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Permanence in ecological systems with spatial heterogeneity

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Synopsis

A basic problem in population dynamics is that of finding criteria for the long-term coexistence of interacting species. An important aspect of the problem is determining how coexistence is affected by spatial dispersal and environmental heterogeneity. The object of this paper is to study the problem of coexistence for two interacting species dispersing through a spatially heterogeneous region. We model the population dynamics of the species with a system of two reaction–diffusion equations which we interpret as a semi-dynamical system. We say that the system is permanent if any state with all components positive initially must ultimately enter and remain within a fixed set of positive states that are strictly bounded away from zero in each component. Our analysis produces conditions that can be interpreted in a natural way in terms of environmental conditions and parameters, by combining the dynamic idea of permanence with the static idea of studying geometric problems via eigenvalue estimation.

1. Introduction

A basic problem in population dynamics is that of finding criteria for the long-term coexistence of interacting species. An important aspect of the problem is determining how coexistence is affected by spatial dispersal and environmental heterogeneity. The object of this paper is to study the problem of coexistence for two interacting species dispersing through a spatially heterogeneous region. We model the population dynamics of the species with a system of two reaction–diffusion equations which we interpret as a semi-dynamical system. There are a number of ways of characterising coexistence; here we shall use the criterion of permanence. A system is said to be permanent if any state with all components positive initially must ultimately enter and remain within a fixed set of positive states that are strictly bounded away from zero in each component (for further clarification, see Corollary 3.7 and Remark 3.8).

The advantage of the idea of permanence is that it provides a criterion for long-term coexistence that does not require a complete knowledge of the dynamics of the system. Since our models have infinite dimensional phase spaces, we can almost never hope to describe their dynamics completely. Furthermore,

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the conditions for permanence do not impose many restrictions on the interactions of the species under consideration. Hence, permanence allows us to consider competition, predation and other more complicated forms of density-dependent interaction from a unified point of view. The specific hypotheses implying permanence involve the stability of equilibria where the density of at least one species is identically zero. The stability properties of such equilibria are determined by the principal eigenvalues of elliptic partial differential operators obtained through linearisation. Since the eigenvalues of elliptic operators depend on the coefficients and the geometry of the underlying spatial domain in a fairly direct way, they provide a natural method of quantifying the effects of spatial variation.

The idea of modelling the dynamics of interacting populations with a system of nonlinear differential equations dates back at least to the pioneering work of Lotka and Volterra in the 1920s. The idea of using diffusion to model the spatial dispersal of alleles in population genetics was introduced by Fisher in the 1930s and applied to population dynamics by Skellam and others in the early 1950s. Currently, reaction–diffusion systems are some of the most widely used models for population dynamics or genetics in situations where spatial dispersal plays a significant role. The history and derivation of such models are discussed in [**11**, **17**, **28**, **34**]. The models we consider have the form

$$\frac{\partial u_i}{\partial t} = \mu_i \Delta u_i + u_i f_i(x, u) \quad \text{in } \Omega \times \mathbb{R}_+ \quad (i = 1, 2) \tag{1.1}$$

with $u_i = 0$ or $\partial u_i/\partial \nu = 0$ on $\partial\Omega \times \mathbb{R}_+$, where $\Omega \subseteq \mathbb{R}^m$ is a bounded domain. For our applications we are interested in $m = 1$, 2, or 3 only, but some of our results on reaction–diffusion systems are stated in more generality. The variables u_i represent population densities of the interacting species. The boundary condition $u_i = 0$ describes a situation where crossing the boundary of Ω is lethal to members of the ith species; the condition $\partial u_i/\partial \nu = 0$ corresponds to the boundary of Ω acting as a barrier. It turns out to be very useful to view (1.1) as a semi-dynamical system; in particular, such a viewpoint allows us to use the idea of permanence. A general discussion of how reaction–diffusion equations give rise to semi-dynamical systems is given in [**21**]; a more detailed analysis which is well suited to the problems we consider is given in [**33**].

There are several ways in which coexistence can be interpreted. One simple characterisation is to require (1.1) to have a componentwise positive equilibrium which is a global attractor for non-trivial non-negative solutions. Such an approach works fairly well for a single reaction–diffusion equation (see for example [**8**]), but is not well suited to the analysis of systems since even classical Lotka–Volterra competition models may admit multiple steady states in the presence of diffusion [**4**, **9**, **12**], and the problem of finding and analysing the equilibria for more complicated interactions is quite difficult. In addition, from a biological point of view, it is probably inappropriate to require that orbits tend to a single steady state. The criterion of permanence in the context of zero Dirichlet conditions requires the existence of a region $U = \{(u_1, u_2): v_1 \leqq u_1 \leqq w_1, v_2 \leqq u_2 \leqq w_2\}$ with $v_1, v_2 > 0$ on Ω and $\partial v_1/\partial \nu$, $\partial v_2/\partial \nu < 0$ on $\partial\Omega$ such that all solutions with non-trivial, non-negative initial data are attracted to U.

Another interpretation of permanence is that the boundary of the positive cone in a space where our model generates a semiflow must act as a repeller. The significance of such an interpretation is that to establish permanence we need a detailed knowledge of the dynamics of our system only in or near the boundary of a positive set, which can be arranged to consist of states in which at most one species is present. Since multiple coexistence states, periodic orbits and more complicated dynamics are permitted when both species are present, the idea of permanence turns out to be biologically realistic as well as mathematically tractable. An interesting discussion of the role and history of the idea of permanence in population dynamics, genetics and evolutionary theory is given by Hofbauer and Sigmund in [**23**]. Permanence and/or related criteria for coexistence are discussed in [**3, 7, 20**] and the references therein. Some aspects of such ideas in the reaction–diffusion context are discussed in [**16, 26**].

The conditions we obtain for permanence involve the principal eigenvalues of a class of elliptic problems that has already been considered in establishing the existence (but not stability) of coexistence equilibria in [**4, 9, 29, 31**]. Specifically, suppose that the population of the first species has a positive equilibrium $\bar{u}_1$ in the absence of the second species; then a typical condition for permanence would involve the principal eigenvalue σ_1 of the problem

$$\mu_2 \Delta\phi + f_2(x, \bar{u}_1, 0)\phi = \sigma\phi \quad \text{in } \Omega, \tag{1.2}$$

with boundary conditions on ϕ corresponding to those on u_2. Giving a criterion for permanence in terms of such eigenvalues is of interest from both the mathematical and biological points of view. On the mathematical side, the conditions for permanence are close to those used previously to establish the existence of a coexistent equilibrium state (as in [**4, 9**]), as opposed to the stronger conditions used to establish long time coexistence by proving the uniqueness and stability of such a state (as in [**10, 12**]). We shall prove that permanence actually implies the presence of a coexistent equilibrium (possibly unstable) for (1.1). Similar results for other models are obtained in [**25**]. From the biological viewpoint, it is interesting to find conditions for permanence based on eigenvalues of problems such as (1.2), because those eigenvalues can often be estimated in ways that yield biologically useful information about the effects of various parameters describing the environment, the populations, or their interactions.

Sections 2–5 of this paper are devoted to the application of the idea of permanence to models such as (1.1). Those sections are arranged roughly in order of decreasing abstraction and generality. Section 6 explores the connections between permanence and the existence of coexistence equilibria, and Section 7 gives a summary of our results and their biological implications. In Section 2 we provide the necessary terminology and background information on semiflows and abstract permanence. The ideas are related to those discussed in [**20, 24, 26, 27**]. Section 3 describes how reaction–diffusion systems such as (1.1) can be interpreted as generating semidynamical systems in the spirit of [**21, 33**]. To apply the abstract ideas of Sections 2 and 3 to specific biological models, we must establish that the semiflows they generate are dissipative on the positive cone of an appropriate space and possess average Lyapunov functionals implying that boundary of the positive cone acts as a repeller. The problem of dissipativity is discussed in Section 4. For most of our models, it is easy to establish dissipativity via standard comparison theorems based on the maximum principle, but for one class of models we must use a refinement of some of the ideas on invariance introduced in [1] and used in [16]. We construct our average Lyapunov functions in Section 5. That construction requires a detailed knowledge of the asymptotic behaviour of the model for each species in the absence of the other. The results of Section 4 and 5 impose some structure conditions on the interaction terms f_i, but they are relatively weak. In particular, we may take $f_1(x, u_1, u_2) = m_1 - b_{11}u_1 - b_{12}u_2$, $f_2(x, u_1, u_2) = m_2 \pm b_{21}u_1 - b_{22}u_2$ with $b_{11} > 0$, $b_{12}, b_{21}, b_{22} \geqq 0$ for all x and $m_1 > 0$ for some x. Hence, we can treat many classical models for ecological interactions. (Our results also apply to many other specific forms of interactions.) In Section 6 we return to a fairly general viewpoint and show that permanence implies the existence of a coexistent equilibrium. The approach is based on an asymptotic version of the Schander fixed point theorem as in [25]. Finally, in Section 7 we review our results and discuss their connections with other work and their biological interpretation.

2. Semiflows

In this section we establish our terminology and present the central results from the theory of semiflows which will be used in treating permanence.

Let (Y, d) be a metric space, points in Y being denoted by $u, v, \ldots$ and subsets of Y by $U, V, \ldots$. The following two unsymmetric distances of sets will be used:

$$\bar{d}(U, V) = \sup_{u \in U} d(u, V),$$

$$\underline{d}(U, V) = \inf_{u \in U} d(u, V).$$

The triple $(Y, \pi, \mathbb{R}_+)$ is said to be a *semiflow* if $\pi: Y \times \mathbb{R}_+ \to Y$ is continuous and satisfies:

(i) $\pi(u, 0) = u$,

(ii) $\pi(\pi(u, t), s) = \pi(u, t + s)$ $(s, t \in \mathbb{R}_+)$,

for all $u \in Y$. For convenience, we often write $\pi(u, t) = u \,.\, t$. The symbols $\gamma^+(u)$ and $\omega(u)$ denote the semi-orbit through u and the omega limit set of u, respectively, and the equivalent expressions for sets are defined by taking unions.

A *solution* ϕ through u is a continuous map $\phi: \mathbb{R} \to Y$ such that $\phi(0) = u$ and $\pi(\phi(\tau), t) = \phi(t + \tau)$ for $t \in \mathbb{R}_+$, $\tau \in \mathbb{R}$. The range of ϕ is denoted by $\gamma(u)$ and is called an orbit through u. We *assume* that the backward continuation when it exists is unique. Note that the existence of a backward continuation is not assured, so an assertion as to existence (for example in Theorem 2.1 below) is a strong restriction on the semiflow with wide ranging consequences.

A set U is said to be *forward invariant* if $\gamma^+(U) \subset U$ and *invariant* if $\gamma(U) \subset U$.

The semiflow is said to be *dissipative* if there is a bounded set U such that $\lim_{t \to \infty} d(u \,.\, t, U) = 0$ for all $u \in Y$. U is said to be a *global attractor* if it is compact invariant and $\lim_{t \to \infty} \bar{d}(V \,.\, t, U) = 0$ for all bounded V.

THEOREM 2.1 [20]. *Let Y be complete and suppose that the semiflow is dissipative. Assume that there is a $t_0 \geqq 0$ such that $\pi(\cdot, t)$ is compact for $t > t_0$. Then there is a non-empty global attractor, $\mathscr{A}$ say.*

Consider next the concept of permanence in the abstract semiflow context. We suppose that $Y = Y_0 \cup \partial Y_0$, where Y_0 is open, and assume that Y_0, ∂Y_0 are forward invariant. In relation to the remarks in the introduction, ∂Y_0 will consist of the states with at least one species identically zero.

DEFINITION 2.2. The semiflow is said to be *permanent* if there exists a bounded set U with $\underline{d}(U, \partial Y_0) > 0$ such that $\lim_{t\to\infty} d(v\,.\,t, U) = 0$ for all $v \in Y_0$.

We can now give the following definitions and theorem from [20]. A set $U \subset Y_0$ is said to be *strongly bounded* if it is bounded and $\underline{d}(U, \partial Y_0) > 0$. $\mathscr{A}_0$ is said to be a global attractor relative to strongly bounded sets if it is a compact invariant subset of Y_0 and $\lim_{t\to\infty} \bar{d}(U\,.\,t, \mathscr{A}_0) = 0$ for all strongly bounded U.

THEOREM 2.3. *Assume that the conditions of Theorem 2.1 hold, and let Y_0 and ∂Y_0 be defined as above. Then if permanence holds, there are global attractors $\mathscr{A}$, $\mathscr{A}_\gamma$ for π_γ (that is π restricted to ∂Y_0), and a global attractor $\mathscr{A}_0$ relative to strongly bounded sets.*

Permanence is obviously an asymptotic property. It can thus be studied by examining the semiflow restricted to a forward invariant set derived from an ε-neighbourhood $B(\mathscr{A}, \varepsilon)$ of the global attractor $\mathscr{A}$ of Theorem 2.1. Set then $X = cl\pi(B(\mathscr{A}, \varepsilon), [1, \infty))$, and take $S = X \cap \partial Y_0$. In the next section, it will be shown that X is compact in the context of the present investigation. The following theorem [24] is the basic tool that will be used here for establishing permanence.

THEOREM 2.4. *Assume that the conditions of Theorem 2.1 hold, and let X, S be as defined above. Suppose that $P: X\backslash S \to \mathbb{R}_+$ is continuous, strictly positive and bounded, and for $u \in S$ define*

$$\alpha(t, u) = \liminf_{\substack{v\to u \\ v\in X\backslash S}} \left(\frac{P(v\,.\,t)}{P(v)}\right). \tag{2.1}$$

Then the system is permanent if

$$\sup_{t>0} \alpha(t, u) > \begin{cases} 1 & u \in \omega(S), \quad (2.2a) \\ 0 & u \in S. \quad (2.2b) \end{cases}$$

3. Basic results for the reaction–diffusion system

After describing in detail the conditions on the model, our first task in this section is to show that the solution generates semiflows on appropriate subsets of the Banach spaces $[C^k]^2$ for $k = 0, 1$, and that the compactness required for Theorem

2.1 holds. We shall then examine the concept of permanence in more detail and show how the relatively weak condition of Definition 2.2 can be strengthened.

Consider the following initial/boundary value problem:

$$\begin{aligned} &\frac{\partial u_i}{\partial t} = \mu_i \Delta u_i + u_i f_i(x, u) \quad \text{on } \Omega \times \mathbb{R}_+ \quad (i = 1, \ldots, n), \\ &u_i|_{\partial\Omega} = 0 \left(\text{or } \frac{\partial u_i}{\partial \nu} = 0\right) \quad \text{on } \partial\Omega \times \mathbb{R}_+, \\ &u(x, 0) = u_0(x) \quad \text{on } \Omega, \end{aligned} \tag{3.1}$$

where $u = (u_1, \ldots, u_n)$. We shall impose the following condition on the system:

(H1) (a) $\mu_i > 0$ for $i = 1, \ldots, n$,

(b) $\Omega \subset \mathbb{R}^m$ is bounded and open, with $\partial\Omega$ uniformly $C^{3+\alpha}$ for some $\alpha > 0$,

(c) $f_i: \Omega \times \mathbb{R}^n_+ \to \mathbb{R}$ is C^2 jointly in x and u for $i = 1, \ldots, n$.

Some of our results are valid under weaker hypotheses, which are in some cases stated in the relevant sections of the paper. In particular, the smoothness conditions on f_i may often be weakened; (H1)(c) is sufficient for all results. The results we obtain are derived from [**33**], and we may remark that spatial dependence may be introduced into the diffusion quite easily. For example, instead of Δu we may treat

$$\nabla . (K(x)\nabla u)$$

where K is diagonal, $k_{ii} \in C^{2+\alpha}(\bar{\Omega})$ for some $\alpha > 0$ and the k_{ii} are bounded below away from zero. Finally, with minor amendments, the theory in this section extends to more general boundary conditions.

As usual $C^k(\bar{\Omega})$ for $k = 0, 1$ will denote the Banach spaces of continuous and once continuously differentiable functions, respectively, with the sup norm on the functions and derivatives when appropriate. The norms will be denoted by $\|\cdot\|_k$, and the closed subspaces of functions vanishing on $\partial\Omega$ by $C^k_0(\bar{\Omega})$. $C^k_{0^+}(\bar{\Omega})$ will denote the positive cone with respect to the usual ordering.

As usual, the key step is showing that there is an operator A derived from $-\Delta$ which generates an analytic semigroup. Then $\mathbf{A}$ also generates an analytic semigroup, where $\mathbf{A}$ is the diagonal matrix with A's along the diagonal. The next result follows from [**33**]; the precise specification of the domain of $\mathbf{A}$ is not needed here. For further details, see [**33**]. For a Banach space E, E^β will denote the usual fractional power spaces, with norm $\|\cdot\|_{E^\beta}$. (See [**21**], for example.)

LEMMA 3.1. *Suppose* (H1)(b) *holds. Then there is an operator* $\mathbf{A}$ *derived from* $-\Delta$ *which generates an analytic semigroup on* $[C^k_0(\bar{\Omega})]^n$ *for* $k = 0, 1$. *With* $E = [C^k_0(\bar{\Omega})]^n$,

$$E^\beta \hookrightarrow [C^{k+q}_0(\bar{\Omega})]^n$$

for $q = 0, 1$ *and* $2\beta > q$.

Proof. This is derived from [**33**, Theorem 2.4], and the references below are to [**33**]. (H1) and the remarks following are (M4$_s$) on p. 27 with $s = 1$. The spaces $C_0(\hat{C}$ in Mora's equation) are defined on p. 33 (equation 2.5). The necessary technical conditions on these spaces are verified in [**33**, § 3], and Lemma 3.1 then follows from [**33**]. □

The following abstract results pertaining to the solution of linear and nonlinear differential equations are fairly standard.

LEMMA 3.2. (i) *Consider the linear differential equation*

$$\frac{du}{dt} + \mathbf{A}u = \mathbf{g}(t) \quad (t>0),$$

$$u(0) = u_0.$$

Assume that $u_0 \in E = E^0 = [C_0^0(\bar{\Omega})]^n$, $\mathbf{g}\colon [0,\infty) \to E$ with $\sup_{s\in[0,\infty)} \|\mathbf{g}(s)\|_{E^0} < \infty$. *Then if* $\beta < 1$, *we have* $u(t) \in E^\beta$ $(t>0)$, *and given* $t_0 > 0$ *there exist* $M_1(t_0)$, $M_2(t_0)$ *depending only on* t_0 *such that for* $t \geqq t_0$,

$$\|u(t)\|_{E^\beta} \leqq M_1(t_0)\, \|u_0\|_{E^0} + M_2(t_0) \sup_{s\in[0,\infty)} \|g(s)\|_{E^0}. \tag{3.2}$$

(ii) *Consider the differential equation*

$$\frac{du}{dt} + \mathbf{A}u = \mathbf{f}(u),$$

where $\mathbf{f}\colon E \to E$ *is locally Lipschitz and maps bounded sets into bounded sets.*

Then given $U \subseteq \tilde{U}$ *bounded, there are constants* k, c (*depending on* $\tilde{U}$) *such that for* $u_0, v_0 \in U$

$$\|u(t) - v(t)\|_{E^0} \leqq k\, \|u_0 - v_0\|_{E^0}\, e^{ct}$$

so long as $u(t), v(t) \in \tilde{U}$.

Proof. (i) We write the equation as an integral equation in the usual way, and then apply $\mathbf{A}^\beta$ to obtain the following:

$$\begin{aligned}
\|u(t)\|_{E^\beta} &= \|\mathbf{A}^\beta u(t)\|_{E^0} \\
&\leqq \|\mathbf{A}^\beta e^{-\mathbf{A}t} u_0\|_{E^0} + \left\| \int_0^t \mathbf{A}^\beta e^{-\mathbf{A}(t-s)} \mathbf{g}(s)\, ds \right\|_{E^0} \\
&\leqq C_\beta \left[t^{-\beta} e^{-\delta t}\, \|u_0\|_{E^0} + \sup_{s\in[0,t]} \|\mathbf{g}(s)\|_{E^0} \int_0^t \frac{e^{-\delta(t-s)}}{(t-s)^\beta}\, ds \right],
\end{aligned}$$

where a standard estimate $\|\mathbf{A}^\beta e^{-\mathbf{A}t}\| \leqq C_\beta t^{-\beta} e^{-\delta t}$ for the operator has now been used – see [**21**, Theorem 1.4.3].

(ii) The proof is similar to start with, and then a Gronwall-type inequality is used. □

We assume the following *a priori* bounds:

(H2) *Uniform boundedness.* Given $\alpha > 0$, there exists $B(\alpha)$ such that $\|u(0)\|_{E^0} \leqq \alpha \Rightarrow \|u(t)\|_{E^0} \leqq B(\alpha)$ $(t>0)$.

(H3) *Dissipativity in* $[C_0^0(\bar{\Omega})]^n$. There exists γ such that given $u_0 \in [C_0^0(\bar{\Omega})]^n$, there is a $t(u_0)$ such that $\|u(t)\|_{E^0} \leqq \gamma$ $(t \geqq t(u_0))$.

THEOREM 3.3. *Let* (H2) *and* (H3) *hold. Then the reaction–diffusion system* (3.1) *generates a semigroup on* $[C_0^0(\bar{\Omega})]^n$, *and its restriction to* $[C_0^1(\bar{\Omega})]^n$ *is also a semigroup. Dissipativity in* $[C_0^1(\bar{\Omega})]^n$ *holds. Also* $\pi(\cdot, t)$ *is a compact operator on* $[C_0^1(\bar{\Omega})]^n$ *for every* $t > 0$. *There is a bounded set* U_2 *in* $[C^2(\bar{\Omega})]^n$ *such that if* $U \subset [C_0^1(\bar{\Omega})]^n$ *is bounded, then* $U.t \subset U_2$ *for* $t \geqq 1$.

Proof. The boundedness in (H2) ensures existence for $t > 0$, see [**21**, Theorem 3.3.4]. Continuity of the solution in t of course holds (by the definition of solution). Lemma 3.2(ii) with $U = B(0; \alpha)$ and $\tilde{U} = B(0; B(\alpha))$ from (H2) shows that the solution is actually Lipschitz in the initial condition, and so joint-continuity follows. Also, backward uniqueness holds, see [**18**, Thm. 4.1].

Take now a bounded subset U_0 of $[C_0^0(\bar{\Omega})]^n$. We apply Lemma 3.2(i) treating the reaction term in (3.1) as known. The uniform boundedness ensures that for $u \in U_0$, $\|u\|_{E^0} \leqq B(U_0)$ for some constant $B(U_0)$, and as $\mathbf{f}$ is continuous, there is a constant $B_1(U_0)$ such that $\|\mathbf{g}(u)\|_{E^0} = \|u\mathbf{f}(u)\|_{E^0} \leqq B_1(U_0)$. Hence from (3.2), there is a constant $m(t_0, U_0)$ with

$$\|u(t)\|_{E^\beta} \leqq m(t_0, U_0) \quad \text{for } t > t_0,$$

for $\beta < 1 - \varepsilon$ and any $\varepsilon \in (0, 1)$. Take next $q = 1$ in Lemma 3.1, getting $E^\beta \hookrightarrow [C_0^1(\bar{\Omega})]^n$ for $\beta > \frac{1}{2}$. This yields a constant $m_1(t_0, U_0)$.

$$\|u(t)\|_{C^1} \leqq m_1(t_0, U_0) \quad \text{for } t > t_0. \tag{3.3}$$

As dissipativity holds in $[C_0^0(\bar{\Omega})]^n$, dissipativity in $[C_0^1(\bar{\Omega})]^n$ follows.

We now broadly repeat the argument, this time taking $E = [C_0^1(\bar{\Omega})]^n$. Take any bounded $U_1 \subset [C_0^1(\bar{\Omega})]^n$. Then local existence holds from the standard theory, and from results of the previous paragraph global existence follows (as there is a C^1 bound for $t \geqq t_0$). Hence, by Lemma 3.1, π restricted to $[C_0^1(\bar{\Omega})]^n$ is a semigroup. Use Lemma 3.2(i) again in E, restarting the flow at t_0. By (3.3) there is a bound in E for $t \geqq t_0$, and a $[C^2(\bar{\Omega})]^n$ bound follows for $t > 2t_0$ from the E^β bound and the embedding result of Lemma 3.1. □

COROLLARY 3.4. *There is a global attractor* $\mathscr{A}$ *in* $[C_0^1(\bar{\Omega})]^n$. *The set* $X = cl\pi(B(\mathscr{A}, \varepsilon), [1, \infty))$ *is compact in* $[C_0^1(\bar{\Omega})]^n$ *and forward invariant.*

Proof. The first statement follows from Theorem 2.1 and Theorem 3.3. The compactness is from the last statement of Theorem 3.3. □

Remark 3.5. It follows from the strong maximum principle (see [**18, 35, 37**]) that if $u_i(x, 0) \geqq 0$, $u_i(x, 0) \not\equiv 0$ then $u_i(x, t) > 0$ on Ω (and under Dirichlet boundary conditions $\partial u_i / \partial \nu < 0$ on $\partial\Omega$) for all $t > 0$. Hence, if $(u_1, u_2, \ldots, u_n) \in X$ is also in the boundary of the positive cone, we have $u_i \equiv 0$ in Ω for some i. It turns out that the strong maximum principle has further implications regarding permanence, which we explore in the next result.

The tactic in the next sections will be to use Theorem 2.4 to establish permanence. This will ensure that for solutions with the initial value of no component equal zero (i.e. $u(0) \in X \setminus S$), $\|u_i(\cdot, t)\|_\infty$ for each i is eventually greater than some fixed $\varepsilon > 0$. However, this condition is not completely satisfactory from the point of view of applications, as it does not preclude the possibility that $u_i(x, t)$ for some i should approach zero on "most" of Ω. In fact we shall now show that this is not possible, and such solutions are bounded uniformly below rather strongly, in fact in the strongest sense that can be expected under zero Dirichlet conditions. Let $e \in C^2(\bar{\Omega})$ be such that $e(x) > 0$ for $x \in \Omega$ and $\partial e/\partial \nu < -\gamma$ for $x \in \partial\Omega$, where $\gamma > 0$. The solution of $\Delta e = -1$ with zero Dirichlet conditions is one possible choice.

LEMMA 3.6. *There exists $\underline{\alpha}, \bar{\alpha} \in (0, \infty)$ such that for all $u \in \mathcal{A}_0$ (defined in Theorem 2.3)*

$$\underline{\alpha} e(x) \leqq u_i(x) \leqq \bar{\alpha} e(x) \quad \text{for } x \in \bar{\Omega} \text{ and } i = 1, \ldots, n.$$

Proof. Since $\mathcal{A}_0$ is invariant, given $u \in \mathcal{A}_0$ there is a v and a $t > 0$ such that $v \,.\, t = u$. An obvious application of the strong maximum principle (see [**37**, p. 89, Theorem 9.12 and Corollary 9.14] or [**35**, Theorem 3, p. 170]) shows that $u(x) > 0$ for $x \in \Omega$, and that there is $\varepsilon(u) > 0$ such that $\partial u_i/\partial \eta < -\varepsilon(u)$ on $\partial\Omega$ for $i = 1, \ldots, n$ (actually using also compactness of $\partial\Omega$).

The upper bound in the above is obvious as $\mathcal{A}_0$ is a $[C_1(\bar{\Omega})]^n$ bounded set. Suppose then that the first inequality is false. Then there are sequences $\{u_n\} \in \mathcal{A}_0$ and $\{x_n\} \in \Omega$ such that $\lim_{n\to\infty} (u_n)_i(x_n)/e(x_n) = 0$ for some i. As $\mathcal{A}_0$ and $\bar{\Omega}$ are compact, we can select convergent subsequences, which we continue to denote by $\{(u_n)_i\}$, $\{x_n\}$, and it follows that there exist $u \in \mathcal{A}_0$, $x \in \bar{\Omega}$ with $(u_n)_i(x_n) \to u(x)$. Clearly $x \notin \Omega$, for as $e(x) > 0$ it would follow that $u_i(x) = 0$ which is ruled out by the remarks above. Suppose then that $x \in \partial\Omega$. Draw the tangent plane at x and drop a perpendicular to it from x_n. Let it cut $\partial\Omega$ at y_n. Then this is "almost" the normal to $\partial\Omega$. It is thus clear that there is a $\beta_1 > 0$ such that

$$u_i(x_n) = u_i(x_n) - u_i(y_n) \geqq \beta_1 |x_n - y_n|.$$

Since $e(x_n) \leqq \beta_2 |x_n - y_n|$ for some β_2, there is a $\beta > 0$ such that $u_i(x_n)/e(x_n) > \beta$.

We need to show that $|((u_n)_i(x_n) - u_i(x_n))/(e(x_n))| \to 0$. This is a consequence of C^1 convergence, from which we see that as $n \to \infty$,

$$\left| \frac{(u_n)_i(x_n) - (u_n)_i(y_n)}{x_n - y_n} - \frac{u_i(x_n) - u_i(y_n)}{x_n - y_n} \right| \to 0$$

and the result follows easily.

The last step is to write

$$\frac{(u_n)_i(x_n)}{e(x_n)} = \frac{(u_n)_i(x_n) - u_i(x_n)}{e(x_n)} + \frac{u_i(x_n)}{e(x_n)},$$

by which the result follows from the conclusion of the previous two paragraphs. □

COROLLARY 3.7. *Suppose permanence holds in $[C^1_{0+}(\bar{\Omega})]^n$. Then there is a $\beta > 0$ such that given any $u \notin S$, there is $t(u)$ such that*

$$u_i(x, t) \geqq \beta e(x) \quad \text{for } t \geqq t(u),\ x \in \bar{\Omega}, \text{ and } i = 1, \ldots, n.$$

Proof. This follows from the preceding lemma and Theorem 2.3 upon using convergence in $[C_0^1(\bar{\Omega})]^n$. □

Remarks 3.8. We shall sometimes also treat cases where some component (or components), say u_j, satisfies a zero Neumann condition. In that case a simplified version of the above argument shows that for a component u_j satisfying Neumann boundary conditions the inequality $u_j(x, t) \geqq \beta e(x)$ above may be replaced by $u_j(x, t) \geqq \beta$ for $t \geqq t(u)$ and $x \in \bar{\Omega}$.

4. Dissipativity

In this section we shall establish that the dissipativity hypotheses of the abstract results from the previous section are satisfied by a number of systems modelling ecological interactions with diffusion. The lemmas on dissipativity are proved via fairly standard methods such as invariance principles and comparison theorems for differential inequalities. For one class of systems a variation on a method of Alikakos **[1]** is used. We shall use without specific reference the observation that local existence plus L^∞ ***a priori*** bounds yield global existence in the context of the systems we study; see **[1, 2, 21, 27, 33]** for further discussion.

We shall consider systems of the form

$$\frac{\partial u_i}{\partial t} = \mu_i \, \Delta u_i + u_i f_i(x, u_1, u_2) \quad \text{in } \Omega, \quad i = 1, 2, \tag{4.1}$$

where $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with smooth boundary, and we shall impose either homogeneous Dirichlet or Neumann boundary conditions. We shall always assume that the functions f_i are at least locally Lipschitz in x, u_1 and u_2. Since some of the results may be of independent utility, they are stated under weaker hypotheses than those required for the full semidynamical system formulation of Section 3. In all our models, u_1 and u_2 represent population densities and we consider only models in which the first population is self-limiting. We allow a variety of dynamics for the second population so that we can model both competition and predator–prey interactions, among others.

Our initial observation is that solutions of (4.1) under our smoothness hypotheses on the functions f_i and the domain Ω will in fact be classical; that follows from the Schauder estimates for parabolic equations, as discussed in **[19]**. The next observation is that the first quadrant is always a positively invariant region for (4.1) and in fact if $u_i(x, 0) \geqq 0$, $u_i(x, 0) \not\equiv 0$ then $u_i(x, t) > 0$ in Ω for all $t > 0$ such that u_1 and u_2 remain finite. The forward invariance of the first quadrant follows immediately from invariant set theorems such as those of **[36]** or **[37]**, or could be established directly via the maximum principle. The strict positivity on the interior of Ω follows from the strong maximum principle, since once we have a solution pair (u_1, u_2), each of the equations in (4.1) may be viewed as a linear scalar equation with zero order coefficient $f_i(x, u_1(x, t), u_2(x, t))$.

The key step in establishing dissipativity is that of showing that any solution (u_1, u_2) must satisfy a uniform bound of the form $0 \leqq u_i \leqq K_i$ for some constants K_i, $i = 1, 2$, within finite time. The smoothing properties of the semiflow then imply dissipativity in $C^1(\bar{\Omega})$. In fact, if (4.1) is simply viewed as a parabolic system, then solutions which belong to $C^1(\bar{\Omega})$ must have Hölder-continuous second derivatives on Ω because of the Schauder estimates for parabolic equations (see [**19**]). Thus, we may use maximum principles to obtain *a priori* bounds, even though we will ultimately want to view our semiflow as acting on $C^1(\bar{\Omega})$.

To obtain bounds for u_1 and u_2, we shall first impose conditions on f_1 leading to a bound for u_1, and then consider some weaker conditions on f_2 which then yield an asymptotic bound on u_2.

LEMMA 4.1. *Suppose that there exists a Lipschitz function $F_1(u_1)$ such that*

$$\sup\{f_1(x, u_1, u_2): x \in \bar{\Omega}, u_2 \geqq 0\} \leqq F(u_1) \tag{4.2}$$

for all $u_1 \geqq 0$, and for some M_0,

$$F_1(u_1) < 0 \text{ if } u_1 > M_0. \tag{4.3}$$

If (u_1, u_2) is a solution of (4.1) for $t \in (0, T]$ under homogeneous Dirichlet or Neumann boundary conditions and with non-negative initial data, then $0 \leqq u_1 \leqq y$ on $(0, T]$ where y satisfies

$$\frac{dy}{dt} = yF_1(y), \quad y(0) = y_0 \geqq \sup\{u_1(x, 0): x \in \bar{\Omega}\}. \tag{4.4}$$

If $M_1 > M_0$ and (u_1, u_2) is a solution of (4.1) for all $t > 0$ then $u_1 \leqq M_1$ for t sufficiently large, and if $u_1(x, 0) \leqq M_1$ then $u_1 \leqq M_1$ for all $t > 0$.

Proof. We have already observed that $u_1, u_2 \geqq 0$ on $(0, T]$. Inequality (4.2) implies that

$$0 = \frac{\partial u_1}{\partial t} - \mu_1 \Delta u_1 - u_1 f_1(x, u_1, u_2) \geqq \frac{\partial u_1}{\partial t} - \mu_1 \Delta u_1 - u_1 F_1(u_1). \tag{4.5}$$

Thus, u_1 is a subsolution and y is a solution to the scalar parabolic problem

$$\frac{\partial u}{\partial t} - \mu_1 \Delta u - uF(u) = 0 \quad \text{in } \Omega.$$

If u_1 satisfies homogeneous Dirichlet conditions on $\partial\Omega \times (0, T]$, then $u_1 \leqq y$ on $\partial\Omega \times (0, T]$; if u_i satisfies homogeneous Neumann conditions, we observe that y does so as well. In either case we have $u_1 \leqq y$ on Ω for $t \in (0, T]$ by standard comparison principles for scalar reaction–diffusion equations (see for example [**17**, **37**]). By (4.3) and the structure of (4.4) we have that the interval $[0, M_0]$ is forward invariant and is in fact a global attractor for all non-negative solutions of (4.4). Any solution of (4.4) will thus exist globally and be smaller than M_1 for t sufficiently large. If (u_1, u_2) is a global solution of (4.1), then $u_1 \leqq y < M_1$ for t sufficiently large. If $u_1(x, 0) \leqq M_1$, we may compare u with the solution of (4.4) with $y(0) = M_1$ and draw the same conclusion for all $t > 0$. □

Remark 4.2. The hypotheses on f_1 will be met by any function of the form

$$f_1(x, u_1, u_2) = m_1(x) - b_{11}(x)u_1 - b_{12}(x)u_2,$$

with $b_{11} \geqq b_0 > 0$ and $b_{12} \geqq 0$. Much more general forms of f_1 are also possible; in particular f_1 need not be monotone in either variable.

LEMMA 4.3. *Suppose that f_1 satisfies the hypotheses of Lemma* 4.1 *and that for any $M > 0$ there exists a Lipschitz function $F_2(u_2, M)$ such that*

$$\sup\{f_2(x, u_1, u_2): x \in \bar{\Omega}, 0 \leqq u_1 \leqq M\} \leqq F_2(u_2, M) \tag{4.6}$$

and a constant $M_2(M)$ such that

$$F_2(u_2, M) < 0 \quad \text{if} \quad u_2 > M_2(M). \tag{4.7}$$

Under these hypotheses, any non-negative solution of (4.1) *with homogeneous Dirichlet or Neumann boundary conditions will exist for all $t > 0$. If M_1 is as in Lemma* 4.1 *and $M_3 > M_2(M_1)$, then $u_2 \leqq M_3$ for t sufficiently large. If $u_1(x, 0) \leqq M_1$ and $u_2(x, 0) \leqq M_3$, then $u_1 \leqq M_1$ and $u_2 \leqq M_3$ for all $t > 0$.*

Proof. If (u_1, u_2) is a solution of (4.1) on $(0, T]$, then by Lemma 4.1 there is a constant M such that $u_1 \leqq M$ on $(0, T]$. We may now compare u_2 to the solution of

$$\frac{dy}{dt} = yF_2(y, M), \quad y(0) = y_0 \geqq \sup\{u_2(x, 0): x \in \bar{\Omega}\} \tag{4.8}$$

as in the proof of Lemma 4.1, and conclude that $u_2(x, t) \leqq y(t)$ on $(0, T]$. By (4.7), any non-negative solution of (4.8) must be global in t, so $\sup\{y(t): 0 \leqq t \leqq T\}$ is finite, so that u_2 is bounded on $(0, T]$. Since the solution of (4.1) is bounded on any finite interval in t, it must exist globally (see for example **[2]**). By Lemma 4.1, we will have $u_1 \leqq M_1$ for t sufficiently large. Choosing t_0 so that $u_1(x, t_0) \leqq M_1$ for all $x \in \bar{\Omega}$, let y be a solution to (4.8) with $M = M_1$ and $y(t_0) \geqq \sup\{u_2(x, t_0): x \in \bar{\Omega}\}$. Again we have $u_2 \leqq y$ for $t > t_0$, and the interval $[0, M_2(M_1)]$ is a global attractor for non-negative solutions of (4.8) with $M = M_1$, so if $M_3 > M_2(M_1)$ we have $u_2 \leqq M_3$ for t sufficiently large. If we have $u_1(x, 0) \leqq M_1$, then by Lemma 4.1 $u_1 \leqq M_1$ for all $t > 0$, so we may compare u_2 with the solution of (4.8) wth $y(0) = M_3$ an conclude that $u_2 \leqq y \leqq M_3$ for all $t > 0$. □

Remark 4.4. Lemmas 4.1 and 4.3 suffice to establish dissipativity for the system (4.1) if $f_1(x, u_1, u_2) = m_1(x) - b_{11}(x)u_1 - b_{12}(x)u_2$ and $f_2(x, u_1, u_2) = m_2(x) +$

$b_{21}(x)u_1 - b_{22}(x)u_2$, where b_{11} and b_{22} are bounded below by positive constants and b_{12} is non-negative. The coefficient b_{21} could be of either sign or could change sign in Ω. Such dynamics correspond to the Lotka–Volterra models for competition or predator–prey interaction with both species subject to logistic self-limitation. Of course much more general forms of interactions will also satisfy the conditions of Lemmas 4.1 and 4.3. Lemma 4.3 does not cover the case $f_2(x, u_1, u_2) = m_2(x) + b_{21}(x)u_1$ with $b_{21} > 0$, which occurs in some predator–prey models. To treat that sort of dynamics requires a separate argument.

LEMMA 4.5. *Suppose that the hypotheses of Lemma* 4.1 *are satisfied, that* $f_2(x, u_1, u_2)$ *is bounded from above uniformly in x and* u_2 *if* $\|u_1\|_\infty$ *is bounded, and there exist positive constants* α, β, *and* γ *and a continuous function* $f_3(u_1)$ *such that*

$$\alpha u_1[f_1(x, u_1, u_2) + \gamma] + \beta u_2[f_2(x, u_1, u_2) + \gamma] \leqq f_3(u_1) \tag{4.9}$$

for all $x \in \bar{\Omega}$, $u_1, u_2 \geqq 0$. *Under these hypotheses, any non-negative solution of* (4.1) *with homogeneous Dirichlet or Neumann boundary conditions will exist for all* $t > 0$, *and there is a constant* M_3 *such that* $0 \leqq u_2 \leqq M_3$ *for t sufficiently large.*

Remark 4.6. To prove Lemma 4.5, we show that any solution u_2 must satisfy an L^1 *a priori* estimate independent of the initial data after a finite amount of time. We then use the L^1 bound to obtain an L^∞ bound. The method of obtaining the L^1 bound is similar to that used in [**16**]. The L^∞ bound is derived by using ideas due to Alikakos [**1**]. Specifically, we use [**1**, Theorem 3.1] and the following related technical lemma:

LEMMA 4.7. *Suppose that* $u \geqq 0$ *satisfies*

$$\begin{aligned} u_t &= \mu\, \Delta u + a(x, t)u \quad \text{in } \Omega \times (0, \infty), \\ u\frac{\partial u}{\partial \nu} &\leqq 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{4.10}$$

with $a(x, t)$ *locally Lipschitz in* (x, t), *and satisfying* $a(x, t) \leqq A$ *for some constant A. Suppose also that there exist constants* B_0 *independent of u and* $E^*(B_0, u(x, 0))$ *such that in finite time* $\|u\|_1 \leqq B_0$ *and* $\|u\|_\infty \leqq E^*(B_0, u(x, 0))$. *It follows that there exists a constant* B^* *independent of u such that* $\|u\|_\infty \leqq B^*$ *in finite time.* (*Here* $\| \ \|_p$ *denotes the norm of* $L^p(\Omega)$.)

Remark 4.8. Lemma 4.7 is a refinement of [**1**, Theorem 3.1] and has a similar proof. Theorem 3.1 of [**1**] states that if u satisfies (4.10) and it is known that $\|u\|_1 \leqq B$, then $\|u\|_\infty \leqq E^*(B, u(x, 0))$ for some E^*. Such an estimate is sufficient to establish global existence of solutions (see for example [**1, 2**]) but not sharp enough to show dissipativity. Combining [**1**, Theorem 3.1] with Lemma 4.7 gives conditions under which the uniform boundedness of solutions in L^1 after finite time implies uniform boundedess in L^∞ after finite time.

Proof of Lemma 4.7. The proof is essentially a reworking of the proof of [**1**, Theorem 3.1]. Let

$$E_k = \int_\Omega u^{2^k}, \quad k = 0, 1, 2, \ldots.$$

Then for t large we have

$$\begin{aligned}\frac{dE_k}{dt} &\leqq -\mu 2^k(2^k-1)\int_\Omega u^{2^k-2}\,|\nabla u|^2 + 2^k\int_\Omega a(x,t)u^{2k}\\ &\leqq -\mu\frac{(2^k-1)}{2^{k-2}}\int |\nabla(u^{2^{k-1}})|^2 + 2^k A\int u^{2^k}\\ &\leqq -\nu\int |\nabla(u^{2^{k-1}})|^2 + 2^k A\int u^{2^k},\end{aligned} \tag{4.11}$$

where $\nu = 2\mu$. (See [**1**, equations (3.5)–(3.8)].) Also, we have for $0<\varepsilon<\frac{1}{2}$ and any $v \in W^{1,2}(\Omega)$ that ([**1**, equation (3.9)])

$$\|v\|_2^2 \leqq \varepsilon\,\|\nabla v\|_2^2 + C_0\varepsilon^{-(n/2)}\,\|v\|_1^2, \tag{4.12}$$

with C_0 depending only on n and Ω, where n is the dimension of Ω. From (4.11) and (4.12) with $v = u^{2^{k-1}}$, we obtain

$$\frac{dE_k}{dt} \leqq [-(\nu/\varepsilon) + 2^k A]E_k + C_0\varepsilon^{-(n+2)/2}E_{k-1}^2. \tag{4.13}$$

Choosing $\varepsilon_0 < 2\nu/(2+A)$ and setting $\varepsilon = \varepsilon_k = 4^{-k}\varepsilon_0$, we obtain $-(\nu/\varepsilon_k) + 2^k A \leqq -4^k(1+A/2) + 2^k A \leqq -4^k$ so that (4.13) yields

$$\frac{dE_k}{dt} \leqq -4^k E_k + C_1 4^{[(n+2)/2]k}E_{k-1}^2, \tag{4.14}$$

where C_1 depends on Ω, n, ν, and A, all of which are independent of $u(x, 0)$.

We know that for large t, $E_0 \leqq B_0$ and $\|u\|_\infty \leqq E^*(B_0, u(x,0))$ so that $E_k \leqq (E^*)^{2^k}$ (where we replace the original bound E^* on $\|u\|_\infty$ with $|\Omega|\,E^*$ if $|\Omega|>1$). We shall construct a sequence of bounds B_k and show by induction that $E_k \leqq B_k$ for all k if t is large enough. Let $\delta_k = \sum_{j=1}^k j2^{k-j}$. Then $\delta_k = k + 2\delta_{k-1}$ and $\delta_k/2^k \leqq \sum_{j=1}^\infty j2^{-j} = 2$ for all k. Let $B_k = C_1^{2^k-1}2^{2^k-1}4^{(n/2)\delta_k}B_0^{2^k}$. Choose t_0 such that for all k,

$$(E^*)^{2^k}e^{-2^k t_0} \leqq B_k/2. \tag{4.15}$$

(Notice that $\delta_k/2^k$ is bounded, so that $B_k \leqq (B^*)^{2^k}$ for some B^* and also that (4.15) holds, if $t_0 \geqq \ln E^* - \ln C_1 + 2^{-k}\ln C_1 - \ln 2 - (n\delta_k/2^{k+1})\ln 4 - \ln B_0 + 2^{-k+1}\ln 2$, which can clearly be satisfied.) We can now perform the induction. Choose t^* large enough that for $t \geqq t^*$ we have $E_k \leqq (E^*)^{2^k}$ and suppose that for $t \geqq t^*$, $E_{k-1} \leqq B_{k-1}$. We have by (4.14) that, for $t > t^*$,

$$\frac{dE_k}{dt} \leqq -4^k E_k + C_1 4^{[(n+2)/2]k}B_{k-1}^2$$

so that

$$E_k \leqq C_1 4^{(n/2)k}B_{k-1}^2 + (E^*)^{2^k}e^{-4^k(t-t^*)}. \tag{4.16}$$

For $t \geqq t^* + (t_0/2^k)$, inequality (4.16) yields

$$E_k \leqq C_1(4)^{(n/2)k} B_{k-1}^2 + (E^*)^{2^k} e^{-2^k t_0} \leqq C_1(4)^{(n/2)k} B_{k-1}^2 + B_k/2. \tag{4.17}$$

Also, $B_{k-1}^2 = C_1^{2^k-2} 2^{2^k-2} 4^{(n/2)(2\delta_{k-1})} B_0^{2^k}$ so $C_1(4)^{(n/2)k} B_{k-1}^2 = C_1^{2^k-1} 2^{2^k-2} 4^{(n/2)\delta_k} B_0^{2^k} = B_k/2$ and (4.17) implies $E_k \leqq B_k$ for $t \geqq t^* + t_0/2^k$. (We have used $\delta_k = k + 2\delta_{k-1}$ here.) This completes the inductive step, and since we have $E_0 \leqq B_0$ when $t \geqq t^*$ for some t^*, we may conclude $E_k \leqq B_k$ when $t \geqq t^* + t_0 \sum_{i=1}^k 2^{-i}$. Hence, for $t > t^* + t_0$ we have

$$\|u\|_{2^k} = E_k^{1/2^k} \leqq B_k^{1/2^k} \leqq B^* \tag{4.18}$$

for all k. (We have used the fact that $\delta_k/2^k$ is bounded.) Since (4.18) implies a uniform bound on the norm of u in L^{2^k} for any k, it yields the corresponding uniform bound on $\|u\|_\infty$ for $t > t^* + t_0$. □

Proof of Lemma 4.5. Let α, β, and γ be as in (4.9) and let $G = \int_\Omega (\alpha u_1 + \beta u_2)$. We have

$$\begin{aligned}\frac{dG}{dt} &= \int_\Omega (\alpha u_{1t} + \beta u_{2t}) \\ &= \int_\Omega (\alpha\mu_1 \Delta u_1 + \beta\mu_2 \Delta u_2) \\ &\quad + \int_\Omega \alpha u_1(f_1 + \gamma) + \beta u_2(f_2 + \gamma) \\ &\quad - \gamma \int_\Omega (\alpha u_1 + \beta u_2) \\ &\leqq \int_\Omega f_3(u_1) - \gamma G.\end{aligned}$$

Since u_1 is uniformly bounded on its interval of existence by Lemma 4.1, we have $dG/dt \leqq G_0 - \gamma G$ for some constant G_0. We may conclude that G is bounded, and since u_1 is non-negative and bounded and u_2 is non-negative, the boundedness of G implies the boundedness of u_2 in $L^1(\Omega)$. It follows from [**1**, Theorem 3.1] and the remarks following the proof of that theorem that u_2 is uniformly bounded in $L^\infty(\Omega)$ on its interval of existence. Hence any solution must be global in time and bounded in the L^∞ norm. By Lemma 4.1 we have $u_1 \leqq M_1$ when t is sufficiently large for any global solution, so for large enough t (4.9) implies that we have $(dG/dt) \leqq G_1 - \gamma G$ with G_1 independent of (u_1, u_2). We may conclude that $G \leqq (G_1/\gamma) + G_2 e^{-\gamma t}$, so that, for t sufficiently large, G is bounded by a constant not depending on the initial values of (u_1, u_2). Since $0 \leqq u_1 \leqq M_1$ for large t, such a bound on G implies that $\|u_2\|_1 \leqq B_0$ for some constant B_0 independent of (u_1, u_2), provided t is large enough. Theorem 3.1 of [**1**] now implies that $\|u_2\|_\infty \leqq E^*(B_0, u_2(x, 0))$ for t sufficiently large where E^* is a constant depending on $u_2(x, 0)$. Since $f_2(x, u_1, u_2)$ is uniformly bounded from above, u_2 satisfies the hypotheses of Lemma 4.7 so we must have $\|u_2\|_\infty \leqq B^*$ in finite time for some constant B^* independent of u_1, u_2. We already know $u_2 \geqq 0$, so it follows that, for t large, $0 \leqq u_2 \leqq M_3 \equiv B^*$. □

Remark 4.9. An example of the sort of situation where Lemma 4.5 is required is the type of predator–prey model considered in **[16]**. In that case, $f_1 = a - bu_1 - cu_2$ and $f_2 = -d + eu_1$. We shall allow all the coefficients to depend on x, but require them to be bounded and assume that b, c and d are bounded below by positive constants. Lemma 4.1 immediately yields a bound for u_1 when t is large, and we have

$$\alpha u_1(f_1 + \gamma) + \beta u_2(f_2 + \gamma) = \alpha[a - bu_1 + \gamma]u_1 + \beta(\gamma - d)u_2 + (\beta e - \alpha c)u_1 u_2.$$

To satisfy (4.9) we can choose α and β so that $\alpha/\beta > \sup e/\inf c$ and γ with $\gamma < \inf d$. Hence Lemma 4.5 implies the desired dissipativity.

5. Average Lyapunov functions

In this section we accomplish the main task of this article. Namely, we construct average Lyapunov functions so that Theorem 2.4 implies permanence for a large class of models of the form (1.1). Our results immediately suggest an important topic for further investigation: the biological interpretation of the theorems of this section. Such an investigation is not only of obvious interest, but is also quite natural, in that our permanence results are expressed in terms of eigenvalues of certain related linear elliptic equations whose coefficients have natural biological interpretations. We consider this topic of sufficient import to warrant separate attention, and shall devote a subsequent article to it, which we hope will be of particular interest to the mathematical biology community.

Recall that 'abstract' permanence as defined in Definition 2.2 implies in the present context boundedness away from zero for large t in a rather strong sense; see Corollary 3.7 and Remark 3.8. To construct the average Lyapunov functions we must have a detailed knowledge of the ω-limit set of the semiflow generated in the boundary of the positive cone. The maximum principle implies that solutions of (4.1) with non-negative non-zero initial data in a given component will have that component strictly positive in Ω for $t > 0$; in the case of Neumann conditions, such solutions will be positive on $\bar{\Omega}$ and for Dirichlet conditions they will have normal derivatives on $\partial\Omega$ which are bounded above by a negative constant. Hence, the only trajectories which remain in the boundary of the positive cone have one or both components identically zero. Thus, to determine the ω-limit set of the semiflow on the boundary we need only consider scalar equations. The point $(0, 0)$ is always an equilibrium point. We shall impose conditions on the interaction terms in our models so that the equation for each species in the absence of the other has at most a single positive equilibrium point. The following result may be obtained via the methods of **[8]** (see **[8**, Theorem 2.3**]**).

LEMMA 5.1. *Suppose that $f(x, u)$ is Lipschitz in x on $\bar{\Omega}$ and continuously differentiable in u with $\partial f/\partial u \leqq 0$ for $u \geqq 0$, $f(x, u) \leqq 0$ if $u \geqq \ell$ for some constant* *ℓ, and* $f(x_0, 0) > 0$ *for some* $x_0 \in \bar{\Omega}$. *Let* $\lambda_1^+(f(x_0, 0))$ *be the principal positive eigenvalue for the problem*

$$-\Delta\phi = \lambda f(x, 0)\phi \quad \text{in } \Omega, \qquad \phi = 0 \quad \text{on } \partial\Omega. \tag{5.1}$$

The problem

$$u_t = \mu\,\Delta u + f(x, u)u \quad \text{on } \Omega \times (0, \infty), \qquad u = 0 \quad \text{on } \partial\Omega \times (0, \infty), \tag{5.2}$$

has no positive steady state if $\mu \geqq 1/\lambda_1^+(f(x, 0))$ *and a unique positive steady state* $\bar{u}$ *which is a global attractor for non-trivial non-negative solutions if* $\mu < 1/\lambda_1^+(f(x, 0))$.

Remark 5.2. The existence of the principal eigenvalue $\lambda_1^+(f(x, 0))$ is shown in [**32**]. The regularity assumptions on f may be relaxed somewhat for the purposes of Lemma 5.1, but are needed to ensure the smoothness of solutions. In fact, we need to assume that our nonlinearities are C^2 to utilise the abstract framework of Sections 2 and 3. The condition that $\partial f/\partial u \leqq 0$ is used to establish uniqueness of the positive steady state. Without that condition, there may be several positive steady states. If all the other hypotheses on f are satisfied and $\mu < 1/\lambda_1^+(f(x, 0))$, then a permanence result could be obtained for (5.2) via the methods we shall describe in the context of systems of the form (4.1). The condition $\mu < 1/\lambda_1^+(f(x, 0))$ is equivalent to the condition $\sigma_0 > 0$ where σ_0 is the largest eigenvalue for the problem

$$\mu\,\Delta\psi + f(x, 0)\psi = \sigma\psi \quad \text{in } \Omega, \qquad \psi = 0 \quad \text{on } \partial\Omega. \tag{5.3}$$

The equivalence may be shown via positivity lemmas such as the one stated in [**22**].

The case of Neumann boundary conditions is somewhat more complicated. If $\int_\Omega f(x, 0)\,dx < 0$ then there is again a principal positive eigenvalue under Neumann boundary conditions and Lemma 5.1 extends directly to that case. If $\int_\Omega f(x, 0)\,dx \geqq 0$, then (5.2) has a unique positive steady state which is an attractor for non-trivial non-negative solutions for any $\mu > 0$. The arguments needed to establish these facts are to an extent analogous to those in the case of Dirichlet boundary data. Consequently, in the interest of brevity, we omit them from this article. However, we do feel that they are of sufficient interest, both mathematically and biologically, to warrant inclusion in the literature, and hence we shall include them in our subsequent article.

In the case of predator–prey models without self-limitation on the predator, we shall typically assume that $f_2(x, 0, u) < 0$, since otherwise we cannot expect the predator density to remain bounded. In that case, the single species model (5.2) with $f(x, u) = f_2(x, 0, u)$ will have $u \equiv 0$ as the only non-negative steady state.

Our average Lyapunov functions will involve eigenfunctions of linearised problems with the general form of (5.3) derived from the components of (4.1). If we assume that the functions $f_1(x, u_1, 0)$ and $f_2(x, 0, u_2)$ satisfy the hypotheses of

Lemma 5.1 with $\mu_i < 1/\lambda_1^+(f_i(x, 0, 0))$ for $i = 1, 2$, then each of the problems

$$\begin{aligned} &u_{1t} = \mu_1 \Delta u_1 + f_1(x, u_1, 0)u_1 \quad \text{in } \Omega \times (0, \infty), \\ &u_1 = 0 \quad \text{on } \partial\Omega \times (1, \infty), \end{aligned} \tag{5.4}$$

and

$$\begin{aligned} &u_{2t} = \mu_2 \Delta u_2 + f_2(x, 0, u_2)u_2 \quad \text{in } \Omega \times (0, \infty), \\ &u_2 = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{5.5}$$

has a unique positive steady state $\bar{u}_i$. The same is true for Neumann boundary conditions, except that if $\int_\Omega f_i(x, 0, 0)\, dx \geqq 0$ then the condition $\mu_i < 1/\lambda_1^+(f_i(x, 0, 0))$ is no longer needed. To construct average Lyapunov functions in the case of Dirichlet boundary conditions, we shall use the positive eigenfunctions ψ_1 and ψ_2 corresponding to the largest eigenvalues σ_1 and σ_2 of

$$\begin{aligned} \mu_1 \Delta\psi_1 + f_1(x, 0, \bar{u}_2)\psi &= \sigma\psi_1 \quad \text{in } \Omega, \\ \psi_1 &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{5.6}$$

and

$$\begin{aligned} \mu_2 \Delta\psi_2 + f_2(x, \bar{u}_1, 0)\psi_2 &= \sigma\psi_2 \quad \text{in } \Omega, \\ \psi_2 &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{5.7}$$

respectively. (The case of Neumann boundary conditions is treated similarly, using the steady states and linearised problems arising from those conditions.)

THEOREM 5.3. *Suppose that $f_1(x, u_1, u_2)$ and $f_2(x, u_1, u_2)$ are C^2 in all arguments and satisfy the hypotheses of Lemmas* 4.1 *and* 4.3 *and that $f_1(x, u_1, 0)$ and $f_2(x, 0, u_2)$ satisfy the hypotheses of Lemma* 5.1 *with $\mu_i < 1/\lambda_1^+(f_i(x, 0, 0))$. Suppose also that $f_1(x, 0, 0) \geqq f_1(x, 0, \bar{u}_2)$ where $\bar{u}_2$ is the positive solution of* (5.5). *The semiflow on $[C_0^1(\bar{\Omega})]^2$ generated by* (4.1) *under homogeneous Dirichlet boundary conditions is permanent if the eigenvalues σ_1 and σ_2 of* (5.6) *and* (5.7) *are both positive.*

Remark 5.4. The condition $f_1(x, 0, 0) \geqq f_1(x, 0, \bar{u}_2)$ is a weak formulation of the requirement that the population modelled by u_2 either preys upon or competes with that modelled by u_1. The smoothness requirement is needed for the application of the abstract results in Section 2 to systems as described in Section 3.

Proof of Theorem 5.3. The hypotheses imply that (4.1) is dissipative and that the ω-limit set in the boundary of the positive cone consists of $(0, 0)$, $(\bar{u}_1, 0)$ and $(0, \bar{u}_2)$. Thus we need only find an average Lyapunov function to conclude permanence. Since the semiflow is dissipative, we may restrict our attention to a bounded (in fact compact) absorbing subset X of the positive cone in $[C_0^1(\bar{\Omega})]^2$ that contains the global attractor whose existence is asserted in Theorem 2.1. Recall that the construction of X in Section 3 was performed by allowing the semiflow to act for a positive time on a neighbourhood of the attractor, so that X is compact by the smoothing action of the semiflow and the intersection of X with the boundary of the positive cone consists of states with at least one of u_1 and u_2 identically zero. Let S denote the intersection of X with the boundary of the positive cone. Choose eigenfunctions ψ_1, $\psi_2 > 0$ for (5.6), (5.7), respectively, and define

$$P((v_1, v_2)) = \left(\int_\Omega \psi_1 v_1\, dx\right)^{\beta_1}\left(\int_\Omega \psi_2 v_2\, dx\right)^{\beta_2}$$
$$= \exp\left[\beta_1 \log\int_\Omega \psi_1 v_1\, dx + \beta_2 \log\int_\Omega \psi_2 v_2\, dx\right], \tag{5.8}$$

where β_1, β_2 are positive constants. We have for $(u_1, u_2) \in S$ that

$$\alpha(t, (u_1, u_2)) = \liminf_{\substack{(v_1,v_2)\to(u_1,u_2)\\ (v_1,v_2)\in X\setminus S}} \frac{P((v_1, v_2) \,.\, t)}{P((v_1, v_2))}. \tag{5.9}$$

We need $\sup_{t>0} \alpha(t, (u_1, u_2)) > 0$ for $(u_1, u_2) \in S$ and $\sup_{t>0} \alpha(t, (u_1, u_2)) > 1$ for $(u_1, u_2) \in \omega(S)$. Let $(w_1(t), w_2(t)) = ((v_1, v_2) \,.\, t)$. Since our semiflow is on $X \subseteq [C_0^1(\bar{\Omega})]^2$, the functions v_1 and v_2 need not be twice differentiable in x. However, the semiflow is generated by a system of parabolic equations and the smoothness assumptions on the nonlinearities imply that, for $t > 0$ solutions of the partial differential equations are at least C^2. Computation using (5.8) yields

$$\frac{P((v_1, v_2) \,.\, t)}{P((v_1, v_2))} = \exp\left[\beta_1\left(\log\int_\Omega \psi_1 w_1\, dx\Big|_t - \log\int_\Omega \psi_1 w_1\, dx\Big|_0\right)\right.$$
$$\left. + \beta_2\left(\log\int_\Omega \psi_2 w_2\, dx\Big|_t - \log\int_\Omega \psi_2 w_2\, dx\Big|_0\right)\right]$$
$$= \exp\left[\beta_1 \int_0^t \left(\int_\Omega \psi_1 w_{1t}\, dx \Big/ \int_\Omega \psi_1 w_1\, dx\right)\right.$$
$$\left. + \beta_2 \int_0^t \left(\int_\Omega \psi_2 w_{2t}\, dx \Big/ \int_\Omega \psi_2 w_2\, dx\right)\right]. \tag{5.10}$$

We have for $t > 0$

$$\int_\Omega \psi_1 w_{1t}\, dx = \int_\Omega \psi_1[\mu_1 \Delta w_1 + f(x, w_1, w_2) w_1]\, dx$$
$$= \int_\Omega [(\mu_1 \Delta\psi_1) w_1 + f(x, w_1, w_2)\psi_1 w_1]\, dx$$
$$= \int_\Omega [\sigma_1 - f_1(x, 0, \bar{u}_2) + f_1(x, w_1, w_2)]\psi_1 w_1\, dx, \tag{5.11}$$

and similarly

$$\int_\Omega \psi_2 w_{2t}\, dx = \int_\Omega [\sigma_2 - f_2(x, \bar{u}_1, 0) + f_2(x, w_1, w_2)]\psi_2 w_2\, dx. \tag{5.12}$$

Since X is bounded, $\sigma_1 - f_1(x, 0, \bar{u}_2) + f_1(x, w_1, w_2)$ and $\sigma_2 - f_2(x, \bar{u}_1, 0) + f_2(x, w_1, w_2)$ are bounded below on $X \setminus S$, so that the ratios $(\int_\Omega \psi_i w_{it}\, dx / \int_\Omega \psi_i w_i\, dx)$ are bounded below. It follows that $P((v_1, v_2) \,.\, t)/P((v_1, v_2))$ has a strictly positive lower bound since the expression inside the exponential in (5.10) is bounded away from $-\infty$. To see what happens as $(v_1, v_2) \to \omega(S)$, we must examine how

$$\beta_1\Big(\int_\Omega [\sigma - f_1(x,0,\bar u_2) + f_1(x,w_1,w_2)]\psi_1 w_1\,dx \Big/ \int_\Omega \psi_1 w_1\,dx\Big)$$
$$+\beta_2\Big(\int_\Omega [\sigma_2 - f_2(x,\bar u_1,0) + f_2(x,w_1,w_2)]\psi_2 w_2\,dx \Big/ \int_\Omega \psi_2 w_2\,dx\Big)$$

behaves as $(v_1, v_2) \to (u_1, u_2) \in \omega(S)$, $(v_1, v_2) \in X\setminus S$. By the continuity of the semiflow π, w_1 and w_2 will be uniformly close to v_1 and v_2, respectively, for $t > 0$ sufficiently small. Hence, if we can show that the expression

$$\sigma^*(v_1,v_2) = \beta_1\Big(\int_\Omega [\sigma - f_1(x,0,\bar u_2) + f_1(x,v_1,v_2)]\psi_1 v_1\,dx \Big/ \int_\Omega \psi_1 v_1\,dx\Big)$$
$$+\beta_2\Big(\int_\Omega [\sigma_2 - f_2(x,\bar u_1,0) + f_2(x,v_1,v_2)]\psi_2 v_2\,dx \Big/ \int_\Omega \psi_2 v_2\,dx\Big) \tag{5.13}$$

always has a positive lim inf as $(v_1, v_2) \to (u_1, u_2) \in \omega(S)$, then by (5.9), (5.10), (5.11) and (5.12) we have $\alpha(t, (u_1, u_2)) > 1$ for $(u_1, u_2) \in \omega(S)$ and t sufficiently small. If we let $(v_1, v_2) \to (0, 0)$, then

$$\sigma_1 - f_1(x,0,\bar u_2) + f_1(x,v_1,v_2) \to \sigma_1 - f_1(x,0,\bar u_2) + f_1(x,0,0) \geqq \sigma_1,$$

since $f_1(x, 0, 0) \geqq f_1(x, 0, \bar u_2)$ by hypothesis. Also,

$$\sigma_2 - f_2(x,\bar u_1,0) + f_2(x,v_1,v_2) \to \sigma_2 - f_2(x,\bar u_1,0) + f_2(x,0,0).$$

If we choose β_1 and β_2 so that

$$\beta_1\sigma_1 + \beta_2\sigma_2 + \beta_2 \inf_{x\in\Omega} [f_2(x,0,0) - f_2(x,\bar u_1,0)] > \sigma_3 > 0, \tag{5.14}$$

then

$$\liminf_{\substack{(v_1,v_2)\to(0,0)\\(v_1,v_2)\in X\setminus S}} \sigma^*(v_1,v_2) \geqq \sigma_3 > 0.$$

As $(v_1, v_2) \to (\bar u_1, 0), \sigma_1 - f(x, 0, \bar u_2) + f_1(x, v_1, v_2) \to \sigma_1 - f_1(x, 0, \bar u_2) + f_1(x, \bar u_1, 0)$, so that

$$\int_\Omega [\sigma_1 - f_1(x,0,\bar u_2) + f_1(x,v_1,v_2)]\psi_1 v_1\,dx \to$$
$$\int_\Omega [\sigma_1 - f_1(x,0,\bar u_2) + f_1(x,\bar u_1,0)]\psi_1 \bar u_1\,dx. \tag{5.15}$$

Also

$$\begin{aligned}\int_\Omega f_1(x,\bar u_1,0)\psi_1 \bar u_1\,dx &= -\int_\Omega \psi_1\mu_1\,\Delta\bar u_1\,dx\\ &= -\int_\Omega \bar u_1\mu_1\,\Delta\psi_1\,dx\\ &= -\int_\Omega \bar u_1(\sigma_1 - f_1(x,0,\bar u_2))\psi_1\,dx,\end{aligned} \tag{5.16}$$

so that as $(v_1, v_2) \to (\bar u_1, 0)$, $\int_\Omega [\sigma_1 - f_1(x, 0, \bar u_2) + f_1(x, v_1, v_2)]\psi_1 v_1 \to 0$. Since

$\int_\Omega \psi_1 v_1\, dx \to \int_\Omega \psi_1 \bar{u}_1\, dx > 0$, the first ratio of integrals in (5.13) has limit 0 as $(v_1, v_2) \to (\bar{u}_1, 0)$. For the second ratio of integrals, note that as $(v_1, v_2) \to (\bar{u}_1, 0)$, $\sigma_2 - f_2(x, \bar{u}_1, 0) + f_2(x, v_1, v_2) \to \sigma_2$, so that for (v_1, v_2) sufficiently near $(\bar{u}_1, 0)$ but $(v_1, v_2) \in X \setminus S$ we have that ratio bounded below by $\sigma_2/2$. Hence we have

$$\liminf_{\substack{(v_1,v_2)\to(\bar{u}_1,0)\\ (v_1,v_2)\in X\setminus S}} \sigma^*(v_1, v_2) \geqq \beta_2\sigma_2/2 > 0.$$

As $(v_1, v_2) \to (0, \bar{u}_2)$, computations similar to (5.15) and (5.16) show that $\int [\sigma_2 - f_2(x, \bar{u}_1, 0) + f_2(x, v_1, v_2)]\psi_2 v_2 \to 0$, and since $\sigma_1 - f_1(x, 0, \bar{u}_2) + f_2(x, v_1, v_2) \to \sigma_1$ the first ratio of integrals in (5.13) is bounded below by $\sigma_1/2$ for (v_1, v_2) near $(0, \bar{u}_2)$. Hence

$$\liminf_{\substack{(v_1,v_2)\to(0,\bar{u}_2)\\ (v_1,v_2)\in X\setminus S}} \sigma^*(v_1, v_2) \geqq \beta_1\sigma_1/2 > 0.$$

Thus

$$\liminf_{\substack{(v_1,v_2)\to\omega(S)\\ (v_1,v_2)\in X\setminus S}} \sigma^*(v_1, v_2) > 0,$$

so that $\alpha(t, (u_1, u_2)) > 1$ for $(u_1, u_2) \in \omega(S)$ and $t > 0$ sufficiently small, and permanence follows from the abstract results of the previous section. □

The case of Neumann conditions is very similar to that of Dirichlet conditions, at least in the construction of average Lyapunov functions. An analogue of Lemma 5.1 for the Neumann case is available under the same hypotheses, as previously noted, except that the condition $\mu < 1/\lambda_1^+(f(x, 0, 0))$ may be omitted if $\int_\Omega f(x, 0, 0)\, dx \geqq 0$.

THEOREM 5.5. *Suppose that $f_1(x, u_1, u_2)$ and $f_2(x, u_1, u_2)$ are C^2 in all arguments and satisfy the hypotheses of Lemmas* 4.1 *and* 4.3, *and that $f_1(x, u_1, 0)$ and $f_2(x, 0, u_2)$ satisfy the hypotheses of Lemma* 5.1. *If $\int_\Omega f_i(x, 0, 0)\, dx < 0$, then suppose $\mu_i < 1/\lambda_{1N}^+(f_i(x, 0, 0))$ where $\lambda_{1N}^+(f_i(x, 0, 0))$ is the principal positive eigenvalue of* (5.1) *under Neumann boundary conditions. Let $\bar{u}_{1N}$ and $\bar{u}_{2N}$ be the unique positive solutions of* (5.4) *and* (5.5) *under Neumann conditions, and let σ_{1N} and σ_{2N} then denote the largest eigenvalues of* (5.6) *and* (5.7) *under Neumann conditions. Suppose that $f_1(x, 0, 0) \geqq f_1(x, 0, \bar{u}_{2N})$. The semiflow generated on $[C(\bar{\Omega})]^2$ by* (2.1) *with Neumann boundary conditions is permanent if σ_{1N} and σ_{2N} are both positive.*

Remarks 5.6. The case of Neumann conditions can be treated somewhat differently to that of Dirichlet conditions, since solutions will be strictly positive on $\bar{\Omega}$. A different approach to permanence in the Neumann case is treated in [**26**]. Theorem 5.5 is proved exactly as Theorem 5.3 with the only changes being the replacement of solutions, eigenvalues, eigenfunctions for Dirichlet conditions with the corresponding ones for Neumann conditions. We could also impose Dirichlet conditions on one species and Neumann on the other.

Theorems 5.3 and 5.5 improve known results on the asymptotic behaviour of solutions to the classical Lotka–Volterra competition system with diffusion:

$$\begin{aligned} u_{1t} &= \mu_1 \Delta u_1 + (m_1 - b_{11}u_1 - b_{12}u_2)u_1, \\ u_{2t} &= \mu_2 \Delta u_2 + (m_2 - b_{21}u_1 - b_{22}u_2)u_1. \end{aligned} \tag{5.17}$$

The permanence criteria of Theorem 5.3 coincide with those for the presence of a coexistence equilibrium given in [**4**, **9**] in the case of relatively weak competition. Of course, Theorem 5.3 also applies to the predator–prey model

$$\begin{aligned} u_{1t} &= \mu_1 \Delta u_1 + (m_1 - b_{11}u_1 - b_{12}u_2)u_2, \\ u_{2t} &= \mu_2 \Delta u_2 + (m_2 + b_{21}u_1 - b_{22}u_2)u_2, \end{aligned} \tag{5.18}$$

and to more general models. We shall return to the connections between permanence and coexistence states in the next section.

The case of a predator–prey model with no self-limitation on the predator requires a slightly different analysis, since there will be no positive steady state for the predator density in the absence of prey.

THEOREM 5.7. *Suppose that $f_1(x, u_1, u_2)$ and $f_2(x, u_1, u_2)$ are C^2 and satisfy the hypotheses of Lemmas* 4.1 *and* 4.5, *that $f_1(x, u_1, 0)$ satisfies the hypotheses of Lemma* 5.1 *with $\mu_1 < 1/\lambda_1^+(f_1(x, 0, 0))$, and that $f_2(x, 0, u_2) \leqq 0$ for $u_2 \geqq 0$. Let σ_0 and ψ_0 be the largest eigenvalue and corresponding positive eigenfunction of*

$$\mu_1 \Delta\psi + f_1(x, 0, 0)\psi = \sigma\psi \quad \text{in } \Omega,$$
$$\psi = 0 \quad \text{on } \partial\Omega,$$

and recall that σ_2 and ψ_2 are the largest eigenvalue and corresponding eigenfunction of (5.7). *The semiflow on $[C_0^1(\bar{\Omega})]^2$ generated by* (4.1) *with Dirichlet boundary conditions is permanent if σ_0 and σ_2 are both positive.*

Discussion. The proof is similar to that of Theorem 5.3. Dissipativity follows from Lemma 4.5. The ω-limit set of the semiflow restricted to the boundary of the positive cone consists of $(0, 0)$ and $(\bar{u}_1, 0)$ in this case, and the average Lyapunov function is

$$P(v_1, v_2) = \left(\int_\Omega \psi_0 v_1\, dx\right)^{\beta_1}\left(\int_\Omega \psi_2 v_2\, dx\right)^{\beta_2}.$$

If we proceed as in the proof of Theorem 5.3, the analysis near $(0, 0)$ imposes the condition $\beta_1\sigma_0 + \beta_2\sigma_2 + \beta_2 \inf_{\bar{\Omega}} [f_2(x, 0, 0) - f_2(x, \bar{u}_1, 0)] > 0$ while the analysis near $(\bar{u}_1, 0)$ requires only that $\beta_2\sigma_2 > 0$. Clearly both conditions can be satisfied for some positive β_1, β_2 if σ_0 and σ_2 are positive.

As in the case of Theorem 5.3, Theorem 5.7 extends directly to the case of Neumann boundary conditions:

THEOREM 5.8. *Suppose that the hypotheses of Theorem* 5.7 *are satisfied when the steady state $\bar{u}_1$ and eigenvalues σ_0 and σ_2 are taken with respect to Neumann rather than Dirichlet boundary conditions. Then the system* (4.1) *with Neumann boundary conditions generates a semiflow on $[C(\bar{\Omega})]^2$ which is permanent.*

Remark 5.9. Theorems 5.7 and 5.8 give permanence criteria for systems including the predator–prey system

$$\begin{aligned} u_{1t} &= \mu_1 \Delta u_1 + (a - bu_1 - cu_2)u_1, \\ u_{2t} &= \mu_2 \Delta u_2 + (-d + eu_1)u_2, \end{aligned} \tag{5.19}$$

studied in [16], to which Theorems 5.3 and 5.5 do not apply.

6. The existence of a stationary state

In recent years there has been considerable mathematical interest in stationary coexistence states for two species models with diffusion, coexistence here being interpreted as meaning that the density of neither species is identically zero. The object of this section is to show that, for systems exhibiting permanence, such a state always exists. The proof of this result is a straightforward application of an asymptotic fixed point theorem to the semiflow. It follows from this simple observation that many of the standard existence results are immediately recoverable, and indeed that in some circumstances existence may be proved for very much more general reaction terms with spatial variation included and with less stringent conditions on the sign of their partial derivatives. For a related approach to a model representing delay effects, see [25].

It is clearly not appropriate to review here the rather extensive literature on coexistence states, and we restrict ourselves to a brief outline, referring the reader who requires more information to the papers cited for extensive further references. We first remark that the problem with zero Neumann conditions is relatively straightforward and has been largely settled in [6] and [15]. We shall not refer to this further and shall only consider the case with zero Dirichlet conditions, noting that more general boundary conditions could be treated by extending the permanence results for such conditions.

It is probably fair to say that by far the greatest effort has been directed towards finding sufficient conditions for the existence of coexistence states. One of the principal methods for tackling this problem is based on bifurcation techniques, typical references being [4], [5] and [9]. A somewhat different approach based on an index method is given by [13], [14] and extended by [31]. For an approximate approach for large domains, see [30]. An attack based on sub- and supersolutions is described in [12]. This method is only applicable to cases where the semiflows are suitably ordered, which probably limits it to competing species or mutualistic cases, and excludes predator–prey examples. Finally, we may mention that uniqueness and stability for competing species problems are treated in [10].

The proof of the existence of a stationary coexistence state will be based on the asymptotic Schaunder fixed point theorem (see [38]), which we quote next for ease of reference.

THEOREM 6.1. *Let U be a non-empty, bounded, open, convex subset of the Banach space E, and suppose that $T: E \to E$ is continuous and compact. Assume that for some fixed prime $p \geqq 2$, $T^k \bar{U} \subset U$ for $k = p, p+1$. Then T has a fixed point in U.*

THEOREM 6.2. *Suppose that zero Dirichlet boundary conditions are imposed and that the hypotheses of Theorem* 5.3 *or* 5.7 *are met, so that dissipativity and permanence hold for* (4.1). *Then the system* (4.1) *has a stationary coexistence state, that is, an equilibrium solution with neither component identically zero.*

Remark 6.3. Systems (5.17)–(5.19) are some specific examples of systems to which Theorem 6.2 applies under appropriate conditions on the parameters.

Proof of Theorem 6.2. Take $E = C_0^1(\bar{\Omega})$. Strictly speaking, our permanence results only apply to $C_{0+}^1(\bar{\Omega})$, but it is clear that the system of partial differential equations may easily be extended by defining a smooth continuation of the reaction terms which is zero outside an ε-neighbourhood of $C_{0+}^1(\bar{\Omega})$.

In Lemma 3.6, take $\underline{\gamma} = \underline{\alpha}/2$, $\bar{\gamma} = 2\bar{\alpha}$, and set

$$U = \Big\{u \in C_0^1(\bar{\Omega}): \underline{\gamma} e(x) < u_i(x) < \bar{\gamma} e(x) \text{ for } x \in \Omega \\ \text{and } \underline{\gamma}\frac{\partial e}{\partial \nu}(x) > \frac{\partial u_i}{\partial \nu}(x) > \bar{\gamma}\frac{\partial e}{\partial \nu}(x) \text{ for } x \in \partial\Omega, i = 1, 2, \dots, n\Big\}.$$

Clearly U is strongly bounded, open and convex. Choose any $t > 0$ and set $T_t = \pi(\cdot, t)$. Then T_t is compact (by Theorem 3.3) and continuous. Furthermore, as U is strongly bounded, by the definition of global attractor relative to strongly bounded sets, Theorem 2.3 and Lemma 3.6, there is a k_0 such that $T_t^k\bar{U} \subset U$ for $k \geqq k_0$. It follows by choosing any prime $p > k_0$ that T_t has a fixed point. As this holds for every $t > 0$, the existence of a fixed point of π follows on applying [**3**, Lemma 3.7] on the closure of $\pi(\bar{U}, [1, \infty))$, which is compact by Theorem 3.3.

As an application, let us consider a predator–prey problem discussed in [**4**], for which the governing equations are

$$d_1 \Delta u + u(a_1 - b_1 u - c_1 v) = 0,$$
$$d_2 \Delta v + v(a_2 - b_2 v + c_2 u) = 0,$$

with zero Dirichlet conditions on $\partial\Omega$. Suppose that $b_1, c_1, b_2, c_2 > 0$ and $a_1 > \lambda_1 d_1$, where λ_1 is the smallest eigenvalue of $-\Delta$ with zero Dirichlet conditions. We take for simplicity $a_2 < 0$, although this restriction may be weakened under appropriate conditions. Let $\bar{u}$ be the (unique) non-zero solution of

$$d_1 \Delta\bar{u} + \bar{u}(a_1 - b_1\bar{u}) = 0 \quad \text{in } \Omega,$$
$$\bar{u} = 0 \quad \text{on } \partial\Omega.$$

Then by Theorem 5.7 permanence holds and there is a stationary coexistence state (by Theorem 6.2) if the smallest eigenvalue λ of the problem

$$d_2 \Delta v + v(a_2 + c_2\bar{u}) = \lambda v \quad \text{in } \Omega$$
$$v = 0 \quad \text{on } \partial\Omega,$$

is greater than zero. This is essentially the existence result [**4**, Theorem 3.5(i)].

One may recover in a similar manner the existence part of [**30**, Theorem 1]. We note that Theorem 5.7 applies in much more general situations than the above, and allows less restrictive conditions on the reaction terms than often assumed, with in particular spatial variation allowed. Similar remarks apply to competing species problems.

We conclude with a general comment on the role of coexistence states in a biological context. On its own the *existence* of a coexistence state is probably of somewhat limited biological interest (though of considerable mathematical interest) as the state may not be stable nor indeed unique. However, we see that in a rather wide range of problems the conditions which have been given for the existence of coexistence states are in fact enough to ensure a considerably stronger condition, that of permanence, which is of course a type of stability condition. One may perhaps speculate then that the standard conditions for existence on its own could in many cases be weakened. There is some discussion of a necessary and sufficient condition in [**14**], but this condition is acknowledged there to be 'rather implicit', and clearly much remains to be done on this problem.

7. Summary and conclusions

The results of the preceding sections span a wide range of levels of abstraction, technicality and applicability. The purpose of this section is to put some of them into perspective so that the whole panorama can be viewed and interpreted. The basic point is that our approach to coexistence provides a method which is quite general in applicability but can also be very precise in its conclusions in specific cases.

The first significant feature of our conditions for permanence (for example in Theorems 5.3, 5.5, 5.7 and 5.8) is that they do not require any special assumptions about the monotonicity of the interaction terms, uniqueness of coexistence states, the existence of a global Lyapunov function, or other such properties. The examples noted in the paper are mainly drawn from classical Lotka–Volterra models, but the methods would apply equally well to a system such as

$$u_{1t} = \mu_1 \Delta u_1 + (m_1 - b_{11}u_1 - b_{12}u_2)u_1,$$
$$u_{2t} = \mu_2 \Delta u_2 + (m_2 + b_{21}u_1 - cu_1^2 - b_{22}u_2)u_2,$$

in which the first species acts as prey for the second at low densities but competes with it at higher densities. Much more complicated interactions or functional forms could also be used. Such an increase in generality would be useless from an applied viewpoint if it were accompanied by a corresponding loss of precision, but such is not the case here.

The second major feature of our approach is that where it overlaps with other techniques it often gives similar or better results. A specific example is the problem of coexistence states discussed in Section 6. We find that our approach yields the existence of a coexistence state under the same hypotheses as used in other investigations, but also provides the stronger conclusion that any initial distribution of populations with both species present can be expected to display long-term coexistence. Since even local stability of the coexistence state is difficult to establish (and may not always hold), and in any case does not suffice to ensure long-term coexistence with arbitrary initial data, our result based on permanence is a genuine improvement on what was known previously.

A third important aspect of our approach is that it produces conditions that can be interpreted in natural and direct ways in terms of environmental conditions and parameters describing the strength of interactions. Our conditions for permanence are cast as inequalities on the eigenvalues of a class of problems which have been widely studied. The dependence of the eigenvalues on the geometry of the underlying domain and on the coefficients in the problem is reasonably well understood, they can be computed explicitly in simple cases and there is a huge literature available on their estimation, numerical approximation, qualitative properties and so on. Eigenvalue-based criteria for coexistence can then be used to reach biological conclusions that have been difficult to deduce through other methods.

Our fourth and final observation is that combining the 'dynamics' idea of permanence with the 'static' idea of studying geometric problems via eigenvalues, we have been able to treat questions about coexistence which would be difficult if not impossible to solve using only one of those viewpoints. The whole is evidently more than the sum of its parts and should provide a strong but flexible tool for studying spatial effects on interacting populations.

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