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Coexistence for systems governed by difference equations of Lotka–Volterra type

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Abstract. The question of the long term survival of species in models governed by Lotka–Volterra difference equations is considered. The criterion used is the biologically realistic one of permanence, that is populations with all initial values positive must eventually all become greater than some fixed positive number. We show that in spite of the complex dynamics associated even with the simplest of such systems, it is possible to obtain readily applicable criteria for permanence in a wide range of cases.

Key words: Difference equations — Lotka–Volterra equations — Permanence — Discrete semi-dynamical systems

1. Introduction

Systems of difference equations have been much used in the modelling of the interactions of species with non-overlapping generations, see Hassell [3] for example. It is well known that even for one species the dynamics may be extremely complex, and it may be very difficult to predict the detailed asymptotic behaviour. However, one of the most important questions from a biological point of view concerns the conditions under which long term survival of all the species is assured, and it is our aim to show here that notwithstanding the complex dynamics which may occur, it is often possible to give rather simple and complete answers to this question for an important class of models.

We consider here the system of difference equations

$$x_i' = x_i \exp\left\{ r_i - \sum_{j=1}^{j=n} a_{ij} x_j \right\} \qquad (i = 1, \ldots, n) \tag{1.1}$$

on $\mathbb{R}^n_+$, where $x = (x_1, \ldots, x_n)^t$ is the vector of populations at one generation, and x' is the corresponding vector at the next generation. The r_i are assumed to be constants and $A = (a_{ij})$ is a constant matrix. For closely spaced generations, these equations may be written in the form

$$x_i(t+\varepsilon) = x_i(t) \exp\{\varepsilon[r_i - (Ax(t))_i]\},$$

and subtracting $x_i(t)$ from each side, dividing by ε, and taking the limit as $\varepsilon \to 0$ we obtain the familiar system of Lotka-Volterra differential equations

$$\dot{x}_i = x_i\{r_i - (Ax)_i\} \qquad (i = 1, \ldots, n). \tag{1.2}$$

For $n = 1$, the map $x' = x\, e^{r-ax}$ has been studied in detail by May and Oster [19], and was shown to exhibit a similar scenario of chaotic behaviour for large r as its more popular but biologically less realistic counterpart $x' = rx(1-x)$. Some two species cases have been considered, for example by Hassell [3], but higher dimensional difference systems of the type (1.1) have rarely been tackled in the literature. In this paper we want to show that (1.1) has been unjustly neglected, and is perhaps the most tractable discrete time model in Mathematical Ecology. We will point out that many results long known for (1.2) directly carry over to (1.1), in particular the crucial "averaging property", noticed originally by Volterra [23, pp. 173 et seq.], on the convergence of the time averages towards the equilibrium point (Lemma 2.4), which brings order from chaos. These remarks suggest that (1.1) is *the* natural analogue of (1.2) for discrete time and may therefore justifiably be termed a system of *Lotka-Volterra difference equations.*

The classical approach to questions of coexistence is through asymptotic stability or global asymptotic stability of a necessarily unique interior equilibrium point. However, from a biological point of view a more realistic criterion, that of permanence, appears to be that long term survival holds if and only if asymptotically (that is as the number of generations becomes very large), the species densities should become and remain greater than some fixed strictly positive quantity which is independent of the initial values if these are positive. This does not impose the restriction that the populations should settle down to fixed values, but on the other hand does not allow populations in the long run to remain near the boundary $\partial\mathbb{R}^n_+$ of the nonnegative cone $\mathbb{R}^n_+$ (corresponding to extinction of at least one species). In contrast, asymptotic stability and global asymptotic stability seem unrealistic in that they are too restrictive in requiring convergence to fixed values, while asymptotic stability is too weak in allowing orbits starting too far from the equilibrium point to converge to the boundary. We shall study the question of long term survival here from the point of view of permanence.

The system (1.1) is said to be *permanent*[1] if there is a compact (that is closed and bounded) set M in the interior $\mathring{\mathbb{R}}^n_+$ of $\mathbb{R}^n_+$, and thus with minimum distance from $\partial\mathbb{R}^n_+$ greater than zero, such that for every initial value in $\mathring{\mathbb{R}}^n_+$ the orbits enter and remain within M. The system is *weakly persistent* if for any initial value in $\mathring{\mathbb{R}}^n_+$, $\limsup_{j\to\infty} x_i(j) > 0$ $(i = 1, \ldots, n)$, where $x_i(j)$ is the population of species i at generation j; clearly permanence is a stronger property than weak persistence, although in certain circumstances the latter implies the former, see [2]. A property, for example permanence, is said to be *robust* if it is preserved under sufficiently small perturbations of the parameters in (1.1); it is clearly desirable that any condition in this area should be robust as it will not then be destroyed by small

[1] The equivalent terms, cooperativeness, permanent coexistence, uniform persistence, and ecological stability have also been used in the literature

changes in the specification of the system, and several of our results here are for robust permanence.

The idea of permanence is implicitly contained in Schuster et al. [20, 22] who studied a certain chemical network. Their ingenious technique has been simplified and adapted to yield a general method, based on the concept of an "average" Liapunov function, for establishing permanence by Hofbauer [4] and Hutson [11]. As shown by Jansen [16], this method is particularly effective for Lotka-Volterra equations because of the averaging property. There is now a considerable amount known concerning permanence in several different types of models, ranging from ordinary differential equations to partial differential equations (reaction-diffusion systems) and differential inclusions which allow for uncertainty in the specification of a system, see [1, 2, 7–15, 17, 24] for a wide range of applications. Permanence for general systems of difference equations has been studied by Hutson and Moran [14], a particular case being treated in [5]. However, our object here is to show that, because an analogous averaging property holds, for the special case of difference equations of Lotka–Volterra type (1.1) a great deal more can be said.

Sufficient conditions for permanence are obtained in Sect. 2; the mathematical technique used here is that of discrete semidynamical systems. Although the proofs are somewhat technical, the principal results, Theorem 2.5 and Corollary 2.6 are simple and easy to apply. Considerations of the limitation of the environment dictate that for the model (1.1) to be realistic some condition of uniform boundedness must apply to the orbits; this question has only recently been resolved for Lotka–Volterra differential equations [6], and for difference equations there appears to be little information available. A discussion is given in Sect. 3. Necessary conditions for permanence based on degree theory are given in Sect. 4 and the results are combined in Sect. 5 to yield a complete characterization for robust permanence for three species problems. In one form these conditions take the form of a simple and attractive geometrical criterion, Theorem 5.2(c). Finally we give two applications in Sect. 6, the first pointing out the difference between conditions leading to asymptotic stability and permanence, the second dealing with perhaps one of the most difficult three species problem, the analogue of the May–Leonard system for three competing species.

2. Sufficient conditions for permanence

The principal aim of this section is to show that there is a set of algebraic conditions, straightforward to check in practice, at the (finite number of) equilibrium points on the boundary, which are enough to ensure permanence. This result, which is given in Theorem 2.5, also has a useful geometrical form, Corollary 2.6. A complementary result, Theorem 2.7, gives a similar criterion for showing that there is an attractor in $\partial\mathbb{R}^n_+$, when of course the system is not permanent.

The theory of discrete semidynamical systems (abbreviated here to SDS) provides the basic mathematical tool, and some standard notation for these is first introduced. Let (X, d) be a locally compact metric space (which will here be a subset of $\mathbb{R}^n_+$), and let $T: X \to X$ be continuous. For $k \in \mathbb{Z}^+$ (the non-negative integers) put $x \cdot k = T^k x$, and note that $x \cdot 0 = x$ and $x \cdot (k_1 + k_2) = (x \cdot k_1) \cdot k_2$ for

$k_1, k_2 \in \mathbb{Z}^+$. The semiorbit through x is the set

$$\gamma^+(x) = \{y\colon y = x \cdot k \text{ for some } k \in \mathbb{Z}^+\}.$$

The Ω-limit set, which essentially describes the asymptotic behaviour of the semiorbit, is defined to be

$$\Omega(x) = \{y\colon x \cdot k_i \to y \text{ for some sequence } (k_i) \to \infty\}.$$

For a subset $X_0 \subset X$ put

$$\gamma^+(X_0) = \bigcup_{x \in X_0} \gamma^+(x), \qquad \Omega(X_0) = \bigcup_{x \in X_0} \Omega(x).$$

X_0 is said to be *forward invariant* if $TX_0 \subset X_0$ and *strictly forward invariant* if $T\bar{X}_0 \subset \mathring{X}_0$. The set M is said to be *absorbing* for X_0 if it is forward invariant and $\gamma^+(x) \cap M \neq \emptyset$ for every $x \in X_0$. As the terminology suggests, this means that every semiorbit starting in X_0 is "sucked into" M from which it cannot then escape. X_0 is a *global attractor* if $\lim_{j\to\infty} d(x \cdot j, X_0) = 0$ for every $x \in X$. The SDS is said to be *dissipative* if there is a bounded global attractor. The proof of the following lemma may be deduced directly from that of Hutson [11, Lemma 2.1] and is omitted.

Lemma 2.1. *Let U be open with compact closure, and suppose that V is open and forward invariant, where $\bar{U} \subset V \subset X$. Then if $\gamma^+(x) \cap U \neq \emptyset$ for every $x \in V$, $\gamma^+(\bar{U})$ is compact and absorbing for V.*

Remark. For a dissipative SDS on $\mathbb{R}^n_+$ with global attractor X_0 an application of the lemma to an open ε-neighbourhood U of X_0 shows that there is a compact absorbing set for $\mathbb{R}^n_+$.

To frame the system (1.1) in this setting, rewrite it as

$$x_i' = x_i \exp\{f_i(x)\} \qquad (i = 1, \ldots, n), \tag{2.1}$$

where

$$f_i(x) = r_i - \sum_{j=1}^{j=n} a_{ij} x_j. \tag{2.2}$$

This may be expressed as $x' = Tx$ where $T\colon \mathbb{R}^n_+ \to \mathbb{R}^n_+$ is the continuous map with ith component

$$(Tx)_i = x_i \exp\{f_i(x)\}. \tag{2.3}$$

In dynamical systems terminology the condition of permanence may be rephrased as follows.

Definition. The system (2.1) is said to be *permanent* if and only if there exists a compact absorbing set M for the interior $\mathring{\mathbb{R}}^n_+$ of $\mathbb{R}^n_+$ which is contained in $\mathring{\mathbb{R}}^n_+$ (and whose minimum distance from the boundary $\partial\mathbb{R}^+_n$ is thus non-zero).

It will be assumed throughout that the SDS on $\mathbb{R}^n_+$ is dissipative, in which case in view of the remark after Lemma 2.1 there is a compact absorbing set for $\mathbb{R}^n_+$. We remark that dissipativity is equivalent to the possibly more familiar notion of ultimate or eventual uniform boundedness, that is the existence of a constant L such that

$$\limsup_{k\to\infty} x_i(k) < L \qquad (i = 1, \ldots, n)$$

for all $x \in \mathbb{R}^n_+$. The question of dissipativity is itself of some interest, and is discussed for (2.1) in detail in Sect. 3. When this condition holds, the analysis may evidently be restricted to the compact absorbing set $\gamma^+(\{x: 0 \leq x_i \leq L\})$. From here on we take this set to be X, which is therefore now a *compact* metric space, and let $S = X \cap \partial\mathbb{R}^n_+$. The condition of permanence may then be thought of intuitively as the requirement that S repels orbits in some strong uniform sense.

The role of the function P below will be discussed shortly after some simple algebraic identities have been derived. For any vector $p = (p_1, \ldots, p_n)$ of strictly positive real numbers, define the continuous function $P: X \to \mathbb{R}_+$ by setting

$$P(x) = \prod_{i=1}^{i=n} x_i^{p_i},$$

and note that $P(x) = 0$ if and only if $x \in S$. Put

$$\alpha(m, x) = P(T^m x)/P(x) \qquad (m \in \mathbb{Z}^+, x \in X \backslash S). \tag{2.4}$$

Let

$$\phi(x) = \sum_{i=1}^{i=n} p_i f_i(x) = \sum_{i=1}^{i=n} p_i \left[r_i - \sum_{j=1}^{j=n} a_{ij} x_j \right]. \tag{2.5}$$

Then from (2.3) and (2.4),

$$\alpha(1, x) = \exp\{\phi(x)\}. \tag{2.6}$$

Since $\phi: X \to \mathbb{R}$ is continuous, (2.6) provides a continuous extension of $\alpha(1, \cdot)$ to X. Now for any $k_1, k_2 \in \mathbb{Z}^+$, $x \in X \backslash S$,

$$\begin{aligned} \alpha(k_1 + k_2, x) &= P[x \cdot (k_1 + k_2)]/P(x) \\ &= \frac{P[x \cdot (k_1 + k_2)]}{P(x \cdot k_1)} \cdot \frac{P(x \cdot k_1)}{P(x)} \\ &= \alpha(k_2, x \cdot k_1)\alpha(k_1, x). \end{aligned} \tag{2.7}$$

In particular the relation $\alpha(s, x) = \alpha(1, Tx) \cdot \alpha(1, x)$ provides a continuous extension of $\alpha(2, \cdot)$ to X, and proceeding inductively, of $\alpha(m, \cdot)$ to X for all $m \in \mathbb{Z}^+$. By repeated application of (2.7),

$$\alpha\left(\sum_{i=0}^{i=t} k_i, x\right) = \alpha(k_0, x) \prod_{j=1}^{j=t} \alpha\left(k_j, x \cdot \sum_{i=0}^{i=j-1} k_i\right) \tag{2.8}$$

for any $k_0, \ldots, k_t \in \mathbb{Z}^+$ and $x \in X$, which implies

$$\alpha(m, x) = \exp\left\{\sum_{j=0}^{j=m-1} \phi(x \cdot j)\right\}. \tag{2.9}$$

Define next

$$\beta(x) = \sup_{m \geq 1} \alpha(m, x), \tag{2.10}$$

and note that since $P(x) > 0$ if $x \in X \backslash S$ and P, T are continuous, $\beta(x)$ is finite for each $x \in X \backslash S$. However, $\beta(x)$ may take the value $+\infty$ if $x \in S$.

We wish to show that orbits are repelled by S, and by a standard Liapunov function type argument we see that the condition $\alpha(1, x) = P(Tx)/P(x) > 1$ for all x in a neighbourhood of S, that is P is increasing along semiorbits, is enough to ensure this. However, this condition will not usually be satisfied for the type of system considered here, nor will it be easy to invent an alternative Liapunov function P. Our objective here is to show that the much weaker condition $\beta(x) > 1$ for $x \in S$, which requires only that P should increase over some (rather than every) section of the orbit, is sufficient for permanence. This justifies the term "average Liapunov function" for P. A preparatory technical lemma is needed.

Lemma 2.2. *Let $K \subset X$ be compact, and suppose that $\beta(x) > 1$ for every $x \in K$. Then there is a closed neighbourhood V of K such that if for some $y \in X$ we have $\Omega(y) \subset V$, then $\beta(y) = +\infty$, and $y \in S$.*

Proof. The proof is divided into two stages. We first claim that there are a neighbourhood W of K, an $\bar{h} > 0$, and a $\bar{k} < \infty$ such that for any $x \in W$ there is a positive integer $k_x \leq \bar{k}$ with $\alpha(k_x, x) \geq 1 + \bar{h}$. For each $h > 0$, $k \in \mathbb{Z}^+$ define the following subsets of X:

$$U(h, k) = \{x\colon \alpha(k, x) > 1 + h\}.$$

As $\alpha(k, \cdot)$ is continuous, each $U(h, k)$ is open, and since $\beta(x) > 1$, from (2.10) these sets form an open cover of K. However, K is compact, so there is a finite subcover. Also $U(h_1, k) \supset U(h_2, k)$ if $h_1 \leq h_2$, so it follows that there are an $\bar{h} > 0$, integers $k_1, \ldots, k_j$, and an open neighbourhood W of K with

$$K \subset W \subset \textstyle\bigcup_{i=1}^{i=j} U(\bar{h}, k_i).$$

This establishes the claim, for on each $U(h, k_j)$, $\alpha(k_j, x) > 1 + \bar{h}$, and $k_j \leq \bar{k} = \max k_i$.

To complete the proof, choose a closed neighbourhood $V \subset W$. If for some $y \in X$, $\Omega(y) \subset V$, from the definition of Ω-limit set, for some k_0, $y \cdot k \in W$ for $k \geq k_0$. From what was proved above, there is a sequence (k_i) in $\mathbb{Z}^+$ with $1 \leq k_i \leq \bar{k}$ such that for every $i \geq 1$,

$$\alpha(k_i, y \cdot (k_0 + \cdots + k_{i-1})) \geq (1 + \bar{h}).$$

Hence from (2.8)

$$\alpha\left(\sum_{i=0}^{i=t} k_i, y\right) \geq \alpha(k_0, y)(1 + \bar{h})^t,$$

and it follows that $\beta(y) = \infty$, since $\alpha(k_0, y) > 0$.

Finally, $y \in S$, for as remarked previously, $\beta(y)$ is finite for each $y \in X \backslash S$.

Our first sufficient condition for permanence is the following theorem. This is a special case of a result of Hutson and Moran [14], but its proof is an immediate consequence of Lemmas 2.1 and 2.2 which are needed later, and is included for completeness.

Theorem 2.3. *Let the system* (2.1) *be dissipative. If $\beta(x) > 1$ for each $x \in S$, permanence holds.*

Proof. With the notation of Lemma 2.2, take $K=S$ and $N=X\backslash S$, from that lemma $\Omega(x)\cap N\neq\varnothing$, for otherwise $x\in S$ contrary to assumption. It then follows from Lemma 2.1 with $U=N$ and $V=X\backslash S$ that $M=\gamma^+(\bar{N})$ is the required compact absorbing set in $X\backslash S\subset\mathring{\mathbb{R}}^n_+$.

Use of this theorem depends on estimates of β at every point $x\in S$. As shown in [14], it is in fact enough if $\beta(x)>1$ for each $x\in\Omega(S)$. However, in view of the complexity of the Ω-limit sets of difference equations even in low dimensions, it will often be difficult to check even this condition. Our next and principal objective is to show, by exploiting the averaging property as in [16], that it is sufficient if $\beta(x^*)>1$ for the boundary equilibria x^* only. At these points it is clear from (2.9) that $\beta(x^*)=+\infty$ if $\phi(x^*)>0$, so this criterion is readily checkable. We will also see in Sect. 4 that $\phi(x^*)$ is a linear combination of the "external eigenvalues", which provides a relationship with the intuitive biological concept of "invasion parameter".

Define the average population vector over m generations $\bar{x}(m)=(\bar{x}_1(m),\dots,\bar{x}_n(m))$ by putting

$$\bar{x}_i(m)=m^{-1}\sum_{k=0}^{k=m-1}(x\cdot k)_i.$$

Then from the linearity of (2.5), (2.9) can be rewritten as

$$\alpha(m,x)=\exp\{m\phi(\bar{x}(m))\}. \tag{2.11}$$

Consider now a subsystem of (2.1) of order q obtained by setting $n-q$ of the populations zero and rearranging the indices so that the non-zero populations correspond to $i=1,\dots,q$.

Lemma 2.4. *Assume that $x_i>0$ $(1\leqslant i\leqslant q)$. Suppose that there are real numbers $b>0$ and b', and a sequence $(k_j)\to\infty$ such that $b<(x\cdot k_j)_i<b'$ $(1\leqslant i\leqslant q, j\geqslant 1)$. Then there are a subsequence, again denoted by (k_j), and an equilibrium point x^* such that*

$$\lim_{j\to\infty}\bar{x}(k_j)=x^*.$$

Proof. The averages satisfy the same inequalities, so by compactness there is a convergent subsequence $\bar{x}(k_j)$. Then for $1\leqslant i\leqslant q$,

$$\begin{aligned}k_j^{-1}\log[(x\cdot k_j)_i/x_i]&=k_j^{-1}\sum_{m=1}^{m=k_j}\log[(x\cdot m)_i/(x\cdot(m-1))_i]\\&=k_j^{-1}\sum_{m=1}^{m=k_j}f_i(x\cdot(m-1))\\&=f_i(\bar{x}(k_j))\end{aligned}$$

by the linearity of the f_i. The left-hand side tends to zero as $j\to\infty$, and hence the limit x^* of the convergent subsequence $\bar{x}(k_j)$ satisfies $f_i(x^*)=0$. Thus x^* is an equilibrium point of (2.1).

Theorem 2.5. *Let the system* (1.1) *be dissipative. Assume that there are real numbers* $p_1, \ldots, p_n > 0$ *such that*

$$\phi(x^*) = \sum_{i=1}^{i=n} p_i f_i(x^*) > 0 \tag{2.12}$$

for each equilibrium point x^* *in* $\partial\mathbb{R}_+^n$. *Then* (1.1) *is permanent. If* (1.1) *is robustly dissipative, robust permanence holds.*

Proof. Broadly this is carried out by induction on the dimension. Regarded as a subset of $\mathbb{R}_+^n$, $\partial\mathbb{R}_+^n$ is composed of n faces of dimension $(n-1)$ obtained by setting $x_1, \ldots, x_n$ zero in turn. Denote the intersection of each of these with X by $F^{(n-1)}$, and the set of all these faces by $\bigcup F^{(n-1)}$. Define $F^{(n-2)}, \ldots, F^{(0)} = \{0\}$ together with their interior and boundary similarly.

From (2.10)-(2.12), $\beta(x^*) > 1$ for each equilibrium point $x^* \in S$. From Theorem 2.3, it is enough to show that $\beta(x) > 1$ for each $x \in S$. Since the origin 0 is an equilibrium point, $\beta(0) > 1$. Suppose next that for some q with $0 \leq q \leq n-2$, $\beta(x) > 1$ for all $x \in \bigcup F^{(q)}$. Let x be an interior point of some $F^{(q+1)}$. Then either $\Omega(x) \subset \bigcup F^{(q)}$, or $\Omega(x)$ contains an interior point x_0, say, of $F^{(q+1)}$. In the first case, by the induction hypothesis and Lemma 2.2 with $K = \bigcup F^{(q)}$, $\beta(x) > 1$. In the second case, there is a sequence $(k_j) \to \infty$ with $\lim_{j\to\infty} x \cdot k_j = x_0$. By Lemma 2.4 the averages $\bar{x}(k_j)$ converge to an equilibrium point x^*, say, and it follows from (2.11) and (2.12) that $\beta(x) > 1$. Thus $\beta(x) > 1$ if $x \in F^{(q+1)}$, and the result follows by induction.

Note finally that for a sufficiently small change in the parameters of (1.1), the number of boundary equilibrium points cannot increase and their position is only slightly changed. Hence ϕ remains positive at these points. Together with robust dissipativity this guarantees robust permanence.

Theorem 2.5 is our central result on sufficient conditions for permanence in Lotka-Volterra systems of difference equations. The principal point of this theorem is that it reduces the question of permanence to a (finite) algebraic problem, that of deciding when there exist n positive numbers p_i, such that the linear expressions $\phi(x^*)$ given by (2.5) are greater than zero at a finite number of equilibrium points. Some remarks concerning this follow.

(i) It can happen that there is a line of equilibrium points, but it has been shown in [16] that only the extreme points in $\mathbb{R}_+^n$ need be checked. Hence, as stated above, only a finite number of inequalities enter into the computation, so the problem is indeed purely algebraic. Furthermore, this algebraic problem is clearly identical with that for systems of Lotka-Volterra differential equations. A useful consequence of this is that the extensive results [7, 8] already available for the differential equation case may be used directly, and this will be done at several places in later sections.

It may also be useful to note that the problem is of linear programming type, so the powerful techniques available there may be exploited, see [16].

(ii) There is a simple geometrical condition for permanence for systems of Lotka-Volterra differential equations, see [7, 8] which in view of the remark above we may quote directly.

Corollary 2.6. *Let D denote the set of points where no species increases, that is*

$$D=\{x\colon r\leqslant Ax\},$$

where $r=(r_1,\ldots,r_n)$. *Then if dissipativity holds, the system* (1.1) *is permanent if D is disjoint from the convex hull C of the boundary fixed points.*

(iii) We will see in Sect. 5 that, at least in low dimensions $n\leqslant 3$, the conditions in Theorem 2.5 or Corollary 2.6 in fact *characterise* the robust permanence of (1.1). For $n\geqslant 4$ this remains an open question.

(iv) Whenever Theorem 2.5 characterises permanence there is a noteworthy consequence, which may be seen by setting $a_{ij}=r_ic_{ij}/K_j$, and rewriting (1.1) in the form

$$x_i'=x_i\exp\left\{r_i\left(1-\sum_{j=1}^{j=n}(c_{ij}x_j/K_j)\right)\right\}.$$

Then permanence is completely independent of the basic growth rates r_i and "carrying capacities", K_i, and is determined solely by the "community matrix" (c_{ij}). This holds under the restriction that changing the r_i does not destroy the boundedness assumption, which is true for a large class of interaction schemes (see Lemma 3.3), but not for mutualists (see Lemma 3.2). On the other hand, as pointed out with some regret by Strobeck [25] for (1.2), the local stability of the interior fixed point may depend critically on the r_i.

The following theorem, a generalization of a result in [1], is a partial converse to Theorem 2.5. It will be useful when necessary conditions for permanence are discussed in Sect. 5.

Theorem 2.7. *Suppose* (1.1) *is dissipative. Assume that there is a subset M of S which is strictly forward invariant (for the SDS restricted to S), and that there are positive numbers* $p_1,\ldots,p_n>0$ *such that* $\phi(x^*)<0$ *for every equilibrium point* $x^*\in M$. *Then M contains an attractor, that is there is a neighbourhood U of M in X such that* $\Omega(x)\subset M$ *for every* $x\in U$.

Proof. This is based on arguments very similar to those used in proving Theorem 2.5 and is therefore only given in outline.

The result is first proved under the assumption that $\delta(x)<1$ for every $x\in M$, where $\delta(x)=\inf_{m\geqslant 1}\alpha(m,x)$. Since $\Omega(\bar{M})\subset T\bar{M}\subset M$, an argument similar to that of Lemma 2.2 (with the inequalities reversed) for the SDS restricted to S shows that $\delta(x)=0$ for every $x\in M$. It follows that there are a neighbourhood W of M in X, an $h>0$ and a $\bar{k}<\infty$ such that if $x\in W$ there is a positive integer $k_x\leqslant\bar{k}$ with $\alpha(k_x,x)\leqslant 1-h$.

Let V be a neighbourhood of $T\bar{M}$ in X such that

$$V\cap S\subset M. \tag{2.13}$$

Then $U=W\cap T^{-1}(V)\cap\cdots\cap T^{-\bar{k}}(V)$ is a neighbourhood of $\bar{M}$ in X. Since $\bar{V}\backslash U$ is disjoint from S, by (2.13) there exists $p>0$ such that $P(x)>p$ for $x\in\bar{V}\backslash U$. Hence with $I(p)=\{x\in X\backslash S\colon P(x)<p\}$, $\overline{I(p)}\cap\bar{V}\subset U$.

Let $x\in I(p)\cap U\subset W$. Then by definition of W there is a k with $1\leqslant k\leqslant\bar{k}$ such that $\alpha(k,x)\leqslant 1-h$. Hence $P(x\cdot k)<P(x)\cdot(1-h)<p$, where $x\cdot k\in I(p)$.

Then $x \cdot k \in T^k U \subset V$ and $x \cdot k \in I(p) \cap V \subset U$, from which it follows that $x \cdot k \in I(p) \cap U$. By iteration we obtain a sequence $(k_i) \to \infty$ with $k_{i+1} - k_i \leq \bar{k}$ such that $x \cdot k_i \in I(p) \cap U$ and $P(x \cdot k_i) \to 0$. Since $P(x \cdot k) \leq \bar{\alpha} P(x \cdot k_i)$ holds for all k with $k_i \leq k \leq k_{i+1}$, where $\bar{\alpha} = \max\{\alpha(m, x): 0 \leq m \leq \bar{k}, x \in X\}$, we conclude that $P(x \cdot k) \to 0$ and $\Omega(x) \subset M$. Thus every orbit in $I(p) \cap U$ converges to M.

Finally, the averaging Lemma 2.4 implies again that $\delta(x^*) < 1$ at every equilibrium point x^* in M is sufficient to ensure that $\delta(x) < 1$ at every $x \in M$.

3. Boundedness

The results throughout are based on the hypothesis that the system (1.1) is dissipative. It is clear from the finiteness of the universe that a hypothesis at least as strong as this is required for biological reality. However, the problem of deciding when the difference equations lead to dissipativity is not a simple one, and appears not to have received much attention in the literature. For the corresponding Lotka-Volterra differential equations (1.2) necessary and sufficient conditions *are* known. However, we shall show that whilst the analogous necessary conditions are still valid (Lemma 3.1), they are not sufficient (Lemma 3.2). It is curious to note that the sufficiency breaks down in what might be regarded as the most "cooperative" system — that of a pair of mutalists. Paradoxically the very fact that mutualists assist each other may lead to orbits which approach infinity, but which also come extremely close to both the axes, thus increasing the probability of extinction under external stresses. A sufficient condition (Lemma 3.3) is given which excludes such mutualist interactions.

We call the matrix A a *B-matrix* if

$$\forall x \in \mathbb{R}^n_+ \setminus \{0\} \, \exists i: x_i > 0 \text{ and } (Ax)_i > 0. \tag{3.1}$$

Biologically this property means that for the interaction matrix A in the Lotka-Volterra equations (1.2) or its discrete time analogue (1.1), at every possible state x of the system, at least one of the species, say i, "suffers" in the sense that its growth rate r_i is reduced to $r_i - (Ax)_i$ due to the interaction of the other species.

These matrices were studied in detail in [6]. In particular, it was shown there that (3.1) is equivalent to the fact that, for every choice of the r_i, dissipativity holds for the Lotka-Volterra differential equations (1.2). The following lemma shows that for the difference equations, it is still a necessary condition.

Lemma 3.1. *If the system* (1.1) *is dissipative and* $r_i > 0$ (*or robustly dissipative and the* r_i *are arbitrary*) *then the interaction matrix is a B-matrix.*

Proof. Suppose A is not a B-matrix, then neither is its transpose A^t (see [6]) and (3.1) gives us a vector $p \geq 0$, $p \neq 0$ with $p_i(Ap)_i \leq 0$ for all i. On the support $I = \{i: p_i > 0\}$ of p we have

$$(A^t p)_i = (p^t A)_i \leq 0 \tag{3.2}$$

for $i \in I$, and so $p \cdot Ax \leq 0$ for all x with $\operatorname{supp} x \subset I$. We restrict our attention to this subsystem henceforth. It follows from (2.4)-(2.6) that $P(x') > P(x)$ if $p \cdot r > 0$. If $p \cdot r \leq 0$ then we exploit the robustness assumption and by slightly decreasing the diagonal terms of A we can achieve strict inequality in (3.2). Then for large

x with $\operatorname{supp} x \subset I$, we get $p \cdot Ax < p \cdot r$ and again $P(x') > P(x)$. So the sets $\{x \in \mathbb{R}_+^I: P(x) \geq \alpha\}$ are strictly forward invariant for large α and all orbits in these sets go to infinity. This gives a contradiction.

In contrast with the differential equation case, (3.1) is not sufficient to guarantee dissipativity of (1.1). This is shown by the following counterexample for two mutualistic species with interactions modelled by the equations

$$x' = Rx \exp(-ax + by)$$
$$y' = Ry \exp(bx - ay), \tag{3.3}$$

with R, a, $b > 0$. The interaction matrix A is a B-matrix if

$$\det A = a^2 - b^2 > 0, \tag{3.4}$$

that is if the mutualistic effects are smaller than the intraspecific competition. Now the line $x = y$ is invariant, and there $x' = Rx \exp[(b-a)x]$, so for $b > a$ (when by (3.4) A is not a B-matrix) there are orbits converging to infinity, which is in accordance with Lemma 3.1. However, the following lemma shows that in addition, for $a > b$ unbounded orbits exist if R is large enough.

Lemma 3.2. *If* $R > a/b > 1$, *then* (3.3) *has unbounded orbits.*

Proof. The idea is to construct orbits which start near the x-axis, that is with x large, y small, and which jump to points near the y-axis with x' small and less than y, y' large and greater than x. To be more precise we consider horn-shaped regions

$$B_{K,M} = \{(x, y) \in \mathbb{R}_+^2: x \geq M, xy \leq K \text{ and } y \geq x\, e^{-bx}\}, \tag{3.5}$$

where $K > 0$ is arbitrary and M is any number satisfying the inequalities

$$M \geq a^{-1}, \tag{3.6}$$

$$M \geq 2(a-b)^{-1} \log R, \tag{3.7}$$

$$M \geq Ka/\log(Rb/a). \tag{3.8}$$

If $B'_{K,M}$ denotes the image of $B_{K,M}$ under the reflection $(x, y) \leftrightarrow (y, x)$ then we claim that (3.3) maps $B_{K,M}$ into $B'_{K,Ma/b}$. By iteration this proves that all orbits starting in $B_{K,M}$ are unbounded.

Let $(x, y) \in B_{K,M}$. Then

$$(xy)' = (xy)R^2\, e^{-(a-b)(x+y)} \leq xy \leq K, \tag{3.9}$$

since $x \geq M$ and (3.7) holds. Moreover

$$y' = yR\, e^{bx-ay} \geq x\, e^{-bx} R\, e^{bx-ay} = Rx\, e^{-ay}.$$

Using $y \leq K/x \leq K/M$ and (3.8) we obtain

$$y' \geq ax/b \geq aM/b \geq 1/b. \tag{3.10}$$

Finally, since the function $y \to y\, e^{-by}$ is monotonically decreasing for $y > 1/b$ we have

$$x'/(y'\, e^{-by'}) \geq xR\, e^{-ax+by}/(ax\, e^{-ax}/b) = Rba^{-1}\, e^{by} \geq 1. \tag{3.11}$$

(3.9), (3.10) and (3.11) imply $(y', x') \in B_{K,Ma/b}$.

We conclude this section with a sufficient condition for boundedness. We call the interaction matrix A *hierarchically ordered* if there exists a rearrangement of the indices such that $a_{ij} \geq 0$ whenever $i \leq j$, and additionally $a_{ii} > 0$ for every i. This means that positive interspecific effects (i.e. $a_{ij} < 0$) occur only from lower to higher levels. This excludes all types of mutalism, but allows for any kind of predator–prey or competitive interaction.

Lemma 3.3. *If A is hierarchically ordered then the difference equation* (1.1) *is dissipative* (*for every choice of the basic growth rates r_i*).

Proof. Since $a_{ij} \geq 0$ for $i \leq j \leq n$, from (1.1) with $i = 1$,

$$x_1' \leq x_1 \exp(r_1 - a_{11} x_1),$$

and it follows that x_1' is bounded by the constant $K_1 = e^{r_1 - 1}/a_{11}$. Inserting this bound into (1.1) with $i = 2$, we find by the same argument that, after at most two generations, x_2 is bounded by a constant K_2. Repeating the argument, we see that T^n maps $\mathbb{R}_+^n$ into the compact set $\{x: 0 \leq x_i \leq K_i\}$, which implies dissipativity.

Lemma 3.2 suggests that this result might be best possible in the sense that for every matrix A which is not hierarchically ordered and hence has what may be described as a "generalized mutualist cycle" (by which we mean a directed cycle of positive interspecific interactions), (1.1) will have unbounded orbits for large r_i. This is in contrast with the situation for the differential equations where the result of Lemma 3.3 holds for all B-matrices.

4. Saturated equilibria and necessary conditions for persistence

Theorem 2.5 provides a sufficient condition for permanence. In an attempt to characterise permanence we now derive a set of necessary conditions, which are in fact valid even for weak persistence. Although these conditions are in general far from sufficient, we will see in Sect. 5 that they are strong enough to give characterisations if $n \leq 3$.

Consider an equilibrium point $\bar{x}$ of the difference equation (1.1) and let $I = \{i: \bar{x}_i > 0\}$ be its support. The entries of the Jacobian matrix $J(\bar{x})$ of (1.1) at $\bar{x}$ are given by

$$J_{ik}(\bar{x}) = \frac{\partial x_i'}{\partial x_k} = (\delta_{ik} - \bar{x}_i a_{ik}) \exp\left(r_i - \sum a_{ij}\bar{x}_j\right),$$

$$= \begin{cases} \delta_{ik} - \bar{x}_i a_{ik} & (i \in I) \\ \exp\left(r_i - \sum_j a_{ij}\bar{x}_j\right) & (i \notin I,\ i = k) \\ 0 & (i \notin I,\ i \neq k). \end{cases} \tag{4.1}$$

Hence $J(\bar{x})$ splits into two blocks: the index set I defines the "internal" block corresponding to the restriction of (1.1) to the species $i \in I$. The "external" block is a diagonal matrix whose entries are the *external eigenvalues* $\rho_i(\bar{x}) = \exp f_i(\bar{x})$, where

$$f_i(\bar{x}) = r_i - \sum_j a_{ij}\bar{x}_j \tag{4.2}$$

are just the external eigenvalues of the Lotka–Volterra differential equations (1.2) at $\bar{x}$. Since $\rho_i(\bar{x}) = \lim_{x\to\bar{x}} x_i'/x_i$, $\rho_i(\bar{x})$ has the biological interpretation of a growth rate or "invasion parameter" of the (missing) species i at $\bar{x}$. At $\bar{x}=0$, the ρ_i and f_i reduce to the basic growth rates R_i and r_i of each species.

The equilibrium $\bar{x}$ is called *saturated* (compare [8]) if all its external eigenvalues $\rho_i(\bar{x}) \leq 1$ $(i \notin I)$ or equivalently $f_i(\bar{x}) \leq 0$. If the system is at a saturated equilibrium $\bar{x}$ then it is proof against the invasion of the missing species $i \notin I$. Note that an interior fixed point is always saturated since it has no external eigenvalues, while $\mathbf{0}$ is saturated only if it is semi-stable. The biological relevance of this concept relies on the following fact. If an orbit $\gamma^+(x)$ with $x \in \mathring{\mathbb{R}}_+^n$ converges, then its limit point is a saturated equilibrium. For our special system (1.1) the same also holds for the time averages $\bar{x}(m)$ (this being shown by an argument similar to that used in proving Lemma 2.4).

Conversely if $\bar{x}$ is a strictly saturated equilibrium (i.e. $\rho_i(\bar{x}) < 1$ for all $i \notin I$) then the stable manifold of $\bar{x}$ intersects the interior of $\mathbb{R}_+^n$ and thus $\bar{x}$ is the limit of interior orbits of (2.1).

In particular, permanence and even weak persistence are incompatible with the existence of a strictly saturated fixed point on the boundary. Moreover if weak persistence or permanence is a robust property of the system, saturated boundary fixed points may not occur either, as at least one of them could be made strictly saturated by a small perturbation. In other words, in a robustly weakly persistent system, at every boundary fixed point $\bar{x}$ at least one of the external eigenvalues $\rho_i(\bar{x})$ is larger than 1 or at least one of the $f_i(\bar{x})$ is positive. In many cases (but not in general) this condition is also sufficient to guarantee weak persistence.

Permanence of (1.1), on the other hand, is guaranteed (and in many cases characterized) by Theorem 2.5 if a certain weighted sum $\sum p_i f_i(\bar{x})$ of the logs of the external eigenvalues is positive at *every* boundary fixed point.

The internal block (i.e. the restriction to the index set I) of the Jacobian $J(\bar{x})$ of (2.1), on the other hand, differs from the Jacobian matrix of the Lotka–Volterra equation (1.2) only by the identity matrix. Thus the *internal eigenvalues* of the difference equation are obtained by adding unity to the internal eigenvalues of the differential equation, in contrast to the connection (4.2) via the exponential function for the external eigenvalues.

Recall that the *index* of a vector field at a fixed point $\bar{x}$ is defined as the sign of the determinant of the Jacobian matrix of the vector field at that point (if $\bar{x}$ is regular, that means that this determinant is non-zero). The above argument shows that at every regular fixed point $\bar{x}$ the index with respect to the differential equation (1.2) is identical with its Lefschetz index for the map (2.1).

Lemma 4.1. *Suppose that* (2.1) *is robustly dissipative* (*or that the interaction matrix A is a B-matrix*). *Then the difference equation* (2.1) *has at least one saturated fixed point. If all saturated fixed points are regular then the sum of their indices equals* $(-1)^n$.

Proof. We have seen that the systems (1.1) and (1.2) have the same fixed points, the same saturated fixed points, and also their respective indices coincide. Now recall Lemma 3.1 and the fact [6] that when A is a B-matrix dissipativity holds for the differential equations (1.2). The assertion of the lemma is then a consequence of the corresponding result for the differential equation proved in [7, 8].

We note that the above result is not restricted to (1.1) but holds for general maps on $\mathbb{R}^n_+$ with appropriate dissipativity assumptions.

Theorem 4.2. *Suppose that* (1.1) *is robustly dissipative* (*or more simply that A is a B-matrix*). *Then the following conditions are necessary for* (1.1) *to be robustly permanent or robustly weakly persistent.*

(i) (1.1) *has an interior fixed point $\bar{x}$.*

(ii) $\det A > 0$.

(iii) *If there exists a fixed point $\bar{y}$ with $\bar{y}_k = 0$ and $\bar{y}_i \geq 0$ for $i \neq k$ then the submatrix $A^{(k)}$ with* kth *row and column deleted has positive determinant.*

Proof. As pointed out above, a robustly weakly persistent system cannot have a saturated fixed point on the boundary. Lemma 4.1 shows that there is at least one saturated fixed point, so an interior fixed point $\bar{x} > 0$ must exist. This interior fixed point $\bar{x}$ is unique. Otherwise there would be a line of fixed points whose intersection with $\partial\mathbb{R}^n_+$ would still be a saturated fixed point. Uniqueness implies $\det A \neq 0$ and hence regularity of $\bar{x}$. Then the second part of the lemma applies and shows that $\operatorname{ind}(\bar{x}) = (-1)^n$ or $\det A > 0$ by (4.1). Finally (iii) is a consequence of the eigenvalue formula

$$f_k(\bar{y}) = \bar{x}_i \det A / \det A^{(k)}$$

established in [7].

A partial converse of this is the following statement which can be proved in the same way as was done for differential equations in [7]: if A is a P-matrix, that is all principal minors $\det(a_{ij})_{i,j \in I} > 0$, and (1.1) has an interior fixed point then there is no saturated fixed point on the boundary and hence no interior orbit can converge to a point on the boundary.

5. The characterisation of permanence for three species

In this section we finally characterise (robust) permanence of (1.1) if the number of species is three or less. Surprisingly it turns out that the sufficient condition in terms of linear inequalities of Theorem 2.5, or the equivalent geometric condition of Corollary 2.6, actually *characterise* robust permanence. On the other hand the necessary conditions given in Theorem 4.2 characterise robust weak persistence and, up to one exceptional case, robust permanence as well. Thus, at least for $n \leq 3$, both the sufficient conditions obtained by use of an average Liapunov function in Sect. 2, and the necessary conditions obtained with index theory in Sect. 4 are good enough to give characterizations. This is noteworthy as difference equations, even with few species, are usually considered to be extremely hard and are rarely treated in the literature.

We start with the case of two species where the proof is an easy application of our previous results and is left to the reader, see also Example 6.1 below.

Theorem 5.1. *If* (2.1) *with $n = 2$ is robustly dissipative, then the following are equivalent.*

(1) (2.1) *is* (*robustly*) *permanent.*

(2) (2.1) *is robustly weakly persistent.*
(3) *The interior fixed point exists and* $\det A = a_{11}a_{22} - a_{12}a_{21} > 0$.
(4) *The interior fixed point lies outside the convex hull of the boundary fixed points.*

The study of three species systems is complicated by one exceptional case discovered by May and Leonard [18] for the differential equation, see Example 6.2. In this case interior orbits can converge to the boundary, but the Ω-limit sets are not contained in one boundary face. The system is then weakly persistent but not permanent.

More precisely we call the system (1.1) a system of *May–Leonard type* if $r_i > 0$ $(i = 1, 2, 3)$, $a_{ii} > 0$ (so the one-species fixed points $F_1(r_1/a_{11}, 0, 0)$, etc. exist), and the external eigenvalues $\rho_j(F_i) = \exp \lambda_{ij}$ at F_i have the following cyclic sign pattern: $\lambda_{12}, \lambda_{23}, \lambda_{31} \geqslant 0$ and $\lambda_{21}, \lambda_{32}, \lambda_{13} \leqslant 0$ (or this pattern reversed), where

$$\lambda_{ij} = r_j - r_i a_{ji}/a_{ii},$$

see Example 6.2. In this case we need to impose an additional condition to guarantee permanence.

(iv) If (1.1) is of May–Leonard type then

$$\lambda_{12}\lambda_{23}\lambda_{31} + \lambda_{21}\lambda_{32}\lambda_{13} > 0. \tag{5.1}$$

Theorem 5.2. *Suppose* (1.1) *with* $n = 3$ *is robustly dissipative. Then the following holds*

(a) (1.1) *is robustly weakly persistent if and only if properties* (i), (ii) *and* (iii) *of Theorem* 4.2 *hold.*
(b) (1.1) *is robustly permanent if and only if properties* (i), (ii), (iii) *and* (iv) *hold.*
(c) (1.1) *is robustly permanent if and only if the two sets C and D of Corollary* 2.6 *are disjoint.*

The corresponding result for the differential equation was established for two-prey one predator systems by Hutson and Vickers [9], for three competitors in [1], and for general three species systems by Hofbauer [7].

Proof. Theorem 4.2 shows that (i), (ii) and (iii) are necessary conditions for robust weak persistence, respectively robust permanence. For the converse we use the result in [7]. The proof there shows that the algebraic conditions (i)–(iv) imply that the system of linear inequalities (2.12) has a positive solution $p_i > 0$. Thus Theorem 2.5 yields permanence.

We are left with showing that (iv) is necessary for robust permanence, and for this we proceed as in [1] or [7] using Theorem 2.7. We first establish the existence of a suitable strictly forward invariant set M. Since the origin 0 is a source, there is an open neighbourhood U of 0 such that the vector Tx points outwards if $x \in U \setminus \{0\}$. Now $X \setminus U$ is compact, and so therefore is $T(X \setminus U)$. Further, clearly $0 \notin T(X \setminus U)$. Thus there is a closed ball B centre 0 with $B \subset U$ such that $B \cap T(X \setminus U) = \varnothing$. Since X is forward invariant, it follows that $X \setminus B$ is strictly forward invariant, and so therefore is $M = S \cap (X \setminus B)$ relative to S.

A simple calculation shows that the only boundary equilibrium points in M are the one species equilibrium points F_i. It is also easy to see that $\lambda_{12}\lambda_{23}\lambda_{31} + \lambda_{21}\lambda_{32}\lambda_{13} < 0$ implies for all i the existence of $p_i > 0$ such that $\sum_j p_j \lambda_{ij} < 0$. If equality occurs in (5.1) we can achieve this by a small perturbation of the parameters using robustness. Thus $P(x)=\prod x_i^{p_i}$ is decreasing near the equilibrium points F_i, and hence in the average near M, and by Theorem 2.7, M contains an attractor. Thus (1.1) is not permanent in this case. Since there is no saturated fixed point on the boundary, the system is nonetheless still weakly persistent.

6. Applications

As an illustration we consider two examples. The first shows that the criterion of asymptotic stability may be highly misleading.

Example 6.1. The difference equation analogue of the standard Lotka–Volterra model for a predator–prey interaction with x, y the respective populations may be expressed in the form

$$\begin{aligned} x' &= x \exp\{r(1-x)-y\}, \\ y' &= y \exp\{s(-1+\beta x)\}, \end{aligned} \tag{6.1}$$

where r, s, $\beta > 0$. An elaboration of the argument in Lemma 3.3 shows that (6.1) is dissipative. Apart from the origin, there is only one boundary equilibrium $F_1(1,0)$, and there the external eigenvalue is $\exp\lambda$ with $\lambda = s(\beta-1)$. If $\lambda \leqslant 0$, that is $\beta \leqslant 1$, F_1 is saturated and it may be shown that $y \to 0$ along all orbits. If $\lambda > 0$ there is an interior equilibrium. The set C is the line segment of the x-axis from the origin to F_1, and D is the intersection of $\{(x,y)\in\mathbb{R}_+^2 : x \leqslant \beta^{-1}\}$ and the region to the right of the line $r(1-x)-y=0$. If $\lambda > 0$ these are disjoint, and by Corollary 2.6 the system is permanent. If intraspecific competition is introduced for the predator, (6.1) becomes robustly dissipative and Theorem 5.1 applies directly. The system is then robustly permanent iff there is an interior equilibrium, iff the boundary equilibrium F_1 is not saturated.

When $\beta > 1$, the condition for asymptotic stability of the interior equilibrium is that both the following hold:

$$s(\beta-1) < 1,$$
$$r[2-s(\beta-1)] < 4\beta.$$

Thus here asymptotic stability is an unnecessarily restrictive condition for the long term survival of species. If r or s is large, it may be expected that the dynamics will be complicated, perhaps leading to chaos, but the system is still permanent.

Example 6.2. Consider the following difference equations for three competing species:

$$\begin{aligned} x_1' &= x_1 \exp[r(1-x_1-\alpha x_2-\beta x_3)] \\ x_2' &= x_2 \exp[r(1-\beta x_1-x_2-\alpha x_3)] \\ x_3' &= x_3 \exp[r(1-\alpha x_1-\beta x_2-x_3)], \end{aligned}$$

where $0<\alpha<1<\beta$ and $r>0$. These are the analogue of a set of Lotka–Volterra differential equations studied in [18, 21]. There are four boundary equilibria $(0,0,0)$, $(1,0,0)$, $(0,1,0)$ and $(0,0,1)$, and an interior equilibrium $(1,1,1)/(1+\alpha+\beta)$. The region D of decrease of all species is the intersection of those regions to the right of each of the planes $1-x_1-\alpha x_2-\beta x_3=0$, $1-\beta x_1-x_2-\alpha x_3=0$, $1-\alpha x_1-\beta x_2-x_3=0$, and it is easy to check that this is disjoint from the convex hull of the boundary equilibria if and only if $\alpha+\beta<2$. By Theorem 5.2(c) this condition is necessary and sufficient for robust permanence. If $\alpha+\beta>2$, in the differential equation case there is a heteroclinic cycle joining the boundary equilibria on the positive coordinate axes which attracts all orbits (except for those starting on the line $x_1=x_2=x_3$), as shown in [21]. For the difference equations, under the same conditions there is an attractor in the boundary, but on general grounds this is likely to be extremely complex if r is large. If $\alpha+\beta<2$ the stability of the interior equilibrium will be lost for large r, and the orbits will be complex perhaps leading to chaos, although the system is permanent.

These examples show that the criterion for permanence is readily checked for three species by the use of Theorem 5.2. For four or more species, whilst theorems 2.5 and 2.6 still provide a simple way of finding sufficient conditions for permanence, it is not known at the present time whether these conditions are also necessary.

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