# Permanence in periodic–parabolic ecological systems with spatial heterogeneity

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**Abstract**

We establish sufficient conditions for permanence phenomena for a class of spatially heterogeneous periodic–parabolic systems arising from ecological models. The conditions are expressed in quantifiable ways in terms of the spectra of associated linear differential operators. In so doing, we connect asymptotic coexistence in such a system to the underlying biological assumptions about the model which are expressed in the parameters and coefficients of these operators.

## 1 Introduction.

In this article we are concerned with a class of reaction–diffusion models motivated by population dynamics. Namely, we consider systems of the form

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1 f_1(x,t,u_1,u_2) \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + u_2 f_2(x,t,u_1,u_2) \end{aligned} \tag{1}$$

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

$$u_1 = 0 = u_2 \tag{2}$$

on $\partial\Omega \times (0, \infty)$. In (1)–(2), $\Omega$ is a bounded domain in $\mathbb{R}^n$ with sufficiently smooth boundary ( say, of class $C^{3+\alpha}$ for some $\alpha > 0$), and $u_i(x,t)$ represents the population density of species $i$ at location $x \in \Omega$ and time $t > 0$. We use the Laplace operator $\Delta = \partial^2/\partial x_1^2 + \ldots + \partial^2/\partial x_n^2$ to represent the random motion of the species within $\Omega$, with diffusion coefficients $d_1 > 0$ and $d_2 > 0$, respectively, and $f_i(x, t, u_1, u_2)$ to represent the *per capita* growth law for species $i$ at location $x$, time $t$ and densities $u_1$ and $u_2$, $i = 1, 2$. A salient feature is that we require

$$f_i(x, t+T, u_1, u_2) = f_i(x, t, u_1, u_2) \tag{3}$$

for some $T > 0$, $i = 1, 2$, so as to idealize that the habitat and species interactions are periodic in time.

The question regarding (1)–(2) of fundamental interest in population dynamics is whether or not the model predicts the ultimate coexistence of species 1 and 2. These models have no nonzero equilibria. Consequently, the notion of a globally attracting (componentwise) positive equilibrium (a widely used mathematical prescription for coexistence in autonomous systems; by globally attracting we mean with respect to nonnegative, (componentwise) nontrivial initial data on $\Omega$) does not obtain in this situation. However, (1)–(2) may very well admit its natural analogue, a globally attracting (componentwise) positive periodic orbit. In this circumstance, it is reasonable to view the model as predicting the coexistence of the interacting species. Moreover, in corresponding single–species propagation models, namely

$$\frac{\partial u}{\partial t} = d\Delta u + uf(x, t, u) \tag{4}$$

in $\Omega \times (0, \infty)$ with $u = 0$ on $\partial\Omega \times (0, \infty)$, there are very natural conditions on $f$ that guarantee the existence of a globally attracting positive periodic orbit. Specifically, such an orbit exists (for appropriate values of $d$) if the per capita growth law is a decreasing function of the density and is in fact negative for large enough values of the density (uniformly in space and time). However, in the case of (1)–(2), such restrictions on $f_1(x, t, u_1, 0)$ and $f_2(x, t, 0, u_2)$ are not sufficient to guarantee the existence of a globally attracting (componentwise) positive periodic orbit for (1)–(2). Indeed, identifying conditions on $d_i$ and $f_i(x, t, u_1, u_2)$ to guarantee such is a formidable task. Moreover, for purposes of addressing the central population dynamical question, i.e., the asymptotic coexistence of the interacting species, having a globally attracting (componentwise) positive periodic orbit is an overly strong requirement. All that is really necessary is that trajectories to (1)–(2) emanating from nonnegative (componentwise) nontrivial data be *eventually* bounded away from $(0, 0)$ in an appropriate and uniform manner. Since both components of all trajectories vanish on the boundary of $\Omega$ for all positive time, a suitable notion of asymptotic coexistence is the existence of positive smooth functions $U_1$ and $U_2$ on $\Omega$ satisfying (2) and having negative outer normal derivatives $\partial U_i/\partial \nu$ on $\partial\Omega$ so that for any initial data $(u_1^0(x), u_2^0(x))$ on $\overline{\Omega}$ with $u_i^0(x) \gneqq 0$, the corresponding trajectory $(u_1(x,t), u_2(x,t))$ has $u_i(x,t) \geq U_i(x)$ on $\overline{\Omega}$ for all $t \geq t_0(u_i^0, u_2^0)$. This notion of asymptotic coexistence for (1)–(2) is usually called *uniform persistence*. If, additionally, there are smooth functions $V_1$ and $V_2$ on $\overline{\Omega}$ with $U_i < V_i$ on $\Omega$ such that $u_i(x,t) \leq V_i(x)$ on $\overline{\Omega}$ for all $t \geq t_0(u_1^0, u_2^0)$, (1)–(2) is said to be *permanent*. In this article, we take *permanence* as our notion of asymptotic coexistence, even though it is a seemingly stronger requirement than uniform persistence, because the hypotheses we impose and the techniques we employ to obtain uniform persistence simultaneously yield permanence.

A clarification is in order at this point. The formulation of permanence just given is tailored to (1)–(2). However, in the mathematical literature, permanence is most often viewed as a property that certain abstract dynamical systems possess. Consequently, in order to utilize the literature, we must first cast (1)–(2) in a dynamical systems framework. Since (1) is non–autonomous, the trajectories of (1)–(2) do not constitute a semi–flow (as do the trajectories for its autonomous analogue [4]). Consequently, in order to cast (1)–(2) in a dynamical systems context, a modification in the spirit of skew–product flows (see, for example [11]) is necessary. To this end, we can follow the recent work of Zhao and Hutson [12] on permanence for (1) (supplemented by homogeneous Neumann boundary data). Once the notion of permanence in the dynamical system framework is verified, it is of course necessary to show that the permanence of (1)–(2) in the sense originally described follows.

In the special case that $f_1$ and $f_2$ describe competitive interactions, an alternate approach to permanence, called *compressibility*, based on monotonicity, is available. This approach is due to Hess and Lazer [8]. (See also [7].) Many interactions of interest, for example, predation, are not suitably monotone, so that an alternate approach to permanence is needed in such cases. However, the results of [7] are posed in terms of spectral properties of appropriate linear differential operators. (The discovery by Lazer [10] of a principal eigenvalue for a periodic–parabolic linear differential operator and its refinement by Hess and his collaborators (see the discussion in [7, pp. 60–61]) is absolutely indispensible in this regard.) The approach we describe in this article also expresses sufficient conditions for permanence in (1)–(2) in terms of the spectra of linear differential operators associated with (1)–(2). In so doing, we connect asymptotic coexistence in the system described by (1)–(2) to the underlying biological assumptions expressed in the parameters of (1). Moreover, this connection is explicitly quantifiable and may be used to make meaningful biological observations. (See, for example [3], where such observations are made for the autonomous analogue of (1)–(2).)

The remainder of this article is structured as follows. In Section 2, we set up a framework for considering (1)–(2) as a suitable semi–dynamical system. To do so, some initial assumptions are made on the *per capita* growth rate terms $f_i$. At this stage, we make explicit the definition of permanence in the dynamical systems context and the criterion (the existence of a so–called "average Lyapunov functional" – see [9]) we use to assert permanence. In Section 3, we establish permanence in the dynamical systems context through the construction of an average Lyapunov function. The verity of the construction is dependent upon spectral properties of certain linear differential operators associated with (1)–(2). Consequently, the permanence results of this section are formulated in a manner analogous to the compressibilty results in [7], [8]; indeed, the results coincide when (1)–(2) represents a competitive interaction. Finally, in Section 4, we show that permanence for (1)–(2) in the dynamical systems context implies our original formulation of permanence for (1)–(2).

# 2 Dynamical systems framework.

We begin this section by establishing a suitable dynamical systems framework for the discussion of permanence for (1)–(2). Our development follows [4] and [12] closely. Consequently, keeping in mind the space constraints on this article, we present here only the barest possible outline and refer the interested reader to [1], [4] and [12] and the references therein for more detail.

Let us assume:

**(H1)** $\Omega \in \mathbb{R}^n$ is a bounded domain, with boundary $\partial\Omega$ uniformly of class $C^{3+\alpha}$.

**(H2)** Condition (3).

**(H3)** $f_i(x,t,u_1,u_2)$ is $C^3$ in all its arguments, $i = 1, 2$.

Under these assumptions, (1)–(2), supplemented by the initial condition $u_i(x,t_0) = \tilde{u}_i(x)$ for $x \in \overline{\Omega}$, where $t_0 \geq 0$, can be reformulated as the initial value problem

$$\begin{aligned} \dot{u} + Au &= F(t,u(t)) \\ u(t_0) &= \tilde{u} \end{aligned} \tag{5}$$

in the space $[C_0^0(\overline{\Omega})]^2$, where $u = (u_1, u_2)$ and $\tilde{u} = (\tilde{u}_1, \tilde{u}_2)$, $A$ is the infinitesimal generator of a semi–group derived from $\begin{pmatrix} -d_1\Delta & 0 \\ 0 & -d_2\Delta \end{pmatrix}$, and $F : [0,\infty) \times [C_0^0(\overline{\Omega})]^2 \to [C_0^0(\overline{\Omega})]^2$ is given by

$$F(t,u) = (u_1(x)f_1(x,t,u_1,u_2), u_2(x)f_2(x,t,u_1,u_2)). \tag{6}$$

Moreover, for any $\tilde{u} \in [C_0^0(\overline{\Omega})]^2$ and $t_0 \geq 0$, (5) admits a unique solution $\phi(\tilde{u},t_0,t)$ on a maximal interval $[t_0, \beta(\tilde{u},t_0))$ so that $\phi(\tilde{u},t_0,t_0) = \tilde{u}$, $\phi(\tilde{u},t_0,t)$ is a classical solution of (1)–(2) on $(t_0, \beta(\tilde{u}, t_0))$ and if $\beta(\tilde{u}, t_0) < \infty$, $\lim_{t\to\infty} \|\phi(\tilde{u}, t_0, t)\|_{[C_0^0(\overline{\Omega})]^2} = \infty$. That such is the case follows as in [4] and [12] and the references there in. Additionally, it follows from [6, p.61 ] that if the components of $\tilde{u}$ are nonnegative, so are those of $\phi(\tilde{u}, t_0, t)$. (Our Hypothesis **(H3)** is stronger than is absolutely necessary. However, it is a clean and easily understood conditon sufficient for our purposes here. For a more precise accounting, see [1].)

Now assume additionally:

**(H4)** For any $\alpha > 0$, there is a $B(\alpha) > 0$ so that if $u \in [C_0^0(\overline{\Omega})]_+^2$ and $\|u\|_{[C_0^0(\overline{\Omega})]^2} \leq \alpha$, $\|\phi(u, \tau, t)\|_{[C_0^0(\overline{\Omega})]^2} \leq B(\alpha)$ for all $\tau \geq 0$ and $t \geq \tau$.

**(H5)** There is a $B > 0$ so that if $u \in [C_0^0(\overline{\Omega})]_+^2$ and $\tau \geq 0$, there corresponds $t_0 = t_0(u, \tau)$ so that $\|\phi(u, \tau, t)\|_{[C_0^0(\overline{\Omega})]^2} \leq B$ for $t \geq t_0$.

Here $[C_0^0(\overline{\Omega})]_+^2$ denotes the positive cone of $[C_0^0(\overline{\Omega})]^2$; i.e., those elements whose components are nonnegative. It follows from **(H4)** that $\phi(u, \tau, t)$ exists on $[\tau, \infty)$ for any $u \in [C_0^0(\overline{\Omega})]_+^2$. Now, let $\tau > 0$ be given, and consider

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i f_i(x, t + \tau, u_1, u_2) \tag{7}$$

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

$$u_i(x, t + \tau) = 0 \tag{8}$$

on $\partial\Omega \times (0, \infty)$, $i = 1, 2$. Let $F_\tau(t, u) = F(t + \tau, u)$ where $F$ is as in (6), and denote by $\varphi(u, F_\tau, t)$ the unique solution to (7)–(8) such that $\varphi(u, F_\tau, 0) = u$. It follows as in [12] that $\phi(u, \tau, t) = \varphi(u, F_\tau, t - \tau)$ for $t \geq \tau$.

We may now formulate (1)–(2) as a semi–dynamical system. Let $S^1 = \{P_\tau \mid \tau \in \mathbb{R}_+\}$, where $P_\tau = e^{2\pi i \tau / T}$. Then $[C_0^0(\overline{\Omega})]_+^2 \times S^1$ admits the metric

$$d((u, P_\tau), (v, P_s)) = \|u - v\|_{[C_0^0(\overline{\Omega})]^2} + \sqrt{1 - \cos\left(\frac{2\pi(\tau - s)}{T}\right)}$$

under which it is complete. Define $\pi : [C_0^0(\overline{\Omega})]_+^2 \times S^1 \times \mathbb{R}_+ \to [C_0^0(\overline{\Omega})]_+^2 \times S^1$ by

$$\begin{aligned} \pi(u, P_\tau, t) &= (\phi(u, \tau, \tau + t), P_{\tau+t}) \\ &= (\varphi(u, F_\tau, t), P_{\tau+t}). \end{aligned}$$

Then, as in [12], $\pi$ is a semi–flow. Modifying the arguments in [4] slightly so as to take into account the $S^1$ component of the semi–flow, we see that $\pi(.,t) : [C_0^0(\overline{\Omega})]_+^2 \times S^1 \to [C_0^0(\overline{\Omega})]_+^2 \times S^1$ is compact for any $t > 0$ and that there is a nonempty bounded set $U \in [C_0^0(\overline{\Omega})]_+^2 \times S^1$ so that for any $(u, P_\tau) \in [C_0^0(\overline{\Omega}]_+^2 \times S^1$, $\pi(u, P_\tau, t) \in U$ for all $t \geq t_0 = t_0(u, P_\tau)$. This last property is called point dissipativity. Since $\pi$ is point dissipative and $\pi(.,t)$ is compact for $t > 0$, a result of Bilotti and Lasalle [2] (cf. [5]) guarantees the existence of a compact set $\mathcal{A}$ in $[C_0^0(\overline{\Omega})]_+^2 \times S^1$ invariant under $\pi$ so that $\lim_{t\to\infty} d(\pi(u, P_\tau, t), \mathcal{A}) = 0$ for any $(u, P_\tau) \in [C_0^0(\overline{\Omega})]_+^2 \times S^1$, i.e. a global attractor. As observed in [4], the regularity theory of parabolic differential equations allows us (under the same assumptions **(H1)**–**(H5)**) to view $\pi$ as a semi–flow on the space $[C_0^1(\overline{\Omega})]_+^2 \times S^1$. $\pi$ is point dissipative and compact for $t > 0$ fixed, relative to $[C_0^1(\overline{\Omega})]_+^2 \times S^1$. Consequently, there is a global attractor for $\pi$ in $[C_0^1(\overline{\Omega})]_+^2 \times S^1$, which we again call $\mathcal{A}$. If we now let $X = \overline{\pi(B(\mathcal{A}, \varepsilon), [t_0, \infty))}$, where $B(\mathcal{A}, \varepsilon)$ is an open neighborhood of $\mathcal{A}$ in $[C_0^1(\overline{\Omega})]_+^2 \times S^1$ and $t_0 > 0$ is arbitrary, we find as in [4] that $X$ is compact and positively invariant. (It is worth noting at this point that we work in $[C_0^1(\overline{\Omega})]_+^2 \times S^1$ primarily to benefit from the fact that the positive cone in $[C_0^1(\overline{\Omega})]^2$ has a nonempty interior, whereas the positive cone in $[C_0^0(\overline{\Omega})]^2$ does not. In the case of (1) supplemented by homogeneous Neumann boundary data, as in [12], such an adjustment is unnecessary, since the positive cone in $[C^0(\overline{\Omega})]^2$ has nonempty interior.)

The upshot of the preceding observations is that all the interesting dynamics for $\pi$ occur in $X$. Let $t' > 0$ be fixed and consider $\tilde{X} = \pi(X, t')$. Then $\tilde{X}$ is compact and positively invariant. Moreover, we may express $\tilde{X}$ as $\tilde{X} = \left(\tilde{X} \cap \{\text{int}[C_0^1(\overline{\Omega})]_+^2 \times S^1\}\right) \cup \left(\tilde{X} \cap \{\partial[C_0^1(\overline{\Omega})]_+^2 \times S^1\}\right)$. It follows from the parabolic maximum principle and the definition of $\tilde{X}$ that $\tilde{X} \cap \{\text{int}[C_0^1(\overline{\Omega})]_+^2 \times S^1\}$ and $\tilde{X} \cap \{\partial[C_0^1(\overline{\Omega})]_+^2 \times S^1\}$ are positively invariant. Let $S = \tilde{X} \cap \{\partial[C_0^1(\overline{\Omega})]_+^2 \times S^1\} = \tilde{X} \cap \partial\{[C_0^1(\overline{\Omega})]_+^2 \times S^1\}$. Then if $(u, P_\tau) \in S$ and $u = (u_1, u_2)$ either $u_1 \equiv 0$ or $u_2 \equiv 0$. We say that $\pi$ is *permanent* provided there is a subset $\tilde{U}$ of $\tilde{X} - S$ so that $\inf_{(u,P_\tau)\in\tilde{U}} \overline{d}((u, P_\tau), S) > 0$ and $\lim_{t\to 0} \overline{d}(\pi(u, P_\tau, t), \tilde{U}) = 0$ for all $(u, P_\tau)$ in $\tilde{X} - S$, where $\overline{d}$ is the metric in $[C_0^1(\overline{\Omega})]^2 \times S^1$.

There are several ways to determine that $\pi$ is permanent. We shall use the following criterion, usually referred to as the method of an average Lyapunov functional. For more background on this approach, see [9].

**Theorem 2.1** *Suppose that $\pi$, $\tilde{X}$ and $S$ are described as above. Suppose that $\rho : \tilde{X} - S \to \mathbb{R}_+$ is continous, strictly positive, and bounded, and for $(u, P_\tau) \in S$ define*

$$\alpha(t, (u, P_\tau)) = \liminf_{\substack{(v,P_s)\to(u,P_\tau) \\ (v,P_s)\in\tilde{X}-S}} \left( \frac{\rho(\pi(v, P_s, t))}{\rho((v, P_s))} \right).$$

*Then $\pi$ is permanent if*

$$\sup_{t>0} \alpha(t, (u, P_\tau)) > \begin{cases} 1 & (u, P_\tau) \in \omega(S) \\ 0 & (u, P_\tau) \in S, \end{cases}$$

*where $\omega(S)$ denotes the $\omega$–limit set of $S$.*

To complete the reformulation of (1)–(2) in a dynamical systems context, we need to give conditions on $f_i(x,t,u_1,u_2)$, $i = 1,2$, under which **(H4)** and **(H5)** hold. The following sufficient conditions hold in situations in which both species exhibit a self–regulation mechanism, and include many instances of predation and competition. The sufficiency of the conditions (for guaranteeing **(H4)** and **(H5)** ) may be verified using sub– and super–solutions techniques and comparison principles as in [4].

**Theorem 2.2** *Suppose there exists a Lipschtiz function $F_1^*(t,u_1)$ which is $T$–periodic in $t$ so that*

$$\sup\{f_1(x,t,u_1,u_2) \mid x \in \overline{\Omega},\ u_2 \geq 0\} \leq F_1^*(t,u_1) \tag{9}$$

*and there exist $a > 0$ and $M_0 > 0$ so that*

$$F_1^*(t,u_1) \leq -a \ \text{ if } u_1 \geq M_0. \tag{10}$$

*Then if $(u_1,u_2)$ is a solution of (1)–(2) for $t \in (0,R]$ with nonnegative initial data, then $0 \leq u_1 \leq y$ on $(0,R]$ where $y$ satisfies*

$$\frac{du}{dt} = yF_1^*(t,y)\ ,\ y(0) = y_0 \geq \sup\{u_1(x,0) \mid x \in \overline{\Omega}\}.$$

*Moreover, if $M_1 > M_0$ and $(u_1,u_2)$ is a solution to (1)–(2) for all time $t > 0$, then $u_1 \leq M_1$ for $t$ sufficiently large, and if $u_1(x,0) \leq M_1$, then $u_1 \leq M_1$ for all $t > 0$.*

**Theorem 2.3** *Suppose that $f_1$ satisfies the hypotheses of Theorem 2.2 and that for any $M > 0$ there exist a Lipschitz function $F_2^*(t,u_2,M)$ which is $T$–periodic in $t$ so that*

$$\sup\{f_2(x,t,u_1,u_2) \mid x \in \overline{\Omega}\ ,\ 0 \leq u_1 \leq M\} \leq F_2^*(t,u_2,M) \tag{11}$$

*for $t \in [0,T]$ and constants $M_2(M) > 0$ and $a(M) > 0$ so that*

$$F_2^*(t,u_2,M) \leq -a(M) \ \text{ if } u_2 \geq M_2(M) \tag{12}$$

*Then solutions to (1)–(2) corresponding to componentwise nonnegative initial data exist for all $t > 0$. Moreover, if $M_1$ is as in Theorem 2.2 and $M_3 > M_2(M_1)$, $u_2 \leq M_3$ for $t$ sufficiently large, and if $u_1(x,0) \leq M_1$ and $u_2(x,0) \leq M_3$, then $u_1(x,t) \leq M_1$ and $u_2(x,t) \leq M_3$ for all $t > 0$.*

## 3 Average Lyapunov functional.

We now employ Theorem 2.1 to assert that $\pi$ is permanent. We see from the statement of Theorem 2.1 that we need to know $\omega(S)$. It follows from the definition of $S$ that we need to determine the asymptotic behavior of solutions when one of the species is extinct. To this end, consider

$$\begin{aligned} \frac{\partial u}{\partial t} &= d\Delta u + uf(x,t,u) \quad \text{in } \Omega \times (0,\infty) \\ u &= 0 \qquad\qquad\qquad\quad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{13}$$

where $f$ is $T$–periodic in $t$ and satisfies

**(L1)** $f$ is $C^3$ in all arguments.

**(L2)** $f(x,t,v) > f(x,t,u)$ if $0 \leq v < u$.

**(L3)** $f(x,t,u) < 0$ if $u \geq K$ for some $K > 0$.

By [8](cf. [7]) the linear eigenvalue problem

$$\begin{aligned} \frac{\partial v}{\partial t} - d\Delta v - f(x,t,0)v = \mu v \qquad & \text{in} \quad \Omega \times \mathbb{R} \\ v = 0 \qquad & \text{on} \quad \partial\Omega \times \mathbb{R} \\ v(x,t+T) = v(x,t) \quad & \text{in} \quad \Omega \times \mathbb{R} \end{aligned} \tag{14}$$

admits a unique $\mu \in \mathbb{R}$ having associated eigenfunction $v \in C^{2+\alpha,1+\frac{\alpha}{2}}(\overline{\Omega} \times [0,T])$ with $v(x,t) > 0$ for $x \in \Omega$ and $t \in \mathbb{R}$. We have the following result.

**Theorem 3.1** *Consider (13) and suppose that $f$ is $T$–periodic in $t$ and satisfies* **(L1)–(L3)**. *Then (13) admits a positive $T$–periodic solution $u(x,t)$ if and only if $\mu$ in (14) is negative. Additionally:*

(i) *If $\mu < 0$, $u$ is the only such solution. Moreover, if $w(x) \in C^1(\overline{\Omega})$ with $w \gneqq 0$ and $u_w$ denotes the solution of (13) with $u_w(x,0) = w(x)$, and if $\varepsilon > 0$ is given, there is $t_0 = t_0(w)$ so that $\|u(x,t) - u_w(x,t)\|_{C^1(\overline{\Omega})} < \varepsilon$ for all $t > t_0$ (i.e., $u$ is globally asymptotically stable with respect to nonnegative initial data).*

(ii) *If $\mu > 0$, $0$ is globally asymptotically stable with respect to nonnegative initial data.*

*Proof:* The special case when $f(x,t,u) = m(x,t) - b(x,t)u$ and $b(x,t) > 0$ on $\overline{\Omega} \times [0,T]$ is given in Theorem 28.1 of [7]. Properties **(L2)** and **(L3)** are the essential features of $m(x,t) - b(x,t)u$ needed in the proof. Consequently, it is relatively easy to adapt the proof there to the general situation and we leave this to the interested reader.

Theorem 3.1 enables us to determine $\omega(S)$. $(u, P_\tau) \in S$ implies that $u = (u_1, 0)$ or $(0, u_2)$. Consequently, Theorem 3.1 implies that if $(u, P_\tau) \in \omega(S)$, $(u, P_\tau) \in \{(0,0,P_\tau),\ (u_1^*(.,\tau),0,P_\tau),\ (0,u_2^*(.,\tau),P_\tau)\}$ , where $u_1^*$ is the unique globally attracting positive $T$–periodic solution of

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1\Delta_1 + u_1 f_1(x,t,u_1,0) \quad \text{in} \quad \Omega \times (0,\infty) \\ u_1 &= 0 \qquad\qquad\qquad\qquad\qquad \text{on} \quad \partial\Omega \times (0,\infty) \end{aligned} \tag{15}$$

and $u_2^*$ is the unique globally attracting $T$–periodic solution of

$$\begin{aligned} \frac{\partial u_2}{\partial t} &= d_2\Delta u_2 + u_2 f_2(x,t,0,u_2) \quad \text{in} \quad \Omega \times (0,\infty) \\ u_2 &= 0 \qquad\qquad\qquad\qquad\qquad \text{on} \quad \partial\Omega \times (0,\infty) \end{aligned} \tag{16}$$

should either exist. Now assume

**(N1)** For $i = 1, 2$, $d = d_i$ and $f(x,t,0) = f_i(x,t,0,0)$ are such that $\mu = \overline{\mu_i} < 0$ in (14).

Let $u_1^*(x,t) = u_1^* = u_1^*(\overline{\mu_1})$ and $u_2^*(x,t) = u_2^* = u_2^*(\overline{\mu_2})$ denote the unique positive $T$–periodic solutions of (15) and (16) respectively. Let $g_1(x,t) = f_1(x,t,0,u_2^*(x,t))$ and $g_2(x,t) = f_2(x,t,u_1^*(x,t),0)$. Then $g_i \in C^{2+\alpha,\,1+\frac{\alpha}{2}}(\overline{\Omega} \times [0,T])$ and there is a unique $\tilde{\mu}_i \in \mathbb{R}$ so that

$$\begin{aligned} \frac{\partial v}{\partial t} - d_i\Delta v - g_i(x,t)v &= \mu_i v \qquad \text{in} \quad \Omega \times \mathbb{R} \\ v &= 0 \qquad\quad \text{on} \quad \partial\Omega \times \mathbb{R} \\ v(x,t+T) &= v(x,t) \quad \text{in} \quad \Omega \times \mathbb{R} \end{aligned} \tag{17$i$}$$

and

$$\begin{aligned} -\frac{\partial w}{\partial t} - d_i\Delta w - g_i(x,t)w &= \mu_i w \qquad \text{in} \quad \Omega \times \mathbb{R} \\ w &= 0 \qquad\quad \text{on} \quad \partial\Omega \times \mathbb{R} \\ w(x,t+T) &= w(x,t) \quad \text{in} \quad \Omega \times \mathbb{R} \end{aligned} \tag{18$i$}$$

admit solutions $\psi_i(x,t) > 0$ and $\psi_i^*(x,t) > 0$ in $\Omega \times \mathbb{R}$, respectively, $i = 1, 2$ [10]. (Note that (18) is the adjoint equation to (17).) Assume

**(N2)** For $i = 1, 2$, $d_i$ and $g_i(x,t)$ are such that $\tilde{\mu}_i < 0$ in (17) (or in (18)).

We may now state our main result.

**Theorem 3.2** *Assume* **(H1)–(H5)** *and that* $f_1(x,t,u_1,0)$ *and* $f_2(x,t,0,u_2)$ *satisfy* **(L2)–(L3)**. *Then if* $f_1(x,t,0,0) > f_2(x,t,0,u_2)$ *for* $u_2 > 0$ *and* **(N1)** *and* **(N2)** *hold,* $\pi$ *is permanent.*

*Proof:* We employ Theorem 2.1. To that end, let $\tilde{X}$ and $S$ be as in Section 2, and define $\rho : \tilde{X} - S \to \mathbb{R}_+$ by

$$\rho\left((v_1, v_2, P_\tau)\right) = \left(\int_\Omega v_1(x)\psi_1^*(x,\tau)dx\right)^{\beta_1} \left(\int_\Omega v_2(x)\psi_2^*(x,\tau)dx\right)^{\beta_2} \tag{19}$$

where $\psi_i^*$ is a normalized eigenfunction for (18) with $\psi_i^*(x,t) > 0$ in $\Omega \times \mathbb{R}$, $i = 1, 2$, and $\beta_i > 0$ is a positive constant to be determined, $i = 1, 2$. The right hand side of (19) may be written

$$\exp\left[\beta_1 \log \int_\Omega v_1(x)\psi_1^*(x,\tau)dx + \beta_2 \log \int_\Omega v_2(x)\psi_2^*(x,\tau)dx\right] \tag{20}$$

For $(u_1, u_2, P_{\tau_0}) \in S$, define

$$\alpha(t, (u_1, u_2, P_{\tau_0})) = \liminf_{\substack{(v_1, v_2, P_\tau) \to (u_1 u_2, P_{\tau_0}) \\ (v_1, v_2, P_\tau) \in \tilde{X} - S}} \left(\frac{\rho(\pi((v_1, v_2, P_\tau), t))}{\rho((v_1, v_2, P_\tau))}\right).$$

If $\sup_{t>0} \alpha(t, (u_1, u_2, P_{\tau_0})) > 0$ for $(u_1, u_2, P_{\tau_0}) \in S$ and $\sup_{t>0} \alpha(t, (u_1, u_2, P_{\tau_0})) > 1$ for $(u_1, u_2, P_{\tau_0}) \in \omega(S)$, Theorem 2.1 implies that $\pi$ is permanent.

By (20), we have

$$\frac{\rho(\pi((v_1, v_2, P_\tau), t))}{\rho((v_1, v_2, P_\tau))} = \frac{\rho(v_1(x,t), v_2(x,t), P_{\tau+t})}{\rho((v_1(x), v_2(x), P_\tau))}$$

$$= \exp\left\{\beta_1[\log \int_\Omega v_1(x,t)\psi_1^*(x,\tau+t)dx - \log \int_\Omega v_1(x,0)\psi_1^*(x,\tau)dx].\right.$$

$$\left. + \beta_2[\log \int_\Omega v_2(x,t)\psi_2^*(x,\tau+t)dx - \log \int_\Omega v_2(x,0)\psi_2^*(x,\tau)dx]\right\}$$

$$= \exp\left\{\beta_1 \int_0^t \left(\frac{\frac{d}{ds}\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx}{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx}\right) ds + \right.$$

$$\left.\beta_2 \int_0^t \left(\frac{\frac{d}{ds}\int_\Omega v_2(x,s)\psi_2^*(x,\tau+s)dx}{\int_\Omega v_2(x,s)\psi_2^*(x,\tau+s)dx}\right) ds\right\}$$

$$= \exp\left\{\sum_{i=1}^{2} \beta_i \int_0^t \left(\frac{\int_\Omega([(\partial v_i/\partial s)(x,s)]\psi_i^*(x,\tau+s) + v_i(x,s)(\partial\psi_i^*/\partial s)(x,\tau+s)dx}{\int_\Omega v_i(x,s)\psi_i^*(x,\tau+s)dx}\right) ds\right\}.$$

But now

$$\int_\Omega [\frac{\partial v_1}{\partial s}(x,s)\psi_1^*(x,\tau+s) + v_1(x,s)\frac{\partial \psi_1^*}{\partial s}(x,\tau+s)]dx$$

$$= \int_\Omega [d_1 \Delta v_1(x,s) + v_1(x,s) f_1(x, \tau+s, v_1(x,s), v_2(x,s))] \psi_1^*(x, \tau+s) dx -$$
$$\int_\Omega v_1(x,s)[d_1 \Delta \psi_1^*(x,\tau+s) + f_1(x,\tau+s,0,u_2^*(x,\tau+s))\psi_1^*(x,\tau+s) + \mu_1 \psi_1^*(x,\tau+s)]dx$$
$$= \int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)[f_1(x,\tau+s,v_1(x,s),v_2(x,s)) - f_1(x,\tau+s,0,u_2^*(x,\tau+s)) - \mu_1]dx$$

and analogously for $i = 2$. So

$$\frac{\rho(\pi((v_1, v_2, P_\tau))}{\rho((v_1, v_2, P_\tau))} =$$
$$\exp\{\beta_1 \int_0^t (\frac{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)[f_1(x,\tau+s,v_1(x,s),v_2(x,s)) - f_1(x,\tau+s,0,u_2^*(x,\tau+s))}{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx}$$
$$- \frac{\mu_1]dx}{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx})ds$$
$$+\beta_2 \int_0^t (\frac{\int_\Omega v_2(x,s)\psi_2^*(x,\tau+s)[f_2(x,\tau+s,v_1(x,s),v_2(x,s)) - f_2(x,\tau+s,u_1^*(x,\tau+s),0)}{\int_\Omega v_2(x,s)\psi_2^*(x,\tau+s)dx}$$
$$- \frac{\mu_2]dx}{\int_\Omega v_2(x,s)\psi_2^*(x,\tau+s)dx})ds\}$$

It follows from the compactness of $\tilde{X}$ and the properties of $f_1$ and $f_2$ that, for example, $f_1(x,\tau+s,v_1(x,s),v_2(x,s)) - f_1(x,\tau+s,0,u_2^*(x,\tau+s)) - \mu_1$ is uniformly bounded below in $x$, $\tau$ and $s$. Consequently, $\sup_{t>0} \alpha(t,u_1,u_2,P_{\tau_0}) > 0$ for any $(u_1,u_2,P_{\tau_0}) \in S$ for any fixed choice of $\beta_1 > 0$ and $\beta_2 > 0$. To see that $\sup_{t>0} \alpha(t,u_1,u_2,P_{\tau_0}) > 1$ for any $(u_1,u_2,P_{\tau_0}) \in \omega(S)$, recall that $(u_1,u_2,P_{\tau_0}) \in \omega(S)$ implies $(u_1,u_2,P_{\tau_0}) \in \{(0,0,\tau_0),(u_1^*(.,\tau_0),0,P_{\tau_0}),(0,u_2^*(.,\tau_0),P_{\tau_0})\}$. If $v_1(x,s) \to 0$, $v_2(x,s) \to 0$ and $\tau \to \tau_0$, $f_1(x,\tau+s,v_1(x,s),v_2(x,s)) - f_1(x,\tau+s,0,u_2^*(x,\tau+s)) - \mu_1 \to f_1(x,\tau_0+s,0,0) - f_1(x,\tau_0+s,0,u_2^*(x,\tau_0+s)) - \mu_1 \geq -\mu_1$ since $f_1(x,\tau_0+s,0,0) - f_1(x,\tau_0+s,u_2^*(x,\tau_0+s)) \geq 0$. Additionally, $f_2(x,\tau+s,v_1(x,s),v_2(x,s)) - f_2(x,\tau+s,u_1^*(x,\tau+s),0) - \mu_2 \to f_2(x,\tau_0+s,0,0) - f_2(x,\tau_0+s,u_1^*(x,\tau_0+s),0) - \mu_2$. If we choose $\beta_1 > 0$ and $\beta_2 > 0$ so that $\beta_1(-\mu_1) + \beta_2(-\mu_2) + \beta_2 \inf_{(x,t)} [f_2(x,t,0,0) - f_2(x,t,u_1^*(x,t),0)] > \beta_3 > 0$ it follows that $\sup_{t>0} \alpha(t,0,0,P_{\tau_0}) > 1$, independent of $\tau_0$. If $v_1(x,s) \to u_1^*(x,\tau_0+s)$, $v_2(x,s) \to 0$ and $\tau \to \tau_0$, observe that

$$\int_0^t \left( \frac{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx}{\int_\Omega v_1(x,s)\psi_1^*(x,\tau+s)dx} \right) ds$$
$$= \log \int_\Omega v_1(x,t)\psi_1^*(x,\tau+t)dx - \log \int_\Omega v_1(x,0)\psi_1^*(x,\tau)dx$$
$$\to \log[\int_\Omega u_1(x,\tau_0+t)\psi_1^*(x,\tau_0+t)dx / \int_\Omega u_1(x,\tau_0)\psi_1^*(x,\tau_0)dx]$$

On the other hand, $f_2(x,\tau+s,v_1(x,s),v_2(x,s)) - f_2(x,\tau+s,u_1^*(x,\tau+s),0) - \mu_2 \to f_2(x,\tau_0+s,u_1^*(x,\tau_0+s),0) - f_2(x,\tau_0+s,u_1^*(x,\tau_0+s),0) - \mu_2 = -\mu_2$.
Consequently,

$$\alpha(T,(u_1^*(.,\tau_0),0,P_{\tau_0})) = \exp\left\{\beta_1 \log\left[\frac{\int_\Omega u_1(x,\tau_0+T)\psi_1^*(x,\tau_0+T)dx}{\int_\Omega u_1(x,\tau_0)\psi_1^*(x,\tau_0)dx}\right] + \beta_2(-\mu_2)T\right\}$$

$$= \exp \beta_2(-\mu_2)T > 1$$

So $\sup_{t>0} \alpha(t,(u_1^*(.,\tau_0),0,P_{\tau_0})) > 1$ for any $\beta_2 > 0$, independent of $\tau_0$. Since $\mu_1 < 0$, an analogous argument shows that $\sup_{t>0} \alpha(t,(0,u_2^*(.,\tau_0),P_{\tau_0})) > 1$ for any $\beta_1 > 0$, independent of $\tau_0$. Consequently, Theorem 2.1 implies that $\pi$ is permanent.

# 4 Permanence of $\pi$ implies permanence.

We complete our discussion by showing that if the semiflow $\pi$ is permanent according to the definition in Section 2, then (1)–(2) is permanent in the sense described in the Introduction. Namely, there are smooth functions $U_i \le V_i$ on $\overline{\Omega}$, $i = 1,2$, with $U_i > 0$ in $\Omega$ and $\partial U_i/\partial\nu < 0$ on $\partial\Omega$, so that if $(u_1(x,t),u_2(x,t))$ is a solution to (1)–(2) with $u_i(x,0) \gneqq 0$ for $i = 1,2$, there corresponds $t_0 = t_0(u_1(x,0),u_2(x,0)) > 0$ so that $U_i \le u_i(x,t) \le V_i$ for all $t \ge t_0$. It follows readily from the dissipativity of $\pi$ that any sufficiently large positive constant is a suitable choice for $V_i$. To obtain $U_i$, we establish the following result. In what follows $e(x)$ is the unique function solving

$$\begin{aligned} -\Delta\phi &= 1 \quad \text{on} \quad \partial\Omega \\ \phi &= 0 \quad \text{on} \quad \partial\Omega. \end{aligned} \tag{21}$$

**Theorem 4.1** *Suppose that the semiflow* $\pi : [C_0^1(\overline{\Omega})]_+^2 \times S^1 \times \mathbb{R}_+ \to [C_0^1(\overline{\Omega})]_+^2 \times S^1$ *induced by (1)–(2) is permanent. Then there exists* $\alpha > 0$ *so that for any solution to (1)–(2)* $(u_1(x,t),u_2(x,t))$ *with* $u_i(x,0) \gneqq 0$ *for* $i = 1,2$ *there corresponds* $t_0 = t_0(u_1(x,0),u_2(x,0)) > 0$ *so that*

$$u_i(x,t) > \alpha\, e(x) \quad on \quad \Omega \tag{22}$$

$$\frac{\partial u_i}{\partial\nu} < \alpha\frac{\partial e(x)}{\partial\nu} \quad on \quad \partial\Omega \tag{23}$$

*for all* $t \ge t_0$, $i = 1,2$.

*Remark:* By (21) and the strong maximum principle, $e(x) > 0$ in $\Omega$ and $\partial e/\partial\nu < -\gamma$ on $\partial\Omega$, where $\gamma > 0$ is constant. It follows from (22) that an appropriate choice for $U_i(x)$, $i = 1,2$, is $\alpha e(x)$.

*Proof:* Let $\mathcal{A}$, $\tilde{X}$, $S$ and $\tilde{U}$ be as in Section 2. It follows from the definition of $\tilde{U}$ that $\overline{\tilde{U}} \cap S = \emptyset$ and from the permanence of $\pi$ that $\mathcal{A} \subseteq \overline{\tilde{U}} \cup S$. Let $\tilde{\mathcal{A}} = \mathcal{A} \cap \overline{\tilde{U}}$. Then $\tilde{\mathcal{A}}$ is a compact invariant set for $\pi$. Moreover, since $\inf_{(u,P_\tau)\in\tilde{U}} \overline{d}((u,P_\tau),S) > 0$, it follows from [5] that $\lim_{t\to\infty}\left(\sup_{(u,P_\tau)\in\tilde{U}} \overline{d}(\pi(u,P_\tau,t),\tilde{\mathcal{A}})\right) = 0$. As a result, since the inequalities in (22) determine an open set in $C_0^1(\overline{\Omega})$ , we need only establish (22) for $u \in [C_0^1(\overline{\Omega})]_+^2$ with the property that $(u,P_\tau) \in \tilde{\mathcal{A}}$ for some $\tau \in \mathbb{R}$. For such a $u$, there is $(v,P_{\tau_1}) \in \tilde{\mathcal{A}}$, with $\tau_1 < \tau$, so that $\pi(v,P_{\tau_1},\tau-\tau_1) = (\varphi(v,F_{\tau_1},\tau-\tau_1),P_\tau) = (u,P_\tau)$. The strong maximum principle implies that $u_i(x) > 0$ in $\Omega$ and $\partial u_i(x)/\partial\nu < 0$ on $\partial\Omega$, $i = 1,2$, where $u = (u_1,u_2)$. It now follows that there is $\alpha(u) > 0$ so that $u_i(x) > \alpha(u)e(x)$ in $\Omega$ and $\partial u_i(x)/\partial\nu < \alpha(u)\partial e(x)/\partial\nu$ on $\partial\Omega$, $i = 1,2$. The compactness of $\tilde{\mathcal{A}}$ shows that (22) holds for $u$ with $(u,P_\tau) \in \tilde{\mathcal{A}}$ for some $\tau$ and the proof is complete.

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