DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS
Volume **33**, Number **10**, October **2013**

doi:10.3934/dcds.2013.33.4627

pp. **4627–4646**

PERSISTENCE AND GLOBAL STABILITY FOR A CLASS OF DISCRETE TIME STRUCTURED POPULATION MODELS

Hal L. Smith and Horst R. Thieme

School of Mathematical and Statistical Sciences
Arizona State University
Tempe, AZ 85287, USA

(Communicated by Jianhong Wu)

Dedicated to Odo Diekmann on the occasion of his 65th birthday

Abstract. We obtain sharp conditions distinguishing extinction from persistence and provide sufficient conditions for global stability of a positive fixed point for a class of discrete time dynamical systems on the positive cone of an ordered Banach space generated by a map which is, roughly speaking, a nonlinear, rank one perturbation of a linear contraction. Such maps were considered by Rebarber, Tenhumberg, and Towney (Theor. Pop. Biol. 81, 2012) as abstractions of a restricted class of density dependent integral population projection models modeling plant population dynamics. Significant improvements of their results are provided.

1. Introduction.

Rebarber, Tenhumberg, and Towney [22] formulate a nonlinear abstract density dependent integral projection model given by

$$x_{n+1} = Ax_n + f(c^T x_n)b, \qquad n \geq 0, \tag{1.1}$$

for the dynamics of stage structured population model with plant populations in mind.

Here, A is a bounded positive linear operator on an ordered Banach space X with spectral radius less than unity, b is a positive vector in X, c^T denotes a positive bounded linear functional on X, and $f : [0, \infty) \to [0, \infty)$.

In the biological applications, X is $\mathbb{R}^N$ or $L^1(D)$, b represents the distribution of new members of the population, $c^T x$ gives the seed-production or off-spring produced by state x, f describes the density dependence of fecundity, and A describes movement and survival.

In the finite dimensional case, the dynamics of similar models, and more general ones, have been well-studied. See the monographs by Caswell [1] and Cushing [2], and the papers [4, 6, 14, 16]. The monograph by the authors [25] contains many newer references to the literature on persistence results for finite dimensional models and proves some new ones. See especially Chapter 7 and Sections 3.1 and 8.6 in [25].

2010 *Mathematics Subject Classification.* Primary: 37N25, 92D25; Secondary: 37B25.

Key words and phrases. Discrete time, structured population model, persistence, persistence attractor, stability.

The first author is supported by NSF grant DMS-0918440.

In this note, we explore the global dynamics of these systems, taking advantage of the special structure. We are motivated by the work of Rebarber et al. [22] to seek sharp conditions distinguishing extinction and uniform persistence of the population as well as global stability. Persistence of the plant population was not addressed directly in [22] although their Theorem 3.2 gives sufficient conditions for nonzero orbits to be unbounded. As a special case of our results, we show that if $f'(0)c^Te < 1$, where $e = (I - A)^{-1}b$, then the extinction equilibrium is locally asymptotically stable while if the reverse inequality holds ($f'(0) = \infty$ is allowed), then the plant population persists in several natural senses. Persistence results are especially important in the general case that f is not assumed to have special properties such as monotonicity or concavity. We provide simple conditions that ensure the existence of a compact global attractor of bounded sets for the dynamical system generated by (1.1). Sufficient conditions for local stability and instability of fixed points are provided. Our global stability result for a unique positive fixed point, Theorem 5.8, is an improvement over Theorem 3.3 in [22]. Indeed, we do not assume that f is monotone and concave and their assumption that c^T is strictly positive implies our hypothesis (b). Finally, two examples are provided which illustrate our results. The principal example is a size-structured integral population projection model where the structure redistribution kernels are measures so the dynamics takes place in the space of measures. In this example, the linear operator A is generally not compact.

For a small selection of continuous rather than discrete time size-structured models and their analysis see [7, 8, 9, 10, 11, 12].

2. **Fundamentals of the dynamics.**

Let A be a positive linear bounded operator on an ordered Banach space X with positive cone X^+, that is, $AX^+ \subset X^+$. Let $\sigma(A)$ denote the spectrum of A and assume that its spectral radius, $r(A)$, satisfies $r(A) < 1$. We point out that A is not assumed to be a compact operator.

In the applications, X is typically $\mathbb{R}^n$, $L^1(D)$ or the space of finite signed measures $\mathcal{M}(E, \mathcal{S})$. The positive cone is the set of vectors with nonnegative components, the set of almost everywhere nonnegative functions, or the set of nonnegative measures.

Let $b \in X^+$ be a nonzero positive vector and c^T be a bounded positive linear functional on X. We write $x \le y$ or $y \ge x$ when $x, y \in X$ and $y - x \in X^+$; similarly, if $S, U \subset X$ we write $S \le U$ if the inequality holds between every pair $u \in U$ and $s \in S$. If $x \le y$, $[x, y] = \{z \in X : x \le z \le y\}$ denotes the order interval with endpoints x and y. We write $x < y$ if $x \le y$ and $x \ne y$.

Occasionally, we will assume that the cone X^+ is normal or, equivalently, the norm is semi-monotone: There exists some $c \ge 0$ such that $\|x\| \le c\|y\|$ whenever $0 \le x \le y$. Then the original norm can be replaced by an equivalent monotone norm ($c = 1$) [20, Sec.4.1] [23].

Let $f : \mathbb{R}^+ \to \mathbb{R}^+$ be continuous, $f(0) = 0$ and $f(s) > 0$ for $s > 0$. Consider the semilinear map $F : X^+ \to X^+$ defined by

$$F(x) = Ax + bf(c^Tx), \qquad x \in X^+. \tag{2.1}$$

Our interest is in the dynamical system generated by the difference equation

$$x_{n+1} = F(x_n),\ n \ge 0,\ x_0 \in X^+, \tag{2.2}$$

i.e., in the discrete semiflow $\{F^n; n \in \mathbb{Z}_+\}$.

The variation of constants formula

$$x_n = A^n x_0 + \sum_{k=1}^{n} f(c^T x_{n-k}) A^{k-1} b, \qquad n \in \mathbb{N}, \tag{2.3}$$

can easily be proved by induction. By the triangle inequality,

$$\|x_n\| \le \|A^n x_0\| + \sum_{k=1}^{n} f(c^T x_{n-k}) \|A^{k-1} b\|, \qquad n \in \mathbb{N}. \tag{2.4}$$

The positive vector e defined by

$$e = (I - A)^{-1} b = \sum_{j \ge 0} A^j b, \tag{2.5}$$

will play a key role. If $c^T e = 0$, the difference equation (1.1) can be explicitly solved and $x_n \to 0$ as $n \to \infty$.

Theorem 2.1. *Let $c^T e = 0$. Then, for all $n \in \mathbb{N}$,*

$$x_n = A^n x_0 + \sum_{k=1}^{n} f(c^T A^{n-k} x_0) A^{k-1} b.$$

Further $x_n \to 0$ as $n \to \infty$.

Proof. Notice that $c^T e = 0$ implies that $c^T A^n b = 0$ for all $n \in \mathbb{Z}_+$. The variation of constants formula implies that $c^T x_n = c^T A^n x_0$ for all $n \in \mathbb{N}$. By (2.4),

$$\|x_n\| \le \|A^n x_0\| + \sum_{k=1}^{n} f(c^T A^{n-k} x_0) \|A^{k-1} b\|.$$

Since $r(A) < 1$, the sequence $(f(c^T A^n x_0))$ is bounded and the series $\sum_{k=1}^{\infty} \|A^{k-1} b\|$ converges. So we can apply Fatou's lemma (with the counting measure) and

$$\limsup_{n\to\infty} \|x_n\| \le \limsup_{n\to\infty} \|A^n x_0\| + \sum_{k=1}^{\infty} \limsup_{n\to\infty} f(c^T A^{n-k} x_0) \|A^{k-1} b\| = 0. \qquad \square$$

Bounded invariant sets are dominated by a multiple of the vector e, a result that will often prove useful.

Lemma 2.2. *Let $S \subset X^+$ be invariant, i.e., $F(S) = S$, and be bounded. Then there exist some $C > 0$ such that $S \subset [0, Ce]$.*

Proof. Let $z \in S$. By [25, Thm.1.40], there exists a sequence $(z_n)_{n\in\mathbb{Z}}$ in S with

$$z_{n+1} = F(z_n) = A z_n + f(c^T z_n) b, \qquad n \in \mathbb{Z}, \qquad z_0 = z.$$

Since (z_n) is bounded, there exists some $C > 0$ such that $f(c^T z_n) \le C$ for all $n \in \mathbb{Z}$ with C not depending on z and n. Hence

$$z_n \le A z_{n-1} + C b, \quad n \in \mathbb{Z}.$$

By induction,

$$z_n \le A^k z_{n-k} + C \sum_{j=0}^{k-1} A^j b, \qquad n \in \mathbb{Z}, k \in \mathbb{N}.$$

The right hand side converges to Ce as $k \to \infty$. Since X^+ is closed, $z_n \le Ce$ for all $n \in \mathbb{Z}$. In particular $z \le Ce$. $\square$

F is said to be *point dissipative* if there exists $N > 0$ such that $\limsup_{n\to\infty} \|x_n\| \le N$, $x_0 \in X^+$, for any sequence (x_n) given by (2.2).

F is said to be *eventually bounded on bounded sets* if for every $M > 0$ there exists some $\tilde{M} > 0$ and $m \in \mathbb{N}$ such that $\|x_n\| \le \tilde{M}$ for all $n \ge m$ whenever $\|x_0\| \le M$.

F is said to be *asymptotically smooth* if every bounded forward invariant subset of X^+ is attracted by a compact set.

See [2, 17, 25] for these definitions. The following result explores their consequences.

Proposition 2.3. *(a) F is asymptotically smooth.*

(b) If $\{c^T F^n(x_0)\}_{n\ge 0}$ is bounded, then the orbit $O(x_0) = \{x_n = F^n(x_0); n \in \mathbb{N}\}$ has compact closure. Its omega limit set $\omega(x_0)$ is nonempty, compact, invariant, and $x_n \to \omega(x_0)$. Moreover, there exists $C > 0$ such that $\omega(x_0) \subset [0, Ce]$.

(c) If F is point dissipative,

$$\Omega = \cup\{\omega(x_0); x_0 \in X^+\} \tag{2.6}$$

has compact closure in X^+, attracts every point of X^+, and $\bar{\Omega} \subset [0, Ce]$ for some $C > 0$.

(d) If F is point dissipative and eventually bounded on bounded sets, the semiflow induced by F has a compact attractor, $\mathcal{A}$, of bounded sets with $\mathcal{A} \subset [0, Ce]$ for some $C > 0$.

Proof. (a) Notice that $F = A + G$ with a compact map G. By induction, for each $n \in \mathbb{N}$, $F^n = A^n + G_n$ with a compact map $G_n : X^+ \to X^+$. By [25, Thm.2.46], F is asymptotically smooth.

(b) By assumption, there exists some $C > 0$ such that $f(c^T x_n) \le C$ for all $n \in \mathbb{Z}_+$. By (2.4),

$$\|x_n\| \le \|A^n\| \, \|x_0\| + m\Big(\sum_{k=0}^{n} \|A^k\|\Big)\|b\|, \qquad n \in \mathbb{N}.$$

The series converges because $r(A) = \lim_{k\to\infty} \|A^k\|^{1/k} < 1$. By the same token, $(\|x_n\|)$ is a bounded sequence. Compactness of $O(x_0)$ follows from (a) and [25, Prop.2.27]. The properties of $\omega(x_0)$ follow in the usual way ([25, Thm.2.11], e.g.). The last statement follows from Lemma 2.2 and the invariance of $\omega(x_0)$.

(c) [25, Thm.2.28] and Lemma 2.2.

(d) [25, Thm.2.33] and Lemma 2.2. □

We give an easy condition for F to be point dissipative and eventually bounded on bounded sets. Before we can do so, we need to observe that linearizations of F, if they exist, are of the form

$$Bx = Ax + \mu(c^T x)b, \qquad x \in X, \tag{2.7}$$

with $\mu \in \mathbb{R}$, and prove an important relation for the spectral radius of B.

Theorem 2.4. *If $\mu > 0$ and $\diamond$ denotes one of the relations $<, >, =$, then $r(B) \diamond 1$ if and only if $\mu c^T e \diamond 1$. Moreover, if $r(B) > r(A)$, then $r(B)$ is an eigenvalue of B with a positive eigenvector.*

If $\mu < 0$, then $r(B) \ge 1$ implies $\mu c^T e \le -1$ with strict inequality in the latter if strict in the former.

This theorem should be compared to the finite-dimensional results [3, Thm.3] [21] and the infinite dimensional result [29, Thm.3.10]. Since the linear operator A

is perturbed by a special rank one operator, one does not need to assume that the cone is regular and normal as in [29, Thm.3.10].

Proof. We pass to the complexification of X. Let

$$v_\lambda = (\lambda I - A)^{-1} b = \sum_{k=0}^{\infty} \frac{A^k b}{\lambda^{k+1}}, \qquad |\lambda| > r(A).$$

Then $v_\lambda \neq 0$ and, if $\lambda > r(A)$, then $v_\lambda \geq 0$. As

$$\lambda I - B = \lambda I - A - \mu b c^T = (\lambda I - A)[I - \mu v_\lambda c^T] \quad \text{ if } |\lambda| > r(A),$$

we conclude that $|\lambda| > r(A)$ satisfies $\lambda \in \sigma(B)$ if and only if $1 \in \sigma(\mu v_\lambda c^T)$. Since the rank one map $\mu v_\lambda c^T$ is compact, $1 \in \sigma(\mu v_\lambda c^T)$ if and only if 1 is an eigenvalue of it. Any eigenvector of $\mu v_\lambda c^T$ is necessarily co-linear with v_λ. Indeed, one is an eigenvalue if and only if $\mu v_\lambda c^T v_\lambda = v_\lambda$, or equivalently, $\mu c^T v_\lambda = 1$. Notice that

$$B v_\lambda = A v_\lambda + \mu b c^T v_\lambda = \lambda v_\lambda + (\mu c^T v_\lambda - 1) b.$$

Thus we conclude that $|\lambda| > r(A)$ satisfies $\lambda \in \sigma(B)$ if and only if $\mu c^T v_\lambda = 1$ and λ is an eigenvalue of B.

Define

$$h(\lambda) := c^T v_\lambda = \sum_{k \geq 0} \frac{c^T A^k b}{\lambda^{k+1}}, \ |\lambda| > r(A).$$

It is strictly decreasing for real $\lambda \in (r(A), \infty)$, $h(1) = c^T e$, and $h(\infty) = 0$. Moreover, since $c^T A^k b \geq 0$, it follows that $|h(\lambda)| \leq h(|\lambda|)$ for $|\lambda| > r(A)$.

If $\mu > 0$ and if $|\lambda| > r(A)$ satisfies $\lambda \in \sigma(B)$, then $1 = \mu h(\lambda) \leq \mu h(|\lambda|)$ by our previous considerations. By the intermediate value theorem, there exists $\lambda' \geq |\lambda|$ such that $1 = \mu h(\lambda')$. This implies that $\lambda' \in \sigma(B)$. Therefore, if $\mu > 0$ and $r(B) > r(A)$, then $r(B)$ is an eigenvalue of B with a positive eigenvector $v_{r(B)}$.

If $r(B) > 1$, then $1 = \mu c^T v_\lambda$ for some $|\lambda| > 1$ so we have $1 \leq |\mu| h(|\lambda|) < |\mu| h(1) = |\mu| c^T e$. Thus, $r(B) > 1$ implies that $|\mu| c^T e > 1$. If $\mu > 0$, then $\mu c^T e > 1$; if $\mu < 0$ then $\mu c^T e < -1$.

If $\mu c^T e = \mu h(1) > 1$ (so $\mu > 0$), then the equation $\mu h(\lambda) = 1$ must have a unique solution $\lambda^* > 1$. This means that $1 \in \sigma(\mu v_{\lambda^*} c^T)$. Consequently, $\lambda^* \in \sigma(B)$ and $r(B) > 1$.

If $r(B) = 1$ and $\mu > 0$, then as shown above, one is an eigenvalue of B with eigenvector v_1 so $\mu h(1) = \mu c^T e = 1$. Now consider the case that $\mu < 0$ (note $B = A$ when $\mu = 0$ so $r(B) = 1$ cannot hold). If $r(B) = 1$, then there exists a sequence (λ_n) in $\sigma(B)$ such that $1 \geq |\lambda_n| \to 1$. Since $r(A) < 1$, we can assume that $|\lambda_n| > r(A)$ for all $n \in \mathbb{N}$. By our previous consideration, $1 \in \sigma(\mu v_{\lambda_n} c^T)$ and $1 = \mu h(\lambda_n) \leq |\mu| h(|\lambda_n|) \to |\mu| h(1) = |\mu| c^T e$ so $|\mu| c^T e \geq 1$ and hence $\mu c^T e \leq -1$. In summary of this and a preceding paragraph, for the case $\mu < 0$, we have shown that if $r(B) \geq 1$, then $\mu c^T e \leq -1$ with strict inequality in case that $r(B) > 1$.

If $\mu c^T e = 1$, then $\mu e c^T e = e$ so $1 \in \sigma(\mu v_1 c^T)$ implying that $1 \in \sigma(B)$. Thus, $r(B) \geq 1$. But if $r(B) > 1$, then $\mu c^T e = |\mu| c^T e > 1$ as shown above. This contradiction proves the implication: $\mu c^T e = 1$ implies that $r(B) = 1$. □

We give a condition in terms of f for F to be point dissipative and for all bounded sets to have bounded forward orbits.

Theorem 2.5. *Let the cone X^+ be normal and*

$$(c^T e)\ f'(\infty) < 1, \qquad f'(\infty) := \limsup_{s\to\infty} \frac{f(s)}{s}. \tag{2.8}$$

Then F is point dissipative and any bounded subset S of X^+ has a bounded orbit $O(S) = \bigcup_{n\in\mathbb{Z}_+} F^n(S)$. So F is eventually bounded on bounded sets and the semiflow induced by F has a compact attractor of bounded sets.

Proof. There exists $a, \epsilon > 0$ such that $f(s) \le a + \epsilon s$ and $(c^T e)\epsilon < 1$. Set $y = ab$ and define $D : X^+ \to X^+$ by $Dx = Ax + \epsilon(c^T x)b$. Then $F(x) \le y + Dx$ for all $x \in X^+$. By Theorem 2.4, $r(D) < 1$. Now apply [25, Prop.7.2]. While [25, Prop.7.2] has only been formulated for $X = \mathbb{R}^N$, the proof works for any ordered Banach space with normal cone. Notice that, if the cone is normal, the original norm can be replaced by an equivalent monotone one.

Then there exists $N > 0$ such that $\limsup_{n\to\infty} \|x_n\| \le N$ for all $x_0 \in X^+$. Further, after switching to an equivalent norm, there exists some $R > 0$ such that $F(X^+ \cap \bar{B}_s) \subset \bar{B}_s$ for all $s \ge R$, where $\bar{B}_s$ is the closed ball with center 0 and radius s. This implies that F is point-dissipative and eventually bounded on every bounded subset of X^+. □

3. **Extinction and stability of the extinction state.**

Obviously, the extinction state $x = 0$ is a fixed point of F. We expect that the zero fixed point is stable when $r(F'(0)) < 1$, equivalently, by Theorem 2.4 with $\mu = f'(0)$, when $f'(0)c^T e < 1$, and unstable if the reverse strict inequality holds.

The positive linear functional

$$y^T = c^T(I - A)^{-1} \tag{3.1}$$

will play a useful role. As $y^T(I - A) = c^T$,

$$y^T = y^T A + c^T \ge c^T. \tag{3.2}$$

By (2.5),

$$y^T b = c^T(I - A)^{-1}b = c^T e. \tag{3.3}$$

Theorem 3.1. *Let $\eta \in (0, \infty]$ be such that $\frac{f(s)}{s} c^T e \le 1$ for all $s \in (0, \eta]$.*

- *(a) Then 0 is stable with respect to y^T: For any $\delta \in (0, \eta)$, $y^T x_n \le \delta$ for all $n \in \mathbb{N}$ whenever $y^T x_0 \le \delta$.*
- *(b) 0 is locally stable with respect to $\|\cdot\|$.*
- *(c) If there is some $\tilde{\eta} \in (0, \infty]$ such that $\frac{f(s)}{s} c^T e < 1$ for all $s \in (0, \tilde{\eta})$, then $x_n \to 0$ whenever $y^T x_0 < \tilde{\eta}$, and 0 is locally asymptotically stable.*

Proof. Let $x \in X^+$ and $y^T x \le \eta$. Then $c^T x \le \eta$, and

$$\begin{aligned} y^T F(x) =& y^T Ax + f(c^T x) y^T b = y^T x - c^T x + f(c^T x) c^T e \\ \le& y^T x - c^T x + c^T x = y^T x. \end{aligned}$$

Let $x_n = F^n x$. Then the terms $y^T x_n$ form a decreasing sequence and (a) follows.

(b) In particular, $c^T x_n \le \delta$ for all $n \in \mathbb{N}$ whenever $\delta \in (0, \eta)$ and $y^T x_0 \le \delta$. By (2.4),

$$\|x_n\| \le \|A^n x_0\| + \sum_{k=1}^{n} \sup f([0, \delta]) \|A^{k-1} b\|.$$

After switching to an equivalent norm, we can assume that $\|A\| < 1$ [19, 2.5.2]. Let $\epsilon > 0$ and $\|x_0\| \le \epsilon$. Then, for $n \in \mathbb{N}$,

$$\|x_n\| \le \|A\|\epsilon + \sup f([0,\delta]) \sum_{k=1}^{\infty} \|A^{k-1}b\|.$$

Choosing $\delta \in (0,\epsilon)$ small enough, we can achieve, $\|x_n\| \le \epsilon$ for all $n \in \mathbb{N}$ provided $\|x_0\| \le \epsilon$ and $y^T x_0 \le \delta$. Now choose $\tilde{\delta} = \min\{\epsilon, \delta/\|y^T\|\}$. Then $\|x_n\| \le \epsilon$ whenever $\|x_0\| \le \tilde{\delta}$.

(c) Let α be the limit of $(y^T x_n)$. If $y^T x_0 < \tilde{\eta}$, $\alpha < \tilde{\eta}$. Then

$$\alpha = \lim_{n\to\infty} y^T x_{n+1} = \lim_{n\to\infty} \big(y^T x_n - c^T x_n + f(c^T x_n)c^T e\big).$$

This implies that $-c^T x_n + f(c^T x_n)c^T e \to 0$ as $n \to \infty$. Suppose that $\beta := \limsup_{n\to\infty} c^T x_n > 0$. There exists a strictly increasing sequence (n_k) of natural numbers such that $c^T x_{n_k} \to \beta$. Since f is continuous and $\beta > 0$, $\beta = f(\beta)c^T e < \beta$, a contradiction. So $\beta = 0$ and $c^T x_n \to 0$ and $f(c^T x_n) \to 0$ as $n \to \infty$. Since $\sum_{n=1}^{\infty} \|A^n b\|$ converges, we can apply Lebesgue's dominated convergence theorem (with the counting measure) to (2.4) and obtain $\|x_n\| \to 0$ as $n \to \infty$. □

Corollary 3.2. *(a) If f is differentiable at 0 and $f'(0)c^T e < 1$, then 0 is locally asymptotically stable.*

(b) If $\frac{f(s)}{s}c^T e < 1$ for all $s > 0$, then $F^n(x) \to 0$ as $n \to \infty$ for all $x \in X^+$, and 0 is globally asymptotically stable.

4. **Persistence.**

Several sets of sufficient conditions for extinction of the population were provided in the preceding section. Here we seek sufficient conditions for the persistence of the population. Recall the positive linear functional y^T defined by (3.1).

Theorem 4.1. *Let $c^T e f'(0) > 1$ hold. Then the semiflow induced by F is uniformly weakly persistent in the following sense:*

There exists some $\epsilon > 0$ such that $\limsup_{n\to\infty} c^T x_n \ge \epsilon$ for any solution (x_n) with $y^T x_0 > 0$.

Proof. Suppose that the semiflow is not uniformly weakly persistent in this sense. Let $\epsilon > 0$. Then there exists a solution (x_n) such that $y^T x_0 > 0$ and $\limsup_{n\to\infty} c^T x_n < \epsilon$. In particular, $(c^T x_n)$ is a bounded sequence in $\mathbb{R}_+$. By Proposition 2.3 (b), (x_n) is a bounded sequence in X^+.

By (3.2) and (3.3),

$$y^T x_{n+1} = y^T A x_n + y^T b f(c^T x_n) = (y^T - c^T)x_n + c^T e f(c^T x_n). \tag{4.1}$$

Suppose that $y^T x_0 > 0$. If $c^T x_0 > 0$, then $y^T x_1 \ge c^T e f(c^T x_0) > 0$. If $c^T x_0 = 0$, then $y^T x_1 = y^T x_0 > 0$. It follows that if $y^T x_0 > 0$, then $y^T x_n > 0$ for all $n \ge 0$.

So, after a shift in time, we can assume that $y^T x_n > 0$ for all $n \in \mathbb{Z}_+$ and $c^T x_n \le \epsilon$ for all $n \in \mathbb{Z}_+$. Now choose $\epsilon > 0$ so small that

$$c^T e f(s) \ge \xi s \qquad 0 \le s \le \epsilon, \tag{4.2}$$

with some $\xi > 1$. Since (x_n) is a bounded sequence in X^+, we can define its generating function (discrete Laplace transform) by

$$\hat{x}(q) = \sum_{n=0}^{\infty} q^n x_n; \qquad 0 \le q < 1. \tag{4.3}$$

With $a_n = f(c^T x_n)b$,

$$x_{n+1} = Ax_n + a_n, \qquad n \in \mathbb{Z}_+, \tag{4.4}$$

with another bounded sequence (a_n) in X^+. We multiply this recursion by q^n and sum from 0 to ∞,

$$q^{-1}(\hat{x}(q) - x_0) = A\hat{x}(q) + \hat{a}(q), \qquad 0 < q < 1. \tag{4.5}$$

Since $q^{-1} > 1 > r(A)$,

$$\hat{x}(q) = q^{-1}(q^{-1} - A)^{-1}x_0 + (q^{-1} - A)^{-1}\hat{a}(q). \tag{4.6}$$

Putting back $a_n = f(c^T x_n)b$, we obtain

$$\hat{x}(q) = q^{-1}(q^{-1} - A)^{-1}x_0 + \sum_{n=0}^{\infty} q^n f(c^T x_n)(q^{-1} - A)^{-1}b. \tag{4.7}$$

By (4.2),

$$\hat{x}(q) \geq q^{-1}(q^{-1} - A)^{-1}x_0 + \sum_{n=0}^{\infty} q^n \xi \frac{c^T x_n}{c^T e}(q^{-1} - A)^{-1}b. \tag{4.8}$$

We apply the functional c^T,

$$c^T\hat{x}(q) \geq q^{-1}c^T(q^{-1} - A)^{-1}x_0 + \xi\frac{c^T\hat{x}(q)}{c^T e}c^T(q^{-1} - A)^{-1}b, \qquad 0 < q < 1. \tag{4.9}$$

Since $0 < y^T x_0 = c^T(I - A)^{-1}x_0$, $q^{-1}c^T(q^{-1} - A)^{-1}x_0 > 0$ and so $c^T\hat{x}(q) > 0$ for all $q \in (0, 1)$. We divide by $c^T\hat{x}(q)$,

$$1 \geq \frac{\xi}{c^T e}c^T(q^{-1} - A)^{-1}b, \qquad 0 < q < 1. \tag{4.10}$$

We take the limit $q \to 1$,

$$1 \geq \frac{\xi}{c^T e}c^T(I - A)^{-1}b = \xi > 1,$$

a contradiction. ☐

Next we convert this weak persistence (limit superior) into strong persistence (limit inferior).

Theorem 4.2. *Assume that the semi-dynamical system generated by F is point dissipative and $c^T ef'(0) > 1$. Then F is uniformly y^T-persistent: There exists some $\epsilon > 0$ such that*

$$\liminf_{n\to\infty} y^T x_n > \epsilon, \ \forall x_0 \in X^+ \ \textit{satisfying} \ y^T x_0 > 0. \tag{4.11}$$

Proof. By Theorem 4.1 and $y^T \geq c^T$, F is uniformly weakly y^T-persistent, i.e., (4.11) holds with limit superior in place of limit inferior.

Now, we leverage the weak persistence (with limit superior) to get strong persistence (with limit inferior). For this we employ a standard "weak persistence implies strong persistence" result, Corollary 4.8 in [25], using the notation of that result. The compact attracting set $\overline{\Omega}$ (see Proposition 2.3)

can serve as the required attracting set B of Corollary 4.8. As already noted in the proof of Theorem 4.1, if $y^T x_0 > 0$, then $y^T x_n > 0$ for all $n \geq 0$; so by Remark 4.9 in [25], it follows that all hypotheses of Corollary 4.8 are satisfied. Corollary 4.8 implies (4.11). ☐

Next, we strengthen our hypotheses in order to obtain a stronger persistence result.

Theorem 4.3. *Let $c^T ef'(0) > 1$ and $\ell \in \mathbb{Z}_+$ and $z^T := \sum_{j=0}^{\ell} c^T \circ A^j$.*

Let at least one of the following two assumptions be satisfied,

(i) $z^T b > 0$,

or

(ii) If $x \in X^+$ and $c^T x > 0$, then $z^T Ax > 0$.

Then the following hold.

(a) If S is a compact invariant subset of $X^+ \setminus \{0\}$, then $\inf z^T(S) > 0$.

(b) If the semi-dynamical system generated by F is point dissipative, there exists $\epsilon > 0$ such that

$$\liminf_{n\to\infty} z^T x_n > \epsilon, \ \forall x_0 \in X^+ \text{ satisfying } y^T x_0 > 0. \tag{4.12}$$

Notice that (i) follows from $c^T ef'(0) > 1$ if ℓ is chosen large enough.

Proof. (a) Let S be a compact invariant subset of $X^+ \setminus \{0\}$. It is sufficient to show that $z^T x > 0$ for all $x \in S$.

Suppose $x \in S$ and $z^T x = 0$. Since S is invariant, by [25, Thm.1.40], there exists a sequence $(x_n)_{n\in\mathbb{Z}}$ in S such that $x_n = F(x_{n-1})$ and $x_0 = x$. Now

$$0 = c^T \Big(\sum_{j=0}^{\ell} A^j x_0 \Big) = c^T \Big(\sum_{j=0}^{\ell} A^j A x_{-1} \Big) + f(c^T x_{-1}) z^T b.$$

So $\sum_{j=1}^{\ell+1} c^T A^j x_{-1} = 0$ and $f(c^T x_{-1}) z^T b = 0$. Now either of the two assumptions implies that $c^T x_{-1} = 0$ and so $z^T x_{-1} = 0$.

By induction, $z^T x_{-n} = 0$ for all $n \in \mathbb{Z}_+$. This implies $x_n = A x_{n-1}$ for $n \le 0$. Again by induction, $x_0 = A^n x_{-n}$ for all $n \in \mathbb{N}$. We take the limit as $n \to \infty$ and, since (x_n) is bounded, $x_0 = 0$, contradicting $0 \notin S$.

(b) We also assume that F is point dissipative. Let $\Omega_1 = \bigcup \{\omega(x_0); x_0 \in X^+, y^T x_0 > 0\}$. Since F is uniformly y^T-persistent by Theorem 4.2, $\inf y^T(\Omega_1) > 0$. Further Ω_1 is invariant and a subset of the compact invariant set $\bar\Omega$ in Proposition 2.3. So $\bar\Omega_1$ is compact and invariant and $0 \notin \bar\Omega_1$. By part (a), $\inf z^T(\bar\Omega_1) > 0$. The statement in (b) now follows from the definition of Ω_1. ☐

If ℓ can be chosen to be zero in Theorem 4.3, we can draw further conclusions.

Theorem 4.4. *Let $c^T ef'(0) > 1$ and at least one of the following two assumptions be satisfied,*

(i) $c^T b > 0$,

or

(ii) if $x \in X^+$ and $c^T x > 0$, then $c^T Ax > 0$.

Then the following hold:

(a) If S is a compact invariant subset of $X^+ \setminus \{0\}$, then $S \subset [\delta e, Ce]$ for appropriate $C \ge \delta > 0$.

(b) If the semi-dynamical system generated by F is point dissipative, there exists $C \ge \delta > 0$ such that

$$\bigcup \{\omega(x_0); x_0 \in X^+, y^T x_0 > 0\} \subset [\delta e, Ce]. \tag{4.13}$$

Assumption (i) essentially means that first-year plants make seeds or first-season animals are fertile. It is weaker than strict positivity of c^T, assumed in [22]. Assumption (ii) means that an individual that reproduces this year also has a chance to reproduce next year. The example in Section 8 shows that these assumptions are necessary.

Proof. (a) Let S be a compact invariant subset of $X^+ \setminus \{0\}$. By Theorem 4.3, with $\ell = 0$, there exists some $C \geq \delta > 0$ such that $C \geq f(c^T x) \geq \delta$ for all $x \in S$.

Let $x \in S$. By [25, Thm.1.40], there exists a sequence $\{x_n\}_{n\in\mathbb{Z}}$ in S such that $x_0 = x$ and $x_{n+1} = Ax_n + f(c^T x_n)b$. Then

$$x_n \geq Ax_{n-1} + \delta b, \qquad x_n \leq Ax_{n-1} + Cb, \qquad n \in \mathbb{Z}.$$

By induction,

$$x_n \geq A^k x_{n-k} + \delta \sum_{j=0}^{k-1} A^j b, \qquad x_n \leq A^k x_{n-k} + C \sum_{j=0}^{k-1} A^j b, \qquad n \in \mathbb{Z}, k \in \mathbb{N}.$$

Since X^+ is closed, by letting $k \to \infty$, $\delta e \leq x_n \leq Ce$. Hence $S \subseteq [\delta e, Ce]$.

For (b), let $S = \cup\{\omega(x_0); x_0 \in X^+, y^T x_0 > 0\}$. Then S has compact closure and S and $\bar{S}$ are invariant. By Theorem 4.3, with $\ell = 0$, $\inf_{x\in\bar{S}} c^T x > 0$. Then statement (b) follows from part (a). □

5. **Global dynamics for general f.**

The special structure of F ensures that existence of nonzero fixed points will not be a difficult challenge.

Lemma 5.1. *$F(x) = x$ if and only if*

$$x = pe \quad \textit{with} \quad f(pc^T e) = p \geq 0. \tag{5.1}$$

Moreover,

$$F(te) = te + t\left(f(tc^T e)/t - 1\right) b, \quad t > 0. \tag{5.2}$$

Proof. $x = Ax + bf(c^T x) \iff x = (I - A)^{-1} bf(c^T x) = f(c^T x)e \iff$ (5.1). □

Equation (5.2) and the fact that $b > 0$ imply that either $F(te) > te$, $F(te) < te$, or $F(te) = te$. This is particularly useful when F is monotone.

The derivative of F at a fixed point $x = pe$, $p \geq 0$, exists if $f'(pc^T e)$ exists, and

$$F'(pe)x = Ax + f'(pc^T e)(c^T x)b, \qquad x \in X. \tag{5.3}$$

We expect that the fixed point pe is stable when $r(F'(pe)) < 1$ and unstable when $r(F'(pe)) > 1$.

Theorem 5.2. *Let $c^T e > 0$ and $p > 0$ such that $f(pc^T e) = p$. Then $x = pe$ is a nonzero fixed point of F. Let f be differentiable at $pc^T e$ and $\frac{d}{ds}\frac{f(s)}{s} < 0$ and $\frac{d}{ds} sf(s) > 0$ at $s = pc^T e$. The $x = pe$ is a locally asymptotically stable fixed point.*

Proof. If $f'(pc^T e) = 0$, then $F'(pe) = A$ and $r(F'(pe)) < 1$.

Consider the case $f'(pc^T e) > 0$. Since $\frac{d}{ds}\frac{f(s)}{s} < 0$ at $s = pc^T e$,

$$0 > f'(pc^T e)pc^T e - f(pc^T e) = p(f'(pc^T e)c^T e - 1).$$

Hence $f'(pc^T e)c^T e < 1$ and $r(F'(pe)) < 1$ by Theorem 2.4.

Now consider the case $f'(pc^T e) < 0$. Since $\frac{d}{ds} sf(s) > 0$ at $s = pc^T e$,

$$0 < f'(pc^T e)pc^T e + f(pc^T e) = p(f'(pc^T e)c^T e + 1).$$

Hence $f'(pc^T e)c^T e > -1$. We take the contrapositive of the last statement in Theorem 2.4 and obtain that $r(F'(pe)) < 1$.

So, in either case, $r(F'(pe)) < 1$. Then

$$F(x) - pe = F'(pe)(x - pe) + G(x), \qquad G(x) = F(x) - F(pe) - F'(pe)(x - pe).$$

After choosing an equivalent norm, $r_p = \|F'(pe)\| < 1$ [19, 2.5.2]. Let $\epsilon = (1-r_p)/2$. Since F is differentiable at pe, there exists some $\delta > 0$ such that $\|G(x)\| \le \epsilon\|x-pe\|$ whenever $\|x - pe\| \le \delta$. Hence

$$\|F(x) - pe\| \le (1 - \epsilon)\|x - pe\|, \qquad \|x - pe\| < \delta.$$

So, if $\|x_0 - pe\| < \delta$ and $x_n = F^n(x_0)$, the terms $\|x_n - pe\|$ form a decreasing sequence which converges to 0. □

Remark 5.3. The assumptions for f can equivalently be condensed in one inequality,

$$s|f'(s)| < f(s) \quad \text{at} \;\; s = pc^T e.$$

Since $f'(s) > 0$ implies $\frac{d}{ds}(sf(s)) > 0$ and $f'(s) < 0$ implies $\frac{d}{ds}\frac{f(s)}{s} < 0$, it follows from the proof of Theorem 5.2 that these inequalities are actually equivalent to $r(F'(pe)) < 1$.

The following abstract instability result holds as expected.

Theorem 5.4. *If $r(F'(pe)) > 1$, then the fixed point $x = pe$ is unstable, i.e., there exists some $\epsilon > 0$ and a sequence $(x_k) \in X_+$ such that $x_k \to x$ and $\|F^n(x_k)-x\| > \epsilon$ for some $n = n_k \in \mathbb{N}$.*

Proof. Since the linear map $x \mapsto f'(pc^T e)(c^T x)b$ is compact and $r(A) < 1 < r(F'(x))$, all spectral values λ of $B = F'(x)$ with $|\lambda| \ge 1$ are eigenvalues and do not belong to the essential spectrum of B; in particular they are poles of the resolvent of B and have finite dimensional generalized eigenspaces [18]. Let $\lambda_1, \dots, \lambda_k$ be the eigenvalues of B whose absolute values equal $r(B)$. Let P_j be the projection onto the generalized eigenspace of λ_j [30, Thm.VIII.8.3]. Then the $P_j : X \to X$ are bounded linear operators such that $BP_j = P_jB$, $P_jP_j = P_j$, $P_jP_i = 0$ if $i \ne j$. Further λ_j is an eigenvalue of BP_j and the only one. Set $P = \sum_{j=1}^k P_j$. Then P is a projection that commutes with B and $\lambda_1, \dots \lambda_k$ are the eigenvalues of PB and $r((I - P)B) < r(B)$. Choose q_1 and q_2 such that

$$r((I - P)B) < q_1 < q_2 < r(B), \qquad q_2 > 1.$$

Let $X_1 = P(X)$ and $X_2 = (I-P)X$. Then $X = X_1 \oplus X_2$ with two forward invariant subspaces, X_1 finite dimensional and invariant. The restriction of B to X_1, B_1, is invertible on X_1 and and $r(B_1^{-1}) < q_2^{-1} < 1$. Thus there exists some $M > 0$ such that $\|(B_1^{-1})^n\| \le Mq_2^{-n}$ for all $n \in \mathbb{N}$. Hence $\|B^n x\| \ge M^{-1}q_2^n\|x\|$ for all $x \in X_1$ and $n \in \mathbb{N}$. Further there is some $M_2 > 0$ such that $\|B^n x\| \le M_2 q_1^n\|x\|$ for all $x \in X_2$ and $n \in \mathbb{N}$. We are now in the situation of [5] (see also [15, Prop.5.10]) and the instability of x follows. □

The following is a partial instability result in terms of f.

Corollary 5.5. *Let $c^T e > 0$ and $p > 0$ such that $f(pc^T e) = p$. Then $x = pe$ is a nonzero fixed point of F. Let f be differentiable at $pc^T e$ and*

$$sf'(s) > f(s) \quad \textit{at} \;\; s = pc^T e.$$

Then $x = pe$ is an unstable fixed point.

Proof. We substitute $s = pc^T e$ into the inequality,

$$pc^T ef'(pc^T e) > f(pc^T e) = p.$$

So $c^T ef'(pc^T e) > 1$. By (5.3) and Theorem 2.4, $r(F'(pe)) > 1$ and the assertion follows from Theorem 5.4. □

To study the global stability of a unique nonzero fixed point, we introduce the y^T-persistence attractor of F.

Theorem 5.6. *Let $c^T ef'(0) > 1 > c^T ef'(\infty)$ and X^+ be a normal cone.*

Then there exists a compact invariant set $\mathcal{A}_1$ which is stable, connected, and $\inf_{x\in\mathcal{A}_1} y^T x > 0$. $\mathcal{A}_1$ attracts neighborhoods of compact sets in $\{x \in X^+; \exists n \in \mathbb{Z}_+ : y^T F^n x > 0\}$. In particular, $\mathcal{A}_1$ attracts all points $x \in X^+$ such that $y^T x > 0$.

$\mathcal{A}_1$ attracts all bounded subsets S of X^+ with $S \geq se$ for some $s > 0$. Moreover, if S is a bounded subset of X^+ with $S \geq se$ for some $s > 0$, $\omega(S) \subseteq [\delta e, Ce]$ for appropriate $C > \delta > 0$.

Finally $\mathcal{A}_1 \subset [\delta e, Ce]$ for some $C \geq \delta > 0$ if $c^T b > 0$ or if $c^T Ax > 0$ for all $x \in X^+$ with $c^T x > 0$.

$\mathcal{A}_1$ is called the y^T-persistence attractor of F

Before proving this result, we require some preliminaries. The monotone unfolding $g : \mathbb{R}^2_+ \to \mathbb{R}_+$ of f is defined by

$$g(s,t) = \begin{cases} \inf f([s,t]), & 0 \leq s \leq t, \\ \sup f([t,s]), & 0 \leq t \leq s. \end{cases} \tag{5.4}$$

Some of its properties are listed below.

Lemma 5.7. *(a) g is increasing in the first argument and decreasing in the second.*
(b) g is continuous.
(c) For any $t > 0$, $\frac{g(s,t)}{s} \to f'(0)$ as $s \to 0+$.
(d) For any $t \geq 0$, $\limsup_{s\to\infty} \frac{g(s,t)}{s} \to f'(\infty)$.
(e) For $0 \leq s \leq t$, $g(s,t) \leq f(s), f(t) \leq g(t,s)$.

These statements are either proved in [26, L.3.7] or follow in a similar way.

Proof of Theorem 5.6. By Theorem 2.5, there exists a compact attractor of bounded sets. By [25, Thm.5.7], there exists a y^T-persistence attractor $\mathcal{A}_1$ that has most of the properties listed above including $\inf y^T(\mathcal{A}_1) > 0$. $\mathcal{A}_1$ is connected by [25, Prop.5.9].

Let S be a bounded subset of X^+ and $S \geq \delta e$ for some $\delta > 0$. By Theorem 2.5, $\{F^n(S); n \in \mathbb{Z}_+\}$ is bounded. So there exists some $M > 0$ such that $c^T F^n u \leq M$ for all $n \in \mathbb{Z}_+$ and $u \in S$. By Lemma 5.7 $g(s,M)/s \to f'(0)$ as $s \to 0$. Since $c^T ef'(0) > 1$, $g(sc^T e, M) \geq s$ for sufficiently small $s > 0$. Let $u_0 \in S$ and $u_n = F(u_{n-1})$. Then

$$u_n \geq Au_{n-1} + g(c^T u_{n-1}, M)b.$$

So

$$u_1 \geq A\delta e + g(c^T \delta e, M)b \geq \delta(e - b) + \delta b = \delta e.$$

By induction, $u_n \geq \delta e$ for all $n \in \mathbb{Z}_+$. Hence $F^n(S) \geq \delta e$ for all $n \in \mathbb{N}$. This implies that the semiflow induced by F is eventually uniformly $\hat{\rho}$-positive for $\hat{\rho}(x) = [x]_e = \sup\{s \geq 0, x \geq se\}$. This implies that F is eventually uniformly y^T-positive and c^T-positive on S. Hence the y^T-persistence attractor attracts S. Further $\omega(S) \geq \delta e$.

Since $\omega(S)$ is compact and invariant, $\omega(S) \subset [\delta e, Ce]$ for some $C \geq \delta$ by Lemma 2.2.

Finally assume that $c^T b > 0$ or that $c^T Ax > 0$ for all $x \in X^+$ with $c^T x > 0$. Since $\mathcal{A}_1$ is a compact invariant subset of $X^+ \setminus \{0\}$, $\mathcal{A}_1 \subset [\delta e, Ce]$ for some $C \geq \delta > 0$ by Theorem 4.4. □

Next, we link the global stability of a nontrivial fixed point of F to that of the scalar function $\phi : \mathbb{R}_+ \to \mathbb{R}_+$,

$$\phi(s) = c^T ef(s), \qquad s \geq 0.$$

Recall

$$f'(\infty) = \limsup_{s\to\infty} \frac{f(s)}{s}.$$

Theorem 5.8. *Let $c^T ef'(0) > 1 > c^T ef'(\infty)$ and X^+ be a normal cone. Then ϕ has a fixed point $p > 0$, and F has the fixed point $x^* = \frac{p}{c^T e} e$. Assume*

(H) p is the only fixed point of ϕ with $p > 0$ and ϕ^2 has no fixed point q such that $0 < q < p < \phi(q)$.

Then the following hold.

(a) If S is a bounded subset of X^+ and $S \geq se$ for some $s > 0$, $F^n(x_0) \to x^*$ as $n \to \infty$ uniformly for $x_0 \in S$.

(b) Additionally assume that $c^T b > 0$ or that $c^T Ax > 0$ for all $x \in X^+$ with $c^T x > 0$. Then x^* is a stable fixed point and all solutions (x_n) of $x_{n+1} = F(x_n)$ with $y^T x_0 > 0$ converge to x^*. Moreover, $\mathcal{A}_1 = \{x^*\}$.

The hypothesis (H) for ϕ is satisfied if

$f(s)/s$ is a strictly decreasing function of $s > 0$

and one of the following hold [28, Cor.9.9]:

(i) f is increasing on $(0, p)$ or (p, ∞)
or
(ii) $sf(s)$ is a strictly increasing function of $s > 0$.

The example in Section 8 will show that the extra assumptions in part (b) are necessary.

Proof of Theorem 5.8. The existence of a non-zero fixed point of ϕ is immediate from Lemma 5.1 and our hypotheses.

$F(x) = \hat{F}(x, x)$ where $\hat{F}(x, y) := Ax + g(c^T x, c^T y)b$ so by Lemma 5.7, F is monotonically decomposable in the sense of [24]. Define $G : X^+ \times X^+ \to X^+ \times X^+$ by

$$G(x, y) = (\hat{F}(x, y), \hat{F}(y, x)).$$

Then $G(x, x) = (F(x), F(x))$ and, by [24, Lemma 1], G is monotone with respect to the "southeast ordering" defined by $(x, y) \leq_C (\bar{x}, \bar{y})$ whenever $x \leq \bar{x}$ and $y \geq \bar{y}$:

$$(x, y) \leq_C (\bar{x}, \bar{y}) \Rightarrow G(x, y) \leq_C G(\bar{x}, \bar{y}).$$

In order to apply [24, Theorem 2 and Corollary 3], we seek $x_0, y_0 \in X^+$ with $x_0 \leq y_0$ and $\hat{F}(x_0, y_0) \geq x_0$ and $\hat{F}(y_0, x_0) \leq y_0$.

By Lemma 5.7(d) and $c^T ef'(\infty) < 1$, we can choose $y_0 = t_0 e$ with $t_0 > 0$ so large that

$$\hat{F}(y_0, 0) = Ay_0 + g(c^T y_0, 0)b \leq y_0. \tag{5.5}$$

Similarly, by Lemma 5.7(c) and $c^T ef'(0) > 1$, we can now choose $x_0 = s_0 e$ with $s_0 > 0$ so small that $x_0 \le y_0$ and

$$\hat{F}(x_0, y_0) = Ax_0 + g(c^T x_0, c^T y_0)b \ge x_0.$$

By the monotonicity properties of g and (5.5),

$$\hat{F}(y_0, x_0) = Ay_0 + g(c^T y_0, x_0)b \le y_0.$$

Therefore, the hypotheses of [24, Theorem 2] are satisfied and therefore $\{(x_n, y_n) = G^n(x_0, y_0)\}_{n\ge 0}$, which satisfy the difference equation

$$x_{n+1} = Ax_n + g(c^T x_n, c^T y_n)b, \qquad y_{n+1} = Ay_n + g(c^T y_n, c^T x_n)b, \tag{5.6}$$

also satisfy

$$x_0 \le x_n \le x_{n+1} \le y_0, \quad x_0 \le y_{n+1} \le y_n \le y_0, \quad x_n \le y_n,\ n \ge 0,$$

and, if $\{(x_n, y_n)\}_{n\ge 0}$ converges, say to (x^*, y^*), then $x^* \le y^*$ and $G(x^*, y^*) = (x^*, y^*)$, or

$$x^* = Ax^* + g(c^T x^*, c^T y^*)b, \qquad y^* = Ay^* + g(c^T y^*, c^T x^*)b, \tag{5.7}$$

so that

$$x^* = g(c^T x^*, c^T y^*)e, \qquad y^* = g(c^T y^*, c^T x^*)e. \tag{5.8}$$

Indeed, since the set $[c^T x_0, c^T y_0]b$ is compact in X^+ and $r(A) < 1$, the sets $\{x_n; n \ge 0\}$ and $\{y_n : n \ge 0\}$ have compact closure in X^+ and therefore $\{(x_n, y_n)\}_{n\ge 0}$ converges to (x^*, y^*) where $x_0 \le x^* \le y^* \le y_0$.

By [24, Theorem 2], $\omega(x) \subset [x^*, y^*]$ for all $x \in [x_0, y_0]$.

To show that $x^* = y^*$, we must verify that whenever $u, v \in [x_0, y_0]$ with $u \le v$ satisfy $\hat{F}(u, v) = u,\ \hat{F}(v, u) = v$, then $u = v$. See [24, Corollary 2]. Since $\hat{F}(u, v) = u,\ \hat{F}(v, u) = v$ is equivalent to (5.7) with (u, v) instead of (x^*, y^*), we conclude that

$$u = g(c^T u, c^T v)e, \qquad v = g(c^T v, c^T u)e. \tag{5.9}$$

Set $\alpha = c^T u$ and $\beta = c^T v$. Then $u \le v$ implies that $0 < \alpha \le \beta$ and

$$\alpha = g(\alpha, \beta)c^T e, \qquad \beta = g(\beta, \alpha)c^T e. \tag{5.10}$$

By the definition of g and the intermediate value theorem, $[\alpha, \beta] = f([\alpha, \beta])c^T e$, i.e., $[\alpha, \beta] = \phi([\alpha, \beta])$. Our assumptions on ϕ and [28, Prop.9.2] imply that $\alpha = \beta$ and therefore $u = v$. This implies that $x^* = y^*$ and thus, $\omega(x) = \{x^*\}$ for all $x \in [x_0, y_0]$.

Given an arbitrary $x \in X^+$ satisfying $x \ge se$ for some $s > 0$, we can always choose x_0, y_0 as above with $x_0 < x < y_0$, so we may conclude that $F^n(x) \to x^*$ as $n \to \infty$.

If $S \subset X^+$ is bounded with $S \ge se$ for some $s > 0$, then $\omega(S) \subset [\delta e, Ce]$ for suitable $C > \delta > 0$ by Theorem 5.6. As we may take x_0 and y_0 as above with $\omega(S) \subset [x_0, y_0]$, we conclude that

$$\omega(S) = \omega(\omega(S)) \subset \omega([x_0, y_0]) = \bigcap_{n\ge 0} \overline{F^n([x_0, y_0])} \subset \bigcap_{n\ge 0} [x_n, y_n] = \{x^*\}.$$

Now assume that $c^T b > 0$ or that $c^T Ax > 0$ for all $x \in X^+$ with $c^T x > 0$. Then the y^T-persistence attractor, $\mathcal{A}_1$, satisfies $\mathcal{A}_1 \subset [\delta e, Ce]$ with appropriate $C \ge \delta > 0$ by Theorem 5.6. Thus $\mathcal{A}_1 = \{x^*\}$ by the previous paragraph and x^* is stable and attracts every x_0 with $y^T x_0 > 0$. □

6. **Global dynamics for monotone f.** Monotonicity can be used to obtain strong persistence type results.

Theorem 6.1. *Assume that X^+ is a normal cone, f is nondecreasing, and $c^Tef'(0) > 1 > c^Tef'(\infty)$.*

Then there exists a minimal positive fixed point $x_{\min} = pe$ and a maximal positive fixed point $x_{\max} = Pe$ for some $P \geq p > 0$.

For all $x_0 \in X^+$ with $x \geq se$ for some $s > 0$, we have

$$\omega(x_0) \subset [x_{\min}, x_{\max}].$$

If $c^Tb > 0$ or if $c^TAx > 0$ for all $x \in X^+$ with $c^Tx > 0$, the compact connected persistence attractor $\mathcal{A}_1$ of Theorem 5.6 is contained in $[x_{\min}, x_{\max}]$, $x_{\min}$ is the minimum of $\mathcal{A}_1$ and $x_{\max}$ the maximum of $\mathcal{A}_1$, and $\mathcal{A}_1$ attracts all bounded subsets S of X^+ with $S \geq \delta e$ for some $\delta > 0$.

Proof. As f is nondecreasing, F is monotone: $0 \leq x \leq y \Rightarrow F(x) \leq F(y)$. There exists $r > 1$ and $\eta > 0$ such that $c^Te(f(s)/s) > r$ if $0 < s < \eta$. Using (5.2), we conclude that $F(te) > te$ if $tc^Te < \eta$ and $t > 0$. If $x_0 = t_0e$ for such a t_0, then $x_1 = F(x_0) > x_0$ leads to $x_{n+1} \geq x_n$, $n \geq 0$. As orbits have compact closure, $x_n \to x_{\min} \geq x_0$ and $F(x_{\min}) = x_{\min}$ by continuity. Hence $x_{\min} = pe$ for some p with $c^Tep \geq \eta$. This fixed point is minimal since any other one must be se for $c^Tes \geq \eta$; as $t_0 < s$, $F^n(t_0e) \leq F^n(se) = se$ and letting $n \to \infty$ yields $x_{\min} \leq se$. It follows that if $x_0 = te$ for $c^Tet \in (0, \eta)$ then $x_n \to x_{\min}$.

As $1 > c^Tef'(\infty)$, there exists $S > 0$ such that $c^Te\frac{f(s)}{s} < 1$ for all $s \geq S$, implying by (5.2) that there are no fixed points $x = te$ for $c^Tet > S$. In fact, $F(te) < te$ for $c^Tet > S$ by (5.2). Consequently, for such t, we have $pe < te$ and $x_{\min} = F(pe) < F(te) < te$. Iterating results in $x_{\min} \leq F^{n+1}(te) < F^n(te) < te$, $n \geq 0$. As before, we conclude that $F^n(te)$ converges monotonically to a fixed point $x_{\max} = Pe$ for some $P \geq p$. It is easy to see, arguing as we did for the minimality of $x_{\min}$, that $x_{\max}$ is the maximal fixed point of F and that $F^n(te) \to x_{\max}$ for $c^Tet > S$.

Now let $x_0 \in X^+$ satisfy $x_0 \geq se$ for some $s > 0$. We may as well assume that $c^Tes < \eta$. Then $F^n(x_0) \geq F^n(se)$ for all $n \geq 0$ and since $F^n(se) \to x_{\min}$, we conclude that $x_{\min} \leq \omega(x_0)$. By Proposition 2.3 and Theorem 2.5, there exists $M > 0$ such that $\omega(x_0) \leq Me$. Clearly, we may assume $c^TeM > S$. By monotonicity and invariance of limit sets, $\omega(x_0) = F^n(\omega(x_0)) \leq F^n(Me)$, $n \geq 0$. Taking the limit results in $\omega(x) \leq x_{\max}$.

We now assume that $c^Tb > 0$ or $c^TAx > 0$ for all $x \in X^+$ with $c^Tx > 0$. Then $\mathcal{A}_1 \subset [\epsilon e, Ce]$ for suitable $C > \epsilon > 0$ by Theorem 5.6. Let $t \in (0, \epsilon)$ be so small that $F(te) \geq te$ and set $x_0 = te$. Let $y \in \mathcal{A}_1$. Since $\mathcal{A}_1$ is invariant, by [25, Thm.1.40] there exists a sequence (y_n) in $\mathcal{A}_1$ such that $y_n = F(y_{n-1})$, $n \in \mathbb{Z}$ and $y_0 = y$. In particular $y_n \geq x_0$ for all $n \in \mathbb{Z}$. Hence $y = y_0 = F^n(y_{-n}) \geq F^n(x_0) = x_n \to x_{\min}$. So $y \geq x_{\min}$. Similarly we prove that $y \leq x_{\max}$.

If $S \subset X^+$ is bounded and $S \geq se$ for some $s > 0$, then $\mathcal{A}_1$ attracts S by Theorem 5.6. □

Remark 6.2. The above results are valid if $f'(0) = +\infty$.

7. **Global dynamics for monotone and strictly concave f.** The result below for nondecreasing and strictly concave f is patterned after Theorem 3.3 and Remark 3.5 of [22]. Note that our extra assumptions in case (c) are weaker than strict positivity of c^T as defined in [22].

Theorem 7.1. *Let f be nondecreasing and strictly concave and let X^+ be normal.*

(a) *If $c^T e f'(0) < 1$, then $x_n \to 0$ for all $x_0 \in X^+$.*
(b) *If $c^T e f'(0) > 1$ and if equation $f(pc^T e) = p$ has a solution $p = p^* > 0$ then $x^* = p^* e$ is the unique fixed point of F.*
(c) *If the hypotheses of (b) hold and if $c^T b > 0$ or $c^T Ax > 0$ whenever $c^T x > 0$, then $x_n \to x^*$ for all x_0 satisfying $y^T x_n > 0$ for some $n \geq 0$.*
(d) *If the hypotheses of (b) hold, then $x_n \to x^*$ for all $x_0 \in X^+$ satisfying $x_0 \geq se$ for some $s > 0$.*

The example in Section 8 will show that the extra assumptions in part (c) are necessary. We can treat (c) and (d) as a special case of Theorem 5.8 or invoke Theorem 6.1. Notice that the strict concavity of f and $f(0) = 0$ imply that $f(s)/s$ is a strictly decreasing function of $s > 0$.

Proof. If $c^T e f'(0) < 1$ and f is strictly concave, then $c^T e \frac{f(s)}{s} < 1$ for all $s > 0$, so (a) follows from Corollary 3.2.

As f is strictly concave, the solution $p = p^*$ of $f(pc^T e) = p$ is unique. By Lemma 5.1, $x^* = pe$ is the unique nontrivial fixed point, proving (b).

Concavity also implies that $c^T e \frac{f(s)}{s} < 1$ for $s > c^T x^*$ so the hypotheses of Theorem 2.5 holds. (c) follows from Theorem 5.6 and the final assertion of Theorem 6.1.

The proof of (d) is immediate from Theorem 6.1 and the uniqueness of x^*.

Alternatively, (c) and (d) follow from Theorem 5.8. □

8. **A simple example.** Although our emphasis in this work is on the infinite dimensional case, the following example has the virtue that its global behavior can be worked out and the relative strength of the various results can be directly compared. In particular, it shows that the extra assumptions in Theorem 5.8 (b) and Theorem 7.1 (c) are necessary. Consider the age-structured model, similar to the one described in [25, Example 7.12], of a species that does not live to a third year. It is given by

$$\begin{aligned} x_1(n+1) &= \frac{a(qx_1(n) + x_2(n))}{1 + d(qx_1(n) + x_2(n))}, \\ x_2(n+1) &= px_1(n), \end{aligned}$$

where $0 < p < 1$ and $a, d > 0$ and $q \geq 0$. With $x = (x_1, x_2)^T$, $b = (1, 0)^T$, $c^T = (q, 1)$, and $f(s) = \frac{as}{1+ds}$, it becomes

$$x_{n+1} = Ax_n + bf(c^T x_n) = F(x_n),$$

where

$$A = \begin{pmatrix} 0 & 0 \\ p & 0 \end{pmatrix}.$$

Easy computations give $e = (1, p)^T$, $y^T = (p + q, 1)$ so $f'(0)c^T e = a(q + p)$.

If $a(q + p) > 1$, then $r(F'(0)) > 1$ so Theorem 4.2 applies and we conclude that there exists $\epsilon > 0$ such that

$$\liminf_{n\to\infty} [(p + q)x_1(n) + x_2(n)] > \epsilon, \tag{8.1}$$

provided $(p + q)x_1(0) + x_2(0) > 0$. We stress that ϵ is independent of the initial data.

If $q > 0$, Theorem 4.3 and Theorem 4.4 apply with $z^T = c^T$ since $c^T b = q > 0$. In that case, we may conclude that there exists $\epsilon > 0$ such that

$$\liminf_{n\to\infty} qx_1(n) + x_2(n) > \epsilon, \tag{8.2}$$

provided $(p+q)x_1(0) + x_2(0) > 0$.

If $q = 0$, the organism reproduces only in its second year of life and the dynamics are more interesting as we will see. Assume that $r(F'(0)) = ap > 1$. Indeed, in this case, non-trivial orbits that initiate on the boundary of the first quadrant remain there, alternating between the positive x_1 axis and the positive x_2 axis. These so-called synchronous orbits, nonzero orbits contained in the boundary of the positive quadrant, converge to a unique period-two orbit of the form $(0,k)^T \to (m,0)^T \to (0,k)^T \to \cdots$ where $m, k > 0$, as shown in [25, Remark 7.14]. This case illustrates that c^T-persistence cannot hold since $c^T x_n = x_2(n)$. Theorem 4.3 applies with $z^T = c^T + c^T \circ A = (p,1)$ but as $y^T = z^T$ it is not an improvement of Theorem 4.2.

Notice that, if $q = 0$, then $c^T b = 0$ and $c^T A = (p,0)$. Therefore, $c^T x \neq 0$ and $c^T Ax = 0$ for all $x \in \mathbb{R}^2$ with $x_1 = 0, x_2 \neq 0$, so hypotheses (i) and (ii) of Theorem 4.4 fail as they must.

As f is nondecreasing and bounded, Theorem 6.1 applies when $a(q+p) > 1$. In this case, there is exactly one fixed point

$$x^* = (s, ps)^T, \ \ s = \frac{a(q+p)-1}{q+p}.$$

Therefore, Theorem 6.1 implies that $\omega(x_0) = \{x^*\}$ for all x_0 belonging to the interior of the first quadrant. Due to the synchronous orbits when $q = 0$, this result is clearly the best possible result in this case.

Clearly, f is concave as well so Theorem 7.1 (c) gives the global stability of the fixed point $\hat{x}$ for non-trivial orbits when $q > 0$ and Theorem 7.1 (d) gives the global stability for strictly positive initial data when $q = 0$.

9. **Example with a general structure redistribution kernel.** As another application, we consider a discrete time structured population model, sometimes called an integral population projection model, like in [22], but we allow structure redistribution kernels that are measures.

Let $(E, \mathcal{S})$ be a measurable space, i.e., E is a set and $\mathcal{S}$ a σ-algebra of subsets of E. Let $K : \mathcal{S} \times E \to \mathbb{R}_+$ be the yearly structure redistribution kernel: If $\eta \in E$ and $S \in \mathcal{S}$, then $K(S,\eta)$ is the probability that the structural state of an individual lies in S if it was equal to η in the previous year. Let $X = \mathcal{M}(E,\mathcal{S})$ be the Banach space of finite (signed) measures on $\mathcal{S}$ with the norm being given by the total variation. The state space for the semiflow is the cone X^+ consisting of the nonnegative measures. As the norm is monotone, the cone X^+ is normal. We assume that $K(\cdot,\eta)$ is a nonnegative measure on $\mathcal{S}$ for any $\eta \in E$ and $K(S,\cdot)$ is measurable on E. Further $\sup_{\eta\in E} K(E,\eta) < 1$. Notice that $K(E,\eta)$ is the probability of surviving the year if the structural state is η.

Let $f : \mathbb{R}_+ \to \mathbb{R}_+$ satisfy the assumptions of Section 2. Then the model takes the form

$$x_{n+1}(S) = \int_E K(S,\eta)x_n(d\eta) + f\Big(\int_E h(\eta)x_n(d\eta)\Big)\mu(S), \qquad S \in \mathcal{S}.$$

The measure x_n describes the structural distribution of the population in the n^{th} year. The nonnegative measure μ gives the structural distribution of individuals that complete their first year. $h(\eta)$ is the fertility of an individual with structural state η and $h : E \to E$ a bounded measurable function. Under our assumptions for K, there is a unique nonnegative measure e on $\mathcal{S}$ such that

$$e(S) = \mu(S) + \int_E K(S, \eta)e(d\eta), \qquad S \in \mathcal{S}.$$

The following is an immediate consequence of Theorem 5.8.

Theorem 9.1. *Assume that $f(0) = 0$ and $f(s)/s$ is strictly decreasing and $sf(s)$ is strictly increasing in $s > 0$,*

$$f'(0) \int_E h(\eta)e(d\eta) > 1 > f'(\infty) \int_E h(\eta)e(d\eta).$$

Then the following hold.

(a) There exists a unique positive measure x such that

$$\sup_{S\in\mathcal{S}} |x_n(S) - x(S)| \to 0$$

for any solution (x_n) for which $x_0(S) \geq \delta e(S)$, $S \in \mathcal{S}$, with some $\delta > 0$.

(b) If $\int_E h(\eta)\mu(d\eta) > 0$ or if $\int_E \int_E h(s)K(ds, \eta)x(d\eta) > 0$ for all nonnegative measures x with $\int_E h(\eta)x(d\eta) > 0$, the convergence holds as in (a) for any solution (x_n) with $\int_E \tilde{h}(\eta)x_0(d\eta) > 0$ where $\tilde{h}$ is the solution of

$$\tilde{h}(\eta) = h(\eta) + \int_E \tilde{h}(\alpha)K(d\alpha, \eta), \qquad \eta \in E.$$

Notice that the operator A on $\mathcal{M}(E, \mathcal{S})$ given by the redistribution kernel K will not be compact in general.

More specifically, let the structural variable be the weight of an individual, $E = \mathbb{R}_+$. Let us assume that the reproductive season is very short and occurs at the turn of the year. Assume that the weight at the end of the year is uniquely determined by the beginning of the year. Let $k(\eta)$ be the weight at the end of a year when the size is η at the beginning. To be specific, $k(\eta) = \eta + \eta_0$ where η_0 is a constant weight increase per year. Set $K(S, \eta) = \chi_S(k(\eta))p(\eta)$ with χ_S being the characteristic function of the set S and $p(\eta)$ the probability of surviving the year. Let $\mathcal{S}$ be the set of Borel subsets of $\mathbb{R}_+$. Recall that $\mathcal{M}(\mathbb{R}_+) = \mathcal{M}(\mathbb{R}_+, \mathcal{S})$ is the dual space of $C_0(\mathbb{R}_+)$, the space of continuous functions that vanish at infinity. Then, for the dual of A, A^*,

$$(A^*g)(\eta) = \int_{\mathbb{R}_+} g(s)K(ds, \eta) = p(\eta)g(\eta + \eta_0), \qquad \eta \in \mathbb{R}_+, g \in C_0(\mathbb{R}_+).$$

Also recall that A^* is compact if and only if A is. If A were compact, A^* would map bounded subsets of $C_0(\mathbb{R}_+)$ into equicontinuous ones which obviously is not the case. Notice that A can be restricted to $L^1(\mathbb{R}_+)$ with

$$(Ag)(s) = p(s - \eta_0)g(s - \eta_0), \qquad s \geq 0, g \in L^1(\mathbb{R}_+),$$

where g and p are extended by 0 to the negative real numbers. If the restriction $\tilde{A}$ to $L^1(\mathbb{R}_+)$ were compact, then its dual $\tilde{A}^*$ would be compact on $L^\infty(\mathbb{R}_+)$ which it is not by the same reason as before.

The choice of $\mathcal{M}(\mathbb{R}_+)$ rather than $L^1(\mathbb{R}_+)$ is necessary, if all individuals completing their first year have the same weight η_1, for then μ is the Dirac measure concentrated at η_1, $\mu(S) > 0$ if and only if $\eta_1 \in S$. Even if $x_0 \in L^1(\mathbb{R}_+)$, it can then easily happen that $x_1 \notin L^1(\mathbb{R}_+)$, where $L^1(\mathbb{R}_+)$ is identified with the set of measures that are absolutely continuous with respect to the Lebesgue measure.

This special case is worth fleshing out a bit. Assume further that there is a threshold weight $\eta^\sharp > 0$ for reproduction such that the fertility function satisfies $h(\eta) = 0$ for $\eta \le \eta^\sharp$ and $h(\eta) > 0$ for $\eta > \eta^\sharp$. Then the first assumption in Theorem 9.1 (b), namely $c^T\mu = \int_E h(\eta)\mu(d\eta) > 0$, is satisfied if and only if $\eta_1 > \eta^\sharp$.

The second assumption in Theorem 9.1 (b) does not refer to the measure μ at all. It holds, for instance, if h and $K((\eta^\sharp,\infty),\cdot)$ are bounded away from 0 on every closed finite interval in $(\eta^\sharp,\infty)$. To see this, assume that $\int_E\int_E h(s)K(ds,\eta)x(d\eta) = 0$. By Tonelli's theorem and the assumptions on h, $\int_E K((\eta^\sharp,\infty),\eta)x(d\eta) = 0$. By our assumption on K, $x(I) = 0$ for every closed finite interval in $(\eta^\sharp,\infty)$. So $x((s^\sharp,\infty)) = 0$ and $\int_E h(\eta)x(d\eta) = 0$. By contraposition, the second assumption in Theorem 9.1 (b) holds.

The assumptions concerning the nonlinear function f, which describes the density dependence of fecundity, are satisfied for the following class of functions,

$$f(s) = \frac{as}{(1+ds^\xi)^\zeta}, \qquad s \ge 0,$$

where $a, d, \xi, \zeta > 0$ and $\xi\zeta \le 2$ [28, p.98]. Notice that f is nondecreasing on $\mathbb{R}_+$ if and only if $\zeta\xi \le 1$.

Discussion. To our knowledge, there is little discussion of persistence in continuous time size-structured population models with the qualitative analysis concentrating on steady states, local stability, and bifurcations [8, 10, 12]. The monograph [25] avoids size-structured population models because establishing existence and uniqueness of their solutions can be highly nontrivial [13, 27] and definitely is page and time consuming [7, 9, 11]. Discrete time models, by their very nature, obviate existence and uniqueness issues completely, and their qualitative behavior can be taken on right away (however, if the modeling is detailed, the continuity of the map may become an issue). Motivated by [22], this paper studies persistence and global stability in a simple discrete time model. The results apply to size-structured models where only the reproduction of individuals (via the function f) but not their growth and survival (represented by the linear operator A) depend on the population density. This restriction allows us to prove global stability results as well. The latter presumably will not extend to density-dependent individual growth while we are fairly optimistic that the persistence results, after suitable modification, may.

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Received September 2012; revised January 2013.

E-mail address: halsmith@asu.edu
E-mail address: hthieme@asu.edu