing u and v appropriately (see [6]), we may also assume that b and f are also both equal to 1. These assumptions yield the steady-state system

$$\begin{aligned} -\Delta u &= u[a-u-cv] \\ -\Delta v &= v[d-eu-v], \qquad \text{in } \Omega \\ u|_{\partial\Omega} &= 0 = v|_{\partial\Omega}. \end{aligned} \tag{1.2}$$

In the context of (1.2), the condition for uniqueness in case $a = d$ may be stated succinctly: let $a > \lambda_1$, where λ_1 is the smallest positive eigenvalue of

$$\begin{aligned} -\Delta\psi &= \lambda\phi \qquad && \text{in } \Omega \\ \psi &\equiv 0 && \text{on } \partial\Omega, \end{aligned} \tag{1.3}$$

and, in addition, let $0 < c < 1$ and $0 < e < 1$. For the remainder of this article we assume that $0 < c < 1$ and $0 < e < 1$. (The constant λ_1 will appear throughout the paper and will always be as in (1.3).) We should note that in case $0 < c \leq 1$ and $e \geq 1$ or $0 < e \leq 1$ and $c \geq 1$, there can sometimes be more than one coexistence state for (1.1) — (1.2). That such is the case for $a = d$ was established independently in [4] and [7], and when $a \neq d$, in [6].

Let us now briefly describe our approach. Specifically, let us define a map $F : \mathbf{R}^4 \times [C_0^{2+\alpha}(\overline{\Omega})]^2 \to [C^\alpha(\overline{\Omega})]^2$ by

$$F(a,d,c,e,u,v) = \begin{bmatrix} -\Delta u + u(u+cv-a) \\ -\Delta v + v(eu+v-d) \end{bmatrix}. \tag{1.4}$$

Here $C^\alpha(\overline{\Omega})$ denotes the space of Hölder continuous functions, where $0 < \alpha < 1$, and $C_0^{2+\alpha}(\overline{\Omega})$ denotes the twice continuously differentiable functions vanishing on $\partial\Omega$ with Hölder continuous second partial derivatives. (See [**9**].) The linearization of F with respect to the $u - v$ variables is readily seen to be

(1.5)
$$\begin{aligned} &\underset{(u,v)}{DF|(a,d,c,e,u,v)} \begin{bmatrix}\varphi\\ \psi\end{bmatrix} \\ &\quad = \begin{bmatrix} (-\Delta + (2u + cv - a)) & cu \\ ev & (-\Delta + (2v + eu - d)) \end{bmatrix} \begin{bmatrix}\varphi\\ \psi\end{bmatrix}. \end{aligned}$$

If $F(a,d,c,e,u,v) = 0$, where $u(x) > 0$ and $v(x) > 0$ on Ω, then a manifold of coexistence states to (1.1) exists about (a,d,c,e,u,v) provided the operator DF in (1.5) is a linear homeomorphism between $[C_0^{2+\alpha}(\overline{\Omega})]^2$ and $[C^\alpha(\overline{\Omega})]^2$. In Section 3, after some preliminaries in Section 2, we show that if $a = d$ and $0 < c < 1$ and $0 < e < 1$, such is always the case. This fact is used in conjunction with the uniqueness results of [**7**] enables us to obtain a uniqueness for result for (a^*, d^*) "sufficiently close" to the diagonal $a = d$. In Section 5, estimates from [**6**] and [**7**] (in particular Theorem 2.3 of [**6**]) enable us to extend (in $a - d$ parameter space) the uniqueness results of Section 4 for "small" c and e. Moreover, how "small" is "small" is made rather explicit in our results.

Although we can give explicit conditions insuring uniqueness when $a \neq d$, these conditions are stronger than the requirement $0 < c < 1$, $0 < e < 1$, which suffices when $a = d$. We conjecture that this last condition is sufficient even if $a \neq d$, but so far have not been able to find a proof.

In Section 5, we obtain stability of the unique steady state described in Sections 3 and 4. In obtaining the invertibility of DF we show that in fact the first eigenvalue of DF is positive; we then use upper and lower solutions for (1.1) constructed from eigenfunctions of DF to obtain stability via a comparison principle. The general approach is similar to that taken in [**11**]; comparison principles and upper/lower solution methods for (1.1) and (1.2) are discussed and further references are given in [**7**].

The system (1.1) models the interaction of two species which diffuse through an environment Ω and compete with each other for resources. The condition $u = v = 0$ on $\partial\Omega$ corresponds to a completely hostile environment outside Ω. The biological implications of our results are essentially that if each species can exist in the absence of the other and if the interactions between the two species are sufficiently weak, then the species can coexist and there is a unique, stable coexistence state. Further, we can give bounds which are sufficiently explicit to permit numerical approximation on the allowable ranges of interaction parameters. Our results sharpen and extend some of those obtained in [7] by giving different and/or weaker conditions on the parameters under which the system (1.1) will have a unique and stable coexistence state. Our attempt to give sharp and explicit conditions on the allowable parameter ranges is motivated largely by the importance of such information in relating the model to applied problems.

2. Some technical preliminaries. Suppose $\Omega \subseteq \mathbf{R}^N$ is a smooth, bounded domain. For $\mu = 1, \ldots, n$, let L^μ be the strongly, uniformly elliptic differential operator given by

$$L^\mu u(x) = -\sum_{i,j=1}^{N} a_{ij}^\mu(x) \frac{\partial^2 u(x)}{\partial x_i \partial x_j} + \sum_{i=1}^{N} b_i^\mu(x) \frac{\partial u}{\partial x_i}(x) + c^\mu(x) u(x)$$

where the coefficient functions are assumed of class $C^\alpha(\overline{\Omega})$ for some $\alpha \in (0,1)$ and $c^\mu \geq 0$ on $\overline{\Omega}$. Now consider the eigenvalue problem

$$(L+M)\overrightarrow{\varphi} = \lambda \overrightarrow{\varphi}, \quad x \in \Omega \tag{2.1}$$

where

$$L = \begin{pmatrix} L^1 & & \\ & \ddots & \\ & & L^n \end{pmatrix}, \quad M = (m_{ij}(x))_{i,j=1}^n, \quad \overrightarrow{\varphi} = \begin{pmatrix} \varphi^1 \\ \vdots \\ \varphi^n \end{pmatrix},$$

subject to the boundary conditions

$$\varphi^\mu(x) = 0 \quad \text{for } x \in \partial\Omega. \tag{2.2}$$

LEMMA 2.1. *Suppose $m_{ij} \in C^\alpha(\overline{\Omega})$ for $i, j = 1, \ldots, n$. Then if $m_{ij} \leq 0$ for $i \neq j$ and $\sum_{j=i}^n m_{ij} \geq 0$ for $i = 1, \ldots, n$, $(L+M)^{-1}$ exists and is a compact positive operator on $[C_0^\alpha(\overline{\Omega})]^n$. Furthermore, if $\tilde{M}(x)$ is irreducible for some $x \in \Omega$, where*

$$\tilde{m}_{ij} = \begin{cases} m_{ij} & \text{if } i \neq j, \\ 0 & \text{if } i = j. \end{cases}$$

(2.1) — (2.2) *has a smallest positive eigenvalue* λ *and a corresponding eigenfunction* $\overrightarrow{\varphi}$ *with* $\varphi^\mu(x) > 0$ *for* $x \in \Omega$.

PROOF: The maximum principle for elliptic systems [**13**, pages 188–192], guarantees that $(L+M)^{-1}$ exists and is a positive operator on $[C_0^\alpha(\overline{\Omega})]^n$. Compactness follows from standard a priori estimates [**1**] and embedding theorems [**9**]. If $\tilde{M}(x)$ is irreducible for some $x \in \Omega$, the maximum principle guarantees that if

$$(L+M)\overrightarrow{u} = \overrightarrow{f}$$
$$\overrightarrow{u}|_{\partial\Omega} = 0,$$

and $f^\mu \geq 0$ on $\overline{\Omega}$ but $\overrightarrow{f} \not\equiv 0$, then $u^\mu(x) > 0$ for $x \in \Omega$ and $\mu = 1, \ldots, n$. Theorem 2.5 of [**10**] may now be employed to assert that $(L+M)^{-1}$ has positive spectral radius $\rho((L+M)^{-1})$. The Krein-Rutman Theorem [**3**] guarantees that $\lambda = 1/\rho((L+M)^{-1})$ is the required eigenvalue. That the corresponding eigenfunction $\overrightarrow{\varphi}$ is as described follows from the maximum principle.

Recall that the linearization of (1.2) at (a,d,c,e,u,v) is given by

$$T\begin{bmatrix}\varphi\\ \psi\end{bmatrix} = \begin{bmatrix}(-\Delta + (2u+cv-a)) & cu\\ ev & (-\Delta + (2v+eu-d))\end{bmatrix}\begin{bmatrix}\varphi\\ \psi\end{bmatrix}. \tag{2.3}$$

Consider the eigenvalue problem

$$T\begin{bmatrix}\varphi\\ \psi\end{bmatrix} = \lambda\begin{bmatrix}\varphi\\ \psi\end{bmatrix}, \tag{2.4}$$

where φ and ψ are requried to vanish on $\partial\Omega$. If we make the substitution $\sigma = -\varphi$, (2.4) is equivalent to

$$\begin{aligned}-\Delta\sigma + (2u+cv+K)\sigma - cu\psi &= (\lambda + a + K)\sigma\\ -\Delta\psi - ev\sigma + (2v+eu+a-d+K)\psi &= (\lambda+a+K)\psi.\end{aligned} \tag{2.5}$$

If we let

$$L = \begin{pmatrix}-\Delta & 0\\ 0 & -\Delta\end{pmatrix}$$

and

$$M = \begin{pmatrix}2u+cv+K & -cu\\ -ev & 2v+eu+a-d+K\end{pmatrix},$$

the hypotheses of Lemma 2.1 are satisfied for some $K > 0$. We have now established

PROPOSITION 2.2. *If T is given by (2.3), then the eigenvalue problem (2.4) has a smallest eigenvalue λ and a corresponding eigenvector $\begin{bmatrix} \varphi \\ \psi \end{bmatrix}$ with $\varphi(x) < 0 < \psi(x)$ for all $x \in \Omega$.*

3. The case $a = d$. We now show that if T is as given in (2.3), $a = d > \lambda_1$, and $0 < c,\ e < 1$, then T is invertible, and in fact has a strictly positive first eigenvalue. Note that (2.5) is equivalent in this case to

$$\begin{aligned} -\Delta\sigma + (2u + cv)\sigma - cu\psi &= (\lambda + a)\sigma \\ -\Delta\psi - ev\sigma + (2v + eu)\psi &= (\lambda + a)\psi. \end{aligned} \tag{3.1}$$

Now fix $a = d > \lambda_1$ and c_0, e_0 with $0 < c_0,\ e_0 < 1$. Let $c(t) = c_0 t$ and $e(t) = e_0 t$, for $t \in [0,1]$. Then there is a unique positive solution [7] to (1.2) at $(a, a, c(t), e(t))$ given by

$$u(t) = \frac{1 - c(t)}{1 - c(t)e(t)}\theta_a, \quad v(t) = \frac{1 - e(t)}{1 - c(t)e(t)}\theta_a,$$

where θ_a is the unique positive solution of

$$\begin{aligned} -\Delta u + u^2 - au = 0 \quad \text{in } \Omega \\ u|_{\partial\Omega} \equiv 0. \end{aligned} \tag{3.2}$$

Consider

$$\begin{aligned} L &= \begin{pmatrix} -\Delta & 0 \\ 0 & -\Delta \end{pmatrix} \\ M(t,x) &= \begin{pmatrix} 2u(t) + c(t)v(t) & -c(t)u(t) \\ -e(t)v(t) & 2v(t) + e(t)u(t) \end{pmatrix}. \end{aligned} \tag{3.3}$$

If $t \in (0,1]$, Lemma 2.1 may be employed to assert the invertibility of $L + M(t,x)$. If $t = 0$, it follows from the invertibility of $-\Delta + 2\theta_a$. Since $M(t,x) = M(t)\theta_a(x)$, where $m_{ij}(t)$ are smooth functions of t on [0,1], Lemma 2, [**12**] implies that $\rho((L+M(t,x))^{-1})$ and hence the first eigenvalue of (3.1) are continuous functions of t on [0,1].

Notice that θ_a is an eigenfunction for

$$
(3.4)\qquad \begin{aligned} -\Delta u + \theta_a u &= au && \text{in } \Omega \\ u &= 0 && \text{on } \partial\Omega. \end{aligned}
$$

A comparison with (3.4) shows that the first eigenvalue for

$$
\begin{aligned} -\Delta u + 2\theta_a u &= \mu u && \text{in } \Omega \\ u &= 0 && \text{on } \partial\Omega \end{aligned}
$$

is necessarily greater than a. It follows that $\rho((L + M(0,x))^{-1}) > 0$. The results of [**12**] now guarantee that if $\mu(t)$ denotes the smallest positive eigenvalue of

$$
(3.5)\qquad [L + M(t,x)] \begin{bmatrix} \sigma_t \\ \psi_t \end{bmatrix} = \mu(t) \begin{bmatrix} \sigma_t \\ \psi_t \end{bmatrix},
$$

where L and $M(t,x)$ are as in (3.3), then $\mu(t)$ and hence $\lambda(t) = \mu(t) - a$ vary continuously with t.

We now claim that $\lambda(t) > 0$ for $t \in [0,1]$. Observe that $\lambda(0) > 0$. Since $\lambda(t)$ is continuous in t, if the claim is not valid, there is a first $t_1 \in (0,1]$ such that $\lambda(t_1) = 0$. At t_1, we have

$$
(3.6)\qquad \begin{aligned} -\Delta\sigma_{t_1} + (2u_{t_1} - c(t_1)v_{t_1} - a)\,\sigma_{t_1} - c(t_1)u_{t_1}\psi_{t_1} &= 0 \\ -\Delta\psi_{t_1} - e(t_1)v_{t_1}\sigma_{t_1} + (2v_{t_1} + e(t_1)u_{t_1} - a)\,\psi_{t_1} &= 0, \end{aligned}
$$

where u_{t_1}, v_{t_1} satisfy

$$
(3.7)\qquad \begin{aligned} -\Delta u_{t_1} + (u_{t_1} + c(t_1)v_{t_1} - a)\,u_{t_1} &= 0 \\ -\Delta v_{t_1} + (v_{t_1} + e(t_1)u_{t_1} - a)\,v_{t_1} &= 0. \end{aligned}
$$

Consider the first equations of (3.6) and (3.7). Multiply the first equation of (3.6) by u_{t_1} and the first equation of (3.7) by σ_{t_1}. Then integrate over Ω and subtract. Integration by parts and the Dirichlet boundary data guarantee that

$$
\int_\Omega u_{t_1}\,(-\Delta\sigma_{t_1}) = \int_\Omega \sigma_{t_1}\,(-\Delta u_{t_1}).
$$

Consequently,

$$\int_\Omega u_{t_1}^2 \sigma_{t_1} - c(t_1) \int_\Omega u_{t_1}^2 \psi_{t_1} = 0.$$

But now

$$u_{t_1} = \frac{1 - c(t_1)}{1 - c(t_1)e(t_1)} \theta_a,$$

whence

$$\int_\Omega \theta_a^2 \sigma_{t_1} - c(t_1) \int_\Omega \theta_a^2 \psi_{t_1} = 0. \tag{3.8}$$

A similar argument with the second equations of (3.6) and (3.7) will give

$$\int_\Omega \theta_a^2 \psi_{t_1} - e(t_1) \int_\Omega \theta_a^2 \sigma_{t_1} = 0. \tag{3.9}$$

Since $0 < t_1 \leq 1$, Lemma 2.1 guarantees that $\sigma_{t_1} > 0$ on Ω and that $\psi_{t_1} > 0$ on Ω. Therefore

$$\int_\Omega \theta_a^2 \sigma_{t_1} > 0 \text{ and } \int_\Omega \theta_a^2 \psi_{t_1} > 0.$$

It follows from (3.8) — (3.9) that

$$\begin{vmatrix} 1 & -c(t_1) \\ -e(t_1) & 1 \end{vmatrix} = 0.$$

Hence $c(t_1)e(t_1) = 1$. But $c(t_1)e(t_1) = t_1^2 c_0 e_0 \leq c_0 e_0 < 1$, since $0 < c_0 < 1$ and $0 < e_0 < 1$. This contradiction establishes the following result.

THEOREM 3.1. *Suppose that $a = d > \lambda_1$ and that $0 < c < 1$ and $0 < e < 1$. Then if T is as given by (2.3), the first eigenvalue of T is positive. In particular, T is invertible.*

Theorem 3.1 allows us to give a uniqueness result for (1.2) as follows.

THEOREM 3.2. *Suppose $a_0 > \lambda_1$ and let $0 < c_0 < 1$ and $0 < e_0 < 1$. Then there is a neighborhood V of (a_0, a_0) in $\mathbf{R}^2$ and a C^1-map $F : V \to [C_0^{2+\alpha}(\overline{\Omega})]^2$ such that the following are equivalent:*

(i) *$(u, v) \in [C_0^{2+\alpha}(\overline{\Omega})]^2$ with $u(x) > 0$ and $v(x) > 0$ for $x \in \Omega$, (u, v) satisfies*

$$\begin{aligned} -\Delta u &= u[a - u - c_0 v] \\ -\Delta v &= v[d - e_0 u - v], \end{aligned} \tag{3.10}$$

and $(a, d) \in V$.
(ii) $(u, v) = F(a, d)$.

PROOF: Theorem 3.1 and the Implicit Function Theorem guarantee that there is a neighborhood W of (a_0, a_0) in $\mathbf{R}^2$ and a C^1-map $F : W \to [C_0^{2+\alpha}(\overline{\Omega})]^2$ such that $(a, d, F(a, d))$ is a componentwise positive solution to (3.10). If the conclusion of the theorem is false, there exist sequences

$$\{(a_n, d_n, u_n, v_n)\}_{n=1}^{\infty}, \{(a_n, d_n, u_n^*, v_n^*)\}_{n=1}^{\infty} \in W \times \left(C_0^{2+\alpha}(\overline{\Omega})\right)^2$$

with u_n, u_n^*, v_n, v_n^* positive on Ω, $(u_n, v_n) \neq (u_n^*, v_n^*)$, and $(a_n, d_n) \to (a_0, a_0)$. From [7], $u_n \leq a_n$ on $\overline{\Omega}$ and $v_n \leq d_n$ on $\overline{\Omega}$, and likewise for u_n^* and v_n^*. Standard a priori estimates and embedding theorems for elliptic equations guarantee that in fact $\{(u_n, v_n)\}_{n=1}^{\infty}$ and $\{(u_n^*, v_n^*)\}_{n=1}^{\infty}$ are bounded sequences in $[C_0^{2+\alpha}(\overline{\Omega})]^2$. By compactness, we may choose a subsequence $\{(a_{n_i}, d_{n_i})\}_{i=1}^{\infty}$ of $\{(a_n, d_n)\}_{n=1}^{\infty}$ such that $(u_{n_i}, v_{n_i}) \to (\overline{u}, \overline{v})$ and $(u_{n_i}^*, v_{n_i}^*) \to (u^*, v^*)$ in $[C_0^{2+\alpha}(\overline{\Omega})]^2$. Furthermore $(\overline{u}, \overline{v})$ and (u^*, v^*) solve (3.10) with $a = d = a_0$, and $\overline{u}, \overline{v}, u^*, v^*$ are all nonnegative. Since $0 < c_0 < 1$ and $0 < e_0 < 1$, from [6], we know that (a_0, a_0) is not a point of bifurcation from extinction to coexistence states. Therefore [7] implies that

$$(\overline{u}, \overline{v}) = (u^*, v^*) = \left(\frac{1 - c_0}{1 - c_0 e_0}\theta_a, \frac{1 - e_0}{1 - c_0 e_0}\theta_a\right).$$

Since

$$(u_{n_i}, v_{n_i}) \neq \left(u_{n_i}^*, v_{n_i}^*\right),$$

we have violated the Implicit Function Theorem. This contradiction establishes the result.

4. The general case. We now consider the invertibility of the operator T in (2.3) for general a and d. We begin by expressing T as

(4.1)
$$T\begin{bmatrix}\varphi\\ \psi\end{bmatrix} = \begin{bmatrix}-\Delta + 2u + cv - a & 0\\ 0 & -\Delta + 2v + eu - d\end{bmatrix}\begin{bmatrix}\varphi\\ \psi\end{bmatrix} + \begin{bmatrix}0 & cu\\ ev & 0\end{bmatrix}\begin{bmatrix}\varphi\\ \psi\end{bmatrix}.$$

Observe that if $u > 0$ on Ω and if

$$(-\Delta + 2u + cv - a)h = \lambda h \qquad \text{in } \Omega,$$

where $h > 0$ in Ω and $h \equiv 0$ on $\partial\Omega$, then

$$\int_\Omega u(-\Delta h) + \int_\Omega 2u^2 h + \int_\Omega cuvh - \int_\Omega auh = \lambda \int_\Omega uh.$$

From integration by parts and the fact that (u, v) solves (1.2) it follows that

$$\int_\Omega (au - u^2 - cuv)h + 2\int_\Omega u^2 h + \int_\Omega cuvh - \int_\Omega auh = \lambda \int_\Omega uh,$$

which implies

$$\int_\Omega u^2 h = \lambda \int_\Omega uh.$$

Hence $\lambda > 0$ and $(-\Delta + 2u + cv - a)^{-1}$ is a compact positive operator and similarly for $(-\Delta + 2v + eu - d)^{-1}$. Thus we have established

PROPOSITION 4.1. *$T : [C_0^{2+\alpha}(\Omega)]^2 \to [C^\alpha(\Omega)]^2$ is invertible if and only if*

$$S = I - \begin{bmatrix} (-\Delta + 2u + cv - a)^{-1} & 0 \\ 0 & (-\Delta + 2v + eu - d)^{-1} \end{bmatrix} \begin{bmatrix} 0 & cu \\ ev & 0 \end{bmatrix}$$

is an invertible operator on $[C_0^{2+\alpha}(\overline{\Omega})]^2$.

REMARK: Once again an appeal to the a priori estimates and embedding theorems of the theory of elliptic partial differential equations [**2**, page 929], allows us to view S as an operator on $[C_0^0(\overline{\Omega})]^2$. Let us denote by $\| \;\|$ the usual supremum norm on $C_0^0(\overline{\Omega})$ and as norm on $[C_0^0(\overline{\Omega})]^2$, we take $\left|\left|\left| \binom{f}{g} \right|\right|\right| = \|f\| + \|g\|$ for $\binom{f}{g} \in [C_0^0(\overline{\Omega})]^2$.

It is a standard result of functional analysis that S is invertible provided $|||I - S||| < 1$. A simple observation shows that such is the case provided

$$\|c(-\Delta + 2u + cv - a)^{-1}(u\cdot)\| < 1 \tag{4.2}$$

and

$$\|e(-\Delta + 2v + eu - d)^{-1}(v\cdot)\| < 1. \tag{4.3}$$

We obtain conditions on a, d, c, and e which guarantee (4.2) and (4.3). Observe that by the generalized resolvent formula we may write

$$\begin{aligned} &c(-\Delta + 2u + cv - a)^{-1} \\ &= c(-\Delta + 2\theta_a - a)^{-1} \\ &\qquad + c[(-\Delta + 2u + cv - a)^{-1} - (-\Delta + 2\theta_a - a)^{-1}] \\ &= c(-\Delta + 2\theta_a - a)^{-1} \\ &\qquad + c[(-\Delta + 2u + cv - a)^{-1}](2\theta_a - 2u - cv)(-\Delta + 2\theta_a - a)^{-1}]. \end{aligned}$$

It follows that

$$\|c(-\Delta + 2u + cv - a)^{-1}\| \le \frac{\|c(-\Delta + 2\theta_a - a)^{-1}\|}{1 - \|2\theta_a - 2u - cf\| \; \|(-\Delta + 2\theta_a - a)^{-1}\|}$$

so long as

$$\|2\theta_a - 2u - cv\| < \frac{1}{\|(-\Delta + 2\theta_a - a)^{-1}\|}. \tag{4.4}$$

It follows from [**6**, Lemma 1.1] that $u \le \theta_a$ and by monotonicity of $\| \;\|$ that $\|u\| \le \|\theta_a\|$. Hence if (4.4) holds, (4.2) is valid so long as

$$\frac{\|\theta_a\| \; \|c(-\Delta + 2\theta_a - a)^{-1}\|}{1 - \|2\theta_a - 2u - cv\| \; \|(-\Delta + 2\theta_a - a)^{-1}\|} < 1 \tag{4.5}$$

or equivalently

$$\|2\theta_a - 2u - cv\| + c\|\theta_a\| < \frac{1}{\|(-\Delta + 2\theta_a - a)^{-1}\|}. \tag{4.6}$$

Proceeding analogously for (4.3), we see that (4.3) holds if

$$\|2\theta_d - 2v - eu\| + e\|\theta_d\| < \frac{1}{\|(-\Delta + 2\theta_d - d)^{-1}\|}. \tag{4.7}$$

PROPOSITION 4.2. *If (u, v) is a componentwise positive solution and T is as given in (2.3), then T is invertible if (4.6) and (4.7) hold.*

Consider now (4.6) and (4.7) in case $\lambda_1 < d \leq a$. In this situation, [**6**, Theorem 2.3] implies that

$$\begin{cases} \frac{1-c}{1-ce}\theta_a \leq u \leq \theta_a \text{ and} \\ v \leq \min\left\{\frac{1-e}{1-ce}\theta_a, \theta_d\right\} \end{cases} \tag{4.8}$$

for any positive solution (u, v) of (1.2). Now let $\lambda_1 < d_0 \leq d \leq a \leq a_0$. Define $K_0 = K_{a_0,d_0}$ by

$$K_{a_0,d_0} = \sup_{d_0 \leq d \leq a \leq a_0} \frac{\theta_a}{\theta_d}. \tag{4.9}$$

If λ_1 is the first eigenvalue of $-\Delta$ with Dirichlet boundary conditions on Ω, and $\varphi_1 > 0$ is the corresponding eigenfunction, normalized with $\sup \varphi_1 = 1$, and τ satisfies $-\Delta\tau = 1$ in Ω, $\tau|_{\partial\Omega} = 0$, then from [**7**] we have the bound

$$K_0 \leq \frac{\max\{a_0^2/4, \lambda_1(a_0 - \lambda_1)\}}{d_0 - \lambda_1} \sup_{x \in \bar{\Omega}} \frac{\tau(x)}{\varphi_1(x)} < \infty.$$

Note that (4.8) and (4.9) imply that

$$u \leq K_0\theta_d.$$

Consequently, if $1 - eK_0 > 0$, Lemma 1.1 of [**6**] implies that

$$(1 - eK_0)\theta_d \leq v, \tag{4.10}$$

since $(1 - eK_0)\theta_d$ solves

$$\begin{aligned} -\Delta w &= w\left[d - eK_0\theta_d - w\right] && \text{in } \Omega \\ w &> 0 && \text{in } \Omega \\ w &\equiv 0 && \text{on } \partial\Omega. \end{aligned}$$

(If $1 - eK_0 < 0$ then (4.10) is trivially satisfied.)

From (4.8) we have

$$(4.11)\qquad \begin{aligned} 2\theta_a - 2u - cv &\le 2\theta_a - \frac{2(1-c)}{1-ce}\theta_a \\ &= \frac{2c(1-e)}{1-ce}\theta_a \end{aligned}$$

and also

$$(4.12)\qquad \begin{aligned} 2\theta_a - 2u - cv &\ge 2\theta_a - 2\theta_a - \frac{c(1-e)}{1-ce}\theta_a \\ &= \frac{-c(1-e)}{1-ce}\theta_a. \end{aligned}$$

Combining (4.11) and (4.12) shows that

$$\begin{aligned} \|2\theta_a - 2u - cv\| + c\|\theta_a\| &\le \left(\frac{2c(1-e)}{1-ce} + c\right)\|\theta_a\| \\ &= \frac{3c - 2ce - c^2 e}{1-ce}\|\theta_a\|. \end{aligned}$$

Consider (4.7). From (4.8) and (4.10),

$$(4.13)\qquad 0 \le 2\theta_d - 2v \le 2eK_0\theta_d.$$

Hence

$$\begin{aligned} \|2\theta_d - 2v - eu\| + e\|\theta_d\| &\le \|2\theta_d - 2v\| + e\|u\| + e\|\theta_d\| \\ &\le 2eK_0\|\theta_d\| + eK_0\|\theta_d\| + e\|\theta_d\| \quad \text{by (4.13)} \\ &\le e(3K_0+1)\|\theta_d\|. \end{aligned}$$

Thus we have established the following theorem.

THEOREM 4.3. *Suppose that (u, v) is a componentwise positive solution to (1.2), $\lambda_1 < d_0 \le d \le a \le a_0$, $0 < c < 1$ and $0 < e < 1$. Then if*

$$(4.14)\qquad \frac{3c - 2ce - c^2 e}{1-ce} < \frac{1}{\|(-\Delta + 2\theta_a - a)^{-1}\| \cdot \|\theta_a\|}$$

and

$$(4.15)\qquad e(3K_0+1) < \frac{1}{\|(-\Delta + 2\theta_d - d)^{-1}\|\ \|\theta_d\|},$$

where K_0 is given by (4.9), the linearization T of (1.2) at (u, v) is an invertible operator from $[C_0^{2+\alpha}(\overline{\Omega})]^2$ to $[C^\alpha(\overline{\Omega})]^2$.

We may now extend Theorem 3.2. We begin with the following lemma.

LEMMA 4.4. *The map $a \to (-\Delta + 2\theta_a - a)^{-1}$ is a continuous function from (λ_1, ∞) into $\mathcal{B}(C_0^0(\overline{\Omega}))$, the bounded linear operators on $C_0^0(\overline{\Omega})$.*

PROOF: From the results of [6] and [7], we know that the map $a \to \theta_a$ is continuous from (λ_1, ∞) into $C_0^\alpha(\overline{\Omega})$. The result now follows via the resolvent formula and the results of [12].

THEOREM 4.5. *Let $\lambda_1 < d_0 < a_0$. Let*

$$B_{[d_0,a_0]} = \min_{d_0 \le a \le a_0} \frac{1}{\|(-\Delta + 2\theta_a - a)^{-1}\| \, \|\theta_a\|}.$$

Suppose that $0 < c < 1$, $0 < e < 1$ and, in addition,

$$d_0 > \lambda_1(e\theta_{a_0}), \tag{4.16}$$

where $\lambda_1(e\theta_a)$ is the first eigenvalue for the problem

$$\begin{aligned} -\Delta\psi + e\theta_a\psi &= \lambda\psi \quad \text{in } \Omega \\ \psi &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

$$\frac{3c - 2ce - c^2 e}{1 - ce} < B_{[d_0,a_0]} \tag{4.17}$$

and

$$e(3K_0 + 1) < B_{[d_0,a_0]}. \tag{4.18}$$

Let $V_{[d_0,a_0]} = \{(a,d) : d_0 \le d \le a \le a_0\}$. Then there is a C^1-map $F : V_{[d_0,a_0]} \to [C_0^{2+\alpha}(\overline{\Omega})]^2$ such that the following are equivalent:

(i) $(u,v) \in C_0^{2+\alpha}(\overline{\Omega})]^2$ *with $u(x) > 0$ and $v(x) > 0$ for $x \in \Omega$, (u,v) satisfies*

$$\begin{aligned} -\Delta u &= u[a - u - c_0 v] \\ -\Delta v &= v[d - e_0 u - v], \end{aligned} \tag{4.19}$$

$(a,d) \in V_{[d_0,a_0]}$, and c_0, e_0 satisfy (4.16) — (4.18).

(ii) $(u,v) = F(a,d)$.

Furthermore, the first eigenvalue for T is positive for $(u,v) = F(a,d)$ with $(a,d) \in V[d_0, u_0]$.

REMARK: $B_{[d_0,a_0]} < \infty$ by Lemma 4.4.

PROOF: Condition (4.16) guarantees that there is no bifurcation from extinction to coexistence states in $V_{[d_0,a_0]}$ for (c_0, e_0). The existence of F now follows from Theorem 3.2, Theorem 4.3, and the Implicit Function Theorem. Suppose now there exist $(a^*, d^*) \in V_{[d_0,a_0]}$ and $(u,v) \in C_0^{2+\alpha}(\overline{\Omega})]^2$ such that $u(x) > 0$ on Ω, $v(x) > 0$ on Ω, (u,v) solves (4.19) and $(u,v) \neq F(a^*, d^*)$. Note that for any $(a,d) \in V_{[d_0,a_0]}$ and for any componentwise positive solution (u,v) to (4.19) at (a,d), $u \leq a_0$ and $v \leq a_0$. Theorem 4.3 and the Implicit Function Theorem may be employed to assert the existence of a C^1-function $g : (d^*, a^*) \to [C_0^{2+\alpha}(\overline{\Omega})]^2$ such that $g(d)$ is a componentwise positive solution to (4.19) at (a^*, d). $g(d^*) \neq F(a^*, d^*)$ by assumption. However, Theorem 3.2 implies that $g(d) = F(a^*, d)$ for $d \geq \tilde{d}$, where $d^* < \tilde{d} < a^*$, a contradiction to the Implicit Function Theorem, which establishes the equivalence of (i) and (ii). To see that the first eigenvalue for T is positive for $(u,v) = F(a,d)$ when $(a,d) \in V_{[d_0,a_0]}$, observe that since $0 < c < 1$ and $0 < e < 1$, Theorem 3.1 implies that the first eigenvalue for T is positive when $a = d$; also, it depends continuously on a, d, u, and v. Hence, since T is invertible for $(u,v) = F(a,d)$ the first eigenvalue can never pass through zero and hence must remain positive as (a,d) varies in $V_{[d_0,a_0]}$.

REMARK: By placing restrictions (conditions (4.17) and (4.18)) on the sizes of c and e, Theorem 4.5 enables us to guarantee the extension of the unique solution manifold for (1.2) from the diagonal $a = d$ in a quantifiable manner which separates conditions on c and e from those on a and d. Condition (4.16) is used only to guarantee that u and v remain positive and hence that $(-\Delta + 2u + cv - a)^{-1}$ and $(-\Delta + 2v + eu - d)^{-1}$ exist. With slightly more care in the statement of Theorem 4.5, this condition can be eliminated.

The last argument in the proof of Theorem 4.5 has the further implication that we can extend the unique solution manifold until the first eigenvalue for the linearized system becomes zero. The positivity of the first eigenvalue is intimately related to the stability of the solution; this relationship is described explicitly in Theorem 5.2 in the next section. Loss of positivity of the first eigenvalue of the linearization of an equation or system often coincides with loss of stability and with bifurcation, so we cannot generally expect uniqueness unless the first eigenvalue is positive.

We now conclude this section with an alternate approach to the invertibility of T of (2.3) in the general case. These results should be compared with those of [7, Section 4].

Suppose that λ is the first eigenvalue for

$$\begin{aligned} -\Delta\varphi + (2u + cv - a)\varphi + cu\psi &= \lambda\phi \\ -\Delta\psi + ev\varphi + (2v + eu - d)\psi &= \lambda\psi. \end{aligned} \tag{4.20}$$

Since the first eigenvalue of $-\Delta + (u + cv - a)$ is zero, and the same for $-\Delta + (v + eu - d)$, we have

$$\begin{aligned} &\int_\Omega (|\nabla\varphi|^2 + (u + cv - a)\varphi^2] \geq 0 \\ &\int_\Omega (|\nabla\psi|^2 + (v + eu - d)\psi^2] \geq 0. \end{aligned} \tag{4.21}$$

From (4.20),

$$\begin{aligned} \int_\Omega [|\nabla\varphi|^2 + (2u + cv - a)\varphi^2 + cu\varphi\psi] &= \lambda \int_\Omega \phi^2 \\ \int_\Omega [|\nabla\psi|^2 + ev\varphi\psi + (2v + eu - d)\psi^2] &= \lambda \int_\Omega \psi^2. \end{aligned} \tag{4.22}$$

Combining (4.21) and (4.22)

$$\int_\Omega [u\varphi^2 + cu\varphi\psi] \leq \lambda \int_\Omega \phi^2$$

and

$$\int_\Omega [ev\varphi\psi + v\psi^2] \leq \int_\Omega \lambda\psi^2.$$

Consequently,

$$\int_\Omega [u\varphi^2 + (cu + ev)\varphi\psi + v\psi^2] \leq \lambda \int_\Omega [\phi^2 + \psi^2]\,. \tag{4.23}$$

The quadratic form in (4.23) is positive definite on Ω (and hence $\lambda > 0$ and T is invertible) if

$$vu - \frac{1}{4}[cu + ev]^2 > 0. \tag{4.24}$$

Condition (4.24) can be established using bounds on ratios of θ_a and θ_d in regions where the appropriate bounds on u and v are available. Specifically, using (4.8) and (4.10) in (4.24) shows that if the inequality

$$\frac{4(1-c)(1-eK_0)}{1-ce} > (cK_0 + e)^2 \tag{4.25}$$

is satisfied then (4.24) must hold. Thus we have the following:

THEOREM 4.6. *Suppose that* (4.25) *holds. Then the first eigenvalue of T is positive and thus T is invertible.*

5. Stability. Given the existence and uniqueness of a coexistence state for (1.1) it is natural to inquire about the stability properties of that state. We assume that $k_1 = k_2 = 1$ and that (1.1) has been normalized to have the form

$$\begin{aligned} u_t - \Delta u &= u[a - u - cv] \\ v_t - \Delta v &= v[d - eu - v] \quad \text{on } \Omega \times (0,\infty) \\ u|_{\partial\Omega\times(0,\infty)} &= 0 = v|_{\partial\Omega\times(0,\infty)} \\ u|_{\overline{\Omega}\times\{0\}} = u_0(x), &\quad v|_{\overline{\Omega}\times\{0\}} = v_0(x). \end{aligned} \tag{5.1}$$

It follows from standard results in the theory of reaction-diffusion systems that (5.1) has a unique classical solution for any $u_0, v_0 \in C^\alpha(\overline{\Omega})$; see [7] and the references cited there. We shall need the following comparison result, which is a special case of the results of Section 1 of [7]:

LEMMA 5.1. *Suppose that u_1, v_1 and u_2, v_2 are C^2 in x and C^1 in t on $\Omega \times (0,\infty)$ and continuous on $\overline{\Omega} \times [0,\infty)$ and satisfy*

$$\begin{aligned} u_{1t} - \Delta u_1 - u_1[a - u_1 - bv_1] &\geq u_{2t} - \Delta u_2 - u_2[a - u_2 - bv_2] \\ v_{1t} - \Delta v_1 - v_1[d - eu_1 - v_1] &\leq v_{2t} - \Delta v_2 - v_2[d - eu_2 - v_2] \ \text{ in } \Omega, \end{aligned} \tag{5.2}$$

$$u_1 \geq u_2 \text{ and } v_1 \leq v_2 \text{ on } [\overline{\Omega} \times \{0\}] \cup [\partial\Omega \times (0,\infty)].$$

Then $u_1 \geq u_2$ *and* $v_1 \leq v_2$ *on* $\overline{\Omega} \times [0, \infty)$.

By applying Lemma 5.1 with appropriate comparison functions constructed from the coexistence state and the eigenfunctions for T we obtain the stability of our steady states with respect to C_0^1 perturbations. Our method is closely related to that used by Hess in [**11**].

THEOREM 5.2. *Suppose that the hypotheses of one of Theorems* 3.1, 4.5, *or* 4.6 *are satisfied, so that* (5.1) *admits a unique coexistence state and the first eigenvalue of* T *is positive. Let* (u^*, v^*) *denote the coexistence state and let* $\lambda > 0$ *denote the first eigenvalue for* T. *For any* $\epsilon \in (0, \lambda_1)$, *there exists a* $\delta > 0$ *such that if* (u, v) *is a solution to* (5.1) *with* $(u_0, v_0) \in [C_0^1(\overline{\Omega})]^2$ *with*

$$\|(u^*, v^*) - (u_0, v_0)\|_{[C_0^1(\overline{\Omega})]^2} < \delta \tag{5.3}$$

then

$$\|(u, v) - (u^*, v^*)\|_{[C(\overline{\Omega})]^2} \to 0$$

exponentially with order $-\epsilon$ *as* $t \to \infty$.

REMARK: Once we know that $(u, v) \to (u^*, v^*)$ in $[C(\overline{\Omega})]^2$ we can use parabolic regularity results to obtain convergence in stronger norms.

PROOF: Let $\begin{bmatrix} \phi \\ \psi \end{bmatrix}$ be an eigenvector for (2.4) normalized by

$$\max \left\{ \sup_{\overline{\Omega}} |\phi|, \sup_{\overline{\Omega}} |\psi| \right\} = 1.$$

Let

$$\begin{aligned} \overline{u} &= u^* + \gamma e^{-\epsilon t} \phi, & \underline{v} &= v^* + \gamma e^{-\epsilon t} \psi \\ \underline{u} &= u^* - \gamma e^{-\epsilon t} \phi, & \overline{v} &= v^* - \gamma e^{-\epsilon t} \psi. \end{aligned}$$

(Recall that we may choose $\phi > 0$, $\psi < 0$ in Ω, so that $\underline{u} < \overline{u}$ and $\underline{v} < \overline{v}$.)

We have in $\Omega \times (0, \infty]$

$$\begin{aligned}(5.4)\qquad &\overline{u}_t - \Delta\overline{u} - \overline{u}[a - \overline{u} - c\underline{v}] \\ &= -\epsilon\gamma e^{-\epsilon t}\phi - \Delta u^* - \gamma e^{-\epsilon t}\Delta\phi \\ &\quad - \left(u^* + \gamma e^{-\epsilon t}\phi\right)\left[a - u^* - \gamma e^{-\epsilon t}\phi - cv^* - \gamma e^{-\epsilon t}c\psi\right] \\ &= -\epsilon\gamma e^{-\epsilon t}\phi - [\Delta u^* + u^*(a - u^* - cv^*)] \\ &\quad + \gamma e^{-\epsilon t}\left[-\Delta\phi + (2u^* + cv^* - a)\phi + cu^*\psi\right] \\ &\quad + \gamma e^{-\epsilon t}\phi\left[\gamma e^{-\epsilon t}\phi + \gamma e^{-\gamma t}c\psi\right] \\ &= \gamma e^{-\epsilon t}\phi\left[-\epsilon + \lambda + ce^{-\epsilon t}\phi + \gamma e^{-\epsilon t}c\psi\right] \\ &\quad \geq \gamma e^{-\epsilon t}\phi\,[\lambda - \epsilon - c\gamma] \geq 0\end{aligned}$$

provided $\epsilon < \lambda$ and $\gamma \leq (\lambda - \epsilon)/c$. Similarly, we have in $\Omega \times (0, \infty]$

$$\begin{aligned}(5.5)\qquad \underline{v}_t - \Delta\underline{v} - \underline{v}[d - e\overline{u} - \underline{v}] &= \gamma e^{-\epsilon t}\psi\left[\lambda - \epsilon + \gamma e^{-\epsilon t}e\phi + \gamma e^{-\epsilon t}\psi\right] \\ &\leq \gamma e^{-\epsilon t}\psi[\lambda - \epsilon - \gamma] \leq 0\end{aligned}$$

provided $\epsilon < \lambda$ and $\gamma \leq \lambda - \epsilon$. Analogous computations show that if $\epsilon < \lambda$, $\gamma \leq \lambda - \epsilon$, and $\gamma \leq (\lambda - \epsilon)/e$, then

$$(5.6)\qquad \underline{u}_t - \Delta\underline{u} - \underline{u}[a - \underline{u} - c\overline{v}] \leq 0$$

and

$$(5.7)\qquad \overline{v}_t - \Delta\overline{v} - \overline{v}[d - e\underline{u} - \overline{v}] \geq 0.$$

By construction we have $\overline{u} = \underline{u} = \overline{v} = \underline{v} = 0$ on $\partial\Omega \times [0, \infty]$. By the hypotheses of Theorem 3.1, 4.5, or 4.6, $c < 1$ and $e < 1$, so we need only $\epsilon < \lambda$ and $\gamma \leq \lambda - \epsilon$. Suppose that u, v satisfy (5.1) with

$$(5.8)\qquad \begin{aligned} u^* - (\lambda - \epsilon)\phi &\leq u_0 \leq u^* + (\lambda - \epsilon)\phi \\ v^* + (\lambda - \epsilon)\psi &\leq v_0 \leq v^* - (\lambda - \epsilon)\psi. \end{aligned}$$

Then we have $\underline{u} \leq u \leq \overline{u}$, $\underline{v} \leq v \leq \overline{v}$ on $[\Omega \times \{0\}] \cup [\partial\Omega \times [0, \infty)]$ and by (5.4) — (5.7) and (5.1) we have in $\Omega \times (0, \infty)$

$$\begin{aligned}\overline{u}_t - \Delta\overline{u} - \overline{u}[a - \overline{u} - c\underline{v}] &\geq u_t - \Delta u - u[a - u - cv] \\ \underline{v}_t - \Delta\underline{v} - \underline{v}[d - e\overline{u} - \underline{v}] &\leq v_t - \Delta v - v[d - eu - v]\end{aligned}$$

and

$$\begin{aligned}\underline{u}_t - \Delta\underline{u} - \underline{u}[a - \underline{u} - c\overline{v}] &\leq u_t - \Delta u - u[a - u - cv]\\ \overline{v}_t - \Delta\overline{v} - \overline{v}[d - e\underline{u} - \overline{v}] &\geq v_t - \Delta v - v[d - eu - v].\end{aligned}$$

Thus, by Lemma 5.1, we have $\underline{u} \leq u \leq \overline{u}$ and $\underline{v} \leq v \leq \overline{v}$ in $\Omega \times [0, \infty)$. Hence $(u, v) \to (u^*, v^*)$ exponentially as $t \to \infty$ provided (5.8) holds. The inequalities (5.8) give an estimate on the size of the region of attraction of (u^*, v^*). It follows from arguments based on the strong maximum principle that $\phi > 0$ in Ω and $\partial\phi/\partial n < 0$ on $\partial\Omega$, with $\psi < 0$ in Ω and $\partial\psi/\partial n > 0$ on $\partial\Omega$; thus, if

$$\|(u^*, v^*) - (u_0, v_0)\|_{[C_0^1(\overline{\Omega})]^2}$$

is sufficiently small, we have (5.8).

(For a detailed discussion of such arguments, see for example [7].) This completes the proof of Theorem 5.2.

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