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INVASION OF A PERSISTENT SYSTEM

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Dedicated to the memory of Geoffrey J. Butler, my doctoral thesis supervisor. His influence and inspiration continue to live on.

1. Introduction. Today, with genetic engineering no longer just a topic of science fiction, but rather a reality, one of the intriguing questions in ecology concerns how to predict the effect of introducing a new species to a thriving ecosystem. In this paper we consider the following special case: When is it possible for an invading population to successfully infiltrate a community?

We formulate the problem in terms of the mathematical notions of *persistence* (see, for example, Butler, Freedman, and Waltman [**2, 3**] and Butler and Waltman [**4**]). Other closely related terminology includes *cooperativity, permanent coexistence, permanence*, and *ecological stability*. For a discussion of how these terms are related, see Gard [**8**], Hofbauer [**10**] and Hutson and Law [**14**]. The notion of *uninvadability* is discussed in Sigmund and Schuster [**16**].

2. Preliminaries. For any positive integer n, define

$$\mathbf{R}^n_+ = \{(x_1, x_2, \dots , x_n) \in \mathbf{R}^n : x_i \geq 0,\ i = 1, \dots , n\}$$

and, for any $J \subseteq \mathcal{N} = \{1, 2, \dots , n\}$, define

$$\mathbf{R}^n_J = \{(x_1, x_2, \dots , x_n) \in \mathbf{R}^n_+ : x_i = 0,\ i \in \mathcal{N}\backslash J\}.$$

Consider the autonomous system

$$\begin{aligned} \dot{z}(t) &= g(z(t)) \quad (z = (z_1, z_2, \dots , z_k)), \\ z(0) &\in \operatorname{int} \mathbf{R}^k_+ \quad \left(\cdot = \frac{d}{dt}\right), \end{aligned} \tag{2.1}$$

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where $g : \mathbf{R}_+^k \to \mathbf{R}^k$ is sufficiently smooth so that global existence and uniqueness of solutions and continuous dependence of solutions on initial conditions and on parameters hold. Assume that both $\mathbf{R}_+^k$ and $\operatorname{int}\mathbf{R}_+^k$ are positively invariant with respect to (2.1). Given $x \in \mathbf{R}_+^k$, let $x(t)$ be the solution of (2.1) satisfying $x(0) = x$. Let $\gamma(x)$ $(\gamma^+(x))$, the trajectory (positive semi-trajectory) through x be defined to be the set $\{x(t) : t \in \mathbf{R}\}$ $(\{x(t) : t \in \mathbf{R}_+\})$. Let $\Lambda^+(x)$ $(\Lambda^-(x))$ denote the positive or omega limit set (negative or alpha limit set) of the solution through x.

System (2.1) is called *dissipative* if, for each $z \in \mathbf{R}_+^k$, $\Lambda^+(z) \neq \varnothing$ and $\cup_{x\in\mathbf{R}_+^k}\Lambda^+(x)$ has compact closure, i.e., all solutions are uniformly asymptotically bounded.

Following Butler, et al. [**2**], we define (2.1) to be *weakly persistent* if $z \in \operatorname{int}\mathbf{R}_+^k$ implies that $\overline{\lim}_{t\to\infty} z_i(t) > 0$, for all $i = 1, \dots, k$. If $\overline{\lim}$ is replaced by $\underline{\lim}$, (2.1) is called *strongly persistent* or simply *persistent*. System (2.1) is *uniformly persistent* if there exists a uniform $\epsilon_0 > 0$ such that $\underline{\lim}_{t\to\infty} z_i(t) \geq \epsilon_0$ for all $i = 1, \dots, k$ and $z \in \operatorname{int}\mathbf{R}_+^k$.

REMARK 2.1. From the results in [**3**], it follows that (2.1) is uniformly persistent in the above sense if, in addition to being persistent, it is dissipative and $\partial\mathbf{R}_+^k$ is isolated and acyclic. If (2.1) is both dissipative and uniformly persistent, there is a global (stable, compact) attractor in $\operatorname{int}\mathbf{R}_+^k$ (where global is with respect to $\operatorname{int}\mathbf{R}_+^k$). (The term attractor used by Conley is the stable attractor of Bhatia and Szegö.)

Any concepts not defined are standard in dynamical systems theory (see, for example, Bhatia and Szegö [**1**], Sell [**15**], and Conley [**7**]).

3. Results. Consider the following model describing the dynamics of interacting populations as well as possibly of the limiting resources of some ecosystem:

$$\begin{aligned} &\dot{x} = F(x, y, \mu), \qquad (x = x_1, x_2, \dots, x_n)), \\ &\dot{y} = yh(x, y, \mu), \qquad x \in \mathbf{R}_+^n,\ y \in \mathbf{R}_+ \text{ and } \mu \in I, \end{aligned} \tag{3.1}$$

and the corresponding subsystem,

$$\dot{x} = F(x, 0, \mu), \qquad x \in \mathbf{R}_+^n \text{ and } \mu \in I, \tag{3.2}$$

where I is some set of parameters and F and h are assumed to be continuously differentiable. Let $(3.1)_{\hat{\mu}}$ and $(3.2)_{\hat{\mu}}$ denote (3.1) and (3.2) for some fixed $\hat{\mu} \in I$. Assume that both the nonnegative cone and the positive cone are positively invariant with respect to each system. Interpret each x_i as the concentration (as a function of time) of some limiting resource being added to the system or the concentration of some reproducing population interacting in the system. Let y represent the concentration of the population attempting to invade (3.2). Assume that, for $\mu \in L \subseteq I$, system $(3.2)_\mu$ is thriving in the sense that the system is persistent. In applications (see Section 5) the parameters $\mu \in I$ can often be thought of as bifurcation parameters. As these parameters vary, the dynamics of the systems and, in particular, which species survive may change.

The main result, Theorem 3.1 below, gives criteria that guarantee that, for some $\hat{\mu} \in I$, the invasion by y of a persistent n-dimensional system $(3.2)_{\hat{\mu}}$ will be successful (at least deterministically) in the sense that they ensure that the resulting $(n+1)$-dimensional system $(3.1)_{\hat{\mu}}$ will be persistent. Theorem 3.3 is a generalization of Theorem 3.1. In Theorem 3.3, invasion by y may drive certain species to extinction.

The proofs of all the results in this section are given in Section 4. The approach is similar to the approach taken in [**9, 11**, and **13**].

THEOREM 3.1. *For $\hat{\mu} \in I$, define*

$$\Omega(\hat{\mu}) \equiv \overline{\bigcup_{x \in \operatorname{int} \mathbf{R}_+^n} \Lambda^+(x)}, \tag{3.3}$$

where $\Lambda^+(x)$ is defined with respect to system $(3.2)_{\hat{\mu}}$. Assume

(i) *system $(3.3)_{\hat{\mu}}$ is dissipative*;

(ii) *all solutions $\varphi(t) = (x(t), y(t))$ of $(3.1)_{\hat{\mu}}$ with $\varphi(0) \in \operatorname{int} \mathbf{R}_+^{n+1}$ satisfy $\underline{\lim}_{t\to\infty} x_k(t) > 0$, $k \in \mathcal{N}$*;

(iii) *for each $x \in \Omega(\hat{\mu})$, there exists a constant $T_x > 0$ such that*

$$\int_{-T_x}^{0} h(x(s), 0, \hat{\mu})\, ds > 0 \tag{3.4}$$

(*where $x(t)$ is the solution of $(3.2)_{\hat{\mu}}$ with $x(0) = x$*).

Then $(3.1)_{\hat{\mu}}$ *is persistent.*

REMARK 3.2. If $(3.2)_{\hat{\mu}}$ is dissipative, then $\Omega(\hat{\mu})$ is a compact, invariant set and if, in addition, $(3.2)_{\hat{\mu}}$ is uniformly persistent, $\Omega(\hat{\mu}) \subseteq \operatorname{int} \mathbf{R}^n_+$.

THEOREM 3.3. *Assume that, for some* $\hat{\mu} \in I$:

(i) *system* $(3.1)_{\hat{\mu}}$ *is dissipative*;

(ii) *there exists* $J \subseteq \mathcal{N}$ *such that, for all solutions* $\varphi(t) = (x(t), y(t))$ *of* $(3.1)_{\hat{\mu}}$ *with* $\varphi(0) \in \operatorname{int} \mathbf{R}^{n+1}_+$ *or* $\varphi(0) \in \operatorname{int} \mathbf{R}^{n+1}_J$, $\lim_{t\to\infty} x_k(t) = 0$ *if* $k \in \mathcal{N} \setminus J$ *and* $\underline{\lim}_{t\to\infty} x_k(t) > 0$ *if* $k \in J$;

(iii) *for each* $x \in \Omega_J(\hat{\mu}) \equiv \overline{\cup_{x \in \operatorname{int} \mathbf{R}^n_J} \Lambda^+(x)}$ (*where* $x(t)$ *is the solution of* $(3.2)_{\hat{\mu}}$ *with* $x(0) = x$), *there exists a constant* $T_x > 0$ *such that*

$$\int_{-T_x}^{0} h(x(s), 0, \hat{\mu})\, ds > 0. \tag{3.5}$$

If $y(0) > 0$, *then* $\underline{\lim}_{t\to\infty} y(t) > 0$ *for* $(3.1)_{\hat{\mu}}$.

COROLLARY 3.4. *The above theorems are also valid if* (3.4) *or* (3.5) *of condition* (iii) *is replaced by*

$$\int_{0}^{T_x} h(x(s), 0, \hat{\mu})\, ds > 0. \tag{3.6}$$

4. Technical lemmas and proofs. The technical lemmas are mainly concerned with the implications of condition (iii) of Theorems 3.1 and 3.3. We state and prove the results in terms of the general system (2.1), since (3.1) and (3.2) are both special cases of this system.

Throughout this section, assume that the set K is compact and invariant with respect to system (2.1) and that the function $f : K \to \mathbf{R}$ is continuous.

LEMMA 4.1. *Assume that, for each $x \in K$, there exists a constant $T_x > 0$ such that*

$$\int_{-T_x}^{0} f(x(s))\, ds > 0, \tag{4.1}$$

where $x(t)$ is the solution of (2.1) *with $x(0) = x$. Then there exist uniform constants $T > 0$ and $\eta > 0$ such that, for any $z \in K$, T_z exists satisfying $0 < T_z \le T$ and*

$$\int_{-T_z}^{0} f(z(s))\, ds \ge \eta, \tag{4.2}$$

where $z(t)$ is the solution of (2.1) *with $z(0) = z$.*

PROOF. Suppose not. Then, for any fixed $\hat{T} > 0$ and $\eta > 0$, there exists a corresponding solution $\hat{x}(t)$ of (2.1) with $\hat{x}(0) \in K$ such that

$$\int_{-\tau}^{0} f(\hat{x}(s))\, ds < \eta \quad \text{for every } 0 \le \tau \le \hat{T}.$$

Hence, there exist sequences of positive constants $\{T_n\} \uparrow \infty$ and $\{\epsilon_n\} \downarrow 0$ as $n \uparrow \infty$ and a sequence of corresponding solutions $\{z_n(t)\}$ of (2.1), with $z_n(0) \in K$ for each n such that

$$\int_{-\tau}^{0} f(z_n(s))\, ds < \epsilon_n \quad \text{for every } 0 \le \tau \le T_n. \tag{4.3}$$

Since $z_n(0) \in K$ for each n and K is compact, without loss of generality, assume $\{z_n(0)\} \to z(0) \in K$ (taking a subsequence and relabelling if necessary). Since $z(0) \in K$, by hypothesis, there exist $T > 0$ and $\eta > 0$ such that $\int_{-T}^{0} f(z(s))\, ds = \eta$, where $z(t)$ is the solution of (2.1) through $z(0)$. By continuous dependence of solutions on initial conditions, it follows that $z_n(t) \to z(t)$ uniformly for $t \in [-T, 0]$. Thus,

$$\eta = \int_{-T}^{0} f(z(s))\, ds = \lim_{n\to\infty} \int_{-T}^{0} f(z_n(s))\, ds \le \lim_{n\to\infty} \epsilon_n = 0,$$

by (4.3), since $T < T_n$ for all sufficiently large n. This is clearly a contradiction since, by definition, $\eta > 0$. □

REMARK 4.2. Lemma 4.1 holds if (4.1) and (4.2) are replaced by $\int_0^{T_x} f(x(s))\,ds > 0$ and $\int_0^{T_z} f(z(s))\,ds \geq \eta$, respectively. (The proof is similar).

LEMMA 4.3. *The following are equivalent*:

(i) *For each* $x \in K$, *there exists a constant* $T_x > 0$ *such that* $\int_{-T_x}^0 f(x(s))\,ds > 0$, *where* $x(t)$ *is the solution of* (2.1) *satisfying* $x(0) = x$.

(ii) *For each* $z \in K$ *there exists a constant* $T_z > 0$ *such that* $\int_0^{T_z} f(z(s))\,ds > 0$, *where* $z(t)$ *is the solution of* (2.1) *satisfying* $z(0) = z$.

PROOF. (i)⇒(ii). Select any $z \in K$. Let $T > 0$ and $\eta > 0$ be the uniform constants (with respect to K) guaranteed by Lemma 4.1. Define

$$\beta = \min_{t\in[0,T]} \int_0^t f(z(s))\,ds. \tag{4.4}$$

Choose any integer $m > 0$ sufficiently large so that

$$m\eta + \beta > 0. \tag{4.5}$$

Define $\tilde{T} = mT$ and

$$\gamma = \max_{t\in[0,\tilde{T}]} \int_t^{\tilde{T}} f(z(s))\,ds. \tag{4.6}$$

Then $\gamma \leq \bar{k}\eta$ for some fixed integer $\bar{k} > 0$. By definition of T, there exists

$$0 < T_1 \leq T \quad \text{such that} \quad \int_{\tilde{T}-T_1}^{\tilde{T}} f(z(s))\,ds = \eta. \tag{4.7}$$

Since (2.1) is autonomous and K is invariant, there exists

$$0 < T_2 \leq T \text{ such that } \int_{\tilde{T}-(T_1+T_2)}^{\tilde{T}-T_1} f(z(s))\,ds = \eta.$$

Continuing thus, we find $\{T_i\}_{i=1}^m$ such that $0 < T_i \le T$, and so

$$\tilde{T} - \sum_{i=1}^{m} T_i \ge 0 \quad \text{and} \quad \int_{\tilde{T}-\sum_{i=1}^m T_i}^{\tilde{T}} f(z(s))\,ds = m\eta.$$

Case I. If $\tilde{T} - \sum_{i=1}^m T_i \in [0,T]$, then

$$\int_0^{\tilde{T}} f(z(s))\,ds = \int_0^{\tilde{T}-\sum_{i=1}^m T_i} f(z(s))\,ds + \int_{\tilde{T}-\sum_{i=1}^m T_i}^{\tilde{T}} f(z(s))\,ds \ge \beta + m\eta > 0,$$

by (4.4) and (4.5). Take $T_z = \tilde{T}$.

Case II. If $\tilde{T} - \sum_{i=1}^m T_i > T$, continue to find $T_{m+1}, T_{m+2}, \dots, T_{m+j}$. Eventually, $\tilde{T} - \sum_{i=1}^{m+j} T_i \in [0,T]$, where $m+j \le \bar{k}$ since, if $m+j > \bar{k}$, then

$$\int_{\tilde{T}-\sum_{i=1}^{m+j} T_i}^{\tilde{T}} f(z(s))\,ds = (m+j)\eta > \bar{k}\eta > \gamma,$$

violating (4.6). Complete the proof now by arguing as in Case I.

(ii)⇒(i). Since K is invariant, this follows by reversing time. □

The final lemma concerns system $(3.2)_{\hat{\mu}}$. Define

$$C(\hat{\mu}) = \{x \in \operatorname{int} \mathbf{R}_+^n : \overline{\gamma(x)} \subset \operatorname{int} \mathbf{R}_+^n \text{ is compact}\}, \tag{4.8}$$

where $\overline{\gamma(x)}$ is the closure of the trajectory through x, with respect to $(3.2)_{\hat{\mu}}$.

LEMMA 4.4. *Assume* $(3.2)_{\hat{\mu}}$ *is dissipative. If, for each* $x \in \Omega(\hat{\mu})$, *there exists a constant* $T_x > 0$ *such that*

$$\int_0^{T_x} h(x(s), 0, \hat{\mu})\,ds > 0, \tag{4.9}$$

where $x(t)$ is the solution of $(3.2)_{\hat\mu}$ *satisfying* $x(0) = x$*, then, for each* $z \in C(\hat\mu)$*, there exists a constant* $T_z > 0$ *such that*

$$\int_0^{T_z} h(z(s), 0, \hat\mu)\, ds > 0, \tag{4.10}$$

where $z(t)$ is the solution of (3.2) *satisfying* $z(0) = z$.

PROOF. Select $z \in C(\hat\mu)$. Define $A = \overline{\gamma(z)} \cup \Omega(\hat\mu)$. Then A is compact and invariant with respect to $(3.2)_{\hat\mu}$. Therefore, there exists a $\delta > 0$ such that, for any $z_1, z_2 \in A$,

$$\text{if } \rho(z_1, z_2) < \delta \text{ then } |h(z_1, 0, \hat\mu) - h(z_2, 0, \hat\mu)| < \frac{\eta}{2T}, \tag{4.11}$$

where $T > 0$ and $\eta > 0$ are the uniform constants guaranteed by Remark 4.2. By continuous dependence of solutions on initial conditions, there exists a $\hat\delta > 0$ such that, for any solutions $u(t)$ and $w(t)$ of $(3.2)_{\hat\mu}$,

$$\text{if } \rho(w(0), u(0)) < \hat\delta \text{ then } \rho(w(t), u(t)) < \delta \text{ for all } t \in [0, T]. \tag{4.12}$$

Since $\Lambda^+(z(0)) \subseteq \Omega(\hat\mu)$, there exists a $\hat T > 0$ such that

$$\rho(z(t), \Omega(\hat\mu)) < \hat\delta \text{ for all } t \geq \hat T. \tag{4.13}$$

If $\int_0^\tau h(z(s), 0, \hat\mu)\, ds > 0$ for some $0 < \tau \leq \hat T$, we are done. Otherwise, it suffices to show that, for some $T_z > \hat T$,

$$\int_{\hat T}^{T_z} h(z(s), 0, \hat\mu)\, ds > -\int_0^{\hat T} h(z(s), 0, \hat\mu)\, ds. \tag{4.14}$$

By (4.13), there exists a $w_1 \in \Omega(\hat\mu)$ such that $\rho(z(\hat T), w_1) < \hat\delta$. Let $w_1(t)$ be the solution of $(3.2)_{\hat\mu}$ with $w_1(0) = w_1$. Then, by (4.12), $\rho(z(\hat T + t), w_1(t)) < \delta$ for all $t \in [0, T]$, and so, by (4.11), $|h(z(\hat T + t), 0, \hat\mu) - h(w_1(t), 0, \hat\mu| < \eta/(2T)$ for all $t \in [0, T]$. Since $w_1 \in \Omega(\hat\mu)$, there exists $0 < T_{w_1} \leq T$ such that $\int_0^{T_{w_1}} h(w_1(s), 0, \hat\mu)\, ds \geq \eta$. But then,

$$\begin{aligned}\int_0^{T_{w_1}} h(z(\hat T + s), 0, \hat\mu)\, ds &\geq \int_0^{T_{w_1}} h(w_1(s), 0, \hat\mu)\, ds \\ &\quad - \int_0^{T_{w_1}} |h(z(\hat T + s), 0, \hat\mu) - h(w_1(s), 0, \hat\mu)|\, ds \\ &\geq \eta - \eta T_{w_1}/(2T) \geq \eta/2.\end{aligned}$$

Therefore, by a simple change of variables, $\int_{\hat{T}}^{\hat{T}+T_{w_1}} h(z(t),0,\hat{\mu})\,dt \geq \eta/2$. Repeating the argument, one can construct a sequence $\{T_{w_n}\}_{n=1}^{\infty}$ with $0 < T_{w_n} \leq T$ such that

$$\int_{\hat{T}}^{\hat{T}+\sum_{n=1}^{k} T_{w_n}} h(z(t),0,\hat{\mu})\,dt \geq k\eta/2.$$

Hence, one can define $T_z = \hat{T} + \sum_{n=1}^{N} T_{w_n}$ for some N large enough to ensure (4.14) holds. □

We are finally in a position to prove the main result.

PROOF OF THEOREM 3.1. By (ii) it suffices to show that, for $\mu = \hat{\mu}$, all solutions $\varphi(t) = (x(t), y(t))$ of (3.1) with $\varphi(0) \in \operatorname{int} \mathbf{R}_+^{n+1}$ satisfy $\underline{\lim}_{t\to\infty} y(t) > 0$. Suppose not. Then there exists a solution $\hat{\varphi}(t) = (\hat{x}(t), \hat{y}(t))$ with $\hat{\varphi}(0) \in \operatorname{int} \mathbf{R}_+^{n+1}$ for which $\underline{\lim}_{t\to\infty} \hat{y}(t) = 0$. Since $\hat{y}(t) > 0$ for all $t \geq 0$, there exists a sequence $\{t_k\} \uparrow \infty$ as $k \uparrow \infty$ such that

$$\hat{y}(t_k) < \hat{y}(t) \quad \text{for all } 0 \leq t < t_k \tag{4.15}$$

and $\{(\hat{x}(t_k), \hat{y}(t_k))\} \to (\tilde{x}, 0) \in \Lambda^+(\hat{\varphi})$ as $k \to \infty$. By (i) $\Lambda^+(\hat{\varphi})$ is compact, and by (ii) $\Lambda^+(\hat{\varphi}) \subset \operatorname{int} \mathbf{R}_+^n \times \mathbf{R}$. By the invariance of $\Lambda^+(\hat{\varphi})$, $\overline{\gamma(\tilde{x})} \times \{0\} \subset \Lambda^+(\hat{\varphi})$ (where γ is defined with respect to $(3.2)_{\hat{\mu}}$), and so $\overline{\gamma(\tilde{x})} \subset \operatorname{int} \mathbf{R}_+^n$. Therefore, $\tilde{x} \in C(\hat{\mu})$.

Let $\tilde{\varphi}(t) = (\tilde{x}(t), 0)$, where $\tilde{x}(t)$ is the solution of $(3.2)_{\hat{\mu}}$ satisfying $\tilde{x}(0) = \tilde{x}$. By (iii) and Lemmas (4.3) and (4.4), it follows that there exist $T > 0$ and $\epsilon > 0$ such that

$$\frac{1}{T}\int_0^T h(\tilde{x}(s-T),0,\hat{\mu})\,ds > 2\epsilon. \tag{4.16}$$

By (i) and the fact that $\overline{\gamma(\tilde{x})}$ is compact, there exists a compact set A containing $\overline{\gamma(\tilde{x})} \times \{0\}$ in which all solutions of $(3.2)_{\hat{\mu}}$ eventually lie. By the uniform continuity of h on A, there exists $\delta > 0$ such that, for all $(x_1, y_1), (x_2, y_2) \in A$,

$$\text{if } \rho((x_1,y_1)(x_2,y_2)) < \delta \text{ then } |h(x_1,y_1,\hat{\mu}) - h(x_2,y_2,\hat{\mu})| < \epsilon. \tag{4.17}$$

By continuous dependence of solutions on initial conditions, there exists $\bar{\delta} > 0$ such that, for any solution $(\bar{x}(t), \bar{y}(t))$ of $(3.2)_{\hat{\mu}}$ satisfying

$$\begin{aligned} &\rho((\tilde{x}(0),0),(\bar{x}(0),\bar{y}(0))) < \bar{\delta}, \\ \text{then} \quad &\rho((\tilde{x}(t),0),(\bar{x}(t),\bar{y}(t))) < \delta \quad \text{for all } t \in [-T,0]. \end{aligned} \tag{4.18}$$

Choose N sufficiently large so that $t_N - T \geq 0$, $(\hat{x}(t), \hat{y}(t)) \in A$, for all $t \geq t_N - T$, and so that $\rho((\tilde{x}(0), 0), (\hat{x}(t_N), \hat{y}(t_N))) < \bar{\delta}$. By (4.18) and the fact that (3.1) is autonomous

$$\rho((\tilde{x}(t),0),(\bar{x}(t_N+t),\hat{y}(t_N+t))) < \delta \quad \text{for all } t \in [-T,0],$$

and, hence, by (4.17),

$$|h(\tilde{x}(t),0,\hat{\mu}) - h(\hat{x}(t_N+t),\hat{y}(t_N+t),\hat{\mu})| < \epsilon \quad \text{for all } t \in [-T,0].$$

From this and (4.16) it follows that

$$\frac{1}{T}\int_0^T h(\hat{x}(s+t_N-T),\hat{y}(s+t_N-T),\hat{\mu})\,ds > \epsilon,$$

or, equivalently,

$$\frac{1}{T}\int_{t_N-T}^{t_N} h(\hat{x}(t),\hat{y}(t),\hat{\mu})\,dt > \epsilon.$$

From the y equation of (3.1), it follows that $\frac{1}{T}\int_{t_N-T}^{t_N}(\dot{\hat{y}}/\hat{y})\,dt > \epsilon$. Integrating yields $\hat{y}(t_N) > \hat{y}(t_N-T)e^{\epsilon T} > \hat{y}(t_N-T)$, contradicting (4.15). □

PROOF OF THEOREM 3.3. This is similar to the proof of Theorem 3.1. □

PROOF OF COROLLARY 3.4. This is an immediate consequence of Theorem 3.1 and Lemma 4.3. □

5. Applications. In many examples it will be possible to apply Theorem 3.1 with very little known about the structure of $\Omega(\hat{\mu})$ (see

Example 5.5 below). In other cases the structure of $\Omega(\hat{\mu})$ may be simple and well understood. It may consist only of equilibrium points (see Example 5.3) or of equilibrium points and periodic orbits. For each equilibrium $\bar{x} \in \Omega(\hat{\mu})$, in order to verify (iii) it suffices to show that $h(\bar{x}, 0, \hat{\mu}) > 0$. For periodic solutions, the following proposition applies.

PROPOSITION 5.1. *Assume that $\gamma(x)$ is a periodic solution of system* (2.1) *with minimum period $T > 0$. Then the following are equivalent*:

(i) $\int_0^T f(x(s))\, ds > 0$;

(ii) *for each $\bar{x} \in \gamma(x)$, there exists $T_{\bar{x}} > 0$ such that the solution $\bar{x}(t)$ with $\bar{x}(0) = \bar{x}$ satisfies $\int_0^{T_{\bar{x}}} f(\bar{x}(s))\, ds > 0$.*

PROOF. (i)$\Rightarrow$(ii). This is obvious; just define $T_x = T$ for each $\bar{x} \in \gamma(x)$.

(ii)$\Rightarrow$(i). Proceed by contradiction. Assume that $\int_0^T f(x(s))\, ds \leq 0$. Define

$$g(t) = \int_0^t f(x(s))\, ds, \quad t \geq 0. \tag{5.1}$$

Then $g(0) = 0$ and $g(T) \leq 0$. Since $g(t)$ is continuous, $x(t)$ is periodic of period $T > 0$ and $g(T) \leq 0$, g attains its maximum at some point $\bar{t} \in [0, T]$. Thus,

$$g(\bar{t}) \geq g(t) \text{ for all } t \geq 0. \tag{5.2}$$

Consider the solution $\bar{x}(t)$ where $\bar{x}(0) = x(\bar{t})$. The periodicity of $\bar{x}(t)$ and (ii) imply that there exists $T_{\bar{x}}$ with $0 < T_{\bar{x}} \leq T$ such that

$$0 < \int_0^{T_{\bar{x}}} f(\bar{x}(s))\, ds = \int_0^{T_{\bar{x}}} f(x(\bar{t} + s))\, ds = \int_{\bar{t}}^{T_{\bar{x}}+\bar{t}} f(x(s))\, ds.$$

But then $g(T_{\bar{x}}+\bar{t}) = g(\bar{t})+\int_{\bar{t}}^{T_{\bar{x}}+\bar{t}}(f(x(s))\, ds > g(\bar{t})$, contradicting (5.2).
□

Next we show how to apply Theorem 3.1 using the following nondimensional version of a system modelling predator-mediated competition in a chemostat:

$$
\begin{aligned}
\dot{S}(t) &= 1 - S(t) - \sum_{i=1}^{2} x_i(t) p_i(S(t)), \\
\dot{x}_1(t) &= x_1(t)(-1 + p_1(S(t))) - y(t) q_1(x_1(t)), \\
\dot{x}_2(t) &= x_2(t)(-1 + p_2(S(t))), \\
\dot{y}(t) &= y(t)(-1 + q(x_1(t))),
\end{aligned} \tag{5.3}
$$

$$S(0) = 0, \quad x_i(0) \geq 0, \quad i = 1, 2, \quad y(0) \geq 0.$$

$S(t)$ denotes the concentration of the growth-limiting resource, $x_1(t)$ and $x_2(t)$ the concentrations of populations competing for the resource and $y(t)$ the concentration of a predator population. $p_i(S)$ represents the per capita growth rate of the i^{th} competitor as a function of resource concentration and $q(x_1(t))$ the per capita growth rate of the predator which predates solely on $x_1(t)$, the superior competitor in the absence of predation.

Assume that $p_i, q : \mathbf{R}_+ \to \mathbf{R}_+$, are continuously differentiable, $p_i'(S) \geq 0$ for all $S \in \mathbf{R}_+$, $q'(x) \geq 0$ for all $x \in \mathbf{R}_+$, $p_i(0) = 0$, $i = 1, 2$, and $q(0) = 0$. Assume, as well, that there exist uniquely defined positive real numbers λ_i and δ such that

$$
\begin{gathered}
p_i(S) < 1 \quad \text{if } S < \lambda_i, \quad p_i(S) > 1 \quad \text{if } S > \lambda_i, \\
q(x) < 1 \quad \text{if } x < \delta, \quad q(x) > 1 \quad \text{if } x > \delta, \\
p_i'(\lambda_i) > 0 \quad \text{and} \quad q'(\delta) > 0.
\end{gathered} \tag{5.4}
$$

Assume also that all λ_i and δ are distinct from each other and from 1 and

$$0 < \lambda_1 < \lambda_2. \tag{5.5}$$

It is this condition that makes x_1 the superior competitor in the absence of predation (see Butler and Wolkowicz [**5**]).

For a more thorough discussion of this model and for references to others who have studied it and its subsystems, see Butler and Wolkowicz [**6**].

REMARK 5.2. Identify (S, x_1, x_2, y)-space with $\mathbf{R}^4 \cdot \mathbf{R}^4_J$ and $\operatorname{int} \mathbf{R}^4_J$ are positively invariant for (5.3) for any $J \subseteq \{1,2,3,4\}$, and (5.4) is dissipative. In fact, the simplex

$$\{(S, x_1, x_2, y) : S, x_1, x_2, y \geq 0;\ S + \sum_{i=1}^{2} x_i + y = 1\}$$

is a global attractor of (5.3). The proofs are straightforward (for similar proofs see, for example, Hsu et al. [**12**]).

EXAMPLE 5.3. Consider the following subsystems of (5.3):

$$\begin{aligned} \dot{S}(t) &= 1 - S(t) - x_1(t)p_1(S(t)), \\ \dot{x}_1(t) &= x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t)), \\ \dot{y}(t) &= y(t)(-1 + q(x_1(t))), \end{aligned} \tag{5.6}$$

$$S(0) = 0, \quad x_1(0) \geq 0, \quad y(0) \geq 0$$

and

$$\begin{aligned} \dot{S}(t) &= 1 - S(t) - x_1(t)p_1(S(t)), \\ \dot{x}_1(t) &= x_1(t)(-1 + p_1(S(t))), \end{aligned} \tag{5.7}$$

$$S(0) = 0, \quad x_1(0) \geq 0.$$

Then (5.6) plays the role of (3.1) and (5.7) of (3.2) in Theorem 3.1, and y plays the role of the invading population. Let the parameter set be $I = \{\lambda_1, \delta\} \in \operatorname{int} \mathbf{R}^2_+$.

If $\lambda_1 < 1$, using the Lyapunov function,

$$V(S, x_1) = \int_{\lambda_1}^{S} \frac{p_1(\xi) - 1}{p_1(\xi)}\, d\xi + x_1 - x_1^* - x_1^* \ln(x_1/x_1^*),$$

where $x_1^* = 1 - \lambda_1$, it follows that the critical point (λ_1, x_1^*) is globally asymptotically stable for (5.7) with respect to solutions initiating in $\operatorname{int} \mathbf{R}^2_+$. Therefore, with respect to (5.7), for any $\lambda_1 < 1$, $\Omega((\lambda_1, \delta)) = \overline{\cup_{x \in \operatorname{int} \mathbf{R}^2_+} \Lambda^+(x)} = \{(\lambda_1, x_1^*)\}$. Thus, by Theorem 3.1, if $\lambda_1 < 1$, (5.6) is persistent provided $-1 + q(x_1^*) > 0$, that is, provided $x_1^* > \delta$. In fact, this result is sharp in the following sense. If $x_1^* \le \delta$, then the critical point $(\lambda_1, x_1^*, 0)$ is globally asymptotically stable for (5.6) with respect to $\operatorname{int} \mathbf{R}_+^3$, and, hence, (5.6) is not persistent (see [**6**, Theorem 6.3]).

REMARK 5.4. If $1 - \lambda_1 = x_1^* > \delta$, it is now possible to apply the theorem in Butler et al. [**3**] (see Remark 2.1) to show that (5.6) is uniformly persistent.

In the previous example, condition (iii) of Theorem 3.1 is easy to verify since $\Omega(\hat{\mu})$ is a single equilibrium point. It is shown in [**17**] that, if the class of response functions p_1 and q is restricted appropriately, then $\Omega(\hat{\mu})$, with respect to (5.6), is again a single equilibrium point. In fact, for (5.6), using the Lyapunov function,

$$\begin{aligned} V(S, x_1, y) = \int_{S^*}^{S} \frac{p_1(\xi) - p_1(s^*)}{p_1(\xi)}\, d\xi + x_1 - x_1^* - x_1^* \ln(x_1/x_1^*) \\ + y - y^* - y^* \ln(y/y^*), \end{aligned}$$

where (S^*, x_1^*, y^*) is the unique equilibrium point in $\operatorname{int} \mathbf{R}_+^3$, it can be shown that provided q is Lotka-Volterra, it is not even necessary to restrict p_1. In this case, (S^*, x_1^*, y^*) is globally asymptotically stable with respect to $\operatorname{int} \mathbf{R}_+^3$. On the other hand, in [**6**] an example is given in which p_1 is Lotka-Volterra, q is Michaelis-Menten and $\Omega(\hat{\mu})$, with respect to (5.6), contains a periodic orbit.

EXAMPLE 5.5. Let (5.3) play the role of (3.1) and (5.6) the role of (3.2) in Theorem 3.1. Consider x_2 as the invading population. Let the parameter set $I = \{\lambda_1, \lambda_2, \delta\}$. In [**6**, Lemma 8.1] it is shown that if $\lambda_1 < 1$ and $x_1(0) > 0$, then $\underline{\lim}_{t\to\infty} x_1(t) > 0$, and if $\lambda_1 + \delta < 1$, $x_1(0) > 0$, and $y(0) > 0$, then $\underline{\lim}_{t\to\infty} y(t) > 0$. That $\underline{\lim}_{t\to\infty} S(t) > 0$ if $S(0) > 0$ is obvious. From this and by Remark 5.2, to verify that Theorem 3.1 applies it remains to find conditions for (iii) to hold.

We assume that we can parameterize $q(x) = q_\delta(x)$, where

$$\lim_{\delta\to 0} q_\delta(\epsilon) = +\infty \quad \text{for every fixed } \epsilon > 0. \tag{5.8}$$

It is easily verified that, for most realistic response functions including Lotka-Volterra, Michaelis-Menten, and multiple saturation, q can be parameterized in this way. Generally, $\delta \to 0$ is equivalent to the maximum growth rate tending to $+\infty$.

By Remarks 2.1, 5.2 and 5.4, it follows that

$$\Omega(\hat{\mu}) \subseteq \{(S, x_1, y) \in \operatorname{int} \mathbf{R}^3_+ : 0 < S, x_1, y \leq 1\}$$

is compact. Also, for each fixed δ satisfying $\delta < 1 - \lambda_1$, there exists $l = l_\delta$ such that $0 < l \leq y$ for all y for which $(S, x_1, y) \in \Omega(\hat{\mu})$.

PROPOSITION 5.6. *Assume* $\lambda_1 < \lambda_2 < 1$. *Define*

$$\bar{\epsilon} = p_2(\lambda_2 + (1 - \lambda_2)/2) - 1. \quad \textit{(Then } \bar{\epsilon} > 0 \textit{ since } \lambda_2 < 1.\textit{)} \tag{5.9}$$

Select ϵ *such that*

$$0 < \epsilon < \min \left(\frac{1}{4}, \left(\frac{1 - \lambda_2}{2p_1(1)} \right)^2, \left(\frac{\bar{\epsilon}}{4(1 + \bar{\epsilon})} \right)^2 \right]. \tag{5.10}$$

Let $\delta > 0$ *such that* $\lambda_1 + \delta < 1$ *and*

$$q_\delta(\epsilon) > \frac{2}{\sqrt{\epsilon}} \left(1 + \frac{p_1(1) + 1}{\epsilon k} \right), \qquad \textit{where } k = \frac{1}{\sqrt{\epsilon}} - 1. \tag{5.11}$$

Let $\hat{\mu} = \{(\lambda_1, \lambda_2, \delta)\}$, *and define* $\Omega(\hat{\mu})$ *with respect to* (5.6). *Take*

$$T > \max[-\ln(l), 2/\epsilon], \qquad \textit{where } l \leq y. \tag{5.12}$$

Then

$$\int_{-T}^{0} (-1 + p_2(S(v)))\, dv > 0, \tag{5.13}$$

for any solution of (5.6) *with* $(S(0), x_1(0), y(0)) \in \Omega(\hat{\mu})$, *and, hence,* (5.3) *is uniformly persistent.*

PROOF. Define

$$M = p_1(1), \qquad (p_1(1) > 1 \text{ since } \lambda_1 < 1), \tag{5.14}$$

$$X = \{t \in [-T, 0] : x_1(t) \geq \epsilon\}, \tag{5.15}$$

$$V = \{t \in [-T, 0] : S(t) \leq 1 - (1 + k)\epsilon M\}, \tag{5.16}$$

$$X^C = [-T, 0] \backslash X, \tag{5.17}$$

$$V^C = [-T, 0] \backslash V. \tag{5.18}$$

If $t \in X$, then $\dot{y}(t)/y(t) \geq -1 + q_\delta(\epsilon)$. If $t \in X^C$, then $\dot{y}(t)/y(t) \geq -1$. Let ν denote the Lebesque measure. Integrating the y equation from $-T$ to 0 yields

$$\begin{aligned} \ln(y(0)/y(-T)) &\geq \int_X (-1 + q_\delta(\epsilon))\, d\nu + \int_{X^C} -1\, d\nu \\ &= (-1 + q_\delta(\epsilon))\nu(X) - (T - \nu(X)) \\ &= T\left(\frac{\nu(X)}{T} q_\delta(\epsilon) - 1\right). \end{aligned}$$

Therefore,

$$\nu(X)/T < 2/q_\delta(\epsilon), \tag{5.19}$$

since otherwise $-\ln(l) \geq \ln(y(0))/y(-T)) \geq T$, contradicting (5.12).

Next, let $[-T, 0] = \cup_{i=1}^4 G_i$, where

$$\begin{aligned} G_1 &= V \cap X^C && (\Longrightarrow \nu(G_1) \geq \nu(V) - \nu(X)), \\ G_2 &= V \cap X && (\Longrightarrow \nu(G_2) \leq \nu(X)), \\ G_3 &= V^C \cap X^C && (\Longrightarrow \nu(G_3) \leq T), \\ G_4 &= V^C \cap X && (\Longrightarrow \nu(G_4) \leq \nu(X)). \end{aligned}$$

Then

$$\begin{aligned} &\dot{S}(t) \geq 1 - (1 - (1+k)\epsilon M) - \epsilon M = \epsilon k M \quad \text{for } t \in G_1, \\ &\dot{S}(t) \geq 1 - (1 - (1+k)\epsilon M) - M^2 \geq -M^2 \quad \text{for } t \in G_2, \\ &\dot{S}(t) \geq 1 - 1 - \epsilon M = -\epsilon M \quad \text{for } t \in G_3, \\ &\dot{S}(t) \geq 1 - 1 - M = -M \quad \text{for } t \in G_4. \end{aligned}$$

Integrating the S equation of (5.6) from $-T$ to 0 yields

$$1 \geq S(0) - S(t) \geq \epsilon k M(\nu(V) - \nu(X)) - M^2\nu(X) - \epsilon M T - M\nu(X).$$

Therefore, $\nu(V)/T \leq 1/(T\epsilon k M) + (\nu(X)/T)(1 + M/(\epsilon k) + 1/(\epsilon k)) + 1/k$. Since $0 < \epsilon < 1/4$, it follows that $k > 1/(2\sqrt{\epsilon})$, and, hence, $1/k < 2\sqrt{\epsilon}$. By (5.12), $T > 2/\epsilon$, and by (5.14), $M > 1$ so that $1/(T\epsilon k M) \leq$

$1/(2k) < \sqrt{\epsilon}$. By (5.11) and (5.19), $(\nu(X)/T)(1 + M/(\epsilon k) + 1/(\epsilon k)) < \sqrt{\epsilon}$. Hence,

$$\nu(V)/T \le 4\sqrt{\epsilon}. \tag{5.20}$$

Thus,

$$\begin{aligned}
&\int_{-T}^{0} (-1 + p_2(S(t)))\,dt \\
&\qquad = \int_V (-1 + p_2(S(t)))\,d\nu + \int_{V^C} (-1 + p_2(S(t)))\,d\nu \\
&\qquad \ge -\nu(V) + \bar{\epsilon}(T - \nu(V)) \qquad \text{(by (5.9), (5.10), (5.11), (5.14)} \\
&\qquad \ge T\left(\frac{-\nu(V)}{T} + \bar{\epsilon} - \bar{\epsilon}\frac{\nu(V)}{T}\right) \qquad \text{and (5.16))} \\
&\qquad = T\left(\frac{-\nu(V)}{T}(1 + \bar{\epsilon}) + \bar{\epsilon}\right) \\
&\qquad \ge T(\bar{\epsilon} - 4\sqrt{\epsilon}(1 + \bar{\epsilon})) \qquad \text{(by (5.20))} \\
&\qquad > T\left(\bar{\epsilon} - 4\left(\frac{\bar{\epsilon}}{4(1 + \bar{\epsilon})}\right)(1 + \bar{\epsilon})\right) \qquad \text{(by (5.10))} \\
&\qquad = 0.
\end{aligned}$$

Thus, (iii) of Theorem 3.1 holds, and, hence, (5.3) is persistent. As in Example 5.3, one can apply the results in [**3**] to obtain uniform persistence. □

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