Persistence and permanence for a class of functional differential equations with infinite delay

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\textit{Dedicated to Professor John Mallet-Paret, on the occasion of his 60th birthday}

\textit{Suggested running head: Persistence and permanence for FDEs with infinite delay}

Abstract

The paper deals with a class of cooperative functional differential equations (FDEs) with infinite delay, for which sufficient conditions for persistence and permanence are established. Here, the persistence refers to all solutions with initial conditions that are positive, continuous and bounded. The present method applies to a very broad class of abstract systems of FDEs with infinite delay, both autonomous and non-autonomous, which include many important models used in mathematical biology. Moreover, the hypotheses imposed are in general very easy to check. The results are illustrated with some selected examples.

\textit{Keywords:} infinite delay, persistence, permanence, quasimonotone condition, Lotka-Volterra model.
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1. Introduction

This paper is concerned with the persistence and permanence for a class of functional differential equations (FDEs) with infinite delay written in abstract form as

\[ x'_i(t) = F_i(t, x_t) - x_i(t)G_i(t, x_t), \quad i = 1, \ldots, n \]  

(1.1)

where $F = (F_1, \ldots, F_n), G = (G_1, \ldots, G_n) : D \to \mathbb{R}^n$ are continuous on $D \subset \mathbb{R} \times \mathcal{B}$, and $\mathcal{B}$ is an adequate Banach space of continuous functions defined on $(-\infty, 0]$ with values in $\mathbb{R}^n$. As usual, $x_t$ denotes the entire past history of the system up to time $t$, or, in other words, $x_t(s) = x(t + s)$ for $s \leq 0$. Special emphasis will be given to the \textit{autonomous} version of (1.1),

\[ x'_i(t) = F_i(x_t) - x_i(t)G_i(x_t), \quad i = 1, \ldots, n \]  

(1.2)

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where $F_i, G_i : \Omega \subset B \rightarrow \mathbb{R}$ are continuous for all $i$.

We shall consider (1.1) as a general framework for some models from mathematical biology, therefore only positive (or non-negative) solutions of (1.1) are meaningful. Initial conditions at a fixed time $\sigma$ will be taken to be $x(s) = \varphi(s), s \leq \sigma$, with $\varphi : (-\infty, 0] \rightarrow \mathbb{R}^n$ continuous, bounded and positive (or non-negative).

The family of FDEs (1.1) is required to satisfy the so-called quasimonotone condition [30] — here, we abuse the standard terminology, and these systems will be also called cooperative systems (see [30] for a rigorous definition). The main technique employed here is the theory of monotone dynamical systems for retarded FDEs well-established in [29,30,34]: the quasimonotone condition implies that the solution operator is monotone relative to the initial condition function $\varphi$ (but not necessarily strongly monotone) and allows comparison of solutions between related FDEs. However, it is not always clear how to apply the tools of this theory to the situation of infinite delays. In particular, for (1.1) it is not obvious which conditions should be imposed in order to guarantee the persistence of all solutions with positive, bounded initial conditions.

From earlier works (see e.g. [16,25,26]), it has been apparent that a rigorous treatment of FDEs with infinite delay requires a particular attention to its abstract formulation. In Section 2, we choose an admissible phase space $B$ to deal with (1.1), in the sense that it should satisfy some fundamental axioms introduced by Hale and Kato [17]. To address the question of permanence, we shall need bounded positive orbits to have compact closure in $B$, so, in addition, we choose a state space that is a fading memory space [14,18,27]. The contents and organization of the remainder of paper are described below.

Section 3 is the core of the paper, where the main theorems are established, referring to persistence (Theorem 3.1) and permanence (Theorem 3.2) of autonomous cooperative systems (1.2). A key point of our research is that quite reasonable sufficient conditions are enough to guarantee the persistence (or even the uniform persistence) of system (1.2) in the entire set of solutions with initial conditions that are bounded, continuous and positive. In Section 4, we use the results and techniques in Section 3 to further deduce some persistence and permanence criteria for non-autonomous cooperative systems (1.1). We emphasize that, both in Section 3 and 4, no global asymptotical constancy is invoked to establish the persistence or permanence of a system.

Section 5 is dedicated to applications and is divided into three subsections, each dealing with a selected important example from population dynamics. In the first example, sufficient conditions are established for the persistence and permanence of a cooperative Lotka-Volterra model with infinite delay and patch structure, improving significantly some results in a former paper of the author [10]. In fact, the study of this Lotka-Volterra model was a main source of motivation for the present study, since there was an open problem concerning the persistence left unsolved in [10]. For alternative techniques for competitive Lotka-Volterra system, see e.g. [1,8,24,32,33]. The second example
refers to an FDE modelling the growth of a single or multiple species divided into \( n \) classes and following a modified delayed logistic law; the system has unbounded discrete time-varying delays, also includes dispersal terms among the classes, and may be interpreted as a generalization of the modified scalar delayed logistic equation proposed by Arino et al. [6]. The last selected example concerns an FDE system for the interaction of two species structured into mature and immature classes, with the two adult populations in competition; this system is based on Aiello and Freedman’s model for a single species [2], and the finite delay case was studied by Al-Omari and Gourley [5], among others. Although the system is competitive, the method in [5] relies on the construction of sequences of auxiliary cooperative systems, which are used to prove the global attractivity of a positive equilibrium. Here, we show that Al-Omari and Gourley’s method can be extended to the case of infinite distributed delay. These examples have been considered by many authors, and additional references will be given in Section 5. Many other examples from the literature could be analyzed, but the main purpose of Section 5 is to illustrate the application of our main results.

2. Preliminaries: phase space and notations

In this preliminary section, we set an abstract framework to deal with FDEs with infinite delay. In view of the unbounded delays, the phase space \( \mathcal{B} \) should satisfy some fundamental axioms which guarantee that the classical results of existence, uniqueness, continuation, and continuous dependence of solutions are valid – a subject well establish in the literature. Secondly, for our purposes, it is desirable that positive orbits of bounded solutions (with bounded derivatives) are precompact in \( \mathcal{B} \). A convenient choice of \( \mathcal{B} \) is set below.

Let \( g \) be a function satisfying the following properties:

\((g1)\) \( g : (-\infty, 0] \to [1, \infty) \) is a nonincreasing continuous function, \( g(0) = 1 \);

\((g2)\) \( \lim_{u \to 0^-} g(s + u) g(s) = 1 \) uniformly on \((-\infty, 0] \);

\((g3)\) \( g(s) \to \infty \) as \( s \to -\infty \).

For \( n \in \mathbb{N} \), define the Banach space \( \mathcal{B} = C^0_g \),

\[
C^0_g = C^0_g(\mathbb{R}^n) := \left\{ \phi \in C((-\infty, 0]; \mathbb{R}^n) : \lim_{s \to -\infty} g(s) = 0 \right\},
\]

with the norm

\[
\| \phi \|_g = \sup_{s \leq 0} \frac{|\phi(s)|}{g(s)},
\]

where \( | \cdot | \) is any chosen norm in \( \mathbb{R}^n \). To fix terminology we suppose that \( \mathbb{R}^n \) is equipped with the supremum norm, \( |x| = |x|_\infty = \max_{1 \leq i \leq n} |x_i|, \) for \( x = (x_1, \ldots, x_n) \in \mathbb{R}^n \). Consider also the space \( BC = BC(\mathbb{R}^n) \) of bounded continuous functions \( \phi : (-\infty, 0] \to \mathbb{R}^n \). Here, \( BC \) is considered as a subspace of some space \( C^0_g \), so \( BC \) is endowed with the norm of \( C^0_g \). The more explicit notation \( BC_g \) will be also used.
The space $C^0_g$ is an admissible phase space [17,18] for $n$-dimensional FDEs with infinite delay written in the abstract form

$$x'(t) = f(t,x_t),$$

(2.1)

where $f : D \subset \mathbb{R} \times C^0_g \to \mathbb{R}^n$ is continuous and, as usual, segments of solutions in the phase space $C^0_g$ are denoted by $x_t: x_t(s) = x(t + s), s \leq 0$. When $f$ is regular enough, the initial value problem is well-posed, in the sense that for each $(\sigma, \varphi) \in D$ there exists a unique solution $x(t)$ of the problem $x'(t) = f(t,x_t), x_{\sigma} = \varphi$, defined on a maximal interval of existence. This solution will be denoted by $x(t;\sigma,\varphi)$ in $\mathbb{R}^n$ or $x_t(\sigma,\varphi)$ in $C^0_g$. For autonomous systems $x'(t) = f(x_t)$ and $\varphi \in C^0_g$, the solution of $x'(t) = f(x_t), x_0 = \varphi$ is often simply denoted by $x(t;\varphi) \in \mathbb{R}^n$ and $x_t(\varphi) \in C^0_g$. When considering more than one FDE of the form $x'(t) = f(t,x_t)$ or $x'(t) = f(x_t)$, the notations $x(t;\sigma,\varphi,f)$ or $x(t;\varphi,f)$ will be also used, where the argument $f$ is included to avoid any confusion over which FDE is being considered. The space $C^0_g$ has important properties, namely it is a fading memory space – although not always a uniform fading memory space. For definitions and results, see [14,18,27]. For FDEs $x'(t) = f(x_t)$ in fading memory spaces, positive orbits of solutions $x(t) = x(t;\varphi)$ with bounded initial conditions (i.e., for $\varphi \in BC$) which are bounded and have bounded derivatives on $[0,\infty)$ are precompact in $C^0_g$ – a property that will be used to prove our results of permanence.

Alternatively, one may consider the phase space $B = UC_g$, where $UC_g = UC_g(\mathbb{R}^n) := \{\phi \in C((-\infty,0];\mathbb{R}^n): \sup_{s \leq 0} \frac{\phi(s)}{g(s)} < \infty, \frac{\phi(s)}{g(s)} \text{ is uniformly continuous on } (-\infty,0]\}$, with the norm $\|\cdot\|_g$ defined above. The space $UC_g$ is an admissible phase space, in the sense of Hale and Kato [17], but it is not necessarily a fading memory space – contrary to what is stated in [19, p. 47]. In fact, Haddock and Hornor [14] completely described the functions $g$ satisfying (g1)-(g2) for which $UC_g$ is a fading memory space; in particular, $g$ must satisfy the condition $e^{-\gamma_1 s} \leq g(s) \leq e^{-\gamma_2 s}$ for $s \leq -M$, for some $\gamma_1, \gamma_2, M > 0$. For example, (g1)-(g3) hold for $g(s) = 1 - s$, but $g$ does not satisfy this latter condition. If $g(s) = e^{-\gamma s}, s \leq 0$, for some $\gamma > 0$, the spaces $C^0_g$ and $UC_g$ are uniform fading memory spaces, and are often denoted by $C^0_\gamma$ and $UC_\gamma$, respectively. Some of the results established here require having precompactness of bounded positive orbits, therefore there is a clear advantage in considering the phase space $C^0_g$ rather than the usual $UC_g$.

We now set some notation. A vector $c$ in $\mathbb{R}^n$ is said to be positive if all its components are positive, and we write $c > 0$. A function $\varphi : (-\infty,0] \to \mathbb{R}^n$ is said to be positive, with notation $\varphi > 0$, if the vectors $\varphi(s)$ are positive for all $s \leq 0$. We define and denote in a similar way non-negative vectors and non-negative functions. In the space $C^0_g$ (or $UC_\gamma$), a vector $c$ is identified with the constant function $\psi(s) = c$ for $s \leq 0$. The non-negative cones of $\mathbb{R}^n$ and $BC$ are $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x \geq 0\}$ and $BC_+ = BC_+(\mathbb{R}^n) = \{\varphi \in BC : \varphi(s) \geq 0 \text{ for all } s \leq 0\}$, respectively. Motivated by the applications to mathematical biology, we shall take the set

$$BC_0 = \{\varphi \in BC : \varphi(s) > 0 \text{ for all } s \leq 0\}$$
as the set of admissible initial conditions for (2.1). However, in applications, frequently more general orders on \( \mathcal{B} \) are considered, induced by other cones \( \mathcal{K} \subset \mathcal{B} \). We use \( (x)_i \) or simply \( x_i \) to designate the component \( i \) of a vector \( x \in \mathbb{R}^n \). If \( f \) is a function with values in \( \mathbb{R}^n \), it is understood that \( f_i \) means the \( i \)th-component of \( f \), for \( 1 \leq i \leq n \).

3. Main results

In this section, we prove the main results of the paper, about persistence and permanence for a class of autonomous FDEs of the form

\[
x'_i(t) = F_i(x_t) - x_i(t)G_i(x_t), \quad i = 1, \ldots, n,
\]

where \( F = (F_1, \ldots, F_n), G = (G_1, \ldots, G_n) : BC \to \mathbb{R}^n \) are continuous. It is understood that \( BC = BC_g \) is taken as a subspace of \( \mathcal{B} = C^0 \) (or \( \mathcal{B} = UC_g \)). As mentioned above, we are concerned with the solutions \( x(t) = x(t; \varphi) \) of (3.1) with initial conditions

\[
x_0 = \varphi \quad \text{with} \quad \varphi \in BC_0.
\]

We start with a preliminary lemma.

**Lemma 3.1.** Consider \( F,G : BC \to \mathbb{R}^n \) continuous. Then:

(i) if \( F,G \) are bounded on bounded sets of \( BC \), and \( x(t) \) is a non-continuable solution of (3.1) defined on \([0,a)\) with \( a < \infty \), then \( \limsup_{t \to a^-} |x(t)| = \infty \);

(ii) if \( F_i(\varphi) \geq 0 \) for all \( \varphi \in BC_+ \) with \( \varphi_i(0) = 0 \) \((1 \leq i \leq n)\), then the solutions \( x(t) \) with initial conditions \( \varphi \in BC_+ \) satisfy \( x(t) \geq 0 \) for \( t \geq 0 \), whenever they are defined.

**Proof.** The statement in (i) is a classical result [17,18]; the proof of (ii) follows from [30,34].

System (3.1) reads as

\[
x'(t) = f(x_t),
\]

where

\[
f = (f_1, \ldots, f_n), \quad f_i(\phi) = F_i(\phi) - \phi_i(0)G_i(\phi) \quad \text{for} \quad \phi \in BC, 1 \leq i \leq n.
\]

In the remainder of this section, \( F = (F_1, \ldots, F_n), G = (G_1, \ldots, G_n) \) are assumed to be continuous, bounded on bounded sets of \( BC \), and regular enough so that the initial value problems (3.1)-(3.2) have unique solutions – which is the case if \( f \) is Lipschitz continuous on bounded sets.

The main assumptions that will be imposed, either in part or in total, are described below.

(A1) for \( \phi, \psi \in BC_+, \phi \leq \psi \) and \( \phi_i(0) = \psi_i(0) \), then (i) \( F_i(\phi) \leq F_i(\psi) \) and (ii) \( G_i(\phi) \geq G_i(\psi) \), \( i = 1, \ldots, n; \)

(A2) for each \( \delta > 0 \) and each \( i = 1, \ldots, n \), there exists \( \varepsilon > 0 \) such that for all \( \phi, \psi \in BC_+, \phi \leq \psi \) with \( \|\psi - \phi\|_g < \varepsilon \) and \( \phi_i(0) = \psi_i(0) \), then \( G_i(\phi) - G_i(\psi) < \delta \);
(A3) there exists a constant $c > 0$ such that for $\phi, \psi \in BC_+, \phi \leq \psi$ and $\phi_i(0) = \psi_i(0)$, then
$$F_i(\phi) - F_i(\psi) \geq -c\|\psi - \phi\|_g, \ i = 1, \ldots, n;$$

(A4) $F$ is sublinear in $\mathbb{R}^n_+$, i.e., for $x \in \mathbb{R}^n_+$ and $\alpha \in (0, 1)$, $F(\alpha x) \geq \alpha F(x)$;

(A5) there exists a vector $v \in \mathbb{R}^n_+$ such that $F(v) - Bv > 0$, where $B = \text{diag} (G_1(0), \ldots, G_n(0))$;

(A6) there exists a vector $q = (q_1, \ldots, q_n) \in \mathbb{R}^n_+$ such that $F_i(q) - q_iG_i(Lq) < 0$ for $L \geq 1, i = 1, \ldots, n$.

Some comments about the choice of the above hypotheses are in order.

It is apparent that if the pair $(F,G)$ satisfies one or more of the above hypotheses, the same happens for the pair $(\tilde{F}, \tilde{G})$, where $\tilde{F}_i(\phi) = F_i(\phi) + G_i(0)\phi(0), \tilde{G}_i(\phi) = G_i(\phi) - G_i(0), 1 \leq i \leq n$. Hence, without loss of generality, we can take $G(0) = 0$, in which case $B = 0$ for the matrix $B$ in (A5). Assumption (A1) asserts that $F$ and $-G$, and thus $f$ in (3.3) as well, satisfy Smith’s quasimonotone condition given by (see [30])

$$\text{(Q)} \text{ for } \phi, \psi \in BC_+, \phi \leq \psi \text{ and } \phi_i(0) = \psi_i(0), \text{ then } f_i(\phi) \leq f_i(\psi), \ i = 1, \ldots, n.$$

This condition implies that the semiflow for (3.3) is monotone on $BC_+$. Here we abuse the terminology, and also refer to systems satisfying (Q) as cooperative systems. Instead of (A2), we could simply demand $G$ to be uniformly continuous on $BC_+$, but this requirement is too strong for our purposes. Another advantage of the above formulation is that (A2) is trivially satisfied if each $G_i(\phi)$ depends only on $\phi_i(0)$. It is clear that (A3) and (A4) are satisfied if $F$ is linear bounded; also, if $F$ is Lipschitz continuous on $BC_+$, then (A3) holds. Condition (A6) is true whenever either $G \equiv 0$ and $F(q) < 0$, or $\lim_{L \to \infty} G_i(Lq) = \infty, i = 1, \ldots, n$, for some vector $q > 0$. A careful analysis of the proofs below shows that, as alternatives to the sets of constraints (A4),(A5) and (A4),(A6), one can simply impose the hypotheses

$(A5')$ there is $v = (v_1, \ldots, v_n) \in \mathbb{R}^n_+$ such that $F_i(lv) - lv_iG_i(lv) > 0$ for $0 < l \leq 1, 1 \leq i \leq n,$

and

$(A6')$ there is $q = (q_1, \ldots, q_n) \in \mathbb{R}^n_+$ such that $F_i(Lq) - Lq_iG_i(Lq) < 0$ for $L \geq 1, 1 \leq i \leq n,$

respectively, without the additional requirement of the sublinearity of $F|_{\mathbb{R}^n_+}$. Although not essential, the sublinearity condition (A4) allied to the quasimonotone condition (A1) implies, however, that solutions with non-negative initial conditions remain non-negative. In fact, for $\varphi \in BC_+$ with $\varphi_i(0) = 0$, from (A1) we have $f_i(\varphi) = F_i(\varphi) \geq F_i(0), 1 \leq i \leq n$. On the other hand, (A4) implies $F(0) \geq 0$. From Lemma 3.1(ii), it follows that $x(t;\varphi) \geq 0$ for $t \geq 0$ in its interval of definition.

For the definitions of persistence and permanence given below, see e.g. [19,31].

**Definition 3.1.** A system $x'(t) = f(x_t)$ with $S \subset BC_+$ as set of admissible initial conditions is said to be persistent (in $S$) if any solution $x(t;\varphi)$ with initial condition $\varphi \in S$ is defined and
bounded below from zero on \([0, \infty)\), i.e.,

\[
\liminf_{t \to \infty} x_i(t; \varphi) > 0, \quad 1 \leq i \leq n,
\]

for any \(\varphi \in S\). The system is said to be permanent (in \(S\)) if it dissipative and uniformly persistent; in other words, all solutions \(x(t; \varphi), \varphi \in S\), are defined on \([0, \infty)\), and there are positive constants \(m, M\) such that, given any \(\varphi \in S\), there exists \(t_0 = t_0(\varphi)\) for which

\[
m \leq x_i(t; \varphi) \leq M, \quad 1 \leq i \leq n, \quad t \geq t_0.
\]

Here, unless stated otherwise, we take \(S = BC_0\) as the set of admissible initial conditions.

As observed above, from (A4) we get \(F(0) \geq 0\). The situation \(F_i(0) > 0\) for one or more components of the vector \(F(0)\) is not excluded from our setting, although \(F(0) = 0\) is a quite natural condition: for many applications of interest, (3.1) corresponds to a population dynamics model, for which zero should be a steady state. If \(F(0) > 0\), the persistence of (3.1) follows immediately from the quasimonotone condition (Q): with \(f(0) = F(0) > 0\), the solution \(x^0(t) := x(t; 0)\) is nondecreasing in \(t \geq 0\) [30, p. 82] and strictly increasing on an interval \([0, \varepsilon]\) (\(\varepsilon > 0\)). From the order-preserving semiflow, this shows that \(\liminf_{t \to \infty} x_i(t; \varphi) \geq \liminf_{t \to \infty} x^0_i(t) \geq x^0_i(\varepsilon) > 0, 1 \leq i \leq n\), for any \(\varphi \in BC_+\).

In the case of bounded delays, there is an extensive literature using the theory of monotone dynamical system to study the persistence of both autonomous and non-autonomous delayed population models. The situation is much more complex for unbounded delays, since some of the usual methods do not work unless additional conditions are imposed: in spite of a careful choice of an appropriate phase space, as the one set in Section 2, it is a rather difficult task to deal with solutions with initial conditions \(\varphi = (\varphi_1, \ldots, \varphi_n)\) in the full set \(BC_0\), due to the fact that one may have

\[
\min_{1 \leq i \leq n} \inf_{s \leq 0} \varphi_i(s) = 0.
\]

An alternative way to by-pass this difficulty, is to consider only solutions with initial conditions whose components are bounded below and above on \((-\infty, 0]\) by positive constants. The challenge here is to obtain sufficient conditions for the persistence of (3.1) in \(BC_0\) — a situation not often addressed in the literature, unless there are additional conditions on \(F, G\) which allow to relate solutions of (1.1) with solutions of an already known permanent system, or the permanence appears as a by-product of the global attractivity of a positive equilibrium.

The main result about persistence is given below.

**Theorem 3.1.** Suppose that the initial value problems (3.1)-(3.2) have unique solutions defined on \([0, \infty)\). If assumptions (A1)-(A5) are satisfied, system (3.1) is persistent (in \(BC_0\)).

**Proof.** For a positive vector \(v = (v_1, \ldots, v_n)\) as in (A5), fix any small \(\delta > 0\) such that

\[
F(v) - (B + \delta I)v > 0.
\]
Consider $c > 0$ as in (A3): for $\phi, \psi \in BC_+$ with $\phi \leq \psi$ and $\phi_i(0) = \psi_i(0)$,

$$0 \leq F_i(\psi) - F_i(\phi) \leq c \|\psi - \phi\|_g, \quad 1 \leq i \leq n.$$ 

By (A1)-(A2), there exists $\varepsilon > 0$ such that for $\phi, \psi \in BC_+, \phi \leq \psi$, with $\phi_i(0) = \psi_i(0)$ and $\|\psi - \phi\|_g < \varepsilon$,

$$0 \leq G_i(\phi) - G_i(\psi) < \frac{\delta}{2} \quad \text{for } i = 1, \ldots, n.$$ 

**Step 1.** Let $\varphi \in BC_0$ be given. Choose $M_0 > 0$ such that

$$\frac{2\|\varphi\|_\infty}{g(-M_0)} < \varepsilon \quad \text{and} \quad \frac{c|\varphi|}{g(-M_0)} < \frac{\delta}{2} \min_{1 \leq i \leq n} v_i,$$

where $|\varphi| = |\varphi|_\infty$. Note that $F_i(v) - (v_iG_i(v/m) + \delta v_i) \to F_i(v) - (G_i(0) + \delta)v_i > 0$ as $m \to \infty$. Fix $m_0 \in \mathbb{N}$ such that

$$F_i(v) - v_iG_i\left(\frac{1}{m}v\right) - \delta v_i > 0, \quad i = 1, \ldots, n, \quad m \geq m_0,$$

and

$$\varphi(s) > \frac{1}{m_0}v \quad \text{on } [-M_0, 0].$$

As before, write (3.1) in the form (3.3). Assumption (A1) implies that (3.1) is cooperative. Together with (3.1), consider the auxiliary FDE

$$x'(t) = f^\delta(x_t),$$

where $f^\delta = (f^\delta_1, \ldots, f^\delta_n)$. $f^\delta_i(\phi) = f_i(\phi) - \delta \phi_i(0)$ for $\phi \in BC_+, i = 1, \ldots, n$. Next, we denote $x(t) = x(t; \varphi, f)$ and $y^m(t) = x(t; \frac{1}{m}v, f^\delta)$ for any $m \geq m_0$.

From (3.6) and the sublinearity of $F$, for $m \geq m_0$ and $i = 1, \ldots, n$,

$$f^\delta_i\left(\frac{1}{m}v\right) \geq \frac{1}{m} \left[ F_i(v) - v_iG_i\left(\frac{1}{m}v\right) - \delta v_i \right] > 0.$$ 

Clearly, system (3.7) is cooperative as well, consequently $y^m_i(t)$ is nondecreasing on $[0, \infty) \ (1 \leq i \leq n)$ (see Theorem 5.1.1 and Corollary 5.2.2 of [30]). In particular, $\inf_{t \geq 0} y^m_i(t) = \frac{v_i}{m} > 0$.

**Step 2.** We now prove the following claim:

$$x(t) \geq y^m(t) \quad \text{for } t \geq 0, m \geq m_0. \quad (3.8)$$

If the claim fails to be true, there are $m \geq m_0$ and $t_0 > 0, i \in \{1, \ldots, n\}$ such that

$$x_j(t) > y^m_j(t) \quad \text{for } t \in [0, t_0), j = 1, \ldots, n,$$

$$x_i(t_0) = y^m_i(t_0).$$
Hence,

\begin{equation}
0 \geq x_i'(t_0) - (y_i^m)'(t_0) \\
= F_i(x(t_0)) - F_i(y_i^m) + x_i(t_0)[\delta - G_i(x(t_0)) + G_i(y_i^m)] \\
= F_i(x(t_0)) - F_i(\tilde{\phi}) + F_i(\tilde{\phi}) - F_i(y_i^m) + x_i(t_0) \left[\delta - G_i(x(t_0)) + G_i(\tilde{\psi}) - G_i(y_i^m) + G_i(y_i^m)\right],
\end{equation}

where we take

\[
\tilde{\phi}(s) = (\tilde{\phi}_1, \ldots, \tilde{\phi}_n), \quad \tilde{\phi}_i(s) = \begin{cases} \min(\varphi_i(t_0 + s), \frac{1}{m}v_i), & s \leq -(M_0 + t_0) \\ y_i^m(t_0 + s), & -(M_0 + t_0) \leq s \leq 0 \end{cases}
\]

and

\[
\tilde{\psi}(s) = \begin{cases} \varphi(-M_0), & s \leq -(M_0 + t_0) \\ x(t_0 + s), & -(M_0 + t_0) \leq s \leq 0 \end{cases}.
\]

Since \(x_{t_0}(s) \geq \tilde{\phi}(s), \tilde{\psi}(s) \geq y_{t_0}^m(s)\) on \((-\infty, 0]\) and \(\tilde{\phi}_i(0) = \tilde{\psi}_i(0) = x_i(t_0) = y_i^m(t_0)\), by (A1) we have

\[
F_i(x(t_0)) - F_i(\tilde{\phi}) \geq 0, G_i(\tilde{\psi}) - G_i(y_{t_0}^m) \leq 0.
\]

On the other hand, from (3.5)

\[
\|y_{t_0}^m - \tilde{\phi}\|_g \leq \frac{1}{m} \max_{1 \leq i \leq n} \frac{v_i}{g(-(M_0 + t_0))} \leq \frac{|v|}{mg(-M_0)} < \frac{\delta v_i}{2mc},
\]

and

\[
\|x_{t_0} - \tilde{\psi}\|_g = \sup_{s \leq -(M_0 + t_0)} \frac{|\varphi(s + t_0) - \varphi(-M_0)|}{g(s)} \leq \frac{2\|\varphi\|_{\infty}}{g(-M_0)} < \varepsilon.
\]

This implies that

\[
0 \leq F_i(y_{t_0}^m) - F_i(\tilde{\phi}) \leq \delta v_i/(2m) \quad \text{and} \quad |G_i(\tilde{\psi}) - G_i(x_{t_0})| < \delta/2. \quad \text{From (3.9), we therefore obtain}
\]

\[
0 > -\frac{\delta v_i}{2m} + \frac{\delta}{2} x_i(t_0).
\]

But \(x_i(t_0) = y_i(t_0) \geq \frac{v_i}{m}\) from Step 1. The above inequality yields \(0 > -\delta \frac{v_i}{2m} + \frac{\delta}{2} x_i(t_0) \geq 0\), which is not possible. This proves the claim (3.8).

From Steps 1 and 2,

\[
\liminf_{t \to \infty} x_i(t) \geq \liminf_{t \to \infty} y_i^m(t) \geq \frac{v_i}{m_0}, \quad i = 1, \ldots, n,
\]

which shows the persistence of (3.1) in \(BC_0\).

\textbf{Remark 3.1.} Consider an FDE with bounded delays, written in abstract form as (3.1) in the usual phase space \(C = C([-\tau, 0]; \mathbb{R}^n)\) with the supremum norm. Let \(C_+\) be the non-negative cone of \(C\), and take \(\text{int}(C_+) = \{\varphi \in C : \varphi(s) > 0 \text{ for } s \in [-\tau, 0]\}\) as the set of admissible initial conditions. In this case, we can compare directly the solutions \(x(t; \varphi)\) and \(x(t; \frac{1}{m}v)\) of (3.1), for \(m \in \mathbb{N}\) small enough so that \(\varphi(s) \geq \frac{1}{m}v\) on \([-\tau, 0]\). In this way, the persistence of (3.1) in \(\text{int}(C_+)\) is trivially obtained by assuming (A1), (A4) and (A5) (or, alternatively, (A1) and (A5'))). Since the system is autonomous, this leads to the persistence of (3.1) in \(C_0 := \{\varphi \in C_+ : \varphi(0) > 0\}\).
Corollary 3.1. Consider $F : BC_+ \to \mathbb{R}^n$ satisfying (Q), (A3), (A4). If there is a vector $v > 0$ such that $F(v) > 0$, the system

$$x'(t) = F(x_t)$$

(3.11)

is persistent in $BC_0$.

In the case of finite delays, again the hypothesis (A3) is not required in the above corollary. It should be stressed that, even in the case of finite delays, this corollary provides a better criterion for persistence of cooperative FDEs than the one in [35].

To address the permanence of (3.1), we start by establishing the boundedness of all solutions.

Lemma 3.2. Assume (A1)-(A4) and (A6). Then the solutions of the systems (3.1)-(3.2) are defined and bounded on $[0, \infty)$.

Proof. Again, write (3.1) in the form (3.3). From the sublinearity of $F|_{\mathbb{R}^n_+}$, for $q = (q_1, \ldots, q_n) > 0$ as in (A6) and $L \geq 1$ we have $F(Lq) \leq LF(q)$, thus

$$f_i(Lq) \leq L(F_i(q) - q_i G_i(Lq)) < 0, \quad i = 1, \ldots, n.$$  

(3.12)

From the quasimonotone condition, $x_i(t; Lq, f)$ is nonincreasing in $t \in [0, \infty)$ and $x(t; \varphi, f) \leq x(t; Lq, f)$ if $\varphi \leq Lq$ [30]. This proves that all solutions are defined and bounded on $[0, \infty)$.

The main result about permanence of system (3.1) in the full set $BC_0$ is stated below and requires a fading memory space as a phase space.

Theorem 3.2. Let $F, G$ be continuous, bounded on bounded sets of $BC$, and sufficiently regular so that the initial value problems (3.1)-(3.2) have unique solutions. If (A1)-(A6) are satisfied, system (3.1) is permanent in $BC_0$. Moreover, there are positive equilibria $x^*, y^*$ of (3.1) such that any solution $x(t)$ of (3.1) with initial condition $x_0 = \varphi \in BC_0$ satisfies

$$x^* \leq \liminf_{t \to \infty} x(t) \leq \limsup_{t \to \infty} x(t) \leq y^*.$$  

(3.13)

Proof. Let $q \in \mathbb{R}^n_+$ be as (A6). Since bounded positive orbits are precompact in $\mathcal{B} = C^0_\gamma$ (or $\mathcal{B} = UC_\gamma$ for some $\gamma > 0$), then $x(t; Lq, f) \searrow y^*(L)$ as $t \to \infty$, where $y^*(L)$ is an equilibrium of (3.1) [30, p. 82].

In a similar way, for $v = (v_1, \ldots, v_n) > 0$ as in (A5) and $\varepsilon \in (0, 1)$ sufficiently small, we get

$$f_i(\varepsilon v) \geq \varepsilon(F_i(v) - v_i G_i(\varepsilon v)) > 0, \quad i = 1, \ldots, n.$$  

(3.14)

Thus $x(t; \varepsilon v, f)$ is nondecreasing in $t \in [0, \infty)$. By Lemma 3.2, all solutions with initial conditions in $BC_0$ are bounded, hence we conclude that $x(t; \varepsilon v, f) \nearrow x^*(\varepsilon)$ as $t \to \infty$, where $x^*(\varepsilon)$ is a positive equilibrium of (3.1).
Let \( \varphi \in BC_0 \) be given, and take \( \delta > 0 \) such that (3.4) holds. From Theorem 3.1 (see (3.8)), we also obtain that there exists \( m_0 \in \mathbb{N} \) with \( x(t; \varphi, f) \geq x(t; \frac{1}{m} v, f^\delta) \) for \( t \geq 0 \) and \( m \geq m_0 \). We further prove the following claims.

**Claim 1.** There is \( \varepsilon_0 > 0 \) such that for \( 0 < \varepsilon \leq \varepsilon_0 \),

\[
x(t; \varepsilon v, f) \nrightarrow x^* \quad \text{as} \quad t \to \infty,
\]

where \( x^* \) is an equilibrium of (3.1).

To prove this claim, we adapt some arguments in [30, pp. 62]. For similar ideas, see also [29,35]. As shown above, if \( \varepsilon_0 > 0 \) is such that \( f_i(\varepsilon v) > 0 \) for \( 0 < \varepsilon \leq \varepsilon_0 \) and \( 1 \leq i \leq n \), then \( x(t; \varepsilon v, f) \nrightarrow x^*(\varepsilon) \) as \( t \to \infty \), where \( x^*(\varepsilon) \) are equilibria, and \( x^*(\varepsilon) \leq x^* =: x^*(\varepsilon_0) \). Moreover, since \( (dx/dt)(t; \varepsilon v, f) = f(\varepsilon v) > 0 \), then \( x(t; \varepsilon v, f) > x(0; \varepsilon v, f) = \varepsilon v \) for all \( t > 0 \) and \( 0 < \varepsilon \leq \varepsilon_0 \). Clearly, there is \( l^* > 0 \) such that \( x^* \leq l^*v \), so the suprema

\[\delta(\varepsilon) = \sup\{\delta \geq 0 : x^*(\varepsilon) \geq \delta v\}\]

are well defined for \( \varepsilon \in (0, \varepsilon_0] \). Note that \( \delta(\varepsilon) \geq \varepsilon > 0 \). If \( \delta(\varepsilon) < \varepsilon_0 \), then \( x^*(\varepsilon) \geq \delta(\varepsilon)v \) implies that \( x^*(\varepsilon) = x(t; x^*(\varepsilon), f) \geq x(t; \delta(\varepsilon)v, f) > \delta(\varepsilon)v \), which contradicts the definition of \( \delta(\varepsilon) \). Hence, \( \delta(\varepsilon) \geq \varepsilon_0 \). We now obtain \( x^*(\varepsilon) = x(t; x^*(\varepsilon), f) \geq x(t; \varepsilon_0 v, f) \nrightarrow x^* \) as \( t \to \infty \). Consequently, \( x^*(\varepsilon) = x^* \) for \( 0 < \varepsilon \leq \varepsilon_0 \).

**Claim 2.** There is \( L_0 > 0 \) such that for \( L \geq L_0 \),

\[
x(t; Lq, f) \nrightarrow y^* \quad \text{as} \quad t \to \infty,
\]

where \( y^* \) is an equilibrium of (3.1).

We argue as in the proof of Claim 1, so some details are omitted. For \( L_0 > 0 \) such that \( L_0 q > \varepsilon_0 v \) and \( f_i(Lq) < 0 \) for \( L \geq L_0, 1 \leq i \leq n \), we derive \( x(t; Lq, f) \nrightarrow y^*(L) \), with \( Lq \geq y^*(L) \geq y^* \) where \( y^* := y^*(L_0) \geq x^* \). For \( L \geq L_0 \), define

\[M(L) := \inf\{M > 0 : y^*(L) \leq Mq\} > 0.\]

If \( M(L) > L_0 \), we get \( y^*(L) \leq x(t; M(L)q, f) < M(L)q \) for \( t > 0 \), which is not possible from the definition of \( M(L) \). Hence \( M(L) \leq L_0 \), and we get \( y^*(L) \leq x(t; L_0q, f) \rightarrow y^* \) as \( t \to \infty \). This proves that \( y^*(L) = y^* \) for \( L \geq L_0 \).

**Claim 3.** For \( x^* = x^*(\varepsilon_0) \) and \( y^* = y^*(L_0) \) as in Claims 1 and 2, the estimates (3.13) hold; in particular, (3.1) is permanent in \( BC_0 \).
To prove the estimates (3.13), fix any \( \varphi \in BC_0 \) and choose \( L > L_0 \) such that \( \varphi \leq Lq \), where \( L_0 \) is as above. From Claim 2 it follows that \( \limsup_{t \to \infty} x_i(t; \varphi, f) \leq \lim_{t \to \infty} x_i(t; Lv, f) = y_i^*, \) \( i = 1, \ldots, n \) hence (3.1) is dissipative.

Next, we remark that system (3.7), obtained from (3.3) by replacing \( G_i(\varphi) \) by \( G_i(\varphi) + \delta \) for \( 1 \leq i \leq n \), also satisfies the assumptions (A1)-(A6) for any \( \delta > 0 \) such that (3.4) holds. Proceeding as in Claim 1, for \( \delta > 0 \) small, we get that there exists \( \varepsilon_0(\delta) > 0 \) such that for \( 0 < \varepsilon \leq \varepsilon_0(\delta) \),

\[
x(t; \varepsilon v, f^\delta) \nearrow x_\delta^* \quad \text{as} \quad t \to \infty,
\]

where \( x_\delta^* > 0 \) is an equilibrium of (3.7). Now, from (3.8), there exists \( m_0(\delta) \in \mathbb{N} \) such that for \( m \geq m_0(\delta) \) we have \( x(t; \varphi, f) \geq x(t; \frac{1}{m}v, f^\delta) =: y_m^\delta(t) \). With \( m \geq 1/\varepsilon_0(\delta) \), we get that \( \liminf_{t \to \infty} x(t; \varphi, f) \geq x_\delta^* \). We choose e.g. \( \delta_k = 1/k \) for \( k \in \mathbb{N} \), and note that \( f^\delta_k \) increases as \( k \) increases. By the definition of \( m_0 = m_0(\delta) \) in the proof of Theorem 3.1 and the definition of \( \varepsilon_0 = \varepsilon_0(\delta) \) in Claim 1, we may take \( m_k := m_0(\delta_k) \nearrow \infty \). Given \( k_1, k_2 \in \mathbb{N} \) with \( k_2 > k_1 \), for \( m \in \mathbb{N} \) with \( m \geq \max(\varepsilon_0(\delta_{k_1}), \varepsilon_0(\delta_{k_2})) \), we get \( y_{m, \delta_{k_2}} \geq y_{m, \delta_{k_1}} \). Thus we deduce that the sequence of vectors \( X^k := x_{\delta_k}^* \) increases at \( k \) increases, and is bounded from above by \( y^* \), thus there exists \( x^* := \lim_k X_k^* \). Moreover, \( X^k = (X_1^k, \ldots, X_n^k) \) is an equilibrium of (3.7) with \( \delta = 1/k \), i.e., \( f_i(X^k) = \frac{1}{k}X_i^k = 0 \), and \( \liminf_{t \to \infty} x(t; \varphi, f) \geq X^k \). By letting \( k \to \infty \), we obtain the estimate \( \liminf_{t \to \infty} x(t; \varphi, f) \geq x^* \), where \( x^* \) is an equilibrium of (3.1).

**Corollary 3.2.** Under conditions (A1)-(A6), there exists a positive equilibrium of (3.1). Furthermore, if this positive equilibrium is unique, then it is a global attractor of all solutions with initial conditions in \( BC_0 \).

**Remark 3.2.** As a consequence of the above proof, the set \( \{ \varphi \in BC : \varepsilon_0 v \leq \varphi \leq L_0 q \} \) is positively invariant and a global attractor for the semiflow of (3.1). However, if the equilibria \( x^*, y^* \) in (3.13) are distinct, this set may contain a very complex dynamics, with more equilibria, periodic orbits, or heteroclinic orbits (see e.g. [22,23]).

The next result is important for applications.

**Corollary 3.3.** Consider an FDE with infinite delay of the form

\[
x_i'(t) = F_i(x_t) - x_i(t)G_i(x_i(t)), \quad i = 1, \ldots, n
\]  

(3.17)

where \( F_i : BC \to \mathbb{R}, G_i : [0, \infty) \to \mathbb{R} \) are Lipschitz continuous on bounded sets of their domains, and \( G_i(0) = 0, 1 \leq i \leq n \). Suppose that \( F \) satisfies (Q), (A3), (A4), and that there are positive vectors \( v, q \) such that \( F(v) > 0, F(q) < 0 \). Then the solutions of (3.17) with initial conditions \( x_0 = \varphi \in BC_0 \) are defined on \([0, \infty)\) and (3.17) is permanent in \( BC_0 \).

**Proof.** Since \( F_i, G_i \) are Lipschitz continuous on bounded sets, initial value problems have unique non-continuable solutions. For (3.17), conditions (A1)(ii) and (A2) are trivially satisfied,
and $F(q) < 0$ for some vector $q > 0$ implies (A6). The latter also implies that solutions are defined on $[0, \infty)$. The permanence follows from Theorem 3.2.

### 4. Persistence and permanence for non-autonomous systems

We now consider a class of non-autonomous FDEs with infinite delay given by

$$x_i'(t) = F_i(t, x_t) - x_i(t)G_i(t, x_t), \quad i = 1, \ldots, n,$$

for $t \geq t_0$, where $F, G : D \subset \mathbb{R} \times C^0_\mathbb{R} \rightarrow \mathbb{R}^n$ are continuous and bounded on bounded sets of $D$, $a \in \mathbb{R}, D = (a, \infty) \times \Omega$, $t_0 > a$ and $\Omega$ is an open set containing $BC_+$. Initial conditions are written as $x_{t_0} = \varphi$ with $\varphi \in BC_0$. In this section, we always assume that solutions to FDEs with initial conditions in $BC_0$ are unique and defined on $[0, \infty)$.

**Theorem 4.1.** (i) Assume that there are continuous functions $F^i, G^u : BC \rightarrow \mathbb{R}^n$ such that

$$F^i(\phi) \leq F(t, \phi), \quad G(t, \phi) \leq G^u(\phi) \quad \text{for} \quad (t, \phi) \in D. \quad (4.2)$$

If the pair $(F^i, G^u)$ satisfies (A1)-(A5), (4.1) is persistent in $BC_0$.

(ii) Assume that there are continuous functions $F^i, F^u, G^l, G^u : BC \rightarrow \mathbb{R}^n$ such that

$$F^l(\phi) \leq F(t, \phi) \leq F^u(\phi), \quad G^l(\phi) \leq G(t, \phi) \leq G^u(\phi) \quad \text{for} \quad (t, \phi) \in D. \quad (4.3)$$

If $(F^l, G^u)$ satisfies (A1)-(A5) and $(F^u, G^l)$ satisfies (A1)-(A6), (4.1) is permanent in $BC_0$.

**Proof.** In what follows, and without loss of generality, suppose that $t_0 = 0$. Write (4.1) as

$$x'_i(t) = f(t, x_t), \quad t \geq 0, \quad (4.4)$$

where $f_i(t, \phi) = F_i(t, \phi) - \phi_i(0)G_i(t, \phi), 1 \leq i \leq n$. Under (4.2), consider the autonomous system

$$x'_i(t) = F^i_l(x_t) - x_i(t)G^l_i(x_t) =: f^i_l(x_t), \quad i = 1, \ldots, n, \quad (4.5)$$

and assume that $(F^l, G^u)$ satisfies (A1)-(A5). Since (Q) holds for $f^l$, for non-negative solutions of (4.1) we have $x(t; \varphi, f) \geq x(t; \varphi, f^l)$ ($\varphi \in BC_0$). Theorem 3.1 guarantees that (4.5) is persistent, so (4.1) is persistent as well. Similarly, if (4.3) holds we further compare the solutions of (4.1) with the solutions of the cooperative system

$$x'_i(t) = F^u_i(x_t) - x_i(t)G^u_i(x_t) =: f^u_i(x_t), \quad i = 1, \ldots, n, \quad (4.6)$$

Since $x(t; \varphi, f^l) \leq x(t; 0, \varphi, f) \leq x(t; \varphi, f^u)$ for $\varphi \in BC_0$, (4.1) is permanent.

Under conditions (4.3), in fact we obtain explicit lower and upper uniform bounds for the solutions $x(t; 0, \varphi, f), \varphi \in BC_0$, of (4.1):

$$x^{*, l} \leq \liminf_{t \to \infty} x(t; 0, \varphi, f) \leq \limsup_{t \to \infty} x(t; 0, \varphi, f) \leq y^{*, u},$$

where $x^{*, l}, y^{*, u}$ are equilibria of (4.5), (4.6), respectively.

Theorem 4.1 is not easily applicable to FDEs with unbounded time-dependent discrete delays, in which case it is better to deal directly with the non-autonomous system.
Theorem 4.2. For (4.1), let the pair \((F,G)\) satisfy the assumptions:

(H1) for \((t,\phi),(t,\psi)\) ∈ \(D\) with \(0 \leq \phi \leq \psi, \phi_i(0) = \psi_i(0)\), then (i) \(F_i(t,\phi) \leq F_i(t,\psi)\) and (ii) \(G_i(t,\phi) \geq G_i(t,\psi), \; i = 1,\ldots,n;\)

(H2) for each \(\delta > 0\) and each \(i = 1,\ldots,n\), there exists \(\varepsilon > 0\) such that for all \(t \geq t_0, \phi, \psi \in BC_+, \phi \leq \psi\) with \(\|\psi - \phi\|_g < \varepsilon\) and \(\phi_i(0) = \psi_i(0)\), then \(G_i(t,\phi) - G_i(t,\psi) < \delta;\)

(H3) there exists a constant \(c > 0\) such that for \(t \geq t_0, \phi, \psi \in BC_+, \phi \leq \psi\) and \(\phi_i(0) = \psi_i(0)\), then \(F_i(t,\phi) - F_i(t,\psi) \geq -c\|\psi - \phi\|_g, \; i = 1,\ldots,n.\)

In addition, suppose that the functions \(x \mapsto F(t,x) =: \hat{F}(x)\) and \(x \mapsto G(t,x) =: \hat{G}(x), x \in \mathbb{R}^n,\) do not depend on \(t\). Then,

(i) if the pair \((\hat{F},\hat{G})\) satisfies (A4) and (A5), system (4.1) is persistent in \(BC_0\).

(ii) if the pair \((\hat{F},\hat{G})\) satisfies (A4) and (A6), all solutions of (4.1) with initial conditions in \(BC_0\) are bounded.

Proof. For non-autonomous systems \(x'(t) = f(t,x_t)\) with \(f : D \subset \mathbb{R} \times C^0_g \rightarrow \mathbb{R}^n\) continuous, the quasimonotone condition (Q) should be replaced by

(Q') for \((t,\phi),(t,\psi)\) ∈ \(D\) with \(0 \leq \phi \leq \psi\) and \(\phi_i(0) = \psi_i(0)\), then \(f_i(t,\phi) \leq f_i(t,\psi), \; i = 1,\ldots,n.\)

Condition (Q') implies that the solution operator \(x_t(\sigma,\phi)\) for \(x'(t) = f(t,x_t)\) is monotone relative to the variable \(\phi\) and that comparison results as in Chapter 5 of [30] are valid.

(i) As before, write (4.1) as (4.4) and take e.g. \(t_0 = 0\). Assuming (H1)-(H3) means that (A1)-(A3) are satisfied with \(F(\cdot)\) and \(G(\cdot)\) replaced by \(F(t,\cdot)\) and \(G(t,\cdot)\), respectively \((t \geq 0)\). In particular, (H1) implies (Q').

We now adapt the proof of Theorem 3.1, by replacing equation (3.1) by (4.1) and (3.7) by

\[ x'(t) = f^\delta(t,x_t), \tag{4.7} \]

where \(f_i^\delta(t,\phi) = f_i(t,\phi) - \delta \phi_i(0), 1 \leq i \leq n,\) and \(\delta > 0\) is such that \(\hat{F}(v) - (B + \delta I)v > 0\) for \(v = (v_1,\ldots,v_n) > 0\) and \(B = \text{diag}(\hat{G}_1(0),\ldots,\hat{G}_n(0))\) as in (A5). Clearly, (4.7) also satisfies (Q').

Let \(\varphi \in BC_0\) be given. It is apparent that the arguments in Step 2 of the proof of Theorem 3.1 apply with very little change to the non-autonomous case, thus there exists \(m_0 \in \mathbb{N}\) such that \(x(t) \geq y^m(t)\) for \(t \geq 0, m \geq m_0\), where \(x(t) := x(t;0,\varphi,f)\) and \(y^m(t) := x(t;0,\frac{1}{m}\varphi,f^\delta)\).

To further prove that \(\inf_{t \geq 0} y_i^m(t) > 0\) for all \(i\) and \(m\) large, we replace Step 1 of the proof of Theorem 3.1 by the following argument: for \(t \geq 0\) and \(\phi \geq \frac{1}{m}v\) with \(\phi_i(0) = \frac{1}{m}v_i\), from (H1) and (A4) we have

\[ f_i^\delta(t,\phi) \geq F_i(t,v/m) - \frac{1}{m}v_i \left(G_i(t,v/m) + \delta\right) \geq \frac{1}{m} \left[\hat{F}_i(v) - v_i(\hat{G}_i(v/m) + \delta)\right] > 0 \]

for \(m \in \mathbb{N}\) sufficiently large and \(1 \leq i \leq n;\) from Remark 5.2.1 of Smith’s monograph [30], we derive that \(y^m(t) \geq \frac{1}{m}v\) for \(t \geq 0\). This ends the proof of the assertion (i).
(ii) In a similar way, under the hypotheses in (ii), a few changes to the proof of Lemma 3.2 allow us to conclude that all solutions are bounded.

The permanence result in Theorem 3.2 is not easily adapted to deal directly with non-autonomous systems, since its proof uses \(\omega\)-limit sets for autonomous FDEs. In fact, an argument often used in the proof is that a bounded solution \(x(t)\) with monotone components should converge to some \(x^*\) as \(t \to \infty\), where \(x^*\) is an equilibrium of the system – which obviously need not happen for a non-autonomous system. However, in concrete applications, one might further derive the permanence of the system, with explicit upper and lower bounds, as shown in the next section.

5. Applications to population models

The above results on persistence and permanence apply to a very broad class of abstract FDEs with infinite delay, which include many important models used in population dynamics. An advantage of our method is that, in general, the validity of hypotheses (A1)-(A6) and (H1)-(H3) is very easy to check. Here, we illustrate the results with some selected examples.

5.1. A cooperative Lotka-Volterra model with patch structure

Consider the following cooperative Lotka-Volterra system with patch structure:

\[
x_i'(t) = x_i(t) \left( \beta_i - \mu_i x_i(t) + \sum_{j=1}^{n} a_{ij} \int_{0}^{\infty} x_j(t-s) \, d\eta_{ij}(s) \right) + \sum_{j=1}^{n} d_{ij} \int_{0}^{\infty} x_j(t-s) \, d\nu_{ij}(s), \quad i = 1, \ldots, n
\]

(5.1)

where \(\beta_i, \mu_i \in \mathbb{R}, a_{ij} \geq 0, d_{ij} \geq 0, \eta_{ij}, \nu_{ij} : [0, \infty) \to \mathbb{R}\) are bounded, nondecreasing functions with total variation one, for all \(i, j\). For results on persistence, permanence and stability for autonomous or non-autonomous Lotka-Volterra with infinite delays, as well as for a biological explanation of the coefficients involved, see [8,10,11,20,21,24,32,33] and references therein. System (5.1) is written in the form (3.1) with \(F_i, G_i : BC \to \mathbb{R}\) linear operators given by

\[
F_i(\phi) = \beta_i \phi_i(0) + \sum_{j=1}^{n} d_{ij} \int_{0}^{\infty} \phi_j(-s) \, d\nu_{ij}(s),
\]

\[
G_i(\phi) = \mu_i \phi_i(0) - \sum_{j=1}^{n} a_{ij} \int_{0}^{\infty} \phi_j(-s) \, d\eta_{ij}(s).
\]

(5.2)

We now insert (5.1) in a phase space \(C^0_g\), to justify the use of Theorems 3.1 and 3.2. As shown in [12,15], given any prescribed \(\delta > 0\), there is a function \(g\) satisfying (g1)-(g3) and such that

\[
\int_{0}^{\infty} g(-s) \, d\nu_{ij}(s) < 1 + \delta, \quad \int_{0}^{\infty} g(-s) \, d\eta_{ij}(s) < 1 + \delta, \quad i, j = 1, \ldots, n.
\]
In this way, $F_i, G_i$ are well-defined by (5.2) as bounded linear operators in $C^q_0 \ [8,18]$, whose operator norms satisfy the estimates $\|F_i\| < |\beta_i| + (1 + \delta) \sum_{j=1}^{n} a_{ij}, \|G_i\| < |\mu_i| + (1 + \delta) \sum_{j=1}^{n} a_{ij}, i, j = 1, \ldots, n$. Clearly, assumptions (A1)-(A4) are fulfilled. Now define the matrices

$$M = \text{diag}(\beta_1, \ldots, \beta_n) + [d_{ij}], \quad N = \text{diag}(\mu_1, \ldots, \mu_n) - [d_{ij}].$$

For any $v \in \mathbb{R}^n$, $F(v) = Mv, G(v) = Nv$. For the present setting, we derive the following criteria:

**Theorem 5.1.** With the above notations,

(i) If there exists a positive vector $v$ such that $Mv > 0$, system (5.1) is persistent in $BC_0$.

(ii) If there exist positive vectors $v$ and $q$ such that $Mv > 0$ and $Nq > 0$, system (5.1) is permanent in $BC_0$ and it has a positive equilibrium.

(iii) In the latter case, if there is a positive equilibrium $x^*$ for which $Mx^* > 0$, then $x^*$ is a global attractor for all solutions of (5.1) with initial conditions in $BC_0$.

**Proof.** If $Mv > 0$ for some positive $v \in \mathbb{R}^n$, then (A5) is satisfied; similarly, $Nq > 0$ for some $q > 0$ implies (A6). The assertions (i) and (ii) follow from Theorems 3.1 and 3.2.

We now further assume that $Mx^* > 0$ for some positive equilibrium. In particular, this means that $Mv > 0$ for $v = \varepsilon x^*$ and $\varepsilon > 0$; moreover, for $\varepsilon$ small, say $\varepsilon \in (0, 1)$, as in (3.15) we have $x(t; \varepsilon x^*) \not\to x^*$ as $t \to \infty$. Then any solution $x(t) = x(t, \varphi)$ ($\varphi \in BC^+_0$) of (5.1) satisfies the estimates (3.13), where $y^*$ is also an equilibrium. We need to show that $x^* = y^*$.

In order to simplify the arguments, we consider the ODE system associated with (5.1), obtained by taking all the delays equal to zero:

$$x_i'(t) = x_i(t) \left( \beta_i - \mu_i x_i(t) + \sum_{j=1}^{n} a_{ij} x_j(t) \right) + \sum_{j=1}^{n} d_{ij} x_j(t), \quad i = 1, \ldots, n. \quad (5.3)$$

Since the equilibria of (5.1) and (5.3) are the same, we only need to show that solutions of (5.3) satisfy $\limsup_{t \to \infty} x_i(t) \leq x_i^*$. For a positive solution $x(t)$ of (5.3), define $L_j = \limsup_{t \to \infty} (x_j(t)/x_j^*)$, and choose $i$ such that $L_i = \max_j L_j$. Choose a sequence $t_k \to \infty$ with $x_i(t_k) \to L_i x_i^*$ and $x_i^*(t_k) \to 0$ as $k \to \infty$. Using (5.3), this yields

$$0 \leq L_i x_i^* \left( \beta_i - \mu_i L_i x_i^* + L_i \sum_{j=1}^{n} a_{ij} x_j^* \right) + L_i \sum_{j=1}^{n} d_{ij} x_j^*$$

$$= L_i (\beta_i x_i^* + \sum_{j=1}^{n} d_{ij} x_j^*) + L_i^2 x_i^* (\mu_i x_i^* + \sum_{j=1}^{n} a_{ij} x_j^*)$$

$$= L_i (1 - L_i) (\beta_i x_i^* + \sum_{j=1}^{n} d_{ij} x_j^*) = L_i (1 - L_i) (Mx^*)_i.$$

Under the condition $Mx^* > 0$, this leads to $L_i \leq 1$. From (3.13) and the definition of $L_i$, we get $x_j^* \leq \liminf_{t \to \infty} x_j(t) \leq \limsup_{t \to \infty} x_j(t) \leq x_j^*$ for $1 \leq j \leq n$. \phantomsection

\hfill \blacksquare
Remark 5.1. As expected, Theorem 5.1 shows that the global dynamics of (5.1) depend heavily on the algebraic properties of the matrices $M, N$. Condition $Nq > 0$ for some vector $q > 0$ is equivalent to saying that $N$ is a non-singular M-matrix; the dissipativeness follows from this property. When $M$ is an irreducible matrix, there is a positive vector $v$ such that $Mv > 0$ if and only if $s(M) > 0$, where $s(M)$ is the spectral bound of $M$, defined by $s(M) = \max \{\text{Re} \lambda : \lambda \in \sigma(M)\}$. If all the coefficients $\beta_i$ are positive, clearly $Mx^* > 0$ if $x^* > 0$ – so, if $Nq > 0$ for some $q > 0$, a positive equilibrium of (5.1) must be a global attractor. Theorem 5.1 significantly improves the results in [10] in what concerns the persistence of cooperative Lotka-Volterra models (5.1): here, the persistence is established in $BC_0$, a question which was left as an open problem in [10]. On the other hand, [10] deals with questions of extinction, persistence, global asymptotic stability for Lotka-Volterra systems (5.1) without any prescribed signs for the coefficients $\beta_i, a_{ij}$. If there is at least one negative coefficient $a_{ij}$, then (5.1) is not cooperative, and the theory of monotone systems cannot be applied directly. In this scenario, auxiliary cooperative FDEs can be used, and results of comparison with cooperative systems invoked, to draw conclusions about the non-cooperative system – a technique often exploited in [10]. This technique will be illustrated in Subsection 5.3.

Consider now the following non-autonomous version of the Lotka-Volterra system (5.1):

$$
x_i'(t) = x_i(t) \left( \beta_i(t) - \mu_i(t)x_i(t) + \sum_{j=1}^{n} a_{ij}(t) \int_{0}^{\infty} x_j(t-s) d\eta_{ij}(s) \right) \\
+ \sum_{j=1}^{n} d_{ij}(t) \int_{0}^{\infty} x_j(t-s) d\nu_{ij}(s), \quad t \geq 0, i = 1, \ldots, n
$$

(5.4)

where $\mu_i(t), \beta_i(t), a_{ij}(t), d_{ij}(t)$ are continuous and bounded on $[0, \infty)$, $a_{ij}(t), d_{ij}(t)$ are non-negative and $\eta_{ij}, \nu_{ij} : [0, \infty) \rightarrow \mathbb{R}$ are bounded, nondecreasing functions with total variation one, for all $i, j$.

A straightforward application of Theorems 4.1 and 5.1 gives the following criterion:

**Theorem 5.2.** Under the above conditions, define the $n \times n$ constant matrices

$$
M^l = \text{diag} (\underline{\beta}_1, \ldots, \underline{\beta}_n) + [\underline{d}_{ij}], \quad M^u = \text{diag} (\overline{\beta}_1, \ldots, \overline{\beta}_n) + [\overline{d}_{ij}],
$$

$$
N^l = \text{diag} (\underline{\mu}_1, \ldots, \underline{\mu}_n) - [\underline{a}_{ij}],
$$

where we use the notations

$$
\underline{f} = \inf_{t \geq 0} f(t), \quad \overline{f} = \sup_{t \geq 0} f(t),
$$

(5.5)

for a function $f : [0, \infty) \rightarrow \mathbb{R}$ bounded. Then: (i) if there exists a vector $v > 0$ such that $M^l v > 0$, system (5.4) is persistent in $BC_0$; (ii) if there exist vectors $v > 0$ and $q > 0$ such that $M^u v > 0$ and $N^l q > 0$, system (5.4) is permanent in $BC_0$. 

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5.2. A system of modified logistic equations with unbounded delays

Consider the classical delayed logistic equation, also known as Wright’s equation, given by
\[ x'(t) = r x(t)(1 - x(t - \tau)/K), \]
where \( x(t) \) is the population of a species at time \( t \), \( r \) the intrinsic growth rate of the species, \( K \) the carrying capacity, and \( \tau \) the maturation delay. In Arino et al. [6], the model
\[ x'(t) = \frac{\gamma \mu x(t - \tau)}{\mu e^{\mu \tau} + k(e^{\mu \tau} - 1)x(t - \tau)} - \mu x(t) - \kappa x^2(t), \quad (5.6) \]
where \( \gamma, \mu, \kappa, \tau > 0 \), was derived as an alternative, and more realistic, formulation for the delayed logistic law. The coefficients in the logistic equation are related to the ones in (5.6) by
\[ \gamma, \mu, \kappa, \tau > 0, \]
where \( \gamma, \mu \) the birth and mortality rates, respectively) and \( K = (\gamma - \mu)/\kappa \). More recently, Bastinec et al. [7] proposed a more general non-autonomous model with multiple time dependent delays:
\[ x'(t) = \sum_{k=1}^{m} \frac{\alpha_k(t)x(t - \tau_k(t))}{1 + \beta_k(t)x(t - \tau_k(t))} - \mu(t)x(t) - \kappa(t)x^2(t), \quad t \geq 0, \quad (5.7) \]
where \( \alpha_k, \kappa : [0, \infty) \to (0, \infty), \beta_k, \mu, \tau_k : [0, \infty) \to [0, \tau] \) (for some \( \tau > 0 \)) are continuous, \( 1 \leq k \leq m \).

The question of the permanence of (5.7) was raised (but not studied) in [7], and a criterion for it given by the author in [9], with explicit uniform lower and upper bounds for all positive solutions.

Here, we pursue the research, and generalize the scalar equation (5.7): not only unbounded time-varying delays are allowed, but also we consider \( n \) classes (of one or multiple species) following the ‘modified delayed logistic equation’ (5.7), with dispersal terms among the classes. This leads to the system
\[ x'_i(t) = \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)x_i(t - \tau_{ik}(t))}{1 + \beta_{ik}(t)x_i(t - \tau_{ik}(t))} + \sum_{j=1}^{n} d_{ij}(t)x_j(t - \sigma_{ij}(t)) - \mu_i(t)x_i(t) - \kappa_i(t)x_i^2(t), \quad t \geq 0, \quad i = 1, \ldots, n \quad (5.8) \]
where all the coefficients \( \alpha_{ik}(t), \beta_{ik}(t), d_{ij}(t), \mu_i(t), \kappa_i(t) \) and delays \( \tau_{ik}(t), \sigma_{ij}(t) \) are non-negative and continuous functions in \( t \in [0, \infty), k = 1, \ldots, m_i, i, j = 1, \ldots, n \); the time-dependent delay functions \( \tau_{ik}(t), \sigma_{ij}(t) \) are possibly unbounded. The migration rates of populations moving from class \( j \) to class \( i \) are given by \( d_{ij}(t) \), with \( \sigma_{ij}(t) \) the time-delays during dispersion; the instantaneous loss term \(-d_{ji}(t)x_j(t)\) may be incorporated in the term \(-\mu_j(t)x_j(t)\) of the \( j \)-th equation. For biological reasons, we usually consider \( d_{ii}(t) \equiv 0 \); in any case for each \( i \in \{1, \ldots, n\} \) the term \( d_{ii}(t)x_i(t - \sigma_{ii}(t)) \) may be included in the first sum on the right-hand side of (5.8).

We now established sufficient conditions for the persistence of (5.8) in \( BC_0 \). This example also illustrates how to combine the techniques in Theorems 4.1 and 4.2.

**Theorem 5.3.** Suppose that \( \alpha_{ik}, \beta_{ik}, d_{ij}, \mu_i, \kappa_i, \tau_{ik}, \sigma_{ij} : [0, \infty) \to [0, \infty) \) are continuous functions, \( A_i := \sum_{k=1}^{m_i} \alpha_{ik}(t) \) and \( \kappa_i(t) \) are bounded below and above by positive constants, and \( \beta_{ik}, d_{ij}, \mu_i \)
are bounded, \( k = 1, \ldots, m, i, j = 1, \ldots, n \). If there exists a positive vector \( v = (v_1, \ldots, v_n) \) such that
\[
Hv > 0,
\]
where \( H \) is the \( n \times n \) matrix \( H = \text{diag}(A_1 - \overline{\alpha}_1, \ldots, A_n - \overline{\alpha}_n) + \begin{bmatrix} d_{ij} \end{bmatrix} \) for
\[
d_{ij} = \inf_{t \geq 0} d_{ij}(t), \quad A_i = \inf_{t \geq 0} A_i(t), \quad \overline{\alpha}_i = \sup_{t \geq 0} \alpha_i(t),
\]
then all solution of (5.8) with initial conditions in \( BC_0 \) are bounded below and above by positive constants.

**Proof.** As in (5.5), we set the notations \( \underline{f} = \inf_{t \geq 0} f(t), \overline{f} = \sup_{t \geq 0} f(t) \) for a function \( f : [0, \infty) \to [0, \infty) \) bounded. Condition (5.9) reads as
\[
(A_i - \overline{\alpha}_i)v_i + \sum_{j=1}^n d_{ij}v_j > 0, \quad i = 1, \ldots, n. \tag{5.10}
\]
Effecting a scaling of the variables, \( \hat{x}_i(t) = x_i(t)/v_i \), we obtain a new system with the form (5.8), where \( \beta_{ik}(t), d_{ij}(t), \alpha_i(t) \) are replaced by \( \hat{\beta}_{ik}(t) = v_i \beta_{ik}(t), \hat{d}_{ij}(t) = v_j d_{ij}(t)/v_i, \hat{\alpha}_i(t) = v_i \alpha_i(t) \) for all \( i, k, j \), and all other coefficients are the same. Dropping the hats for the sake of simplification, we can therefore assume that (5.8) satisfies condition (5.10) with \( v = (1, \ldots, 1) \).

Define \( r_{ik}(t, x) := \frac{\alpha_{ik}(t)x}{1 + \beta_{ik}(t)x}, t \geq 0, x \geq 0, \) and note that \( 0 \leq \frac{\partial}{\partial x} r_{ik}(t, x) \leq \overline{\alpha}_{ik} \). Write (5.8) as
\[
x'_i(t) = F_i(t, x_t) - x_i(t)G_i(t, x_t) =: f_i(t, x_t), \quad t \geq 0, i = 1, \ldots, n,
\]
with
\[
F_i(t, \phi) = \sum_{k=1}^{m_i} r_{ik}(t, \phi_i(-\tau_{ik}(t))) + \sum_{j=1}^n d_{ij}(t)\phi_j(-\sigma_{ij}(t)), \quad t \geq 0, \phi \in BC,
\]
\[
G_i(t, x) = \mu_i(t) + \kappa_i(t)x, \quad t \geq 0, x \in IR.
\]
Define also the functions \( F^l_i(t, \phi), F^u_i(t, \phi) \) and \( G^l_i(x), G^u_i(x) \) whose components are given by
\[
F^l_i(t, \phi) = \sum_{k=1}^{m_i} \frac{\alpha_{ik} \phi_i(-\tau_{ik}(t))}{1 + \beta_{ik} \phi_i(-\tau_{ik}(t))} + \sum_{j=1}^n d_{ij}(t)\phi_j(-\sigma_{ij}(t)),
\]
\[
F^u_i(t, \phi) = \sum_{k=1}^{m_i} \frac{\overline{\alpha}_{ik} \phi_i(-\tau_{ik}(t))}{1 + \overline{\beta}_{ik} \phi_i(-\tau_{ik}(t))} + \sum_{j=1}^n \overline{d}_{ij}(t)\phi_j(-\sigma_{ij}(t)), \quad t \geq 0, \phi \in BC,
\]
\[
G^l_i(x) = \underline{\alpha}_i + \underline{\kappa} x, \quad G^u_i(x) = \overline{\alpha}_i + \overline{\kappa} x, \quad x \in IR.
\]
Clearly,
\[
F^l_i(t, \phi) \leq F_i(t, \phi) \leq F^u_i(t, \phi), \quad G^l_i(x) \leq G_i(t, x) \leq G^u_i(x)
\]
for \( t \geq 0, \phi \in BC_+, x \in IR_+ \). On the other hand, choose \( g \) satisfying (g1)-(g3), and insert (5.8) is a space \( C_G^0 \). The functions \( F^l_i(t, \phi), F^u_i(t, \phi) \) are uniformly (for \( t \in [0, \infty) \) Lipschitz continuous and
nondecreasing with respect to $\phi$ in the non-negative cone $BC_+$, and $G_i^t(x)$, $G_i^u(x)$ are increasing for $x \geq 0$. Therefore the pairs $(F^l, G^u)$ and $(F^u, G^l)$ satisfy (H1)-(H3). Note also that $x \mapsto F^l(t, x), x \mapsto F^u(t, x)$ are autonomous for $x \in \mathbb{R}^n$, and that $\tilde{F}^l(x) := F^l(t, x), \tilde{F}^u(x) := F^u(t, x)$ are sublinear.

Next, consider the auxiliary systems

\begin{align}
\dot{x}_i(t) &= F_i^l(t, x_t) - x_i(t)G_i^u(x_i(t)) =: f_i^l(t, x_t), \quad i = 1, \ldots, n, \\
\dot{x}_i(t) &= F_i^u(t, x_t) - x_i(t)G_i^l(x_i(t)) =: f_i^u(t, x_t), \quad i = 1, \ldots, n.
\end{align}

(5.11) (5.12)

By results of comparison of solutions,

$$x(t; 0, \varphi, f^l) \leq x(t; 0, \varphi, f) \leq x(t; 0, \varphi, f^u),$$

(5.13)

for $\varphi \in BC_0$. From (5.10) with $v = (1, \ldots, 1) =: 1 \in \mathbb{R}_n^+$ and $\varepsilon > 0$ small, we have

$$\tilde{F}_i^l(\varepsilon 1) - G_i^u(0) = \varepsilon \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}}{1 + \varepsilon \beta_{ik}} - \mu_i + \sum_{j=1}^{n} d_{ij} \right) > 0, \quad i = 1, \ldots, n.$$

Theorem 4.2(i) yields the persistence of (5.11), and thus the persistence of (5.8) as well. Moreover, $\lim_{x \to \infty} G_i^l(x) = \infty, 1 \leq i \leq n$, which implies that $(\tilde{F}^u, G^l)$ satisfies (A6). Theorem 4.2(ii) and (5.13) allow us to conclude the boundedness of solutions $x(t; 0, \varphi, f)$ on $[0, \infty)$, for any $\varphi \in BC_0$. \blacksquare

With an additional condition on the (possibly unbounded) delay functions, the permanence of (5.8) is established, with explicit lower and upper bounds for the asymptotic behavior of solutions.

**Theorem 5.4.** Assume the hypotheses of Theorem 5.3, and in addition that $\lim_{t \to \infty} (t - \tau_{ik}(t)) = \lim_{t \to \infty} (t - \sigma_{ij}(t)) = \infty$ for $i, j = 1, \ldots, n, k = 1, \ldots, m_i$. Then, system (5.8) is permanent. Moreover, for $v = (v_1, \ldots, v_n)$ as in (5.9), the solutions $x(t) = x(t; 0, \varphi)$ of (5.8) with $\varphi \in BC_0$ satisfy the uniform estimates

$$m_0 \leq \liminf_{t \to \infty} x_i(t)/v_i \leq \limsup_{t \to \infty} x_i(t)/v_i \leq M_0, \quad i = 1, \ldots, n,$$

(5.14)

where

$$M_0 = \max_{1 \leq i \leq n} \limsup_{t \to \infty} \frac{1}{v_i^2 \kappa_i(t)} \left[ v_i \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)}{1 + \beta_{ik}(t)v_i} \right) + \sum_{j=1}^{n} d_{ij}(t)v_j \right]$$

(5.15)

and

$$m_0 = \min_{1 \leq i \leq n} \liminf_{t \to \infty} \frac{1}{v_i^2 \kappa_i(t)} \left[ v_i \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)}{1 + \beta_{ik}(t)v_i} - \mu_i(t) \right) + \sum_{j=1}^{n} d_{ij}(t)v_j \right].$$

(5.16)

**Proof.** For $x(t) := x(t; 0, \varphi, f)$, set $x_j := \liminf_{t \to \infty} x_j(t), \bar{x}_j := \limsup_{t \to \infty} x_j(t), 1 \leq j \leq n$. From Theorem 5.3, $0 < \underline{x}_j \leq \bar{x}_j < \infty$ for all $j$. Consider $i$ such that $\bar{x}_i/v_i = \max_{1 \leq j \leq n} (\bar{x}_j/v_j)$, for
\( v > 0 \) as in (5.9). By the fluctuation lemma, take a sequence \((t_m)\) with \(t_m \to \infty\), \(x'_i(t_m) \to 0\) and \(x_i(t_m) \to \xi_i\). For any \(\varepsilon > 0\) small and \(m\) sufficiently large, we have \(x_i(t_m - \tau_{ik}(t_m)) \leq \xi_i + \varepsilon\) and \(v_i x_j(t_m - \sigma_{ij}(t_m))/v_j \leq \xi_i + \varepsilon\) for all \(k, j\). Recalling that the functions \(\tau_{ik}(t, \cdot)\) are nondecreasing on \(x \in [0, \infty)\), for sufficiently large \(m\) we derive

\[
x'_i(t_m) \leq (\xi_i + \varepsilon) \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t_m)}{1 + \beta_{ik}(t_m)(\xi_i + \varepsilon)} + \frac{(\xi_i + \varepsilon)}{v_i} \sum_{j=1}^n d_{ij}(t_m)v_j - \mu_i(t_m)x_i(t_m) - \kappa_i(t_m)x_i^2(t_m),
\]

\[
\leq \kappa_i(t_m) \left[ \frac{\xi_i + \varepsilon}{v_i \kappa_i(t_m)} \left( \sum_{k=1}^{m_i} \alpha_{ik}(t_m) + \sum_{j=1}^n d_{ij}(t_m)v_j \right) - \frac{\mu_i(t_m)}{\kappa_i(t_m)}x_i(t_m) - x_i^2(t_m) \right].
\]

Taking limits \(m \to \infty, \varepsilon \to 0^+\), this estimate yields

\[
0 \leq \limsup_{t \to \infty} \frac{\xi_i - \varepsilon}{v_i \kappa_i(t)} \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)}{1 + \beta_{ik}(t)(\xi_i - \varepsilon)} \right) + \sum_{j=1}^n d_{ij}(t)v_j - \frac{\mu_i(t)}{\kappa_i(t)}x_i(t) - x_i^2(t),
\]

thus

\[
\xi_i \leq \limsup_{t \to \infty} \frac{1}{v_i \kappa_i(t)} \left[ \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)}{1 + \beta_{ik}(t)} \right] + \sum_{j=1}^n d_{ij}(t)v_j .
\]

This leads to \(\xi_j/v_j \leq M_0\), for \(1 \leq j \leq n\) and \(M_0\) as in (5.15).

To prove the uniform lower bound given by (5.14), (5.16), we reason along the lines above, and some details are omitted. Let \(i \in \{1, \ldots, n\}\) be such that \(\bar{x}_i/v_i = \min_{1 \leq j \leq n} \bar{x}_j/v_j\), and take a sequence \((s_m)\) with \(s_m \to \infty\), \(x'_i(s_m) \to 0\) and \(x_i(s_m) \to \bar{x}_i\). For \(\varepsilon > 0\) small and \(m\) large, we get

\[
\frac{x'_i(s_m)}{\kappa_i(s_m)} \geq \frac{\bar{x}_i - \varepsilon}{v_i \kappa_i(s_m)} \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}(s_m)v_i}{1 + \beta_{ik}(s_m)(\bar{x}_i - \varepsilon)} \right) + \sum_{j=1}^n d_{ij}(s_m)v_j - \frac{\mu_i(s_m)}{\kappa_i(s_m)}x_i(s_m) - x_i^2(s_m)
\]

Since \(\bar{x}_i \leq v_iM_0\), taking limits \(m \to \infty, \varepsilon \to 0^+\), this leads to

\[
0 \geq \bar{x}_i \liminf_n \left[ \frac{1}{v_i \kappa_i(s_m)} \left( \sum_{k=1}^{m_i} \frac{\alpha_{ik}(s_m)v_i}{1 + \beta_{ik}(s_m)v_iM_0} \right) - \frac{\mu_i(s_m)v_i + \sum_{j=1}^n d_{ij}(s_m)v_j}{M_0} \right] - \bar{x}_i ,
\]

and therefore \(\bar{x}_i/v_i \geq m_0\) for \(m_0\) as in (5.16).

Note that when \(\beta_{ik}(t) \equiv 0\) in (5.8), the lower bound \(m_0\) in (5.16) does not depend on \(M_0\).

In the case \(n = 1\), we get a criterion which improves and generalizes Theorem 3.2 in [9].

**Corollary 5.1.** Consider the scalar equation (5.7), where \(\alpha_k, \beta_k, \mu, \kappa : [0, \infty) \to [0, \infty)\) are continuous and bounded, \(t_k : [0, \infty) \to [0, \infty)\) are continuous, \(1 \leq k \leq m\), and \(\kappa(t) > \kappa_0, A(t) := \sum_{k=1}^{m} \alpha_k(t) > A_0\) for some constants \(\kappa_0, A_0 > 0\). If

\[
\inf_{t \geq 0} \left( \sum_{k=1}^{m} \alpha_k(t) \right) > \sup_{t \geq 0} \mu(t),
\]

then...
then (5.7) is persistent (in \(BC\)) and all positive solutions are bounded. If in addition \(\lim_{t \to \infty} (t - \tau_k(t)) = \infty\) for \(k = 1, \ldots, m\), (5.7) is permanent and positive solutions \(x(t) = x(t; 0, \varphi) (\varphi \in BC)\) satisfy

\[
m_0 \leq \liminf_{t \to \infty} x(t) \leq \limsup_{t \to \infty} x(t) \leq M_0,
\]

where \(M_0 = \limsup_{t \to \infty} \frac{1}{\kappa(t)} \left( \sum_{k=1}^{m} \alpha_k(t) - \mu(t) \right)\), \(m_0 = \liminf_{t \to \infty} \frac{1}{\kappa(t)} \left( \sum_{k=1}^{m} \alpha_k(t)M_0 - \mu(t) \right)\).

### 5.3. Permanence for a competitive compartmental system with infinite delay

In 1990, Aiello and Freedman [2] proposed and studied a model for a single species with immature and mature stages and a discrete time-delay:

\[
\begin{align*}
u'_i(t) &= \alpha u_i(t) - \gamma u_i(t) - \alpha e^{-\gamma \tau} u_i(t - \tau) \\
u'_m(t) &= \alpha e^{-\gamma \tau} u_m(t - \tau) - \beta u_m(t),
\end{align*}
\]

(5.17)

where \(\alpha, \beta, \gamma, \tau > 0\). In (5.17), \(u_i, u_m\) stand for the immature and mature populations, respectively, \(\tau\) is the maturation time since birth, \(\alpha\) is the birth rate for the species, and \(\beta, \gamma\) the death rates for matures and immatures, respectively. Since the second equation is decoupled from the first, to describe the qualitative behavior of solutions to (5.17) it is sufficient to study the second equation of the system. This model has received great attention over the last decades, a large number of generalizations has been derived, and many aspects of their dynamics analyzed, in several contexts. Besides the early works [2,3,13], see [4,5,28] and references therein for more results on related models. A natural extension is to introduce non-constant delay; in fact, it may even be infinite, leading to a second equation given by

\[
u'_m(t) = \alpha \int_{0}^{\infty} f(s)e^{-\gamma s} u_m(t - s) ds - \beta u_m^2(t)
\]

for some \(f\) summable with \(\int_{0}^{\infty} f(s) ds = 1\). More recently, models with two or more stage-structured species have been proposed. In [5], two species, structured in matures and immatures and in competition, were considered. Disregarding the immature populations, this leads to a Lotka-Volterra type model of the form

\[
\begin{align*}
u'_1(t) &= \alpha_1 \int_{0}^{\infty} f_1(s)e^{-\gamma_1 s} u_1(t - s) ds - \beta_1 u_1^2(t) - c_1 u_1(t)u_2(t) \\
u'_2(t) &= \alpha_2 \int_{0}^{\infty} f_2(s)e^{-\gamma_2 s} u_2(t - s) ds - \beta_2 u_2^2(t) - c_2 u_2(t)u_2(t),
\end{align*}
\]

(5.18)

where \(\alpha_j, \beta_j, \gamma_j, c_j > 0\) and the kernels \(f_j : [0, \infty) \to [0, \infty)\) are continuous (or at least measurable) with \(\int_{0}^{\infty} f_j(s) ds = 1, j = 1, 2\). However, due to technical difficulties, in [4,5] the authors restricted their analyses to the case of kernels \(f_1(s), f_2(s)\) with compact support – of course, if \([0, \tau]\) contains both the supports of \(f_1\) and \(f_2\), the framework is restricted to a system of differential equations with finite distributed delay on \([-\tau, 0]\). The theorem below was proven by Al-Omari and Gourley [5] for the case of a finite delay.
Theorem 5.5. [5] Consider (5.18) with \(\alpha_j, \beta_j, \gamma_j, c_j > 0, f_j : [0, \infty) \to [0, \infty)\) continuous, \(f_j(s) = 0\) for \(s \geq \tau\) for some \(\tau \in (0, \infty)\), and \(\int_0^\tau f_j(s)\,ds = 1, j = 1, 2\). Assume that

\[
c_2\alpha_1 \int_0^\tau f_1(s)e^{-\gamma_1 s}\,ds < \beta_1\alpha_2 \int_0^\tau f_2(s)e^{-\gamma_2 s}\,ds, \tag{5.19}
\]
\[
c_1\alpha_2 \int_0^\tau f_2(s)e^{-\gamma_2 s}\,ds < \beta_2\alpha_1 \int_0^\tau f_1(s)e^{-\gamma_1 s}\,ds. \tag{5.20}
\]

Then \(u^* = (u_1^*, u_2^*)\), where

\[
u_1^* = \frac{1}{\beta_1\beta_2 - c_1c_2} \left( \beta_1\alpha_2 \int_0^\tau f_2(s)e^{-\gamma_2 s}\,ds - c_2\alpha_1 \int_0^\tau f_1(s)e^{-\gamma_1 s}\,ds \right),
\]
\[
u_2^* = \frac{1}{\beta_1\beta_2 - c_1c_2} \left( \beta_2\alpha_1 \int_0^\tau f_1(s)e^{-\gamma_1 s}\,ds - c_1\alpha_2 \int_0^\tau f_2(s)e^{-\gamma_2 s}\,ds \right), \tag{5.21}
\]
is the unique positive equilibrium of (5.18), and \(u^*\) is a global attractor of all solutions to (5.18) with initial conditions in \(C_0 := \{\varphi : [-\tau, 0] \to \mathbb{R}^2 \mid \varphi\text{ is continuous and } \varphi(0) > 0\}\).

Here, as an application of the techniques in Section 3, we prove that the above result is still valid for the case of \(\tau = \infty\). We use the ideas and arguments in [5], inserting them in the present framework, which enables us to deal with the infinite delay. Clearly (5.18) is not cooperative, and consequently Theorems 3.1 and 3.2 cannot be applied directly.

Consider (5.18) with kernels \(f_1, f_2 : [0, \infty) \to [0, \infty)\) continuous with \(L^1\)-norm equal to 1, and assume (5.19)-(5.20) with \(\tau = \infty\). Choose \(\delta > 0\) such that

\[
c_2 \left( \delta\beta_1 + \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}\,ds \right) < \beta_1\alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}\,ds, \tag{5.22}
\]
\[
c_1 \left( \delta\beta_2 + \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}\,ds \right) < \beta_2\alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}\,ds. \tag{5.23}
\]

Fix any solution \(u(t) = u(t; \varphi)\) of (5.18) with \(\varphi \in BC_0\). In \(C_0^0\) or \(UC_\gamma\) with \(0 < \gamma < \min(\gamma_1, \gamma_2)\), we write (5.18) in the form (3.1) with \(n = 2\), where \(F = (F_1, F_2), G = (G_1, G_2)\) are linear functions given by

\[
F_i(\phi) = \alpha_i \int_0^\infty f_i(s)e^{-\gamma_i s}\phi_i(-s)\,ds \quad \text{for} \quad \phi = (\phi_1, \phi_2) \in BC, i = 1, 2,
\]
and \(G(\phi) = G(\phi_1(0), \phi_2(0))\), with

\[
G_1(u) = \beta_1u_1 + c_1u_2, \quad G_2(u) = \beta_2u_2 + c_2u_1 \quad \text{for} \quad u = (u_1, u_2) \in \mathbb{R}^2.
\]

Since \(F(\phi) \geq 0\) for \(\phi \in BC_+\), from Lemma 3.1 the solutions \(u(t)\) of (5.18) with initial conditions in \(BC_0\) are non-negative in their maximal interval of existence. For such solutions, we derive

\[
u_1'(t) \leq \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t - s)\,ds - \beta_1u_1^2(t)
\]
\[
u_2'(t) \leq \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t - s)\,ds - \beta_2u_2^2(t),
\]

\[23\]
and we now compare with solutions to the auxiliary cooperative system

\[
\begin{align*}
  u_1'(t) &= \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t-s)\,ds - \beta_1 u_1^2(t) \\
  u_2'(t) &= \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t-s)\,ds - \beta_2 u_2^2(t).
\end{align*}
\]

System (5.24) satisfies (A1)-(A6), so in particular it is dissipative in \( BC_0 \). Thus, \( u(t) \) satisfies

\[
\limsup_{t \to \infty} u_i(t) \leq u_i^{1,u}, \quad i = 1, 2,
\]

where \( u^{1,u} = (u_1^{1,u}, u_2^{1,u}) \) is the unique positive equilibrium of (5.24), with coordinates given by

\[
  u_i^{1,u} = \frac{\alpha_i}{\beta_i} \int_0^\infty f_i(s)e^{-\gamma_i s}\,ds, \quad i = 1, 2.
\]

For \( t > 0 \) sufficiently large, we get

\[
\begin{align*}
  u_1'(t) &\geq \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t-s)\,ds - \beta_1 u_1^2(t) - c_1 u_1(t)(u_2^{1,u} + \delta) \\
  u_2'(t) &\geq \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t-s)\,ds - \beta_2 u_2^2(t) - c_2 u_2(t)(u_1^{1,u} + \delta),
\end{align*}
\]

and compare \( u(t) \) with solutions to the new auxiliary system

\[
\begin{align*}
  u_1'(t) &= \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t-s)\,ds - \beta_1 u_1^2(t) - c_1 u_1(t)(u_2^{1,u} + \delta) \\
  u_2'(t) &= \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t-s)\,ds - \beta_2 u_2^2(t) - c_2 u_2(t)(u_1^{1,u} + \delta).
\end{align*}
\]

System (5.24) has the form (3.1) and satisfies (A1)-(A4) and (A6). Also, for (5.24) the matrix \( B \) in (A5) reads as \( B = \begin{pmatrix} c_1(u_2^{1,u} + \delta) & 0 \\ 0 & c_2(u_1^{1,u} + \delta) \end{pmatrix} \). Formulae (5.22), (5.23) yield

\[
F(u) - Bu = \left( \alpha_1 u_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}\,ds - c_1(u_2^{1,u} + \delta)u_1, \alpha_2 u_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}\,ds - c_2(u_1^{1,u} + \delta)u_2 \right) > 0,
\]

for any \( u = (u_1, u_2) > 0 \). In particular, (A5) holds. From Theorem 3.2, we now obtain

\[
\liminf_{t \to \infty} u_i(t) \geq u_i^{1,l}, \quad i = 1, 2,
\]

where \( u^{1,l} = (u_1^{1,l}, u_2^{1,l}) \) is the unique positive equilibrium of (5.24), given by

\[
  u_1^{1,l} = \frac{\alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}\,ds - c_1(u_2^{1,u} + \delta)}{\beta_1}, \quad u_2^{1,l} = \frac{\alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}\,ds - c_2(u_1^{1,u} + \delta)}{\beta_2}.
\]
Next, we observe that, for $t > 0$ sufficiently large, the solution $u(t)$ satisfies

$$u_1'(t) \leq \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t-s)\,ds - \beta_1 u_1^2(t) - c_1 u_1(t)(u_2^1 - \delta)$$

$$u_2'(t) \leq \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t-s)\,ds - \beta_2 u_2^2(t) - c_2 u_2(t)(u_1^1 - \delta),$$

and compare it with solutions of the second-upper auxiliary system

$$u_1'(t) = \alpha_1 \int_0^\infty f_1(s)e^{-\gamma_1 s}u_1(t-s)\,ds - \beta_1 u_1^2(t) - c_1 u_1(t)(u_2^1 - \delta)$$

$$u_2'(t) = \alpha_2 \int_0^\infty f_2(s)e^{-\gamma_2 s}u_2(t-s)\,ds - \beta_2 u_2^2(t) - c_2 u_2(t)(u_1^1 - \delta),$$

which satisfies (A1)-(A6). Proceeding in this way, in [5] the arguments above were iterated and auxiliary cooperative systems (5.24$_{n,u}$), (5.24$_{n,l}$) with positive equilibria $u$$_{n,u}$, $u$$_{n,l}$, respectively, constructed, providing upper and lower bounds for $u(t)$:

$$u_{n,l}^i \leq \liminf_{t \to \infty} u_i(t) \leq \limsup_{t \to \infty} u_i(t) \leq u_{n,u}^i, \quad i = 1, 2, \quad n \in \mathbb{N}.$$ 

Moreover, explicit recursive formulae can be obtained for the sequences $u_{n,l}^i$, $u_{n,u}^i$, showing that $u_{n,l}^i$ increases and $u_{n,u}^i$ decreases, $i = 1, 2$, with $\lim_n u_{n,l}^i = \lim_n u_{n,u}^i = u^*$. See [5] for details. Thus,

**Theorem 5.6.** For (5.18), Theorem 5.5 is valid with $\tau = +\infty$ and $C_0$ replaced by $BC_0$.

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