

## Some persistence results for systems of difference equations

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### Abstract

The dynamical systems theory of persistence, sometimes called permanence, derives from population dynamics where it is understood to be the opposite of extinction. Mathematically, it means that there exists an attractor for non-extinction starting states, that is bounded away from the set of extinction states. Here, we briefly review some results and applications that are treated in more depth in [5].

## 1 Persistence

The year-to-year development of populations is often modeled by systems

$$x(n+1) = F(x(n)), n \in \mathbb{Z}_+,$$

where  $F : \mathbb{R}_+^m \rightarrow \mathbb{R}_+^m$ . Of particular interest are nonlinear matrix models where  $F(x) = A(x)x$  with nonnegative matrix  $A(x)$  such that  $x \rightarrow A(x)$  is continuous on  $\mathbb{R}_+^m$ . It is of interest to know whether or not a population persists over the long run or whether it ultimately goes extinct. If the system represents the time evolution of various life stages of an organism, one also wants to know if each life stage persists. Mathematically, uniform persistence can be defined in terms of a persistence function  $\rho : \mathbb{R}_+^m \rightarrow [0, \infty)$  which measures persistence ( $\rho > 0$ ) or the lack of persistence ( $\rho = 0$ ). Once a suitable choice of  $\rho$  is made, define  $\rho$ -persistence as follows: there exists  $\epsilon > 0$  such that

$$\rho(x(0)) > 0 \Rightarrow \liminf_{n \rightarrow \infty} \rho(x(n)) \geq \epsilon.$$

The independence of  $\epsilon$  on initial data  $x(0)$  is stressed using the adjective “uniform” in uniform persistence, although it will typically be dropped for brevity.

If  $\rho(x) = \sum_i a_i x_i$  for some choice of positive  $a_i$  then we are measuring population persistence; if  $\rho(x) = \prod_i x_i^{p_i}$  for some choice of positive  $p_i$  or if  $\rho(x) = \min_i x_i$ , then we are measuring stage persistence.

In my talk, I presented some persistence results some of which are described below. All results presented here are discussed in more detail in the monograph [5] as well as in the papers cited below. See also [2].

As an example, consider the LPA model of flour beetle demographics [1]. The dynamics of change in the densities of life-cycle stages of (feeding) larva ( $x_1$ ), pupa ( $x_2$ ), and adult ( $x_3$ ) are given by:

$$\begin{aligned}x_1(n+1) &= dx_3(n) \exp(-ax_1(n) - bx_3(n)), \\x_2(n+1) &= px_1(n), \\x_3(n+1) &= qx_2(n) \exp(-cx_3(n)) + rx_3(n).\end{aligned}\tag{1}$$

$r$  is adult survival probability,  $p$  is transition/survival probability from the larval to the pupal stage,  $q$  is transition/survival probability from the pupal to the adult stage, and coefficients  $a$ ,  $b$ , and  $c$  are related to cannibalism and  $d$  to fecundity of adults.

The right hand side of (1) is  $F(x) = A(x)x$  where matrix  $A$  is defined by:

$$A(x) = \begin{pmatrix} 0 & 0 & d \exp(-ax_1 - bx_3) \\ p & 0 & 0 \\ 0 & q \exp(-cx_3) & r \end{pmatrix}$$

The following is an example of a persistence result. We denote by  $r(A)$  the spectral radius of matrix  $A$ .

**Theorem 1.1.** ([3]) *Suppose that*

- (a)  $\mathbb{R}_+^m \setminus \{0\}$  is forward invariant:  $x \neq 0 \Rightarrow A(x)x \neq 0$ .
- (b)  $r(A(0)) > 1$  and  $A(0)$  is irreducible.
- (c)  $\exists$  compact  $B \subset \mathbb{R}_+^m$  such that  $x(n) \rightarrow B$ ,  $\forall x(0) \in \mathbb{R}_+^m$ .

Then for any norm  $|\cdot|$ ,  $\exists \epsilon > 0$  such that  $\liminf_{n \rightarrow \infty} |x(n)| > \epsilon$ ,  $x(0) \neq 0$ .

If the norm is  $x = \sum_i |x_i|$ , then our persistence function  $\rho(x) = \sum x_i$  is the total population density. Theorem 1.1 gives conditions for the total population to persist.

For the LPA model (1),

$$A(0) = \begin{pmatrix} 0 & 0 & d \\ p & 0 & 0 \\ 0 & q & r \end{pmatrix}$$

is irreducible if  $pqd > 0$  and

$$r(A(0)) > 1 \Leftrightarrow \frac{pqd}{1-r} > 1.$$

Population persistence holds:  $\exists \epsilon > 0$  such that if  $x(0) \neq 0$ , then

$$\liminf_{n \rightarrow \infty} [x_1(n) + x_2(n) + x_3(n)] > \epsilon.$$

Population persistence does not preclude one of the life-cycle stages from becoming arbitrarily small or even vanishing. Take, for example, the model of a population that reproduces only in its 2nd year of life and then dies (e.g. biennial plant), given by

$$\begin{aligned}x_1(n+1) &= \frac{fx_2(n)}{1 + ax_1(n) + bx_2(n)}, \\x_2(n+1) &= px_1(n), \quad n = 0, 1, 2, \dots,\end{aligned}\tag{2}$$

where  $a, b, f > 0$  and  $0 < p < 1$ .

It is easily shown that the following hold for (2):

- (a) population persistence holds if  $fp > 1$ ; extinction holds if  $fp < 1$ .
- (b) If  $pf > 1$ , then the following hold:
  1. there is a unique period-two orbit  $P: (0, d) \rightarrow (c, 0) \rightarrow (0, d) \rightarrow \dots$ .
  2. every orbit starting in  $\partial\mathbb{R}_+^2 \setminus \{0\}$  converges to  $P$  or its phase shift.
  3. there is a unique equilibrium  $E = (\bar{x}_1, \bar{x}_2)$  with  $\bar{x}_i > 0, i = 1, 2$ .
  4. If  $a < bp$  then  $E$  is stable and  $P$  is unstable; if  $a > bp$  then  $E$  is unstable and  $P$  is stable.

A synchronous orbit  $O = \{x(n) : n \geq 0\}$  is defined to be one for which  $O \subset \partial\mathbb{R}_+^m$ . As the above example shows, synchronous orbits are consistent with population persistence. However, they may be undesirable. The following result precludes synchronous orbits. For matrix  $Q$ , define  $\text{support}(Q) = \{(i, j) : q_{ij} \neq 0\}$ .

**Theorem 1.2.** ([4]) *Assume that*

- (a)  $\exists$  compact  $B \subset \mathbb{R}_+^m$  such that  $x(n) \rightarrow B, \forall x(0) \in \mathbb{R}_+^m$ .
- (b)  $\exists$  a nonnegative, primitive matrix  $Q$  such that  $\text{support}(Q) \subset \text{support}(A(x)), x \in \mathbb{R}_+^m$ .
- (c)  $r(A(0)) > 1$ .

Then there exists an  $\epsilon > 0$  such that

$$\liminf_{n \rightarrow \infty} \min_j x_j(n) \geq \epsilon, x(0) \neq 0. \tag{3}$$

Stage-persistence is our term for conclusion (3). It is stronger than population persistence and it guarantees that every component is eventually bounded away from zero by an amount that is independent of initial data, so long as the initial population is nonzero.

The LPA model (1) is stage-persistent by Theorem 1.2 if  $\frac{pqd}{1-r} > 1$ . Indeed,

$$Q = \begin{pmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} \Rightarrow Q^4 = \begin{pmatrix} 1 & 1 & 2 \\ 1 & 1 & 1 \\ 1 & 2 & 3 \end{pmatrix}$$

so  $Q$  is primitive and  $\text{support}(Q) = \text{support}(A(x))$  for

$$A(x) = \begin{pmatrix} 0 & 0 & d \exp(-ax_1 - bx_3) \\ p & 0 & 0 \\ 0 & q \exp(-cx_3) & r \end{pmatrix}$$

A key hypothesis of both Theorem 1.1 and Theorem 1.2 is the existence of a compact attracting set  $B$ . It can be weakened but not dropped altogether. A useful technique to verify the hypothesis is to find  $y \in \mathbb{R}_+^m$  and nonnegative matrix  $D$  with  $r(D) < 1$  such that  $F(x) \leq y + Dx$ . Then,  $x(n+1) \leq y + Dx(n), n \geq 0$ , which leads to the estimate

$$x(n) \leq \sum_{i=0}^{n-1} D^i y + D^n x(0).$$

As  $r(D) < 1$ , the right side converges to  $(I - D)^{-1}y$  because  $(I - D)^{-1} = \sum_{i=0}^{\infty} D^i \geq 0$  and  $D^n \rightarrow 0$ . The existence of a compact attracting set follows immediately.

For the LPA model, we have

$$\begin{pmatrix} 0 & 0 & de^{-ax_1-bx_3} \\ p & 0 & 0 \\ 0 & qe^{-cx_3} & r \end{pmatrix} x \leq \begin{pmatrix} d/eb \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ p & 0 & 0 \\ 0 & q & r \end{pmatrix} x.$$

$r(D) < 1$  if  $0 \leq r < 1$ , where  $D$  is square matrix on the right.

I would like to conclude this brief review by thanking Professor Eduardo Liz and members of the organizing committee of the conference for the great hospitality that they extended to me during the conference. The conference was mathematically stimulating and the local environment was wonderful.

## References

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