

ON COMPETITION-MEDIATED COEXISTENCE*

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Abstract. Two competing species, denoted B and C , currently inhabit a common habitat patch. Left alone, B can be expected to exclude C from the patch over time. An exotic species A is introduced into the patch. A competes with both B and C . Absent B , A can also be expected to exclude C from the patch over time, whereas absent C , A and B can be expected to coexist. Whether or not the introduction of A into the habitat patch makes for the long-term coexistence of all three species is examined in this article via reaction-diffusion models. It is shown that such an outcome depends on the precise qualitative nature of the pairwise competitive interactions. In particular, long-term coexistence of all three species cannot be expected in the case of Lotka–Volterra models but can be expected for suitable modifications of such models.

Key words. theoretical ecology, persistence of ecological communities, permanence, competition mediated coexistence, reaction-diffusion models

AMS subject classifications. 92D40, 92D25, 35K57, 58F12

PII. S0036139995292367

1. Introduction. In this article, we are concerned with an important topic in theoretical ecology. Namely, does the introduction of an exotic species into an existing community of species serve to enhance the long-term persistence of the community? Here we address the question for the case in which the existing community consists of two species and in which each of the three species competes with remaining two. Our approach is through the analysis of models based on differential equations, chiefly reaction-diffusion systems on a bounded habitat patch subject to absorbing (i.e., homogeneous Dirichlet) boundary data.

To be more specific, let us denote the exotic species as A and the resident species as B and C . Then we shall assume that A and B coexist long-term in the absence of C , that A drives C to extinction in the long term in the absence of B , and that B drives C to extinction in the long term in the absence of A . Moreover, we assume that these long-term outcomes are independent of initial populations or initial population densities, so long as both initial populations are positive or both initial population densities are nonzero. In particular, absent the introduction of A , the existing community of B and C collapses to the single species B in the long term.

In order to speak of long-term persistence of a species or long-term coexistence of the members of a community of species, we need a quantitative definition of these terms. Since we are dealing exclusively with competitive systems, we assume that each species exhibits a self-regulatory mechanism, meaning that its growth rate becomes negative if its population or population density exceeds a threshold value, usually called its carrying capacity. Consequently, the population or population density of each species is bounded above long term by a value which is independent of its initial

*Received by the editors September 25, 1995; accepted for publication (in revised form) May 17, 1996.

<http://www.siam.org/journals/siap/57-5/29236.html>

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the set of initial data. It is clear that if this second requirement fails, permanence is not possible. The first requirement is usually expressed as the acyclicity of π_σ , and the corresponding sufficient conditions for permanence as the acyclicity theorem. If π_σ is acyclic, Hale and Waltman [12] show that π is permanent if and only if the second requirement obtains. If π_σ fails to be acyclic, π can fail to be permanent even if the second requirement holds. (See, for example, [16].) The article [10] contains an accounting of the possibilities for $\{M_1, \dots, M_k\}$ in the case of three-species competition models employing ordinary differential equations. The ω -limit set for π_σ in the situation under consideration in this article in the ordinary differential equations setting can be expressed as $\{(0, 0, 0), (\bar{a}, 0, 0), (0, \bar{b}, 0), (0, 0, \bar{c}), M_5\}$, where \bar{a} , \bar{b} , and \bar{c} are the carrying capacities for A , B , and C absent competition and M_5 denotes the ω -limit set for the competition for A and B absent C . It is known that there exist equilibria $(a_1, b_1, 0)$ and $(a_2, b_2, 0)$ for π with $0 < a_1 < a_2$ and $0 < b_2 < b_1$ so that if $(a, b, 0) \in M_5$, then $a_1 \leq a \leq a_2$ and $b_2 \leq b \leq b_1$. (This property is called *compressivity*. The terminology is due to Hess and Lazer, who established compressivity in the more general context of periodic-parabolic two-species competition systems. See, for example, [14] and [15].) As follows in [10], π_σ is acyclic in this situation and permanence boils down to the second aforementioned requirement. (In the reaction-diffusion setting, a precise analogue holds. We detail these results with references in our next section.)

It is evident from the postulated outcomes of the pairwise interactions among A , B , and C that $\{(0, 0, 0), (\bar{a}, 0, 0), (0, \bar{b}, 0), (0, 0, \bar{c}), M_5\}$ is the appropriate decomposition of the ω -limit set of π_σ for any suitable semiflow π . However, verifying conditions (i) and (ii) plus isolatedness, so that the acyclicity theorem can be used to assert permanence, leads directly to conditions on the coefficients of the model equations. Consequently, it is instructive to examine a specific set of model equations at this time. To this end, let us consider the Lotka-Volterra system

$$(1.1) \quad \begin{aligned} u'_1 &= [a - u_1 - \alpha_{12}u_2 - \alpha_{13}u_3]u_1, \\ u'_2 &= [a - \alpha_{21}u_1 - u_2 - \alpha_{23}u_3]u_2, \\ u'_3 &= [a - \alpha_{31}u_1 - \alpha_{32}u_2 - u_3]u_3, \end{aligned}$$

where u_1 denotes the population of species A at time t , u_2 denotes species B , u_3 denotes species C , and the coefficients are all positive constants. Since $a > 0$, each equation in the system is linearly unstable at $(0, 0, 0)$. Hence $(0, 0, 0)$ is a strong repeller (i.e., $W^s((0, 0, 0)) = \{(0, 0, 0)\}$) so that it is isolated and satisfies condition (ii). Moreover, if $u_i^0 > 0$ and u_i solves

$$\begin{aligned} u'_i &= (a - u_i)u_i, \quad t > 0, \\ u_i(0) &= u_i^0, \end{aligned}$$

then $u_i \rightarrow a$ as $t \rightarrow \infty$. Consequently, the restriction of the model to any one of the "edges" $(u_1, 0, 0)$, $(0, u_2, 0)$, $(0, 0, u_3)$ is globally attractive to an equilibrium. Think now of linearizing the first equation about $(0, a, 0)$ and $(0, 0, a)$. We require A to coexist with B and to drive C to extinction, and so we must have $a - \alpha_{12}a > 0$ and $a - \alpha_{13}a > 0$, or equivalently $\alpha_{12} < 1$ and $\alpha_{13} < 1$. Similar considerations show that we must require $\alpha_{21} < 1$ and $\alpha_{23} < 1$ in the second equation and $\alpha_{31} > 1$ and $\alpha_{32} > 1$ in the third. Consequently, there is at least one direction of growth at $\{(a, 0, 0)\}$, $\{(0, a, 0)\}$, and $\{(0, 0, a)\}$. So $\{(a, 0, 0)\}$, $\{(0, a, 0)\}$, and $\{(0, 0, a)\}$ are isolated hyperbolic equilibria and satisfy condition (ii). Moreover,

population or initial population density. (Of course, how long it takes for the upper bound to go into effect *does* depend upon initial conditions.) For such systems, we take long-term persistence or long-term coexistence to mean the existence of corresponding positive asymptotic lower bounds. In the ordinary differential equations setting, this requires that the population of each species under consideration exceed some fixed positive value after some elapsed time and remain above this fixed value thereafter. (The length of the elapsed time depends on the initial state of the system.) In the reaction-diffusion setting, since we impose an absorbing condition on the boundary of the habitat patch, it is not possible for the population densities in question to exceed a positive value on the entire patch. Consequently, we understand the positive asymptotic lower bound in this case to be a fixed smooth function, positive on the interior of the habitat patch and vanishing on its boundary, with its outward normal derivative negative at each point of the boundary of the habitat patch. When such positive asymptotic lower bounds exist, we say that the system in question is *uniformly persistent* or *permanent*. Uniform persistence or permanence is the definition of long-term persistence or coexistence that we shall employ throughout this article.

General three-species competition models have been studied in both the ordinary differential equation and reaction-diffusion settings, and there is now a good understanding of when such systems are permanent. (See, for example, [10] and references therein in the ordinary differential equations case and [8] and references therein in the reaction-diffusion case.) The approach here is to view the solution trajectories (which necessarily exist for all time by the self-regulatory assumptions) as forming a semidynamical system π on the space of initial data ($\mathbb{R}_+^3 = [0, \infty) \times [0, \infty) \times [0, \infty)$ in the ordinary differential equations case; $[C_0^1(\bar{\Omega})_+]^3$ in the reaction-diffusion setting, where Ω is the habitat patch and $C_0^1(\bar{\Omega})_+$ is the cone of nonnegative smooth functions on $\bar{\Omega}$ which vanish on the boundary of Ω). The aforementioned asymptotic upper bounds on the components of such a system guarantee that π is what is known as *point dissipative*, and the theory of differential equations guarantees that, for any fixed positive value of t , π is a compact map on the space of initial data. (See, for example, [13].) Dynamical systems theory [4] then guarantees that π admits a global attractor, i.e., a compact, invariant set \mathcal{A} for π to which any trajectory becomes and stays arbitrarily close after some elapsed time (dependent upon initial data). Permanence or uniform persistence as we have defined it follows if (i) the intersection of \mathcal{A} with the interior of the space of initial data, say \mathcal{A}' , is uniformly bounded away from the boundary of the space of initial data (essentially the so-called extinction states where at least one of the populations or population densities vanishes); and (ii) any trajectory with initial data in the interior of the space of initial data approaches \mathcal{A}' as time tends to infinity. (See, for example, [5] and [7].) Pioneering work by Freedman and Waltman [10], [11] and Hale and Waltman [12] shows that these criteria are met if the omega limit set of the boundary of the set of initial data (which is invariant under π) can be written as a finite union $\cup_{n=1}^k M_n$ of compact invariant sets (isolated for π and for the restriction π_σ of π to the boundary of the set of initial data) meeting two requirements. The first requirement (i) is that when considered as compact invariant sets for the semiflow π_σ , there is no subcollection $\{M_{i_1}, \dots, M_{i_r}\}$ of $\{M_1, \dots, M_k\}$ so that the intersection of the unstable manifold of $M_{i_j}(W^u(M_{i_j}))$ with the stable manifold of $M_{i_{j+1}}(W^s(M_{i_{j+1}}))$ is nonempty for $i = 1, \dots, r$, where $M_{i_{r+1}} = M_{i_1}$. This requirement says that there is no way to chain this collection of sets together via orbits for π_σ . The second (ii) is that the stable manifold for M_n , $n = 1, \dots, k$, when viewed as a compact invariant set for π , contains no element of the interior of

the set of initial data. It is clear that if this second requirement fails, permanence is not possible. The first requirement is usually expressed as the acyclicity of π_σ , and the corresponding sufficient conditions for permanence as the acyclicity theorem. If π_σ is acyclic, Hale and Waltman [12] show that π is permanent if and only if the second requirement obtains. If π_σ fails to be acyclic, π can fail to be permanent even if the second requirement holds. (See, for example, [16].) The article [10] contains an accounting of the possibilities for $\{M_1, \dots, M_k\}$ in the case of three-species competition models employing ordinary differential equations. The ω -limit set for π_σ in the situation under consideration in this article in the ordinary differential equations setting can be expressed as $\{(0, 0, 0), (\bar{a}, 0, 0), (0, \bar{b}, 0), (0, 0, \bar{c}), M_5\}$, where \bar{a} , \bar{b} , and \bar{c} are the carrying capacities for A , B , and C absent competition and M_5 denotes the ω -limit set for the competition for A and B absent C . It is known that there exist equilibria $(a_1, b_1, 0)$ and $(a_2, b_2, 0)$ for π with $0 < a_1 < a_2$ and $0 < b_2 < b_1$ so that if $(a, b, 0) \in M_5$, then $a_1 \leq a \leq a_2$ and $b_2 \leq b \leq b_1$. (This property is called *compressivity*. The terminology is due to Hess and Lazer, who established compressivity in the more general context of periodic-parabolic two-species competition systems. See, for example, [14] and [15].) As follows in [10], π_σ is acyclic in this situation and permanence boils down to the second aforementioned requirement. (In the reaction-diffusion setting, a precise analogue holds. We detail these results with references in our next section.)

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where u_1 denotes the population of species A at time t , u_2 denotes species B , u_3 denotes species C , and the coefficients are all positive constants. Since $a > 0$, each equation in the system is linearly unstable at $(0, 0, 0)$. Hence $(0, 0, 0)$ is a strong repeller (i.e., $W^s((0, 0, 0)) = \{(0, 0, 0)\}$) so that it is isolated and satisfies condition (ii). Moreover, if $u_i^0 > 0$ and u_i solves

$$\begin{aligned} u_i' &= (a - u_i)u_i, \quad t > 0, \\ u_i(0) &= u_i^0, \end{aligned}$$

then $u_i \rightarrow a$ as $t \rightarrow \infty$. Consequently, the restriction of the model to any one of the "edges" $(u_1, 0, 0)$, $(0, u_2, 0)$, $(0, 0, u_3)$ is globally attractive to an equilibrium. Think now of linearizing the first equation about $(0, a, 0)$ and $(0, 0, a)$. We require A to coexist with B and to drive C to extinction, and so we must have $a - \alpha_{12}a > 0$ and $a - \alpha_{13}a > 0$, or equivalently $\alpha_{12} < 1$ and $\alpha_{13} < 1$. Similar considerations show that we must require $\alpha_{21} < 1$ and $\alpha_{23} < 1$ in the second equation and $\alpha_{31} > 1$ and $\alpha_{32} > 1$ in the third. Consequently, there is at least one direction of growth at $\{(a, 0, 0)\}$, $\{(0, a, 0)\}$, and $\{(0, 0, a)\}$. So $\{(a, 0, 0)\}$, $\{(0, a, 0)\}$, and $\{(0, 0, a)\}$ are isolated hyperbolic equilibria and satisfy condition (ii). Moreover,

$\{(0, 0, 0), (a, 0, 0), (0, a, 0), (0, 0, a), M_5\}$ is acyclic (condition (i)). Letting $u_3 = 0$ in (1.1), it is easy to see that

$$(u_1, u_2) = \left(\frac{a(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}}, \frac{a(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} \right)$$

is the only equilibrium to

$$(1.2) \quad \begin{aligned} u_1' &= [a - u_1 - \alpha_{12}u_2]u_1, \\ u_2' &= [a - \alpha_{21}u_1 - u_2]u_2 \end{aligned}$$

with both components positive, and it is not hard to show that

$$M_5 = \left\{ \left(\frac{a(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}}, \frac{a(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} \right) \right\}.$$

Therefore, permanence obtains for (1.1), provided that the third equation is linearly unstable at

$$\left(\frac{a(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}}, \frac{a(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}}, 0 \right).$$

For such to obtain, we need

$$a - \alpha_{31} \frac{(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}} a - \alpha_{32} \frac{(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} a > 0,$$

or equivalently

$$\frac{\alpha_{31}(1 - \alpha_{12}) + \alpha_{32}(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} < 1.$$

But

$$\frac{\alpha_{31}(1 - \alpha_{12}) + \alpha_{32}(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} > \frac{1 - \alpha_{12} + (1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} = \frac{2 - \alpha_{12} - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}.$$

Since $\alpha_{12} < 1$ and $\alpha_{21} < 1$, $\alpha_{12}(1 - \alpha_{21}) + \alpha_{21} < 1$, which implies $-\alpha_{12}\alpha_{21} < 1 - \alpha_{12} - \alpha_{21}$ or $1 - \alpha_{12}\alpha_{21} < 2 - \alpha_{12} - \alpha_{21}$. Hence

$$\frac{2 - \alpha_{12} - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} > 1$$

and so

$$a - \frac{\alpha_{31}(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}} a - \frac{\alpha_{32}(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} a < 0,$$

and (1.1) fails to be permanent.

The problem with (1.1) is that the combined populations of A and B at their coexistence equilibrium exceed the carrying capacity of either A or B , a common feature of stable Lotka-Volterra models. (See [3, p. 354].) So the effect of the competition between A and B is not strong enough to provide a "slot" for C . Geometrically, the coexistence state

$$\left(\frac{a(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}}, \frac{a(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} \right)$$

lies above the line segment joining the extinction states $(a, 0)$ and $(0, a)$. There have been numerous investigations of the relative positions of coexistence states and extinction states in the biological literature. These are intimately connected with efforts to distinguish various forms of competition, such as interference and exploitation, and with efforts to address various drawbacks in Lotka-Volterra interactions. (See, for example, [1], [3], [17], [18], [20].) In [3], Ayala, Gilpin, and Ehrenfeld fitted a number of phenomenologically derived alternatives to Lotka-Volterra interactions to data from two competing species of *Drosophila*, finding several that match the data much better. One such would add $-\beta_1 u_1 u_2$ to the per capita growth law in the first equation of (1.1) and $-\beta_2 u_1 u_2$ in the second, yielding the system

$$(1.3) \quad \begin{aligned} u_1' &= [a - u_1 - \alpha_{12}u_2 - \beta_1 u_1 u_2 - \alpha_{13}u_3]u_1, \\ u_2' &= [a - \alpha_{21}u_1 - \beta_2 u_1 u_2 - u_2 - \alpha_{23}u_3]u_2, \\ u_3' &= [a - \alpha_{31}u_1 - \alpha_{32}u_2 - u_3]u_3. \end{aligned}$$

Let us consider (1.3) with $\beta_1 = \beta_2 = \beta > 0$. The analysis regarding $\{(0, 0, 0), (a, 0, 0), (0, a, 0), (0, 0, a)\}$ is the same as for (1.1). In particular, A and B coexist, provided that $\alpha_{12} < 1$ and $\alpha_{21} < 1$, independent of β . This phenomenon reflects the fact that $\alpha_{12}u_2$ and $\alpha_{12}u_2 + \beta u_1 u_2$ are very nearly equal for u_1 small for u_2 in bounded ranges of positive values, in particular for u_2 near a . However, β has a definite effect on the location of M_5 , for if (u_1, u_2) is a componentwise positive equilibrium for the subsystem of (1.3) which results from setting $u_3 = 0$, $a - u_1 - \alpha_{12}u_2 = \beta u_1 u_2 = a - \alpha_{21}u_1 - u_2$, which implies that $u_2 = \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}}\right)u_1$. It follows that $M_5 = \{(\bar{u}_1(\beta), \bar{u}_2(\beta))\} =$

$$\left\{ \left(\frac{- (1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a\beta(1 - \alpha_{21})(1 - \alpha_{12})}}{2\beta(1 - \alpha_{21})}, \right. \right. \\ \left. \left. \frac{- (1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a\beta(1 - \alpha_{21})(1 - \alpha_{12})}}{2\beta(1 - \alpha_{12})} \right) \right\}.$$

Asymptotically, both components are proportional to $\frac{1}{\sqrt{\beta}}$, and an easy calculation shows that

$$\lim_{\beta \rightarrow 0^+} \{(\bar{u}_1(\beta), \bar{u}_2(\beta))\} = \left\{ \left(\frac{a(1 - \alpha_{12})}{1 - \alpha_{12}\alpha_{21}}, \frac{a(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}} \right) \right\}.$$

So if $a, \alpha_{12}, \alpha_{21}, \alpha_{31}$, and α_{32} are fixed, $a - \alpha_{31}\bar{u}_1(\beta) - \alpha_{32}\bar{u}_2(\beta) > 0$ for β sufficiently large. For such values, (1.3) is permanent and the introduction of species A serves to preserve the preexisting community, whereas it does not for (1.1).

The preceding might suggest to the reader that the failure of (1.1) to be permanent is connected somehow with the assumption that all three species have the same intrinsic growth rate a . However, such is not the case. Indeed, any Lotka-Volterra model capturing our basic assumptions about the outcomes of the pairwise species interactions for A, B , and C will fail to be permanent. (We leave the modification of the proof to the interested reader.) Consequently, this form of competition-mediated coexistence contrasts with that in the so-called cyclic case (A drives B to extinction absent C , B drives C to extinction absent A , C drives A to extinction absent B , independent of (nontrivial) initial data), where permanence is sometimes possible for Lotka-Volterra dynamics. (See, for example, [19].) Indeed, for appropriate choices of

parameters, permanence results obtain in the cyclic case with Lotka–Volterra dynamics in the reaction-diffusion setting with absorbing boundary conditions [8]. The same can also be said of the companion phenomenon of predator-mediated coexistence. (See [8], [11], for example.)

The body of this article is concerned with establishing competition-mediated coexistence for the situation we have described in the setting of reaction-diffusion models over bounded habitat patches subject to absorbing boundary data. To this end, we show first by the acyclicity theorem that permanence fails to obtain for Lotka–Volterra models over a range of parameter values. Then by modifying the competitive interaction between A and B by adding the term $-\beta_1 u_1^2 u_2$ to the equation for A and the term $-\beta_2 u_1 u_2^2$ to the equation for B , we obtain competition-mediated coexistence, again using the acyclicity theorem. The reaction-diffusion case is considerably more difficult mathematically than is the ordinary differential equations case, since direct calculation is much less useful than in the analysis of (1.1) or (1.3). Consequently, we will need more conditions on the parameters of the system than was the case before. However, we still obtain competition-mediated coexistence for a range of parameter values, so the results are fairly robust. In the ordinary differential equations case (1.3), conditions for permanence were expressed in terms of the instability of the zero solution for certain linearized equations associated with the original system, the instability itself expressed in terms of the positivity of certain combinations of the system parameters. These combinations may be regarded as eigenvalues for the one-dimensional linear operators given by the right-hand side of the linearized equations. (For example, if one has the equation $u' = \alpha u$, α is the eigenvalue of the linear operator $u \rightarrow \alpha u$.) In the reaction-diffusion setting, we express conditions for the instability of the zero solution of the relevant equations in this way, as the right-hand sides are now given by linear elliptic operators. In either case, the instability conditions should be interpreted as an expression of invasibility.

The rest of this article is structured as follows. In section 2, we show that the failure of (1.1) to be permanent extends to the reaction-diffusion setting for appropriate ranges of parameter values. We also obtain some crucial upper bounds on the components of component-positive equilibria to the diffusive analogues of the subsystems of (1.3) which arise by letting C vanish. We use these estimates in section 3 to establish permanence (i.e., competition-mediated coexistence) in the reaction-diffusion setting for a range of parameter values. Finally, we offer some conclusions in section 4.

2. Mathematical background. Consider

$$(2.1) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= \Delta u_1 + u_1[a - u_1 - (\alpha_{12}u_2 + \beta_1 u_1 u_2) - \alpha_{13}u_3], \\ \frac{\partial u_2}{\partial t} &= \Delta u_2 + u_2[a - (\alpha_{21}u_1 + \beta_2 u_1 u_2) - u_2 - \alpha_{23}u_3], \\ \frac{\partial u_3}{\partial t} &= \Delta u_3 + u_3[a' - \alpha_{31}u_1 - \alpha_{32}u_2 - u_3] \end{aligned}$$

in $\Omega \times (0, \infty)$ subject to

$$u_1 = 0 = u_2 = u_3 \quad \text{on } \partial\Omega \times (0, \infty).$$

Assume

(i) $a \geq a' > \lambda_1$, where $\lambda = \lambda_1 > 0$ is the unique real number so that the eigenvalue problem

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

admits a solution $\phi > 0$ on Ω .

(ii) $\alpha_{12}, \alpha_{13}, \alpha_{21}, \alpha_{23} \in (0, 1)$.

(iii) $\alpha_{31} > 1, \alpha_{32} > 1$.

(iv) $\beta_1 \geq 0, \beta_2 \geq 0$.

Our first observation is that condition (i) guarantees the long-term survival of any one of the three species in the absence of the other two. Indeed, it is well known [9] that $a > \lambda_1$ implies the existence of unique $\theta_a > 0$ so that

$$(2.2) \quad \begin{aligned} -\Delta\theta_a &= \theta_a[a - \theta_a] & \text{in } \Omega, \\ \theta_a &= 0 & \text{on } \partial\Omega \end{aligned}$$

and so that for any nonnegative nontrivial continuous initial data $u_0(x)$ on $\bar{\Omega}$, the solution $u(x, t)$ of

$$(2.3) \quad \begin{aligned} \frac{\partial u}{\partial t} &= \Delta u + u[a - u] & \text{in } \Omega \times (0, \infty), \\ u &= 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) &= u_0(x) & \text{on } \Omega \end{aligned}$$

has the property that $u(x, t)$ converges to $\theta_a(x)$ as $t \rightarrow \infty$, uniformly for $x \in \bar{\Omega}$. Additionally, if $\lambda_1 < a_1 < a_2$, it follows from direct inspection of (2.2) that θ_{a_1} is a strict subsolution for (2.2) with $a = a_2$ and hence that $\theta_{a_1}(x) < \theta_{a_2}(x)$ for $x \in \Omega$. Observe now that condition (i) is equivalent to the positivity of σ and σ' , where σ and σ' are the unique values so that

$$(2.4) \quad \begin{aligned} \Delta\phi + a\phi &= \sigma\phi & \text{in } \Omega, \\ \phi &= 0 & \text{on } \partial\Omega \end{aligned}$$

and

$$(2.5) \quad \begin{aligned} \Delta\psi + a'\psi &= \sigma'\psi & \text{in } \Omega, \\ \psi &= 0 & \text{on } \partial\Omega \end{aligned}$$

admit solutions $\phi > 0$ and $\psi > 0$ in Ω . Having $\sigma > 0$ may be interpreted as saying that a species with density u_1 can invade Ω in the absence of the species with densities u_2 and u_3 and that a species with density u_2 can invade Ω if $u_1 \equiv 0$ and $u_3 \equiv 0$. Likewise, having $\sigma' > 0$ may be interpreted as saying that a species with density u_3 can invade Ω , provided that $u_1 \equiv 0$ and $u_2 \equiv 0$. Consequently, the invasibility conditions given by $\sigma > 0$ and $\sigma' > 0$ in (2.4) and (2.5), respectively, imply that $\{(\theta_a, 0, 0), (0, \theta_a, 0), (0, 0, \theta_{a'})\}$ represent the global attractors for (2.1) restricted to the “edges” $\{(u_1, 0, 0), (0, u_2, 0), (0, 0, u_3)\}$, respectively.

Now consider the subsystems of (2.1) which result when either u_2 or u_1 is absent, namely,

$$(2.6) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= \Delta u_1 + u_1[a - u_1 - \alpha_{13}u_3], \\ \frac{\partial u_3}{\partial t} &= \Delta u_3 + u_3[a' - \alpha_{31}u_1 - u_3] && \text{in } \Omega \times (0, \infty), \\ u_1 = 0 = u_3 &&& \text{on } \partial\Omega \times (0, \infty); \end{aligned}$$

$$(2.7) \quad \begin{aligned} \frac{\partial u_2}{\partial t} &= \Delta u_2 + u_2[a - u_2 - \alpha_{23}u_3], \\ \frac{\partial u_3}{\partial t} &= \Delta u_3 + u_3[a' - \alpha_{32}u_2 - u_3] && \text{in } \Omega \times (0, \infty), \\ u_2 = 0 = u_3 &&& \text{on } \partial\Omega \times (0, \infty). \end{aligned}$$

Since $a' \leq a$ and $\alpha_{13} < 1 < \alpha_{31}$, Theorem 2.1 of [6] implies that there is no equilibrium solution to (2.6) with $u_1 > 0$ and $u_3 > 0$. Since $\alpha_{13} < 1$, the value of σ_{13} so that

$$(2.8) \quad \begin{aligned} \Delta\phi + (a - \alpha_{13}\theta_{a'})\phi &= \sigma_{13}\phi && \text{in } \Omega, \\ \phi &= 0 && \text{on } \partial\Omega, \\ \phi &> 0 && \text{in } \Omega \end{aligned}$$

admits a solution is positive. (To see that such is the case, note that $a - \alpha_{13}\theta_{a'} > a - \theta_a$ and that, for $\rho = 0$,

$$\begin{aligned} \Delta\psi + (a - \theta_a)\psi &= \rho\psi && \text{in } \Omega, \\ \psi &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits the solution $\psi = \theta_a$. Hence $\sigma_{13} > 0$ by a standard comparison argument.) Therefore, Lemma 3.3 of [8] asserts that any solution to (2.6) with $u_1(x, 0) > 0$ and $u_3 \geq 0$ converges to $(\theta_a, 0)$ as $t \rightarrow \infty$, uniformly for $x \in \bar{\Omega}$. Since $\alpha_{23} < 1 < \alpha_{32}$, a completely analogous result obtains for (2.7).

Now consider the subsystem of (2.1) resulting from the absence of the species with density u_3 :

$$(2.9) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= \Delta u_1 + u_1[a - u_1 - (\alpha_{12}u_2 + \beta_1u_1u_2)], \\ \frac{\partial u_2}{\partial t} &= \Delta u_2 + u_2[a - (\alpha_{21}u_1 + \beta_2u_1u_2) - u_2] && \text{in } \Omega \times (0, \infty), \\ u_1 = 0 = u_2 &&& \text{on } \partial\Omega \times (0, \infty). \end{aligned}$$

Since α_{12} and α_{21} both lie in the interval $(0, 1)$, the value of σ_{ij} , $i = 1, 2$, $j \neq i$, is positive when

$$(2.10) \quad \begin{aligned} \Delta\psi_i + [a - \alpha_{ij}\theta_a]\psi_i &= \sigma_{ij}\psi_i && \text{in } \Omega, \\ \psi_i &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits a positive solution ψ_i . Consequently, Theorem 5.3 of [7] guarantees that (2.9) is permanent. However, saying that (2.9) is permanent is not the strongest general statement that we can make regarding the system. Indeed, it follows from Theorem 33.3 of [14] that there are equilibrium solutions $(\underline{u}_1, \underline{u}_2)$ and (\bar{u}_1, \bar{u}_2) of (2.9) with $\underline{u}_1 \leq \bar{u}_1$ and $\underline{u}_2 \geq \bar{u}_2$ so that if (u_1, u_2) lies on the global attractor for (2.9), then $\underline{u}_1 \leq u_1 \leq \bar{u}_1$ and $\bar{u}_2 \leq u_2 \leq \underline{u}_2$. If $\beta_1 = \beta_2 = 0$, Theorem 3.2 of [9] implies that $\underline{u}_1 \equiv \bar{u}_1$ and $\underline{u}_2 \equiv \bar{u}_2$. (Indeed, we shall see that such remains the case when β_1 and β_2 are positive, provided that $\beta_1 = \beta_2$.)

Let us concentrate for the moment on the case $\beta_1 = \beta_2 = 0$. Theorem 3.2 of [9] in fact tells us that

$$\underline{u}_1 \equiv \bar{u}_1 \equiv \frac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}\theta_a, \quad \underline{u}_2 \equiv \bar{u}_2 \equiv \frac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}\theta_a.$$

Now, since $\alpha_{31} > 1$ and $\alpha_{32} > 1$,

$$\alpha_{31} \left(\frac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}} \right) + \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right) > \frac{2 - \alpha_{12} - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}.$$

This last exceeds 1 since $\alpha_{12}(1 - \alpha_{21}) + \alpha_{21} < 1$. Consequently,

$$\alpha_{31} \left(\frac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}} \right) \theta_a + \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right) \theta_a \geq \left(\frac{2 - \alpha_{12} - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right) \theta_a$$

and $\sigma_3 < 0$ when

$$\begin{aligned} \Delta\psi + \left[a' - \alpha_{31} \left(\frac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}} \right) \theta_a - \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right) \theta_a \right] \psi &= \sigma_3\psi && \text{in } \Omega, \\ \psi &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits a positive solution. Consequently, the species with density u_3 cannot be successfully introduced in small numbers when the u_1 and u_2 densities are close to their coexistence states, and as previously noted (2.1) fails to be permanent.

Let us now examine (2.9) in the case $\beta_1, \beta_2 > 0$, beginning with the special case $\beta_1 = \beta_2 = \beta$. Let us look for an equilibrium solution with $u_2 = cu_1$, where, of course, $c > 0$. This requires

$$\begin{aligned} -\Delta u_1 &= u_1[a - u_1 - \alpha_{12}cu_1 - \beta cu_1^2], \\ -\Delta(cu_1) &= cu_1[a - cu_1 - \alpha_{21}u_1 - \beta cu_1^2] && \text{in } \Omega. \end{aligned}$$

Consequently, there exists such a solution provided that $1 + \alpha_{12}c = c + \alpha_{21}$, or equivalently $c = \frac{1 - \alpha_{21}}{1 - \alpha_{12}}$, and

$$(2.11) \quad \begin{aligned} -\Delta u_1 &= u_1 \left[a - \left(\frac{1 - \alpha_{12}\alpha_{21}}{1 - \alpha_{12}} \right) u_1 - \beta \frac{(1 - \alpha_{21})}{(1 - \alpha_{12})} u_1^2 \right] && \text{in } \Omega, \\ u_1 &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits a positive solution. As was the case with (2.2), (2.11) admits a positive solution u^* , provided that $a > \lambda_1$ or equivalently σ in (2.4) is positive.

Suppose now that (u_1, u_2) is a componentwise positive equilibrium solution of (2.9), again under the assumption that $\beta_1 = \beta_2 = \beta$. Observe that

$$\begin{aligned}
 & -\Delta \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 &= u_2 [a - \alpha_{21} u_1 - u_2 - \beta u_1 u_2] - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 [a - u_1 - \alpha_{12} u_2 - \beta u_1 u_2] \\
 &= (a - \beta u_1 u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 & \quad - \left[u_2^2 + \left(\alpha_{21} - \alpha_{12} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) \right) u_1 u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1^2 \right] \\
 &= (a - \beta u_1 u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 & \quad - \left[u_2^2 + \left(\frac{\alpha_{21} - \alpha_{12}}{1 - \alpha_{12}} \right) u_1 u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1^2 \right] \\
 &= (a - \beta u_1 u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 & \quad - \left[u_2^2 + \left(\frac{1 - \alpha_{12} - (1 - \alpha_{21})}{1 - \alpha_{12}} \right) u_1 u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1^2 \right] \\
 &= (a - \beta u_1 u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 & \quad - \left[u_2^2 + u_1 u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1^2 \right] \\
 &= (a - \beta u_1 u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \\
 & \quad - \left[(u_2 + u_1) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) \right] \\
 &= (a - \beta_1 u_1 u_2 - u_1 - u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right).
 \end{aligned}$$

Hence

$$(-\Delta + \beta u_1 u_2 + u_1 + u_2) \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right) = a \left(u_2 - \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1 \right),$$

so that either $u_2 \equiv \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1$ or a is an eigenvalue for the operator $-\Delta + \beta u_1 u_2 + u_1 + u_2$. So now suppose that γ is such that

$$\begin{aligned}
 (-\Delta + \beta u_1 u_2 + u_1 + u_2)w &= \gamma w & \text{in } \Omega, \\
 w &= 0 & \text{on } \partial\Omega
 \end{aligned}$$

admits a solution with $w > 0$. Multiplying the equation by u_1 and integrating we find

$$\int_{\Omega} u_1 (-\Delta w) + \int_{\Omega} u_1 (\beta u_1 u_2 + u_1 + u_2) w = \gamma \int_{\Omega} u_1 w.$$

Integrating by parts via the divergence theorem implies that

$$\begin{aligned}
 & \int_{\Omega} u_1 (a - u_1 - \alpha_{12} u_2 - \beta u_1 u_2) w \\
 & + \int_{\Omega} u_1 (\beta u_1 u_2 + u_1 + u_2) w = \gamma \int_{\Omega} u_1 w.
 \end{aligned}$$

Therefore

$$\int_{\Omega} u_1 w (a + (1 - \alpha_{12}) u_2) = \gamma \int_{\Omega} u_1 w.$$

Since $u_2 > 0$ and $1 - \alpha_{12} > 0$, the left hand side exceeds $a \int_{\Omega} u_1 w$, which implies that $\gamma > a$. Consequently, a cannot be an eigenvalue for the operator $-\Delta + \beta u_1 u_2 + u_1 + u_2$ and $u_2 \equiv \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u_1$. Consequently, if $\beta_1 = \beta_2 = \beta$, (2.9) admits the unique componentwise positive equilibrium solution $(u^*, \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u^*)$, where u^* is the unique positive solution to (2.11), which exists when $a > \lambda_1$. We shall shortly see that in this case that we can find upper bounds on u^* sufficient to show that (2.1) is permanent for a' and β sufficiently large.

Let us now consider (2.9) in the case of $\beta_1 > 0$ and $\beta_2 > 0$, $\beta_1 \neq \beta_2$. It is now not necessarily true that (2.9) admits a unique componentwise positive equilibrium solution, let alone one with its components constant multiples of each other. However, we do know from [14] that (2.9) is compressive, and hence that its ω -limit set is contained in the set $\{(u_1, u_2) : \underline{u}_1 \leq u_1 \leq \bar{u}_1, \underline{u}_2 \geq u_2 \geq \bar{u}_2\}$, where $(\underline{u}_1, \underline{u}_2)$ and (\bar{u}_1, \bar{u}_2) are componentwise positive equilibrium solutions to (2.9). We can sometimes use knowledge of the case $\beta_1 = \beta_2$ to obtain upper bounds on \bar{u}_1 and \underline{u}_2 in terms of u^* (for appropriate choices of α_{12}, α_{21} , and β). Then by estimating u^* from above, we can give conditions for permanence in (2.1). To this end, suppose without loss of generality that $\beta_1 < \beta_2$ and let (u_1, u_2) be a componentwise positive equilibrium solution to (2.9). Then

$$\begin{aligned}
 (2.12) \quad & -\Delta u_1 \geq u_1 [a - u_1 - \alpha_{12} u_2 - \beta_2 u_1 u_2], \\
 & -\Delta u_2 \leq u_2 [a - \alpha_{21} u_1 - u_2 - \beta_2 u_1 u_2] \quad \text{in } \Omega.
 \end{aligned}$$

Now let $\phi > 0$ satisfy $-\Delta \phi = \lambda_1 \phi$ in Ω with $\phi = 0$ on $\partial\Omega$. Let $(\bar{u}_1, \bar{u}_2) = (\varepsilon \phi, a)$. Then

$$\begin{aligned}
 (2.13) \quad & -\Delta \bar{u}_1 \leq \bar{u}_1 [a - \bar{u}_1 - \alpha_{12} \bar{u}_2 - \beta_2 \bar{u}_1 \bar{u}_2], \\
 & -\Delta \bar{u}_2 \geq \bar{u}_2 [a - \alpha_{21} \bar{u}_1 - \bar{u}_2 - \beta_2 \bar{u}_1 \bar{u}_2] \quad \text{in } \Omega,
 \end{aligned}$$

provided that

$$\varepsilon \lambda_1 \phi = -\Delta(\varepsilon \phi) \leq \varepsilon \phi [a - \varepsilon \phi - \alpha_{12} a - \beta_2 a \varepsilon \phi],$$

which holds for $\varepsilon > 0$ sufficiently small, provided that

$$(2.14) \quad \lambda_1 < (1 - \alpha_{12})a.$$

Since the strong maximum principle implies that ϕ and u_1 have negative outer normal derivatives at each point of $\partial\Omega$, it follows that $\varepsilon \phi < u_1$ for small enough $\varepsilon > 0$.

Additionally, $u_2 < a$ by the usual maximum principle. Consequently, we may apply the method of upper and lower solutions as in [9] to assert that there is a solution of

$$(2.15) \quad \begin{aligned} -\Delta u &= u[a - u - \alpha_{12}v - \beta_2 uv], \\ -\Delta v &= v[a - \alpha_{21}u - v - \beta_2 uv] && \text{in } \Omega, \\ u = 0 &= v && \text{on } \partial\Omega \end{aligned}$$

with $\bar{u}_1 \leq u \leq u_1$ and $u_2 \leq v \leq a$. We know that (2.15) has only one such solution and hence

$$(2.16) \quad u_2 \leq \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u^*(\beta_2),$$

where $u^*(\beta_2)$ denotes the unique positive solution of (2.11) when $\beta = \beta_2$.

Consider once again a componentwise positive equilibrium solution to (2.9). Then

$$(2.17) \quad \alpha_{21}u_1 + \beta_2u_1u_2 \leq \bar{\alpha}_{21}u_1 + \beta_1u_1u_2$$

for some $\bar{\alpha}_{21} \in (\alpha_{21}, 1)$ if and only if

$$(\beta_2 - \beta_1)u_2 \leq \bar{\alpha}_{21} - \alpha_{21}.$$

Consequently, (2.17) will hold for some $\bar{\alpha}_{21} > \alpha_{21}$, provided that

$$(2.18) \quad \beta_2 - \beta_1 < \frac{(1 - \alpha_{21})}{a}.$$

So let (2.18) hold and choose $\bar{\alpha}_{21}$ so that (2.17) holds. Then

$$(2.19) \quad \begin{aligned} -\Delta u_1 &\leq u_1[a - u_1 - \alpha_{12}u_2 - \beta_1u_1u_2], \\ -\Delta u_2 &\geq u_2[a - \bar{\alpha}_{21}u_1 - u_2 - \beta_1u_1u_2] && \text{in } \Omega, \end{aligned}$$

and if $(\hat{u}_1, \hat{u}_2) = (a, \varepsilon\phi)$,

$$(2.20) \quad \begin{aligned} -\Delta \hat{u}_1 &\geq \hat{u}_1[a - \hat{u}_1 - \alpha_{12}\hat{u}_2 - \beta_1\hat{u}_1\hat{u}_2], \\ -\Delta \hat{u}_2 &\leq \hat{u}_2[a - \bar{\alpha}_{21}\hat{u}_1 - \hat{u}_2 - \beta_1\hat{u}_1\hat{u}_2] && \text{in } \Omega \end{aligned}$$

for $\varepsilon > 0$ sufficiently small, provided that

$$(2.21) \quad a(1 - \bar{\alpha}_{21}) > \lambda_1.$$

In case (2.18) and (2.21) hold, there must be (\hat{u}, \hat{v}) solving

$$(2.22) \quad \begin{aligned} -\Delta \hat{u} &= \hat{u}[a - \hat{u} - \alpha_{12}\hat{v} - \beta_1\hat{u}\hat{v}], \\ -\Delta \hat{v} &= \hat{v}[a - \bar{\alpha}_{21}\hat{u} - \hat{v} - \beta_1\hat{u}\hat{v}] && \text{in } \Omega, \\ \hat{u} = 0 &= \hat{v} && \text{on } \partial\Omega, \end{aligned}$$

with $u_1 \leq \hat{u} \leq a$ and $\varepsilon\phi \leq \hat{v} \leq u_2$ for ε small and positive. Once again, we know that there is only one componentwise positive solution to (2.20), and hence

$$(2.23) \quad u \leq \bar{u}^*(\beta_1),$$

where $\bar{u}^*(\beta_1)$ is the unique positive solution to (2.11) when $\beta = \beta_1$ and α_{21} is replaced by $\bar{\alpha}_{21}$. Summing up, we have the following theorem.

THEOREM 2.1. *Suppose that (2.14), (2.18), and (2.21) hold, and let (u_1, u_2) be a componentwise positive equilibrium to (2.9). Then u_1 satisfies the estimate in (2.23) and u_2 satisfies the estimate in (2.16).*

3. Permanence results. Recall that in the previous section we demonstrated that if $\beta_1 = 0$ and $\beta_2 = 0$, then (2.1) fails to be permanent for any choice whatsoever of the remaining parameters so long as (i), (ii), and (iii) are met. In this section, we show that (2.1) is permanent when

$$(3.1) \quad \alpha_{12} - 1 < (\beta_2 - \beta_1)a < 1 - \alpha_{21},$$

provided that a', β_1 , and β_2 are sufficiently large. What happens here is that by making the competition between the two stronger competitors more severe at intermediate to large values of their densities, we effectively lower their asymptotic coexistence states enough to make possible a successful invasion by the weaker competitor. This phenomenon fails to occur in the Lotka-Volterra case ($\beta_1 = 0, \beta_2 = 0$).

Let us first consider the case $\beta_1 = \beta_2 = \beta$. From the preceding section we have that the conditions for applying the Hale-Waltman acyclicity theorem in order to obtain permanence will be met, provided that $\sigma^* > 0$ when

$$(3.2) \quad \begin{aligned} \Delta \phi^* + \left[a' - \alpha_{31}u^* - \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u^* \right] \phi^* &= \sigma^* \phi^* && \text{in } \Omega, \\ \phi^* &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits a positive solution, where u^* is the unique positive solution of (2.10). The maximum principle implies that

$$\begin{aligned} u^* &\leq \frac{-\left(\frac{1 - \alpha_{12}\alpha_{21}}{1 - \alpha_{12}} \right) + \sqrt{\left(\frac{1 - \alpha_{12}\alpha_{21}}{1 - \alpha_{12}} \right)^2 + 4a \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) \beta}}{2 \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) \beta} \\ &= \frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta}}{2(1 - \alpha_{21})\beta}. \end{aligned}$$

Consequently, we have that (2.1) is permanent, provided that $\beta_1 = \beta_2 = \beta$, so long as $\sigma^{**} > 0$ when

$$(3.3) \quad \begin{aligned} \Delta \phi + \left\{ a' - \left(\alpha_{31} + \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) \right) \right. \\ \left. \times \left[\frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta}}{2(1 - \alpha_{21})\beta} \right] \right\} \phi &= \sigma^{**} \phi, \end{aligned}$$

where $\phi > 0$ satisfies $\Delta \phi + \lambda_1 \phi = 0$ in Ω with $\phi = 0$ on $\partial\Omega$. The definition of ϕ implies that

$$(3.4) \quad \begin{aligned} \sigma^{**} &= a' - \lambda_1 - \left(\alpha_{31} + \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) \right) \\ &\times \left[\frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta}}{2(1 - \alpha_{21})\beta} \right]. \end{aligned}$$

From (3.4), we find that $\sigma^{**} > 0$, provided that

$$(3.5) \quad a < \left\{ \beta \left[\frac{(1 - \alpha_{12})(1 - \alpha_{21})}{(\alpha_{31}(1 - \alpha_{12}) + \alpha_{32}(1 - \alpha_{21}))^2} \right] (a' - \lambda_1) + \frac{(1 - \alpha_{12}\alpha_{21})}{\alpha_{31}(1 - \alpha_{12}) + \alpha_{31}(1 - \alpha_{21})} \right\} (a' - \lambda_1).$$

It is clear from inspection that (3.5) holds, for example, for any $a' > \lambda_1$ provided that β is large, and for $a = a'$ large enough, provided that

$$\beta \left[\frac{(1 - \alpha_{12})(1 - \alpha_{21})}{(\alpha_{31}(1 - \alpha_{12}) + \alpha_{32}(1 - \alpha_{21}))^2} \right] (a' - \lambda_1) + \frac{(1 - \alpha_{12}\alpha_{21})}{\alpha_{31}(1 - \alpha_{12}) + \alpha_{31}(1 - \alpha_{21})} > 1.$$

When β_1 is no longer assumed equal to β_2 , recall that our knowledge of the asymptotic behavior of the subsystem (2.9) in the $u_1 - u_2$ variables is less precise than in the case $\beta_1 = \beta_2$. Namely, we know that (2.9) is compressive but we do not know that it has a single globally attracting componentwise positive equilibrium. However, when (3.1) holds, we showed in the previous section that we can get upper bounds on the components of any componentwise positive equilibrium solution to (2.9). Since compressivity of (2.9) means that it has a global attractor contained in a order interval with endpoints componentwise positive equilibria, such upper bounds provide a "worst case" for the competition the species with density u_3 faces if it tries to invade the $u_1 u_2$ -system (2.9) long after it has been established. This enables us to give conditions under which (2.1) is permanent. More specifically, suppose that $0 < \beta_2 - \beta_1 < \frac{1 - \alpha_{21}}{a}$. Choose $\bar{\alpha}_{21} \in (\alpha_{21}, 1)$ so that $\beta_2 - \beta_1 < \frac{\bar{\alpha}_{21} - \alpha_{21}}{a}$. Then for any equilibrium solution (u_1, u_2) of (2.9), so long as $a(1 - \bar{\alpha}_{21}) > \lambda_1$ and $a(1 - \alpha_{12}) > \lambda_1$, $u_1 \leq \bar{u}^*(\beta_1)$, where $\bar{u}^*(\beta_1)$ is the unique positive solution to (2.11) with $\beta = \beta_1$ and α_{21} replaced with $\bar{\alpha}_{21}$, and $u_2 \leq (\frac{1 - \alpha_{21}}{1 - \alpha_{12}})u^*(\beta_2)$, where $u^*(\beta_2)$ is the unique positive solution to (2.11) with $\beta = \beta_2$. It follows as in [2] that no componentwise positive state (u_1, u_2, u_3) lies in the stable manifold of the global attractor to (2.9), provided that $\sigma^\# > 0$ when

$$(3.6) \quad \Delta\phi^\# + \left[a' - \alpha_{31}\bar{u}^*(\beta_1) - \alpha_{32} \left(\frac{1 - \alpha_{21}}{1 - \alpha_{12}} \right) u^*(\beta_2) \right] \phi^\# = \sigma^\# \phi^\# \quad \text{in } \Omega, \\ \phi^\# = 0 \quad \text{on } \partial\Omega$$

admits a positive solution. Consequently, the hypotheses of the Hale-Waltman acyclicity theorem are met, and we may conclude that (2.1) is permanent, provided that $\sigma^\# > 0$ when (3.6) admits a positive solution. (A precisely analogous result can be formulated when $0 < \beta_1 - \beta_2 < \frac{1 - \alpha_{12}}{a}$.) Now, as before,

$$\bar{u}^*(\beta_1) \leq \frac{-(1 - \alpha_{12}\bar{\alpha}_{21}) + \sqrt{(1 - \alpha_{12}\bar{\alpha}_{21})^2 + 4a(1 - \bar{\alpha}_{21})(1 - \alpha_{12})\beta_1}}{2(1 - \bar{\alpha}_{21})\beta_1}$$

and

$$u^*(\beta_2) \leq \frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta_2}}{2(1 - \alpha_{21})\beta_2}.$$

Consequently, (2.1) is permanent, provided that $\sigma^{\#\#} > 0$, when

$$(3.7) \quad \Delta\phi + \left\{ a' - \alpha_{31} \left(\frac{-(1 - \alpha_{12}\bar{\alpha}_{21}) + \sqrt{(1 - \alpha_{12}\bar{\alpha}_{21})^2 + 4a(1 - \bar{\alpha}_{21})(1 - \alpha_{12})\beta_1}}{2(1 - \bar{\alpha}_{21})\beta_1} \right) - \alpha_{32} \left(\frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta_2}}{2(1 - \alpha_{12})\beta_2} \right) \right\} \phi = \sigma^{\#\#} \phi,$$

where $\Delta\phi + \lambda_1\phi = 0$ in Ω with $\phi = 0$ on $\partial\Omega$. We have established the following theorem.

THEOREM 3.1. *Suppose that (3.1) holds.*

(i) *If $0 < (\beta_2 - \beta_1)a < 1 - \alpha_{21}$, $\bar{\alpha}_{21} \in (\alpha_{21}, 1)$ is such that $\beta_2 - \beta_1 < (\bar{\alpha}_{21} - \alpha_{21})/a$, $a(1 - \alpha_{12}) > \lambda_1$, and $a(1 - \bar{\alpha}_{21}) > \lambda_1$, then (2.1) is permanent if $\sigma^{\#\#} > 0$ in (3.7).*

(ii) *If $\alpha_{12} - 1 < (\beta_2 - \beta_1)a < 0$, $\bar{\alpha}_{12} \in (\alpha_{12}, 1)$ is such that $\beta_1 - \beta_2 < (\bar{\alpha}_{12} - \alpha_{12})/a$, $a(1 - \bar{\alpha}_{12}) > \lambda_1$, and $a(1 - \alpha_{21}) > \lambda_1$, then (2.1) is permanent if $\sigma^{\#\#\#} > 0$ when*

$$(3.8) \quad \Delta\phi + \left\{ a' - \alpha_{31} \left(\frac{-(1 - \alpha_{12}\alpha_{21}) + \sqrt{(1 - \alpha_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \alpha_{12})\beta_1}}{2(1 - \alpha_{21})\beta_1} \right) - \alpha_{32} \left(\frac{-(1 - \bar{\alpha}_{12}\alpha_{21}) + \sqrt{(1 - \bar{\alpha}_{12}\alpha_{21})^2 + 4a(1 - \alpha_{21})(1 - \bar{\alpha}_{12})\beta_2}}{2(1 - \bar{\alpha}_{12})\beta_2} \right) \right\} \phi = \sigma^{\#\#\#} \phi,$$

where ϕ is as in (3.7).

4. Conclusion. It is evident from the preceding discussion and analysis that in the scenario we have postulated for species A, B , and C , whether the introduction of A into the preexisting community results in its long-term preservation depends very much on the particular forms of the pairwise interactions. The crucial factor is whether the competition between A and B reduces their populations or population densities sufficiently long-term to allow C to invade. In the case of Lotka-Volterra dynamics in the setting of ordinary differential equations, the competition between A and B is simply too weak to permit C to invade. We have shown such is sometimes also the case in the setting of reaction-diffusion equations over bounded habitat patches subject to absorbing boundary conditions, and we have shown by example how to modify the interaction between A and B so as to foster the long-term persistence of C .

Our analysis does suggest how competition between A and B which does not mediate the persistence of C can be modified to do so. Namely, one should add a term of the form $-\beta_1 f_1(u_1, u_2)u_1$ to the reaction terms of the first equation and a term of the form $-\beta_2 f_2(u_1, u_2)u_2$ to the reaction terms of the second equation, where β_1 and β_2 are free positive scale parameters and $f_i(u_1, u_2) > 0$ for $i = 1, 2$ and $u_1 > 0, u_2 > 0$. Additionally, we must require that $f_1(u_1, 0) = 0$ and $f_2(0, u_2) = 0$ for any $u_1 \geq 0$ and $u_2 \geq 0$ if it is only the competition between A and B that is to be modified, and that $f_1(0, u_2) = 0$ and $f_2(u_1, 0) = 0$ for any $u_2 \geq 0$ and $u_1 \geq 0$ in order not to make the coexistence of A and B a more stringent requirement.

To see the importance of this last requirement, consider (1.1) again with $\alpha_{12} = \alpha_{21} = \alpha < 1$ and modify the system by adding $-\beta u_2^2 u_1$ to the right-hand side of the first equation and $-\beta u_1^2 u_2$ to the right-hand side of the second (i.e., $f_1(u_1, u_2) = u_2^2$

and $f_2(u_1, u_2) = u_1^2$ so that $f_1(0, u_2) > 0$ if $u_2 > 0$ and $f_2(u_1, 0) > 0$ if $u_1 > 0$). Then the requirement for the coexistence of A and B is modified from $a - \alpha a > 0$ in the case of (1.1) to $a - \alpha a - \beta a^2 > 0$. This last means that $\alpha + \beta a < 1$ or $\beta < \frac{1-\alpha}{a}$. In the modified system, having a componentwise positive equilibrium requires that $a - \alpha u_2 - u_1 - \beta u_2^2 = 0$ and that $a - \alpha u_1 - u_2 - \beta u_1^2 = 0$. By subtracting the two equations, it is not difficult to see that if $(\hat{u}_1, \hat{u}_2, 0)$ is an equilibrium solution with $\hat{u}_1 > 0$ and $\hat{u}_2 > 0$, then either $\hat{u}_1 + \hat{u}_2 = \frac{1-\alpha}{\beta}$ or

$$\hat{u}_1 = \hat{u}_2 = \frac{-(1+\alpha) + \sqrt{(1+\alpha)^2 + 4a\beta}}{2\beta}.$$

The modified system will fail to be permanent if $a - \alpha_{31}\hat{u}_1 - \alpha_{32}\hat{u}_2 < 0$ for any such equilibrium $(\hat{u}_1, \hat{u}_2, 0)$. Since $\alpha_{31} > 1$ and $\alpha_{32} > 1$, $\alpha_{31}\hat{u}_1 + \alpha_{32}\hat{u}_2 > \hat{u}_1 + \hat{u}_2$ so that $a - \alpha_{31}\hat{u}_1 - \alpha_{32}\hat{u}_2 < a - \hat{u}_1 - \hat{u}_2$. If there is an equilibrium with $\hat{u}_1 + \hat{u}_2 = \frac{1-\alpha}{\beta}$, $\beta < \frac{1-\alpha}{a}$ implies that $\hat{u}_1 + \hat{u}_2 = \frac{1-\alpha}{\beta} > (1-\alpha)\left(\frac{a}{1-\alpha}\right) = a$. Consequently, permanence fails in the modified system except possibly if

$$\left(\frac{-(1+\alpha) + \sqrt{(1+\alpha)^2 + 4a\beta}}{2\beta}, \frac{-(1+\alpha) + \sqrt{(1+\alpha)^2 + 4a\beta}}{2\beta}, 0 \right)$$

is the unique such equilibrium. In this case

$$\hat{u}_1 + \hat{u}_2 = \frac{-(1+\alpha) + \sqrt{(1+\alpha)^2 + 4a\beta}}{\beta}$$

and $a - (\hat{u}_1 + \hat{u}_2) > 0$ if and only if $a\beta + (1+\alpha) - \sqrt{(1+\alpha)^2 + 4a\beta} > 0$. An easy calculation shows that this last inequality is equivalent to $\beta > \frac{2(1-\alpha)}{a}$. However, $\beta < \frac{1-\alpha}{a}$ is necessary for the coexistence of A and B . The upshot is that the modified system fails to be permanent, illustrating the need to have $f_1(0, u_2) = 0$ and $f_2(u_1, 0) = 0$ as we suggested.

Finally, there is one additional comment that we should make. The *analysis* in sections 2 and 3 depends in a crucial way on species A and B having equal intrinsic growth rates. It is of considerable interest to ask whether the phenomenon we have described in this article (i.e., the collapse of the existing community under Lotka-Volterra dynamics and competition-mediated coexistence for the modified dynamics) carries over to cases in which A and B have unequal growth rates. Our expectation is that certainly such is the case. A preliminary analysis in the setting of ordinary differential equation models supports this view. However, it also demonstrates that if the growth rates for A and B are unequal, the equilibrium corresponding to $(\bar{u}_1(\beta), \bar{u}_2(\beta))$ need not converge to $(0, 0)$ as $\beta \rightarrow \infty$. In such a case, having the model (with the modified dynamics) predict permanence places an additional condition on the system parameters which can be understood as a restriction on the disparity between the growth rates for A and B . Such is not entirely surprising. Indeed, even in a two-species Lotka-Volterra model, fixed interaction coefficients restrict the disparity between growth rates compatible with a prediction of permanence. Extending such results to the reaction-diffusion case in a quantifiably precise manner is an on going effort at this time which should serve to enhance further the robustness of the phenomenon we have noted in this article.

REFERENCES

- [1] P. ANTONELLI, X. LIN, AND R.H. BRADBURY, *On Hutchinson's competition equations and their homogenization: A higher-order principle of competitive exclusion*, Ecol. Modelling, 60 (1992), pp. 309-320.
- [2] E.J. AVILA-VALES, *Permanence in Seasonal Ecological Models with Spatial Heterogeneity*, Ph.D. thesis, University of Miami, 1995.
- [3] F.J. AYALA, M.E. GILPIN, AND J.G. EHRENFELD, *Competition between species: Theoretical models and experimental tests*, Theoret. Population Biol., 4 (1973), pp. 331-356.
- [4] J. BILOTTI AND J.P. LASALLE, *Periodic dissipative processes*, Bull. Amer. Math. Soc., 6 (1971), pp. 1082-1089.
- [5] G. BUTLER AND P. WALTMAN, *Persistence in dynamical systems*, J. Differential Equations, 63 (1986), pp. 255-263.
- [6] R.S. CANTRELL AND C. COSNER, *On the steady-state problem for the Volterra-Lotka competition model with diffusion*, Houston J. Math., 13 (1987), pp. 337-352.
- [7] R.S. CANTRELL, C. COSNER, AND V. HUTSON, *Permanence in ecological systems with spatial heterogeneity*, Proc. Roy. Soc. Edinburgh Sect. A., 123 (1993), pp. 533-559.
- [8] R.S. CANTRELL, C. COSNER, AND V. HUTSON, *Permanence in some diffusive Lotka-Volterra models for three interacting species*, Dynamical Systems and Appl., 2 (1993), pp. 505-530.
- [9] C. COSNER AND A.C. LAZER, *Stable coexistence states in the Volterra-Lotka competition model with diffusion*, SIAM J. Appl. Math., 44 (1984), pp. 1112-1132.
- [10] H.I. FREEDMAN AND P. WALTMAN, *Persistence in a model of three competitive populations*, Math. Biosci., 73 (1985), pp. 89-101.
- [11] H.I. FREEDMAN AND P. WALTMAN, *Persistence in models of three interacting predator-prey populations*, Math. Biosci., 68 (1984), pp. 213-231.
- [12] J.K. HALE AND P. WALTMAN, *Persistence in infinite-dimensional systems*, SIAM J. Math. Anal., 20 (1989), pp. 388-395.
- [13] D. HENRY, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics 840, Springer-Verlag, Berlin, 1981.
- [14] P. HESS, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Research Notes in Mathematics 247, Longman, Harlow, UK, 1991.
- [15] P. HESS AND A.C. LAZER, *On an abstract competition model and applications*, Nonlinear Anal., 16 (1991), pp. 917-940.
- [16] R. MAY AND W.J. LEONARD, *Nonlinear aspects of competition between three species*, SIAM J. Appl. Math., 29 (1975), pp. 243-253.
- [17] T.W. SCHOENER, *Alternatives to Lotka-Volterra competition: Models of intermediate complexity*, Theoret. Population Biol., 10 (1976), pp. 309-333.
- [18] T.W. SCHOENER, *Population growth regulated by intraspecific competition for energy or time: Some simple representations*, Theoret. Population Biol., 4 (1973), pp. 56-84.
- [19] P. SCHUSTER, K. SIGMUND, AND P. WOLFF, *On ω -limits for competition between three species*, SIAM J. Appl. Math., 37 (1979), pp. 49-54.
- [20] G. SUN, Q. CUI, AND B. SONG, *A new mathematical model of interspecific competition—an expansion of the classical Lotka-Volterra competition equations*, Ecol. Modelling, 58 (1991), pp. 273-284.