

PERMANENCE OF THREE COMPETITORS IN SEASONAL ECOLOGICAL MODELS WITH SPATIAL HETEROGENEITY

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ABSTRACT. We obtain conditions for permanence in a reaction-diffusion system modelling the interaction of three competing species in a bounded habitat whose exterior is lethal to each species under the assumption that the local inter- and intraspecific interactions are temporally periodic. Our results are based upon the Hale-Waltman acyclicity theorem, a skew-product flow approach having been employed to convert the reaction-diffusion system into a continuous time semi-dynamical system. The conditions we derive all are expressed in terms of the sign of the principal eigenvalue for certain associated periodic-parabolic linear operators and may be interpreted biologically as invasibility conditions.

1. Introduction. In the study of any population dynamical model of interacting species, a natural and fundamental question is whether or not the model predicts the long term survival of each of the interacting species. Implicit in this question is another related question: just what is meant by “long term survival” of a species in such a model? This second question has been at the heart of numerous recent analyses of population dynamical models in various contexts, see, e.g., [7, 8, 12, 16, 17, 20] and references therein, and a consensus answer has emerged, reflecting the twin imperatives of biological interpretability and mathematical tractability. Namely, there should be a “positive threshold” with the property that any positive initial state for the model eventually will evolve to a state exceeding the threshold and thereafter remain above the threshold. This concept is usually referred to as *uniform persistence*.

To be more specific about what constitutes a “positive threshold” requires a particular modelling context. In this article, the context is

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that of competition models for three interacting species via reaction-diffusion equations on a bounded spatial domain, supplemented by absorbing, i.e., homogeneous Dirichlet, boundary data. The basic biological interpretation for such models is that three competing species share a common habitat patch, denoted Ω , which is surrounded by a lethal exterior. The states of the model are denoted u_1 , u_2 and u_3 , where $u_i(x, t)$ expresses the population density of the i th species at locale x and time t . Uniform persistence in this context requires the existence of functions U_1, U_2, U_3 on $\bar{\Omega}$ with

$$\begin{aligned} U_i &> 0 && \text{in } \Omega \\ U_i &= 0 && \text{on } \partial\Omega \\ \nabla U_i \cdot \eta &< 0 && \text{on } \partial\Omega \end{aligned}$$

for $i = 1, 2, 3$, where η is a unit outer normal vector to $\partial\Omega$, to serve as the threshold. Namely, for any initial data

$$(u_1(x, 0), u_2(x, 0), u_3(x, 0)) \quad \text{with} \quad u_i(x, 0) \not\equiv 0,$$

the corresponding solution $(u_1(x, t), u_2(x, t), u_3(x, t))$ is required to satisfy $u_i(x, t) \geq U_i(x)$ on $\bar{\Omega}$ and $u_i \geq u_0(u_1(x, 0), u_2(x, 0), u_3(x, 0))$. If, additionally, there are fixed positive constants V_1, V_2, V_3 so that $u_i(x, t) \leq V_i$ once $t \geq t_0(u_1(x, 0), u_2(x, 0), u_3(x, 0))$, the system is said to be *permanent*. Clearly, permanence implies uniform persistence and is in general a stronger requirement. However, the models we consider are regulated by intraspecific as well as interspecific competition. Consequently, the densities of the component species of the system have asymptotic upper bounds; i.e., the system is dissipative. As a result, in this setting, permanence is more or less tantamount to uniform persistence, and we elect to use the more descriptive term.

The most salient feature of the models we consider is that the local interaction terms are both spatially heterogeneous and temporally periodic. Spatial heterogeneity and/or temporal periodicity have figured prominently in several preceding studies (of reaction-diffusion models) which have informed and influenced our current efforts. Hess and Lazer [14, 15] allowed both spatial heterogeneity and temporal periodicity in their studies of reaction-diffusion models for *two* competing species. Solution trajectories for such models respect the ordering of state space

given by $(u_1, v_1) \leq (u_2, v_2)$ if and only if $u_1 \leq u_2$ and $v_1 \geq v_2$. Hess and Lazer exploited this ordering to examine the models via the theory of discrete dynamical systems. They found conditions under which the model exhibits a particularly nice form of permanence, namely that solution trajectories evolve toward a periodically varying family of order intervals. They called this property *compressivity*. Compressivity techniques apply whether absorbing or reflecting, i.e., homogeneous Neumann, boundary data are assumed. However, the requirement that solution trajectories respect an ordering of state space means that compressivity techniques alone cannot be used to analyze a three species competition system. Consequently, we employ a continuous time semi-dynamical system to reformulate our model so as to access the permanence literature to obtain reasonable sufficient conditions for long term coexistence of the component species of our model. This approach was used by Cantrell, Cosner and Hutson in [5] to analyze the general two-species reaction-diffusion models with absorbing or reflecting boundary data under the assumption that the local interaction terms are spatially heterogeneous but independent of time, and in [6] to treat certain three-species competition and predator-prey systems having local interaction terms of constant coefficient Lotka-Volterra type. Converting reaction-diffusion models to semi-dynamical systems is made substantially more difficult by the introduction of temporal periodicity into the model. Hutson and Zhao demonstrated in [18] how to adapt the reformulation approach of [5] to reaction-diffusion models with temporal periodicity as well as spatial heterogeneity in the reaction terms in the case of reflecting boundary data by utilizing the concept of a skew-product flow [22]. In [1] and [2] we modified the results of [18] so that such reaction-diffusion models with absorbing boundary data can be reformulated as semi-dynamical systems.

Once we reformulate the model as a semi-dynamical system π , we show that π is permanent according to a dynamical systems definition. It then follows as in [1] or [2] that the model is permanent in the sense previously described. To show that π is permanent we invoke the Hale-Waltman acyclicity theorem [11]. The sufficient conditions for permanence that we obtain are expressed in terms of the negativity of the principal eigenvalues for certain related periodic-parabolic differential operators. (Such conditions have a natural biological interpretation as conditions for invasibility, a point we amplify at a suitable moment

in our exposition.) Somewhat similar conditions for permanence in reaction-diffusion models of n competing species, reaction terms again spatially heterogeneous and temporally periodic, are given by Cantrell and Cosner in [4] for the case of absorbing boundary data and by Zhao in [23] for the case of reflecting boundary data. Both [4] and [23] rely primarily on comparison principles for single reaction-diffusion equations to obtain asymptotic lower bounds on the components of the system. Our conditions for permanence for the three species case are somewhat less restrictive than those of either of the two other studies when $n = 3$. The basic reason is that compressivity techniques are applicable to the study of the subsystems which arise when one species is absent when $n = 3$ but not for general n .

The remainder of this article is as follows. In Section 2 we describe the reaction-diffusion model, show how to convert it to a semi-dynamical system π and discuss the Hale-Waltman acyclicity theorem. In Section 3 we analyze the subsystems of the model which arise when one or two species are absent from the model. Our main permanence results are given in Section 4. Finally, in Section 5 we extend a result of Fan and Leung [10] on the local asymptotic stability of componentwise positive periodic solutions to reaction-diffusion models for two competing species to situations in which the reaction terms are spatially heterogeneous and temporally periodic. In so doing, we obtain conditions under which solutions to the two-species subsystems of the model evolve to a componentwise positive periodic orbit, providing an additional refinement of the results of Section 4.

2. Set-up and preliminaries. Consider the system

$$(2.1) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1 f_1(x, t, u_1, u_2, u_3) \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + u_2 f_2(x, t, u_1, u_2, u_3) \\ \frac{\partial u_3}{\partial t} &= d_3 \Delta u_3 + u_3 f_3(x, t, u_1, u_2, u_3) \end{aligned}$$

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

$$(2.2) \quad u_i = 0$$

on $\partial\Omega \times (0, \infty)$ for $i = 1, 2, 3$, where Ω is a sufficiently smooth bounded domain in \mathbf{R}^n . Assume

- (H1) $d_i > 0$ for $i = 1, 2, 3$.
- (H2) $f_i \in C^{\alpha, \alpha/2, 2}(\bar{\Omega} \times \mathbf{R} \times \mathbf{R}^3)$
for $i = 1, 2, 3$, where $\alpha \in (0, 1)$.
- (H3) $f_i(x, t + T, u_1, u_2, u_3) = f_i(x, t, u_1, u_2, u_3)$
for $x \in \bar{\Omega}$, $u_i \geq 0$ and $t \in \mathbf{R}$, for $i = 1, 2, 3$.
- (H4) $\frac{\partial f_i}{\partial u_j} \leq 0$ for $i, j = 1, 2, 3$.
- (H5) $f_i(x_i, t_i, 0, 0, 0) > 0$ for some $x_i \in \Omega$
and $t_i \in (0, T)$, for $i = 1, 2, 3$.

There exist $K_1, K_2, K_3 > 0$ so that

$$(H6) \quad \begin{cases} f_1(x, t, u_1, 0, 0) < 0 & \text{if } u_1 \geq K_1 \\ f_2(x, t, 0, u_2, 0) < 0 & \text{if } u_2 \geq K_2 \\ f_3(x, t, 0, 0, u_3) < 0 & \text{if } u_3 \geq K_3 \end{cases}$$

for any $x \in \bar{\Omega}$ and $t \in [0, T]$.

Now let $\vec{u} = (u_1, u_2, u_3) \in [C^1(\bar{\Omega})]^3$ and $t_0 \in [0, \infty]$. Denote by $\phi(\vec{u}, t_0, t)$ the unique solution to (2.1)–(2.2) satisfying $\phi(\vec{u}, t_0, t_0) = \vec{u}$. (Here $\phi = (\phi_1, \phi_2, \phi_3)$.) Let S^1 be parametrized by $P_\tau = e^{2\pi i \tau/T}$, $\tau \in \mathbf{R}^+$. Then, as in [1] or [2], (H1)–(H3) imply that the map $\pi : [C^1_{0+}(\bar{\Omega})]^3 \times S^1 \times [0, \infty) \rightarrow [C^1_{0+}(\bar{\Omega})]^3 \times S^1$ given by

$$\pi(\vec{u}, P_\tau, t) = (\phi(\vec{u}, \tau, \tau + t), P_{\tau+t})$$

is a semiflow, where by $[C^1_{0+}(\bar{\Omega})]^3$ we mean the cone consisting of triples of nonnegative C^1 functions on $\bar{\Omega}$ which vanish on $\partial\Omega$. Hence (2.1)–(2.2) can be reformulated as a semi-dynamical system. (See also [18, 22].) Hypotheses (H4)–(H6) imply, again as in [1] or [2], that there is an $M > 0$ so that $\|\phi(u, \tau, t)\| \leq M$ for $t \geq t(u, \tau)$, where $\|\cdot\|$ denotes the norm in $[C^1(\bar{\Omega})]^3$. It follows from this observation that there is a bounded attracting set for the semiflow π , i.e., π is point dissipative. Moreover, $\pi(\cdot, t)$ is a compact mapping on $[C^1_{0+}(\bar{\Omega})]^3 \times S^1$

for any $t > 0$. (See [1, 2] again, and also [5, 13].) By a result of Bilotti and LaSalle [3], these two properties of π are sufficient to guarantee the existence of a global attractor for π , i.e., a compact set \mathcal{A} , invariant under π , such that for any bounded subset V of $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$,

$$\lim_{t \rightarrow \infty} \left\{ \sup_{(u, P_\tau) \in V} d(\pi(u, P_\tau, t), \mathcal{A}) \right\} = 0,$$

where d denotes the metric in $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$. Consequently, we may restrict our attention to $X = \overline{\pi(B(\mathcal{A}, \varepsilon), [t_0, \infty))}$, where $B(\mathcal{A}, \varepsilon)$ is an ε -neighborhood of \mathcal{A} in $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$ and $t_0 > 0$. It follows as in [1] or [2] that X is compact and positively invariant under π . Since π is continuous, the same is true for $\hat{X} = \pi(X, t')$ where $t' > 0$. \hat{X} can be written $\hat{X} = (\hat{X} \cup \{\text{int}([C_0^1(\bar{\Omega})]^3 \times S^1)\}) \cup (\hat{X} \cap \{\partial([C_{0+}^1(\bar{\Omega})]^3 \times S^1)\})$, both of which are positively invariant under π . Let $\mathcal{S} = \hat{X} \cap \{\partial([C_{0+}^1(\bar{\Omega})]^3 \times S^1)\} = \hat{X} \cap \partial\{[C_{0+}^1(\bar{\Omega})]^3 \times S^1\}$. We say π is *permanent* provided that there is a subset \hat{U} of $\hat{X} - \mathcal{S}$ so that $\inf_{(u, P_\tau) \in \hat{U}} d((u, P_\tau), \mathcal{S}) > 0$ and $\lim_{t \rightarrow \infty} d(\pi(u, P_\tau, t), \hat{U}) = 0$ for all $(u, P_\tau) \in \hat{X} - \mathcal{S}$.

As noted in the introduction, π being permanent by the definition above implies that (2.1) is permanent under the criteria given in the introduction. To establish that π is permanent, we employ the Hale-Waltman acyclicity theorem [11]. The acyclicity theorem applies to a point dissipative semiflow π with the property that $\pi(\cdot, t)$ is compact for $t > 0$ (such as ours) when there is a certain partial knowledge of the geometry of the semiflow in the interior at a distinguished set in a complete metric space. In our case, $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$ is the complete metric space, \hat{X} the distinguished set, and $\hat{X} - \mathcal{S}$ its interior. The partial knowledge needed for a determination of permanence by the acyclicity theorem is expressed in terms of the omega limit set $\omega(\mathcal{S})$ of the boundary \mathcal{S} of \hat{X} where, for our purposes, $\omega(\mathcal{S})$ is defined in a nonstandard manner as $\cup_{(u, P_\tau) \in \mathcal{S}} \omega((u, P_\tau))$. First of all, $\omega(\mathcal{S})$ must have an *isolated covering*, by which we mean that it can be written as $\cup_{n=1}^k M_n$, where the M_n are pairwise disjoint compact isolated invariant sets, each of which is isolated both for π and its restriction π_∂ to \mathcal{S} . Secondly, $\omega(\mathcal{S})$ must be *acyclic*, meaning there is no subcollection $\{M_{n_1}, \dots, M_{n_r}\}$ of $\{M_1, \dots, M_k\}$ which is chained together by the semiflow π in the sense that $M_{n_1} = M_{n_r}$ and for each $i \in \{1, \dots, r-1\}$

there is $u \in S - (M_{n_i} \cup M_{n_{i+1}})$ so that $u \in W^u(M_{n_i}) \cap W^s(M_{n_{i+1}})$, where $W^u(M_{n_i})$ is the unstable manifold of M_{n_i} and $W^s(M_{n_{i+1}})$ is the stable manifold of $M_{n_{i+1}}$. Then the Hale-Waltman acyclicity theorem asserts that if $\omega(S)$ is isolated and acyclic, π is permanent provided $W^s(M_n) \cap (\hat{X} - S) = \phi$ for $n = 1, \dots, k$.

Summarizing, in the context of (2.1)–(2.2), subject to (H1)–(H6), the Hale-Waltman acyclicity theorem may be stated as follows: π is permanent provided that $\omega(S)$ has an acyclic isolated covering $\cup_{n=1}^k M_n$ with the property that $W^s(M_n) \cap (\hat{X} - S) = \phi$ for $n = 1, \dots, k$. This last condition is that π is unstable at M_n with respect to the interior of the distinguished set \hat{X} .

In order to apply the Hale-Waltman result, we must

- (i) find a candidate for the covering, i.e., identify M_1, \dots, M_k ;
- (ii) verify the acyclicity and isolatedness of the covering;
- (iii) establish the required instability conditions.

We essentially perform (i) in the next section. The acyclicity will follow immediately, and we obtain the isolatedness by showing each M_n has a neighborhood which contains no full orbit for π distinct from M_n . The instability condition at M_n will be a consequence of showing that in $\hat{X} - S$ near M_n at least one of the population densities evolves in time away from M_n . In biological terms, M_n is invisable by the species in question.

3. Analysis of subsystems. The sets M_n necessarily lie in $\partial([C_{0+}^1(\bar{\Omega})]^3) \times S^1$. It follows from the construction of \hat{X} and the strong maximum principle that if $(u, P_\tau) = (u_1, u_2, u_3, P_\tau) \in M_n$, then $u_i \equiv 0$ for at least one $i \in \{1, 2, 3\}$. Consequently, in order to employ the acyclicity theorem to assert that π is permanent, consideration must be given to the one and two equation subsystems of (2.1) arising from the assumption that some $u_i \equiv 0$. Here our analysis is greatly facilitated by the theory of periodic-parabolic boundary value problems as developed by Hess, Lazer and others and recorded in [14, 15, 19] among other sources. (See [14] for a rather complete treatment with a substantial list of references.)

The fundamental observation underlying the theory of periodic-parabolic boundary value problems is that of Lazer [19] that the eigen-

value problem

$$(3.1) \quad \begin{aligned} \frac{\partial v}{\partial t} - d\Delta v - \tilde{f}(x, t)v &= \mu v \quad \text{in } \Omega \times \mathbf{R} \\ v &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

has a unique eigenvalue μ (necessarily real) admitting an eigenfunction v which is positive on $\Omega \times \mathbf{R}$ and T -periodic in t , so long as the reaction coefficient \tilde{f} is of class $C^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbf{R})$ for some $\alpha \in (0, 1)$ and is T -periodic in t . The asymptotic behavior of nonnegative solutions to

$$(3.2) \quad \begin{aligned} \frac{\partial u}{\partial t} &= d\Delta u + uf(x, t, u) \quad \text{in } \Omega \times (0, \infty) \\ u &= 0 \quad \text{or } \partial\Omega \times (0, \infty) \end{aligned}$$

is consequently determined so long as (H1)–(H6) hold. In particular, it is shown in [14] that (3.2) admits a unique globally attracting T -periodic positive solution \bar{u} provided $\mu < 0$ in (3.1) with $\tilde{f}(x, t) = f(x, t, 0)$ and that all nonnegative solutions to (3.2) converge uniformly to 0 on $\bar{\Omega}$ as $t \rightarrow \infty$ if $\mu \geq 0$ in (3.1).

It is clear that the restriction of (2.1) arising under the assumption that two of the u_i 's vanish identically is of the form (3.2). Consequently, we may identify some of the isolated invariant sets M_n by converting (3.2) into a semi-dynamical system (which we will call n for convenience) and finding $\omega((u_0, P_{\tau_0}))$. We have the following result.

Lemma 3.1. *If $u_0 \not\equiv 0$ and $(u, P_\tau) \in \omega((u_0, P_{\tau_0}))$, then*

- (i) $u(x) = \bar{u}(x, \tau)$ if $\mu < 0$ in (3.1);
- (ii) $u(x) \equiv 0$ if $\mu \geq 0$ in (3.1).

Proof. (ii) is evident from the preceding observations so we shall show only (i). Let us first show that we may assume $\tau_0 = 0$. There exist $\{t_n\} \rightarrow +\infty$ so that

$$\pi(u_0, P_{\tau_0}, t_n) \longrightarrow (u, P_\tau) \quad \text{as } n \rightarrow \infty.$$

If $t_n > T - \tau_0$,

$$\begin{aligned} \pi(u_0, P_{\tau_0}, t_n) &= \pi(\pi(u_0, P_{\tau_0}, T - \tau_0), t_n - (T - \tau_0)) \\ &= \pi(\tilde{u}_0, P_0, t_n - (T - \tau_0)) \end{aligned}$$

and $t_n - (T - \tau_0) \rightarrow \infty$ as $n \rightarrow \infty$.

So let us now assume $\tau_0 = 0$. For $t > 0$, let $[[t]] = kT$, where $kT \leq t < (k + 1)T$. Notice that $\pi(u_0, P_0, t_n) = \pi(\pi(u_0, P_0, [[t_n]]), t_n - [[t_n]])$ and that if $[[t_n]] = k_n T, \pi(u_0, P_0, [[t_n]]) = (S^{k_n} u_0, P_0)$, where S^n is the n th iteration of the natural Poincaré map. By [14, Theorem 28.1], $S^n u_0 \rightarrow \bar{u}(x, 0)$ as $n \rightarrow \infty$. Hence, so does $S^{k_n} u_0$. Since $t_n - [[t_n]]$ is bounded, it must have a convergent subsequence, converging to \bar{t} , say. Continuity of π implies for this subsequence that $\pi(u_0, P_0, t_n) \rightarrow \pi(\bar{u}(x, 0), P_0, \bar{t}) = (\bar{u}(x, \bar{t}), P_{\bar{t}})$. Consequently, $\tau = \bar{t}$ and $u(x) = \bar{u}(x, \tau)$ as required. \square

When (2.1) is restricted by the assumption that one of the u_i 's vanishes, there arises a two species competition system of the form

$$\begin{aligned}
 (3.3) \quad & \frac{\partial u}{\partial t} = D_1 \Delta u + uf(x, t, u, w) \\
 & \frac{\partial w}{\partial t} = D_2 \Delta w + wg(x, t, u, w) \\
 & u = 0 = w \quad \text{on } \partial\Omega \times (0, \infty),
 \end{aligned}
 \quad \text{in } \Omega \times (0, \infty)$$

with (H1)–(H6) holding. Solution trajectories to such systems preserve the order relation on pairs (u, w) given by $(u_1, w_1) \leq (u_2, w_2)$ if and only if $u_1 \leq u_2$ and $w_1 \geq w_2$. This feature of (3.3) makes it possible to obtain a particularly nice form of permanence for (3.3), called compressivity by Hess and Lazer [15], under appropriate conditions. Specifically, suppose first that $\mu_1 < 0$ and $\mu_2 < 0$ when

$$\begin{aligned}
 (3.4) \quad & \frac{\partial v}{\partial t} - D_1 \Delta v - f(x, t, 0, 0)v = \mu_1 v, \\
 & v = 0 \quad \text{in } \Omega \times \mathbf{R} \quad \text{on } \partial\Omega \times \mathbf{R}
 \end{aligned}$$

and

$$\begin{aligned}
 (3.5) \quad & \frac{\partial z}{\partial t} - D_2 \Delta z - g(x, t, 0, 0)z = \mu_2 z \\
 & z = 0 \quad \text{in } \Omega \times \mathbf{R} \quad \text{on } \partial\Omega \times \mathbf{R}
 \end{aligned}$$

admit positive T -periodic eigenfunctions v and z , respectively. Having $\mu_1 < 0$ in (3.4) and $\mu_2 < 0$ in (3.5) implies that

$$\begin{aligned}
 (3.6) \quad & \frac{\partial u}{\partial t} = D_1 \Delta u + uf(x, t, u, 0) \quad \text{in } \Omega \times (0, \infty) \\
 & u = 0 \quad \text{on } \partial\Omega \times (0, \infty)
 \end{aligned}$$

and

$$(3.7) \quad \begin{aligned} \frac{\partial w}{\partial t} &= D_2 \Delta w + wg(x, t, 0, w) \quad \text{in } \Omega \times (0, \infty) \\ w &= 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned}$$

admit globally attracting positive T -periodic solutions \bar{u} and \bar{w} , respectively. Then suppose further that $\bar{\mu}_1 < 0$ and $\bar{\mu}_2 < 0$ when

$$(3.8) \quad \begin{aligned} \frac{\partial \phi}{\partial t} - D_1 \Delta \phi - f(x, t, 0, \bar{w}(x, t))\phi &= \bar{\mu}_1 \phi \quad \text{in } \Omega \times \mathbf{R} \\ \phi &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

and

$$(3.9) \quad \begin{aligned} \frac{\partial \rho}{\partial t} - D_2 \Delta \rho - g(x, t, \bar{u}(x, t), 0)\rho &= \bar{\mu}_2 \rho \quad \text{in } \Omega \times \mathbf{R} \\ \rho &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

admit positive T -periodic eigenfunctions ϕ and ρ , respectively. Then there are componentwise positive and T -periodic solutions $(\underline{u}, \underline{w})$ and (\bar{u}, \bar{w}) to (3.3) with $(\underline{u}(\cdot, 0), \underline{w}(\cdot, 0)) \leq (\bar{u}(\cdot, 0), \bar{w}(\cdot, 0))$ (and hence $(\underline{u}(\cdot, t), \underline{w}(\cdot, t)) \leq (\bar{u}(\cdot, t), \bar{w}(\cdot, t))$ for all $t > 0$) so that, for any initial data (u_0, w_0) with $u_0 \not\equiv 0, w_0 \not\equiv 0, S^n((u_0, w_0))$ converges to the order interval $[(\underline{u}(\cdot, 0), \underline{w}(\cdot, 0)), (\bar{u}(\cdot, 0), \bar{w}(\cdot, 0))]$. (For details of these results, see [14] or [15].)

When one of the u_i 's in (2.1) vanishes identically, a system of the form (3.3) arises. We will be able to identify the remaining sets M_n from the preceding section by converting (3.3) into a semi-dynamical system π and finding $\omega((u_0, w_0, P_{\tau_0}))$. We have the following result.

Lemma 3.2. *Suppose $u_0 \not\equiv 0, w_0 \not\equiv 0$ and that $(u, w, P_\tau) \in \omega((u_0, w_0, P_{\tau_0}))$. Then if $\mu_1 < 0$ in (3.4), $\mu_2 < 0$ in (3.5), $\bar{\mu}_1 < 0$ in (3.8), and $\bar{\mu}_2 < 0$ in (3.9), $\underline{u}(x, \tau) \leq u(x) \leq \bar{u}(x, \tau)$ and $\bar{w}(x, \tau) \leq w(x) \leq \underline{w}(x, \tau)$ for all $x \in \bar{\Omega}$.*

Proof. As in the case of the proof of Lemma 3.1, we may assume that $\tau_0 = 0$. Then there are $\{t_n\}_{n=1}^\infty$ with $t_n \rightarrow \infty$ as $n \rightarrow \infty$ so that

$\pi(u_0, w_0, P_0, t_n) \rightarrow (u, w, P_\tau)$ as $n \rightarrow \infty$. Letting $[[t_n]]$ be defined as in Lemma 3.1, we have that $\pi(\pi(u_0, w_0, P_0, [[t_n]]), t_n - [[t_n]]) \rightarrow (u, w, P_\tau)$ as $n \rightarrow \infty$. Point dissipativity implies the boundedness of the sequence $\pi(u_0, w_0, P_0, [[t_n]] - T)$ as $n \rightarrow \infty$. Consequently, $\pi(\cdot, T)$ compact implies that $\pi(u_0, w_0, P_0, [[t_n]])$ has a convergent subsequence which we relabel if need be so that $\pi(u_0, w_0, P_0, [[t_n]]) \rightarrow (u^*(x), w^*(x), P_0)$. Since $S^n(u_0, w_0) \rightarrow [(\underline{u}(\cdot, 0), \underline{w}(\cdot, 0)), (\bar{u}(\cdot, 0), \bar{w}(\cdot, 0))]$, $\underline{u}(x, 0) \leq u^*(x) \leq \bar{u}(x, 0)$ and $\bar{w}(x, 0) \leq w^*(x) \leq \underline{w}(x, 0)$ on $\bar{\Omega}$. Continuity of π implies that $(u, w, P_\tau) = \pi(u^*, w^*, P_0, \tau)$. Hence the order preserving property of solution trajectories implies that $\underline{u}(x, \tau) \leq u(x) \leq \bar{u}(x, \tau)$ and $\bar{w}(x, \tau) \leq w(x) \leq \underline{w}(x, \tau)$, as required. \square

4. Permanence results. Under assumptions (H1)–(H6), as we have noted, (2.1) can be reformulated as a semiflow π on $[C^1_+(\bar{\Omega})]^3 \times S^1$. We now formulate conditions under which π is permanent. These conditions all are expressed in terms of the sign of the principal eigenvalue of problems of the form (3.1), where by principal eigenvalue of (3.1) we mean the unique and necessarily real-valued eigenvalue of (3.1) admitting an eigenfunction which is positive on $\Omega \times \mathbf{R}$ and T periodic in t .

We first require:

(P1) The principal eigenvalue μ_i of

$$(4.1) \quad \begin{aligned} \frac{\partial v_i}{\partial t} - d_i \Delta v_i - f_i(x, t, 0, 0, 0)v_i &= \mu_i v_i \quad \text{in } \Omega \times \mathbf{R} \\ v_i &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

is negative for $i = 1, 2, 3$.

We know from Section 3 that if (P1) holds there is a unique globally attracting positive T -periodic solution \bar{u}_i of

$$(4.2) \quad \begin{aligned} \frac{\partial u_i}{\partial t} &= d_i \Delta u_i + \tilde{f}_i(x, t, u_i)u_i \quad \text{in } \Omega \times (0, \infty) \\ u_i &= 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned}$$

$i = 1, 2, 3$, where $\tilde{f}_1(x, t, u_1) = f_1(x, t, u_1, 0, 0)$, $\tilde{f}_2(x, t, u_2) = \tilde{f}_2(x, t, 0, u_2, 0)$ and $\tilde{f}_3(x, t, u_3) = f_3(x, t, 0, 0, u_3)$.

We next require:

(P2) The principal eigenvalue μ_{ij} of

$$(4.3) \quad \begin{aligned} \frac{\partial w_{ij}}{\partial t} - d_i \Delta w_{ij} - \tilde{f}_{ij}(x, t) w_{ij} &= \mu_{ij} w_{ij} \quad \text{in } \Omega \times \mathbf{R} \\ w_{ij} &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

is negative, for $i, j = 1, 2, 3, i \neq j$, where $\tilde{f}_{12}(x, t) = f_1(x, t, 0, \bar{u}_2(x, t), 0)$, $\tilde{f}_{13}(x, t) = f_1(x, t, 0, 0, \bar{u}_3(x, t))$, $\tilde{f}_{21}(x, t) = f_2(x, t, \bar{u}_1(x, t), 0, 0)$, $\tilde{f}_{23}(x, t) = f_2(x, t, 0, 0, \bar{u}_3(x, t))$, $\tilde{f}_{31}(x, t) = f_3(x, t, \bar{u}_1(x, t), 0, 0)$ and $\tilde{f}_{32}(x, t) = f_3(x, t, 0, 0, \bar{u}_3(x, t))$.

If (P1) and (P2) hold, then, in particular, we have $\mu_1 < 0, \mu_2 < 0, \mu_{12} < 0$ and $\mu_{21} < 0$. It follows from Section 3 that the system

$$(4.4) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + f_1(x, t, u_1, u_2, 0) u_1 \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + f_2(x, t, u_1, u_2, 0) u_2 \\ u_1 &= 0 = u_2 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \quad \text{in } \Omega \times (0, \infty)$$

admits componentwise positive T -periodic solutions $(\underline{u}_1(x, t), \underline{u}_2(x, t))$ and $(\bar{u}_1(x, t), \bar{u}_2(x, t))$ with $\underline{u}_1(x, t) \leq \bar{u}_1(x, t)$ and $\underline{u}_2(x, t) \geq \bar{u}_2(x, t)$ for $x \in \bar{\Omega}$ and $t \in \mathbf{R}$. Moreover, if $[v, w]$ denotes an order interval in $C_{0+}^1(\bar{\Omega})$, these solutions have the property that any solution $(u_1(x, t), u_2(x, t))$ to (4.4) arising from componentwise nonnegative nontrivial initial data is such that the distance from $u_1(x, t)$ to the order interval $[\underline{u}_1(x, t), \bar{u}_1(x, t)]$ and the distance from $u_2(x, t)$ to the order interval $[\bar{u}_2(x, t), \underline{u}_2(x, t)]$ both tend to zero as t tends to infinity. Moreover, by (P1) and (P2), there are analogous pairs of componentwise positive T -periodic solutions for each of the other two-equation subsystems of (2.1). Let us denote them $(\underline{u}_1(x, t), \underline{u}_3(x, t))$ and $(\bar{u}_1(x, t), \bar{u}_3(x, t))$ and $(\underline{u}_2(x, t), \underline{u}_3(x, t))$ and $(\bar{u}_2(x, t), \bar{u}_3(x, t))$, respectively, where $\underline{u}_1(x, t) \leq \bar{u}_1(x, t), \underline{u}_2(x, t) \leq \bar{u}_2(x, t), \underline{u}_3(x, t) \geq \bar{u}_3(x, t)$ and $\underline{u}_3(x, t) \geq \bar{u}_3(x, t)$ for $x \in \bar{\Omega}$ and $t \in \mathbf{R}$.

The preceding considerations show that if (P1) and (P2) hold and $\omega(S)$ is as in Section 2, then

$$\begin{aligned} \omega(S) &= \bigcup_{n=1}^7 M_n, \text{ where} \\ M_1 &= \{(0, 0, 0) \times S^1\}, \\ M_2 &= \{((\bar{u}_1(x, \tau), 0, 0), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\}, \\ M_3 &= \{((0, \bar{u}_2(x, \tau), 0), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\}, \\ M_4 &= \{((0, 0, \bar{u}_3(x, \tau)), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\}, \\ M_5 &\subseteq \{((\underline{\tilde{u}}_1(x, \tau), \underline{\tilde{u}}_2(x, \tau), 0), (\bar{u}_1(x, \tau), \\ &\quad \bar{u}_2(x, \tau), 0)), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\} \\ M_6 &\subseteq \{((\underline{\tilde{u}}_1(x, \tau), 0, \underline{\tilde{u}}_3(x, \tau)), (\bar{u}_1(x, \tau), 0, \\ &\quad \bar{u}_3(x, \tau))), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\} \\ M_7 &\subseteq \{((0, \underline{\tilde{u}}_2(x, \tau), \underline{\tilde{u}}_3(x, \tau)), (0, \bar{u}_2(x, \tau), \\ &\quad \bar{u}_3(x, \tau))), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\}. \end{aligned}$$

Additionally, the considerations show that $\omega(S)$ is, in fact, acyclic.

In order to employ the Hale-Waltman acyclicity theorem to conclude that π is permanent, $\omega(S)$ must satisfy the two additional criteria noted in Section 2, namely that $\omega(S)$ is isolated and that $W^s(M_n) \cap (\hat{X} - S) = \phi$ for $n = 1, \dots, 7$. For such to obtain, we require:

(P3) The principal eigenvalue $\tilde{\mu}_i$ of

$$(4.5) \quad \begin{aligned} \frac{\partial z_i}{\partial t} - d_i \Delta z_i - f_i(x, t) z_i &= \tilde{\mu}_i z \quad \text{in } \Omega \times \mathbf{R} \\ z_i &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

is negative, for $i = 1, 2, 3$, where

$$\begin{aligned} \tilde{f}_1(x, t) &= f_1(x, t, 0, \bar{u}_2(x, t), \underline{\tilde{u}}_3(x, t)), \\ \tilde{f}_2(x, t) &= f_2(x, t, \bar{u}_1(x, t), 0, \underline{\tilde{u}}_3(x, t)), \end{aligned}$$

and

$$\tilde{f}_3(x, t) = f_3(x, t, \tilde{u}_1(x, t), \tilde{u}_2(x, t), 0).$$

We may now establish:

Theorem 4.1. *Suppose hypotheses (H1)–(H6) hold for (2.1), and let π denote the associated semiflow on $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$. Then if (P1), (P2) and (P3) hold, π is permanent.*

Remark. (i) Figure 4.1 illustrates the invasibility conditions we require in order to assert that π is permanent.

(ii) Before proving Theorem 4.1, we shall need the following auxiliary lemma.

Lemma 4.2. *Suppose $\gamma \in C^{\alpha, \alpha/2}(\bar{\Omega} \times [0, T])$ for some $\alpha \in (0, 1)$ and T -periodic in t and that $\bar{d} > 0$. Let λ be the principal eigenvalue of*

$$\begin{aligned} \frac{\partial \phi}{\partial t} - \bar{d}\Delta\phi - \gamma(x, t)\phi &= \lambda\phi \quad \text{in } \Omega \times \mathbf{R} \\ \phi &= 0 \quad \text{on } \partial\Omega \times \mathbf{R} \end{aligned}$$

with associated positive T -periodic eigenfunction ϕ , and assume $\lambda < 0$. Suppose for some $\varepsilon \in (0, -\lambda)$ that $u(x, t)$ satisfies the differential inequality

$$\frac{\partial u}{\partial t} \geq \bar{d}\Delta u + [\gamma(x, t) - \varepsilon]u$$

for $t \in [t_0, t_1]$. Then if, for some $k > 0$,

$$u(x, t_0) \geq k\phi(x, t_0)$$

for $x \in \bar{\Omega}$, $u(x, t) \geq ke^{-(\lambda+\varepsilon)(t-t_0)}\phi(x, t)$ for $t \in [t_0, t_1]$.

Proof of Lemma 4.2. Let $v(x, t) = ke^{-(\lambda+\varepsilon)(t-t_0)}\phi(x, t)$. Then

$$\begin{aligned} &\left\{ \frac{\partial u}{\partial t} - \bar{d}\Delta u - [\gamma(x, t) - \varepsilon]u \right\} - \left\{ \frac{\partial v}{\partial t} - \bar{d}\Delta v - [\gamma(x, t) - \varepsilon]v \right\} \\ &= \frac{\partial u}{\partial t} - \bar{d}\Delta u - [\gamma(x, t) - \varepsilon]u - ke^{-(\lambda+\varepsilon)(t-t_0)} \\ &\quad \cdot [\lambda\phi(x, t) - \lambda\phi(x, t) - \varepsilon\phi(x, t) + \varepsilon\phi(x, t)] \geq 0. \end{aligned}$$

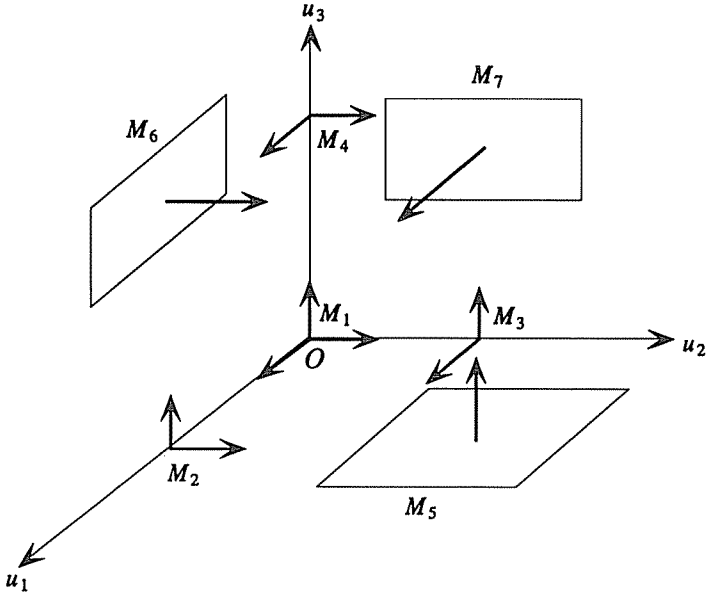


FIGURE 4.1. The eigenvalue sign conditions (invasibilities) postulated in (P1)–(P3) of Theorem 4.1 are indicated by the arrows. Notice that there are 12 such conditions all total: three on M_1 (the origin), two each on M_2, M_3 and M_4 (the single species global attractors absent competition), and one each on M_5, M_6 and M_7 (the global attractors for pairwise competition).

The result now follows from a standard comparison theorem for single reaction-diffusion equations. Compare with [6, Lemma 4.2]. \square

Proof of Theorem 4.1. As previously noted, $\omega(S)$ is acyclic. Consequently, to establish that $\omega(S)$ is isolated and that $W^s(M_n) \cap (\hat{X} - S) = \emptyset$ for $n \in \{1, 2, 3, 4, 5, 6, 7\}$, we need only to show that M_n is isolated relative to $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$ and that $W^s(M_n) \cap [(int [C_{0+}^1(\bar{\Omega})]^3) \times S^1] = \emptyset$ for $n \in \{1, 2, 3, 4, 5, 6, 7\}$. There is a substantial amount of symmetry to the arguments, and so we will present only representative cases. We shall show that M_4 is isolated with respect to $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$ and that $W^s(M_5) \cap [(int [C_0^1(\bar{\Omega})]^3) \times S^1] = \emptyset$.

Suppose that every neighborhood of M_4 contains a full orbit. Suppose that the projection $(u_1(x, t), u_2(x, t), u_3(x, t))$ of such an orbit into

$[C_{0+}^1(\bar{\Omega})]^3$ lies in the u_3 -axis in a small neighborhood of M_4 . The α -limit set of this orbit is nonempty and cannot intersect M_4 , since M_4 is a global attractor. So if every neighborhood of M_4 contains a full orbit, it must be the case that along the projection $(u_1(x, t), u_2(x, t), u_3(x, t))$ of such an orbit into $[C_{0+}^1(\bar{\Omega})]^3$ that $u_1(x, t) > 0$ for $x \in \Omega$ and $t \in \mathbf{R}$ or $u_2(x, t) > 0$ for $x \in \Omega$ and $t \in \mathbf{R}$.

We now show that such an orbit exists from every sufficiently small neighborhood U of M_4 . With no loss of generality, let us suppose that $u_2(x, t) > 0$ for $x \in \Omega$ and $t \in \mathbf{R}$. Consider the equation

$$\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + u_2 f_2(x, t, u_1, u_2, u_3).$$

By (P2), μ_{23} in (4.3) is negative. Let $\sigma > 0$ be given. The uniform continuity of \bar{u}_3 on $\bar{\Omega} \times \mathbf{R}$ implies that there is a $\delta > 0$ so that if $|t_1 - t_2| < \delta$, $|\bar{u}_3(x, t_1) - \bar{u}_3(x, t_2)| < \sigma/2$ for all $x \in \bar{\Omega}$. Let U be a γ -neighborhood of M_4 in $[C_0^1(\bar{\Omega})]^3 \times S^1$, where $\gamma < \sigma/2$ and γ is also small enough so that $|P_{t_1} - P_{t_2}| < \gamma$ implies that $|t_1 - t_2|$ can be assumed less than δ . If $\{(u_1(x, t), u_2(x, t), u_3(x, t), P_t) : t \in \mathbf{R}\}$ is a full orbit in U , then for each t there is a \bar{t} so that $\|(u_1(x, t), u_2(x, t), u_3(x, t)) - (0, 0, \bar{u}_3(x, \bar{t}))\|_{[C^1(\bar{\Omega})]^3} + |P_t - P_{\bar{t}}| < \gamma$. So we can assume \bar{t} is such that $|t - \bar{t}| < \delta$ and hence $\|(0, 0, \bar{u}_3(x, t)) - (0, 0, \bar{u}_3(x, \bar{t}))\|_{[C^1(\bar{\Omega})]^3} < \sigma/2$. So $\|(u_1(x, t), u_2(x, t), u_3(x, t)) - (0, 0, \bar{u}_3(x, t))\|_{[C^1(\bar{\Omega})]^3} < \gamma + \sigma/2 < \sigma$. Now let $\varepsilon \in (0, -\mu_{23})$. Choose $\sigma > 0$ (and hence choose $\gamma > 0$) small enough so that $\|(u_1(x, t), u_2(x, t), u_3(x, t)) - (0, 0, \bar{u}_3(x, t))\|_{[C^1(\bar{\Omega})]^3} < \sigma$ for all $t \in \mathbf{R}$ implies $|f_2(x, t, u_1(x, t), u_2(x, t), u_3(x, t)) - f_2(x, t, 0, 0, \bar{u}_3(x, t))| < \varepsilon$ for all $x \in \bar{\Omega}$ and $t \in \mathbf{R}$. Consequently, if U is a γ -neighborhood of M_4 in $[C_0^1(\bar{\Omega})]^3 \times S^1$ and $\{(u_1(x, t), u_2(x, t), u_3(x, t), P_t) : t \in \mathbf{R}\}$ is a full orbit contained in U ,

$$\frac{\partial u_2}{\partial t} \geq d_2 \Delta u_2 + [\bar{f}_{23}(x, t) - \varepsilon] u_2$$

for all t . Fix $t_0 \in \mathbf{R}$. Lemma 4.2 implies that $u_2(x, t) \geq k e^{-(\mu_{23} + \varepsilon)(t - t_0)} \phi(x, t)$ for $t \geq t_0$, where $\phi(x, t)$ is a positive T -periodic eigenfunction for (4.3) with $i, j = 2, 3$ and $k > 0$ such that $u_2(x, t_0) > k \phi(x, t_0)$ in Ω . Since $\mu_{23} + \varepsilon < 0$, u_2 is not bounded in t . It now follows that M_4 is isolated in $[C_{0+}^1(\bar{\Omega})]^3 \times S^1$.

Suppose now that there exists $(u, P_\tau) \in W^S(M_5)$ with $(u, P_\tau) \in \text{int} [C_{0+}^1(\bar{\Omega})]^3 \times S^1$. Then $\omega((u, P_\tau)) \neq \phi$ and $\omega((u, P_\tau)) \subseteq M_5$. So there

exists $(v, P_{\bar{\tau}}) \in \omega((u, P_{\tau}))$ such that $(v, P_{\bar{\tau}}) \in M_5$. Then there exists $t_n \rightarrow \infty$ as $n \rightarrow \infty$ so that $(\phi(u, \tau, \tau + t_n), P_{\tau+t_n}) \rightarrow ((v_1, v_2, 0), P_{\bar{\tau}})$ as $n \rightarrow \infty$. Now $(v, P_{\bar{\tau}}) \in M_5$ implies that $v_1(x) \leq \tilde{u}_1(x, \bar{\tau})$ and $v_2(x) \leq \tilde{u}_2(x, \bar{\tau})$. By (P3), we know $\tilde{\mu}_3 < 0$, where $\tilde{\mu}_3$ is as in (4.5). Let $\varepsilon \in (0, -\tilde{\mu}_3)$. Choose $\gamma > 0$ so that $f_3(x, t, \tilde{u}_1(x, t) + \gamma, \tilde{u}_2(x, t) + \gamma, \gamma) \geq f_3(x, t, \tilde{u}_1(x, t), \tilde{u}_2(x, t), 0) - \varepsilon$ for $(x, t) \in \bar{\Omega} \times \mathbf{R}$.

We claim that, for sufficiently large n , we must have

$$\begin{aligned} \phi_1(u, \tau, \tau + t_n)(x) &< \tilde{u}_1(x, \tau + t_n) + \gamma/2 \\ \phi_2(u, \tau, \tau + t_n)(x) &< \tilde{u}_2(x, \tau + t_n) + \gamma/2 \\ \phi_3(u, \tau, \tau + t_n)(x) &< \gamma/2 \end{aligned}$$

on $\bar{\Omega}$, where $\phi(u, \tau, \tau + t_n) = (\phi_1(u, \tau, \tau + t_n), \phi_2(u, \tau, \tau + t_n), \phi_3(u, \tau, \tau + t_n))$. Otherwise, we obtain a subsequence of times t_n (where we relabel if need be) and a corresponding sequence of points $\{x_n\} \subseteq \Omega$ so that one of the three inequalities fails at x_n . Without loss of generality, assume

$$\phi_1(u, \tau, \tau + t_n)(x_n) \geq \tilde{u}_1(x_n, \tau + t_n) + \gamma/2$$

for all n . We may assume $x_n \rightarrow \bar{x}$. We have that $\phi_1(u, \tau, \tau + t_n)(x_n) \rightarrow v_1(\bar{x})$ as $n \rightarrow \infty$. Since $P_{\tau+t_n} \rightarrow P_{\bar{\tau}}$, $\tilde{u}_1(x_n, \tau + t_n) \rightarrow \tilde{u}_1(\bar{x}, \bar{\tau})$. Hence, $v_1(\bar{x}) \geq \tilde{u}_1(\bar{x}, \bar{\tau}) + \gamma/2$, a contradiction which establishes our claim. As a consequence, for each large n , there must be an interval $(0, \delta_n)$ so that

$$(4.6) \quad \begin{aligned} \phi_1(u, \tau, \tau + t + t_n)(x) &< \tilde{u}_1(x, \tau + t + t_n) + \gamma \\ \phi_2(u, \tau, \tau + t + t_n)(x) &< \tilde{u}_2(x, \tau + t + t_n) + \gamma \\ \phi_3(u, \tau, \tau + t + t_n)(x) &< \gamma \end{aligned}$$

on $\bar{\Omega}$ for $t \in (0, \delta_n)$. Let $w_3(x, t) = \phi_3(u, \tau, \tau + t + t_n)(x)$. Then by (H4) and the choice of γ ,

$$\frac{\partial w_3}{\partial t} \geq d_3 \Delta w_3 + w_3 [f_3(x, t) - \varepsilon]$$

for $t \in (\tau + t_n, \tau + t_n + \delta_n)$. Moreover, this inequality continues to hold so long as (4.6) does. Lemma 4.2 implies that $w_3(x, t)$ grows

exponentially in t (with order $-(\tilde{\mu}_3 + \varepsilon)$). Therefore, there must be a time $t'_n > t_n$ so that one of the inequalities of (4.6) fails when $t = t'_n - t_n$. Hence the limit of $\pi((u, P_\tau), t'_n)$ as $n \rightarrow \infty$ is not in M_5 , contrary to our assumption. So $W^S(M_5) \cap (\text{int}[C_{0+}^1(\bar{\Omega})]^3 \times S^1) = \emptyset$. The Hale-Waltman acyclicity theorem may now be invoked to guarantee the permanence of π .

5. Globally attracting componentwise positive periodic solutions for two species competition models. In the preceding sections our examination of the asymptotics of the semiflow π associated with (2.1) when one of the species u_1, u_2, u_3 is absent led us to consider two-species competition systems. We established by means of the compressivity theory of Hess and Lazer [14, 15] combined with our construction of the semiflow π that the ω -limit set of the restricted semiflow is contained within a periodically varying family of order intervals in $[C_{0+}^1(\bar{\Omega})]^2$. This observation allowed us to identify "worst case" competition scenarios. A crucial ingredient in a determination that π is permanent is that the absent species will grow when introduced at a low density under such "worst case" competition scenarios. This is the content of (P3), in light of Lemma 4.2. In the biological literature, conditions which permit an absent species to grow when it is introduced at a low density are called "invasibility" conditions.

Of course, the "nicest" possible situation arises when the periodically varying order interval in $[C_{0+}^1(\bar{\Omega})]^2$ collapses to a periodic steady-state, since in such a case we do not need to overestimate the degree of competition to get a "clean" invasibility condition. As a consequence, the question arises of what conditions must be imposed on two-species subsystems, all of which are of the form (3.3), in order to get a unique globally attracting componentwise positive periodic orbit in each "face." An answer for the special case of (3.3) when $D_1 = D_2 = 1$ and

$$(5.1) \quad \begin{aligned} f(x, t, u, w) &= a(t) - bu - cw \\ g(x, t, u, w) &= d(t) - eu - fw \end{aligned}$$

is given in [14, p. 122]. The idea is to find conditions on $a(t), d(t), b, c, e$ and f sufficient to guarantee that (3.3)–(5.1) is compressive and that any componentwise positive periodic orbit of (3.3)–(5.1) is locally asymptotically stable. The theory of periodic parabolic boundary value

problems [14] then guarantees that there can be just one such orbit. Sufficient conditions for the asymptotic stability are available in the work of Fan and Leung [10]. However, the results of [10], as stated, are not applicable to (3.3) in its full generality since they do not allow for spatial heterogeneity. A careful examination of the proof in [10] shows that nevertheless the arguments can be readily modified to account for spatial heterogeneity by replacing expressions of a form such as

$$\sup_{\substack{x \in \Omega \\ t \in [0, T]}} F(t, u(x, t), w(x, t)) \quad \text{with} \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} F(x, t, u(x, t), w(x, t)).$$

Consequently, we have the following stability result.

Theorem 5.1. *Consider the system of reaction-diffusion equations*

$$(5.2) \quad \begin{aligned} \frac{\partial w_1}{\partial t} &= \sigma_1 \Delta w_1 + w_1 [a(x, t) + r_1(x, t, w_1, w_2)] \\ \frac{\partial w_2}{\partial t} &= \sigma_2 \Delta w_2 + w_2 [d(x, t) + r_2(x, t, w_1, w_2)] \\ w_1 = 0 &= w_2 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \quad \text{in } \Omega \times (0, \infty)$$

Assume:

- (i) $a, d \in C^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbf{R})$ for some $\alpha \in (0, 1)$ and a, d are T -periodic in t .
- (ii) $r_i(x, t, w_1, w_2)$ is continuous on $\bar{\Omega} \times \mathbf{R} \times \mathbf{R}_+^2$ for $i = 1, 2$.
- (iii) For each $(w_1, w_2) \in \mathbf{R}_+^2$, $h_i(x, t) = r_i(x, t, w_1, w_2) \in C^{\alpha, \alpha/2}(\bar{\Omega} \times \mathbf{R})$ for some $\alpha \in (0, 1)$ and T -periodic in t .
- (iv) The partial derivatives of r_i with respect to (w_1, w_2) are continuous in $\bar{\Omega} \times \mathbf{R} \times \mathbf{R}_+^2$ with $\partial r_i / \partial w_j < 0$ for $(x, t, w_1, w_2) \in \bar{\Omega} \times \mathbf{R} \times \mathbf{R}_+^2$, $i, j = 1, 2$.

Let $(w_1(x, t), w_2(x, t))$ be a componentwise positive T -periodic solution of (5.2). Then if

$$(5.3) \quad \begin{aligned} &\sup_{(x, t) \in \Omega \times \mathbf{R}} \frac{w_i(x, t) |(\partial r_j / \partial w_i)(x, t, w_1(x, t), w_2(x, t))|}{w_j(x, t) |(\partial r_j / \partial w_j)(x, t, w_1(x, t), w_2(x, t))|} \\ &< \inf_{(x, t) \in \Omega \times \mathbf{R}} \frac{w_i(x, t) |(\partial r_i / \partial w_i)(x, t, w_1(x, t), w_2(x, t))|}{w_j(x, t) |(\partial r_i / \partial w_j)(x, t, w_1(x, t), w_2(x, t))|} \\ &< \infty \end{aligned}$$

for each $1 \leq i, j \leq 2, i \neq j$, the solution (w_1, w_2) is locally asymptotically stable.

Note that (3.3) fits into this framework with $u = w_1, w = w_2, \sigma_i = D_i, a(x, t) = f(x, t, 0, 0), d(x, t) = g(x, t, 0, 0), r_1(x, t, w_1, w_2) = f(x, t, w_1, w_2) - f(x, t, 0, 0)$ and $r_2(x, t, w_1, w_2) = g(x, t, w_1, w_2) - g(x, t, 0, 0)$. Note also that when Theorem 5.1 holds in addition to (P1)–(P3), M_5, M_6 and M_7 in the proof of Theorem 4.1 reduce to periodic orbits (for instance M_5 becomes $\{((\tilde{u}_1(x, \tau), \tilde{u}_2(x, \tau), 0), P_\tau) : x \in \bar{\Omega}, \tau \geq 0\}$) and (P3) reduces to the invasibility of each species along the pertinent periodic orbit. As a consequence, a closer examination of the condition (5.3) when the system (5.2) is compressive seems warranted. We shall devote the remainder of this article to such an examination in the particular but illustrative case of T -periodic Lotka-Volterra interactions, where

$$(5.4) \quad r_1(x, t, w_1, w_2) = -[\alpha_1(x, t)w_1 + \beta_1(x, t)w_2]$$

and

$$r_2(x, t, w_1, w_2) = -[\beta_2(x, t)w_1 + \alpha_2(x, t)w_2].$$

Here $\alpha_i(x, t) > 0$ represents intraspecific competition or self-regulation and $\beta_i(x, t) > 0$ interspecific competition.

In light of the preceding sections, compressivity of (5.2)–(5.4) holds provided the principal eigenvalues for four particular periodic-parabolic differential operators are negative. Namely, we first require $\mu_a < 0$ and $\mu_d < 0$ where μ_a and μ_d represent the principal eigenvalues of the operators $\partial_t - \sigma_1 \Delta - a(x, t)$ and $\partial_t - \sigma_2 \Delta - d(x, t)$, respectively, each operator subject to homogeneous Dirichlet boundary data. A consequence of this first pair of eigenvalue sign conditions is the existence of unique, positive and T -periodic w_1^* and w_2^* satisfying

$$\begin{aligned} \frac{\partial w_1^*}{\partial t} &= \sigma_1 \Delta w_1^* + w_1^* [a(x, t) - \alpha_1(x, t)w_1^*] \\ \frac{\partial w_2^*}{\partial t} &= \sigma_2 \Delta w_2^* + w_2^* [d(x, t) - \alpha_2(x, t)w_2^*]. \end{aligned}$$

Equations (5.2)–(5.4) are compressive if now, in addition, $\mu_{a-\beta_1 w_2^*} < 0$ and $\mu_{d-\beta_2 w_1^*} < 0$ where $\mu_{a-\beta_1 w_2^*}$ and $\mu_{d-\beta_2 w_1^*}$ denote the principal

eigenvalues of the operators $\partial_t - \sigma_1 \Delta - (a(x, t) - \beta_1(x, t)w_2^*(x, t))$ and $\partial_t - \sigma_2 \Delta - (d(x, t) - \beta_2(x, t)w_1^*(x, t))$, respectively, each operator again subject to homogeneous Dirichlet boundary data.

Suppose now that $\mu_a < 0$, $\mu_d < 0$, $\mu_{a-\beta_1 w_2^*} < 0$ and $\mu_{d-\beta_2 w_1^*} < 0$ and that (w_1, w_2) is a componentwise positive T -periodic solution to (5.2)–(5.4). Upper-lower solution arguments for single reaction diffusion equations guarantee that $w_1 < w_1^*$ and $w_2 < w_2^*$, while upper-lower solution arguments for competitive systems (see [9, 14], for example) guarantee that

$$w_1 > w_{1*} \quad \text{and} \quad w_2 > w_{2*},$$

where w_{1*} and w_{2*} are the unique positive T -periodic solutions of

$$(5.5) \quad \frac{\partial w_1}{\partial t} = \sigma_1 \Delta w_1 + w_1 [a(x, t) - \alpha_1(x, t)w_1 - \beta_1(x, t)w_2^*(x, t)]$$

and

$$(5.6) \quad \frac{\partial w_2}{\partial t} = \sigma_2 \Delta w_2 + w_2 [d(x, t) - \beta_2(x, t)w_1^*(x, t) - \alpha_2(x, t)w_2],$$

respectively, whose existence is guaranteed by the negativity of $\mu_{a-\beta_1 w_2^*}$ and $\mu_{d-\beta_2 w_1^*}$. The strong maximum principle [21] now guarantees that, for any such (w_1, w_2) ,

$$(5.7) \quad c_1 < \frac{w_{1*}}{w_2^*} < \frac{w_1}{w_2} < \frac{w_1^*}{w_{2*}} < k_1$$

and

$$(5.8) \quad c_2 < \frac{w_{2*}}{w_1^*} < \frac{w_2}{w_1} < \frac{w_2^*}{w_{1*}} < k_2$$

on $\Omega \times [0, T]$, where c_i and k_i are positive constants, $i = 1, 2$. Condition (5.3) for (w_1, w_2) is the assertion that

$$(5.9) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_1(x, t) \beta_2(x, t)}{w_2(x, t) \alpha_2(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_1(x, t) \alpha_1(x, t)}{w_2(x, t) \beta_1(x, t)}$$

and that

$$(5.10) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_2(x, t) \beta_1(x, t)}{w_1(x, t) \alpha_1(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_2(x, t) \alpha_2(x, t)}{w_1(x, t) \beta_2(x, t)}.$$

In light of (5.7) and (5.8), (5.9) and (5.10) hold provided

$$(5.11) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_1^*(x, t)}{w_{2*}(x, t)} \cdot \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\beta_2(x, t)}{\alpha_2(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_{1*}(x, t)}{w_2^*(x, t)} \cdot \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\alpha_1(x, t)}{\beta_1(x, t)}$$

and

$$(5.12) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_2^*(x, t)}{w_{1*}(x, t)} \cdot \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\beta_1(x, t)}{\alpha_1(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_{2*}(x, t)}{w_1^*(x, t)} \cdot \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\alpha_2(x, t)}{\beta_2(x, t)}.$$

We may now employ (5.11) and (5.12) to obtain computable conditions on the coefficients of (5.2)–(5.4) which guarantee that any componentwise positive T -periodic solution of (5.2)–(5.4) satisfies (5.3). By [14, Lemma 15.7], $\mu_{a-\beta_1 w_2^*}$ and $\mu_{d-\beta_2 w_1^*}$ are continuous in their arguments. Consequently, since w_1^* and w_2^* do not depend on β_1 and β_2 , there will be $\beta_1^0(x, t)$ and $\beta_2^0(x, t)$ small enough so that $\mu_{a-\beta_1^0 w_2^*} < 0$ and $\mu_{d-\beta_2^0 w_1^*} < 0$. Moreover, if $\beta_1(x, t) < \beta_1^0(x, t)$, $\mu_{a-\beta_1 w_2^*} < \mu_{a-\beta_1^0 w_2^*}$ and $w_{1*} > w_{1*}^0$, where w_{1*}^0 is the solution of (5.5) corresponding to $\beta_1^0(x, t)$ and, if $\beta_2(x, t) < \beta_2^0(x, t)$, $\mu_{d-\beta_2 w_1^*} < \mu_{d-\beta_2^0 w_1^*}$ and $w_{2*} > w_{2*}^0$, where w_{2*}^0 is the solution of (5.6) corresponding to $\beta_2^0(x, t)$. So now fix β_1^0 and β_2^0 . Then, for any $\beta_1(x, t) < \beta_1^0(x, t)$ and $\beta_2(x, t) < \beta_2^0(x, t)$, we have (viewing $\sigma_i, a(x, t), d(x, t), \alpha_i(x, t)$ as fixed)

$$\frac{w_{1*}^0}{w_2^*} < \frac{w_{1*}}{w_2^*} < \frac{w_1}{w_2} < \frac{w_1^*}{w_{2*}} < \frac{w_1^*}{w_{2*}^0}.$$

So (5.11)–(5.12) (and thus (5.3)) holds for any componentwise positive T -periodic solution of (5.2)–(5.4) so long as $\beta_1(x, t)$ and $\beta_2(x, t)$ are small enough so that

$$(5.13) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_1^*(x, t)}{w_{2*}^0(x, t)} \cdot \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\beta_2(x, t)}{\alpha_2(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_{1*}^0(x, t)}{w_2^*(x, t)} \cdot \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\alpha_1(x, t)}{\beta_1(x, t)}$$

and

$$(5.14) \quad \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_2^*(x, t)}{w_{1*}^0(x, t)} \cdot \sup_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\beta_1(x, t)}{\alpha_1(x, t)} < \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{w_{2*}^0(x, t)}{w_1^*(x, t)} \cdot \inf_{\substack{x \in \Omega \\ t \in [0, T]}} \frac{\alpha_2(x, t)}{\beta_2(x, t)}.$$

Summarizing, we have the following result.

Corollary 5.2. *Consider (5.2) with r_1 and r_2 as given in (5.4). Suppose $\mu_a < 0$ and $\mu_d < 0$, and let w_1^* and w_2^* denote the unique positive, T -periodic in time solutions to*

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= \sigma_1 \Delta w_1 + w_1[a(x, t) - \alpha_1(x, t)w_1] \\ \frac{\partial w_2}{\partial t} &= \sigma_2 \Delta w_2 + w_2[d(x, t) - \alpha_2(x, t)w_2] \end{aligned}$$

in $\Omega \times \mathbf{R}$ with $w_1^* = 0 = w_2^*$ on $\partial\Omega \times \mathbf{R}$. Let $\beta_1^0(x, t)$ and $\beta_2^0(x, t)$ be positive, T -periodic in time and such that $\mu_a - \beta_1^0 w_2^* < 0$ and $\mu_d - \beta_2^0 w_1^* < 0$, and let w_{1*}^0 and w_{2*}^0 denote the unique positive T -periodic in time solutions to

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= \sigma_1 \Delta w_1 + w_1[a(x, t) - \alpha_1(x, t)w_1 - \beta_1^0(x, t)w_2^*(x, t)] \\ \frac{\partial w_2}{\partial t} &= \sigma_2 \Delta w_2 + w_2[d(x, t) - \beta_1^0(x, t)w_1^*(x, t) - \alpha_2(x, t)w_2] \end{aligned}$$

in $\Omega \times \mathbf{R}$ with $w_{1*}^0 = 0 = w_{2*}^0$ on $\partial\Omega \times \mathbf{R}$. Then any component-wise positive T -periodic in time solution to (5.2) and (5.4) is locally asymptotically stable so long as $\beta_i(x, t) < \beta_i^0(x, t)$ for $i = 1, 2$ and (5.13)–(5.14) holds.

Corollary 5.2 has an immediate biological interpretation. Namely, the two species competitive interaction modeled by (5.2) and (5.4) tends over time to a periodic fluctuation (which remains positive in both species' densities) so long as the interspecific competition (as measured by β_1 and β_2) is weak in comparison to self-regulation (as measured by α_1 and α_2). Conditions (5.13) and (5.14) do allow for temporal and spatial variation in the interaction parameters of the system. However,

they impose a uniform upper bound on such variation. It would be of interest to replace (5.13) and (5.14) with conditions formulated in terms of integrals indicating a bound on the interaction parameters in some average sense. If such were the case, it would be possible to allow larger pointwise variations in the inter- and intraspecific interaction terms and still have the two species competition tend over time to a componentwise positive periodic fluctuation in the densities of the species in question. More generally, our formulation of permanence for (2.1) in terms of the eigenvalue sign conditions (P1)–(P3), i.e., invasibility conditions, raises the question of how temporal periodicity and spatial heterogeneity interact to mediate coexistence. In attacking such a problem, one is quickly led to analyze the relative contributions of space and time to eigenvalues of the form $\mu_{g(x,t)}$, where $g : \bar{\Omega} \times \mathbf{R} \rightarrow \mathbf{R}$ is T -periodic in time. There is a valuable initial investigation of this topic in [14], but much more research is needed if the interplay between temporal and spatial effects is to be thoroughly understood.

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