Asymptotic behaviour for a class of non-monotone delay differential systems with applications

Teresa Faria[a] [b], Rafael Obaya[c], Ana M. Sanz [d]

Suggested running head: Asymptotic behaviour for a class of non-monotone DDEs

Abstract

The paper concerns a class of n-dimensional non-autonomous delay differential equations obtained by adding a non-monotone delayed perturbation to a linear homogeneous cooperative system of ordinary differential equations. This family covers a wide set of models used in structured population dynamics. By exploiting the stability and the monotone character of the linear ODE, we establish sufficient conditions for both the extinction of all the populations and the permanence of the system. In the case of DDEs with autonomous coefficients (but possible time-varying delays), sharp results are obtained, even in the case of a reducible community matrix. As a subproduct, our results improve some criteria for autonomous systems published in recent literature. As an important illustration, the extinction, persistence and permanence of a non-autonomous Nicholson system with patch structure and multiple time-dependent delays are analysed.

Keywords: delay differential equation; non-autonomous Nicholson system; quasi-monotone condition; persistence; permanence; global asymptotic stability.

2010 Mathematics Subject Classification: 34K25, 34K12, 34K27, 34K20, 92D25.

1 Introduction

In the last decades, delay differential equations (DDEs) with patch structure have been largely employed in population dynamics and other fields, since by capturing several features of a heterogeneous environment, they may provide quite realistic models. Structured systems of differential equations have been used in population models when the populations are distributed over different classes (e.g. due to age, size or different food-rich patches), in disease models with several compartments

[a]Corresponding author.
[b]Departamento de Matemática and CMAF-CIO, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal
teresa.faria@fc.ul.pt
[c]Departamento de Matemática Aplicada, E. Ingenierías Industriales, and IMUVA, Instituto de Matemáticas, Universidad de Valladolid, 47011 Valladolid, Spain
rafoba@wmatem.eis.uva.es
[d]Departamento de Didáctica de las Ciencias Experimentales, Sociales y de la Matemática, Facultad de Educación, and IMUVA, Instituto de Matemáticas, Universidad de Valladolid, 34004 Palencia, Spain
anasan@wmatem.eis.uva.es

for a host population, in leukemia models where the infected cells may become inactive, and in a variety of other situations where the transition among the several classes should be considered. See e.g. [6, 20, 25, 26]. Naturally, time delays should be incorporated in such systems to express the maturation time of biological species, the incubation period of diseases, the maturation time of blood cells and several other attributes.

The paper is concerned with a family of non-autonomous DDEs written in abstract form as

$$x'(t) = A(t)x(t) + f(t, x_t), \quad t \geq 0 \tag{1.1}$$

where $A(t)$ is an $n \times n$ matrix of continuous functions, $f : [0, \infty) \times D \to \mathbb{R}^n$ is continuous, $D \subset C([-\tau, 0]; \mathbb{R}^n)$ is equipped with the uniform convergence metric, $\tau > 0$ is the time-delay, and, as usual, x_t denotes the past history of the system on the interval $[t - \tau, t]$, i.e., $x_t(\theta) = x(t + \theta)$ for $\theta \in [-\tau, 0]$. The function f is required to satisfy $f(t, 0) = 0$ for $t \geq 0$, and the ordinary differential equation (ODE) $x'(t) = A(t)x(t)$ to be cooperative, thus $a_{ij}(t) \geq 0$ must hold for all $i \neq j$ and $t \geq 0$, where $a_{ij}(t)$ are the entries of $A(t)$. We restrict our setting to a class of delayed perturbations $f(t, x_t)$ with multiple time-varying discrete delays, having the particular form

$$f(t, \phi) = (f_1(t, \phi_1), \ldots, f_n(t, \phi_n)) \tag{1.2}$$

for $t \geq 0$ and $\phi = (\phi_1, \ldots, \phi_n) \in D$, where $f_i(t, \phi_i) = \sum_{k=1}^{m} n_{ik}(t, \phi_i(-\tau_{ik}(t)))$ and $n_{ik}(t, x), \tau_{ik}(t)$ are continuous, bounded and nonnegative functions, for all i, k. For simplicity, this paper deals with discrete delays only; however, as pointed out later in Section 3, straightforward generalizations to some families of perturbations with distributed delays are possible.

Inserting (1.2) in (1.1) leads to systems of the form

$$x_i'(t) = \sum_{j=1}^{n} a_{ij}(t)x_j(t) + \sum_{k=1}^{m} n_{ik}(t, x_i(t - \tau_{ik}(t))), \; i = 1, \ldots, n, \; t \geq 0, \tag{1.3}$$

which can be interpreted as a structured population model for n populations, see Section 3 for an additional set of hypotheses, as well as for some biological elements of the model.

In the present paper, the main idea is to take full advantage of the properties of the cooperative non-delayed linear system $x'(t) = A(t)x(t)$, to further analyse the large-time behaviour of solutions of system (1.3). We shall impose conditions on the coefficients of the linear system $x'(t) = A(t)x(t)$, in order to have its global exponential stability. This property and the monotonicity of $x'(t) = A(t)x(t)$ will play an important role in the study of (1.3). Although the nonlinearities (1.2) are in general non-monotone, the techniques exploited here are largely based on results of comparison of solutions (see [24]), applied to some convenient auxiliary cooperative DDE systems. This method is used to address the global asymptotic behaviour of solutions of system (1.3), in what concerns its dissipativity, uniform persistence and the global asymptotic stability of the null solution. To some extent and in different frameworks, similar techniques have inspired the papers [8, 9, 16, 17, 28]. Some relevant applications are given. We also hope that the present results can be used to further address other aspects of the global dynamics of (1.3).

As a significant example of systems in the form (1.3), we shall consider a *non-autonomous* Nicholson system with patch structure and multiple time-dependent discrete delays, given by

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) + \sum_{k=1}^{m} \beta_{ik}(t)x_i(t - \tau_{ik}(t))e^{-c_{ik}(t)x_i(t-\tau_{ik}(t))}, \; i = 1, \ldots, n, \tag{1.4}$$

where all the coefficient and delay functions are continuous, nonnegative and bounded. We stress that results concerning multi-dimensional versions of the famous Nicholson's blowflies equation [13] are still quite limited, with most authors treating only *autonomous* systems.

The papers of Faria and Röst [10], on *autonomous* Nicholson systems, and of Obaya and Sanz [22], on uniform and strict persistence for monotone skew-product semiflows, were a strong motivation for the present work. Here, the authors further pursue their previous research, and extend it to general non-autonomous Nicholson systems: in fact, we aim to obtain results on extinction, uniform persistence and permanence of (1.4) as simple illustrations of our main results, proven for a much larger family of DDEs of the form (1.3).

The contents of the paper are now briefly described. In Section 2, we study a cooperative ODE $x'(t) = A(t)x(t)$ and give sufficient conditions for its global exponential stability; in this case, a system of the form (1.1) is dissipative if the delayed perturbation $f(t, x_t)$ is bounded. In Section 3, we start by introducing a set of assumptions for a family of DDEs (1.1), give some biological interpretation of the models and refer to some recent literature. The main results are then presented, providing very general criteria for both the global asymptotic stability of the trivial solution (in biological terms, this implies the extinction of the populations in all patches) and the uniform persistence of such systems. A comparison with results in [9, 18, 28, 30] is also given, and some questions are raised to be left as open problems. Finally, in Section 4 we consider systems with autonomous coefficients (but with possible time-dependent delays): from the results in Section 3 and by a careful analysis of properties of cooperative matrices, we provide necessary and sufficient conditions for both their permanence and extinction, even in the case of a reducible community matrix. These sharp criteria improve and extend results for autonomous systems proven in recent literature. As an important example of application, throughout the paper our results are widely illustrated with versions of the Nicholson system (1.4).

2 Preliminaries

In this section, we establish some preliminary results on stability for non-autonomous linear homogeneous systems of ODEs of cooperative type. Although such systems have been widely studied (see e.g. [5, 12, 14]), some optimal conditions for their asymptotic stability and global exponential stability are given here. For completeness of the reader, the authors opt to include these conditions here, with the proof of a result whenever its precise statement could not be found elsewhere. We start with some standard definitions from the literature [5, 12, 14].

Consider an n-dimensional ODE $x' = f(t, x)$ with $f : [\alpha, \infty) \times D \subset \mathbb{R}^{n+1} \to \mathbb{R}^n$ sufficiently regular so that for any $(t_0, x_0) \in [\alpha, \infty) \times D$ there exists a unique solution, denoted by $x(t, t_0, x_0)$, of the initial value problem $x' = f(t, x), x(t_0) = x_0$, defined on $[\alpha, \infty)$. To simplify the writing, let $D = \mathbb{R}^n$. We further assume that $x = 0$ is a solution, i.e., $f(t, 0) = 0, t \geq \alpha$. The zero solution is said to be *stable* on the interval $[\alpha, \infty)$ if for any $\varepsilon > 0$ and $t_0 \geq \alpha$ there is $\delta = \delta(\varepsilon, t_0) > 0$ such that $|x(t, t_0, x_0)| < \varepsilon$ for all $t \geq t_0$, whenever $|x_0| < \delta$; $x = 0$ is *uniformly stable* if it is stable and δ above can be chosen independently of $t_0 \geq \alpha$. The zero solution is said to be *uniformly asymptotically stable* on $[\alpha, \infty)$ if it is uniformly stable and there is $b > 0$ such that, for any $\varepsilon > 0$, there is $T = T(\varepsilon) > \alpha$ such that, for any $t_0 \geq \alpha$ and $|x_0| < b$, we have $|x(t, t_0, x_0)| < \varepsilon$ for all $t \geq t_0 + T$; and $x = 0$ is *globally exponentially stable* on $[\alpha, \infty)$ if there exist $K, \beta > 0$ such that $|x(t, t_0, x_0)| \leq Ke^{-\beta(t-t_0)}|x_0|$

for all $t \geq t_0 \geq \alpha$ and $x_0 \in \mathbb{R}^n$. In general, the stability of a particular solution $\tilde{x}(t)$ of an ODE $x' = f(t,x)$ is defined as the stability of the zero solution of $y' = f(t, \tilde{x} + y) - f(t, \tilde{x})$.

The usual partial order in $\mathbb{R}^n$ relative to the cone $[0,\infty)^n$ is denoted here by $\leq$, i.e., for $x, y \in \mathbb{R}^n$, $x \leq y$ means $y - x \in [0,\infty)^n$; we write $x \ll y$ whenever $y - x \in (0,\infty)^n$. The notations $\geq$ and $\gg$ have then a clear meaning. In particular, a vector v in $\mathbb{R}^n$ is said to be *positive* (*nonnegative*) if all its components are positive (nonnegative), and we write $v \gg 0$ ($v \geq 0$); by $v > 0$ we mean that $v \geq 0$ and $v \neq 0$.

Lemma 2.1. *Consider a non-autonomous linear ODE*

$$x'(t) = A(t)x(t), \quad t \geq \alpha, \tag{2.1}$$

where $\alpha \in \mathbb{R}$ and $A(t) = [a_{ij}(t)]$ is an $n \times n$ matrix of functions such that:

(a1) a_{ij} are continuous on $[\alpha,\infty)$, $a_{ij}(t) \geq 0, i \neq j, a_{ii}(t) < 0$ for all $t \geq \alpha$ and $i, j \in \{1,\ldots,n\}$;

(a2) there exists a vector $v = (v_1,\ldots,v_n) \gg 0$ such that $A(t)v \leq 0$ for all $t \geq \alpha$.

Then, for any solution $x(t)$ of (2.1), $|x(t)|_{v^{-1}}$ is non-increasing on $t \in [\alpha,\infty)$, where $|\cdot|_{v^{-1}}$ is the norm in $\mathbb{R}^n$ defined by $|x|_{v^{-1}} = \max_{1\leq i\leq n}(v_i^{-1}|x_i|)$ for $x = (x_1,\ldots,x_n)$.

Proof. Rescaling the variables by $\hat{x}_i(t) = v_i^{-1}x_i(t)$ $(1 \leq i \leq n)$, where $v = (v_1,\ldots,v_n) \gg 0$ is a vector as in (a2), we obtain a new linear ODE $\hat{x}'(t) = \hat{A}(t)\hat{x}(t)$, where the matrix $\hat{A}(t) = [\hat{a}_{ij}(t)]$ has entries $\hat{a}_{ij}(t) = v_i^{-1}a_{ij}(t)v_j$. In this way, and after dropping the hats for simplicity, we may consider (2.1) where $v = \mathbf{1} := (1,\ldots,1)$ is the positive vector in (a2) and $|x|_{v^{-1}} = \max_{1\leq i\leq n}|x_i|$.

Let $x(t) \neq 0$ be a solution of (2.1). To prove the claim, we show that $|x(t)|$ is non-increasing on each fixed interval $J = [t_0, t_1]$, $\alpha \leq t_0 < t_1$. Define $u_j = \max_J |x_j(t)|$, and let $u_i = \max_{1\leq j\leq n} u_j$, with $u_i = |x_i(t_*)|$ for some $t_* \in J$. It is sufficient to show that $u_i = |x_i(t_0)|$.

We suppose that $x_i(t_*) > 0$; the case $x_i(t_*) < 0$ is treated in a similar way. Denoting $d_i(t) = -a_{ii}(t)$ and $D_i(t) = \int_{t_0}^t d_i(s)\,ds$, for $t \in J$ we have $x_i'(t) + d_i(t)x_i(t) \leq d_i(t)u_i$. Hence

$$x_i(t) \leq x_i(t_0)e^{-D_i(t)} + u_i(1 - e^{-D_i(t)}), \quad t \in J.$$

In particular for $t = t_*$ we derive $u_i e^{-D_i(t_*)} \leq x_i(t_0)e^{-D_i(t_*)}$, thus $u_i = x_i(t_0)$. □

Lemma 2.2. *For the linear ODE system* (2.1)*, assume*

(a1') a_{ij} are uniformly continuous and bounded on $[\alpha,\infty)$, $a_{ij}(t) \geq 0, i \neq j, a_{ii}(t) < 0$ for all $t \geq \alpha$ and $i, j \in \{1,\ldots,n\}$;

(a2') there exists a vector $v = (v_1,\ldots,v_n) \gg 0$ such that $A(t)v \leq 0$ for all $t \geq \alpha$, and $\liminf_{t\to\infty} A(t)v \ll 0$, in the sense that there exists a sequence $t_k \to \infty$ such that $\lim_k (A(t_k)v)_i < 0$, $i = 1,\ldots,n$.

Then, (2.1) *is asymptotically stable; in other words, $x = 0$ is stable and $\lim_{t\to\infty} x(t) = 0$, for all solutions of* (2.1).

Proof. As in the above proof and without loss of generality, consider $v = \mathbf{1}$ in (a2') and the norm $|x| = \max_{1\leq i\leq n}|x_i|$ in $\mathbb{R}^n$. From Lemma 2.1, (2.1) is uniformly stable. We now prove that the trivial solution is a global attractor of all solutions.

Let $x(t) \neq 0$ be a solution of (2.1), and define $c = \lim_{t\to\infty}|x(t)|$. We want to show that $c = 0$. In order to obtain a contradiction, suppose that $c > 0$. By (a2'), take $t_k \to \infty$ such that

$\alpha_i := \lim_k(-d_i(t_k) + \sum_{j\neq i} a_{ij}(t_k)) < 0$ for all i. In particular for such a sequence, $|x(t_k)| \searrow c$, and thus there exists $i \in \{1, \ldots, n\}$ and a subsequence, still denoted by (t_k), such that either $x_i(t_k) = |x(t_k)| \to c$ or $x_i(t_k) = -|x(t_k)| \to -c$. We only consider the situation $x_i(t_k) \to c$ for some i, the other is treated in a similar way. We now consider separately two cases.

First, suppose that there exists $\lim_{t\to\infty} x_i(t) = c$. Since the entries of $A(t)$ are bounded and uniformly continuous and $x(t)$ is uniformly bounded on $[\alpha, \infty)$, one easily shows that all components $x_j(t)$ and $x_j'(t)$ are uniformly continuous on $[\alpha, \infty)$. From the Barbalat Lemma, we derive that there is $\lim_{t\to\infty} x_i'(t) = 0$, and in particular obtain $\lim_k x_i'(t_k) = 0$. On the other hand, from (2.1) we have

$$x_i'(t_k) \leq x_i(t_k)\Big[- d_i(t_k) + \sum_{j\neq i} a_{ij}(t_k)\Big].$$

Taking limits, the above inequality leads to $0 \leq c\alpha_i$, which is a contradiction.

Next, consider the case when $\underline{x}_i := \liminf_{t\to\infty} x_i(t) < \limsup_{t\to\infty} x_i(t) = c$. From the inequality above, it is clear that t_k are not local extrema points, since $x_i'(t_k) < 0$. However, by reducing to a subsequence if necessary, we may consider that each t_k lies between a local maximum point $\bar{t}_k$ and a local minimum point $\underline{t}_k$, to its left and to its right respectively, with $x_i(\bar{t}_k) \to c, x_i(\underline{t}_k) \to \underline{x}_i$. We may take a sequence (s_k) such that, for all $k \in \mathbb{N}$,

$$t_k < \underline{t}_k < s_k < \bar{t}_{k+1} < t_{k+1}, \quad x_i(s_k) = x_i(t_k), \quad x_i'(s_k) \geq 0.$$

Since the map $t \to |x(t)|$ is non-increasing, we have $x_j(s_k) \leq |x(s_k)| \leq |x(t_k)| = x_i(t_k)$, $1 \leq j \leq n$. We derive

$$0 \leq x_i'(s_k) \leq x_i(t_k)\Big[- d_i(s_k) + \sum_{j\neq i} a_{ij}(s_k)\Big] \leq 0,$$

and therefore $x_i(t_k) = 0$, which is not possible. □

When $f(t, x)$ is periodic in t, a solution of $x' = f(t, x)$ is uniformly asymptotically stable if it is asymptotically stable. This is not true if periodic is replaced by almost periodic (see [12], p. 191 for a counter-example). Moreover, for a linear system $x' = A(t)x$, where $A(t)$ is an $n \times n$ matrix of continuous functions, it is well known that the concepts of global exponential stability and uniform asymptotic stability on an interval $[\alpha, \infty)$ are equivalent (see [5, 14]). Therefore, the following criterion is straightforward for periodic systems, however it applies to the more general case of almost periodic linear systems.

Theorem 2.1. *Let $A(t) = [a_{ij}(t)]$ be an $n \times n$ matrix of almost periodic functions on $\mathbb{R}$ satisfying (a1), (a2) on $\mathbb{R}$, with $A(t_0)v \ll 0$ for some $t_0 \in \mathbb{R}$. Then,* (2.1) *is globally exponentially stable.*

Proof. Let $H(A)$ be the hull of A, that is, the closure for the topology of uniform convergence of the set of shifted maps $\{\theta_t A(\cdot) = A(\cdot + t) \mid t \in \mathbb{R}\}$ [5, 12]. $H(A)$ is a compact metric space. Since A is almost periodic, it follows that A satisfies (a1'), (a2'). The orbit $\{\theta_t A \mid t \in \mathbb{R}\}$ is dense in the hull, thus actually any $B \in H(A)$ satisfies (a1'), (a2') as well. By Lemma 2.2, all solutions of all the systems $x' = B(t)x$, with $B \in H(A)$, tend to 0 as $t \to \infty$. At this point, the spectral theory of Sacker and Sell [23] applies and permits to conclude that (2.1) is globally exponentially stable. □

Usually, the global exponential stability of (2.1) is obtained by assuming that $A(t)$ is *strongly* uniformly row (or column) dominant. The theorem below follows from Proposition 6.3 in [5].

Theorem 2.2. *Consider an $n \times n$ matrix $A(t) = [a_{ij}(t)]$ of bounded continuous functions satisfying (a1), and suppose that*

(a3) there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $T \geq \alpha, \delta > 0$ such that $(A(t)v)_i \leq -\delta$ for all $t \geq T$, $i = 1, \dots, n$.

Then, (2.1) is globally exponentially stable.

Remark 2.1. For any fixed t, the matrix $-A(t)$ is a non-singular M-matrix if and only if there exists a positive vector $v = v(t)$ such that $A(t)v \ll 0$; thus, condition (a3) above not only demands that $-A(t)$ are non-singular M-matrices, for t sufficiently large, but also that there exist positive vectors v, η, which do not depend on t, such that $A(t)v \leq -\eta$ (see [11] and Section 4 for more details on M-matrices).

For $\tau \geq 0$, consider the Banach space $C := C([-\tau, 0]; \mathbb{R}^n)$ equipped with the norm $\|\phi\| = \max_{\theta \in [-\tau,0]} |\phi(\theta)|$, where $|\cdot|$ is a fixed norm in $\mathbb{R}^n$. The case of no delays ($\tau = 0$) is included, in which case C is identified with $\mathbb{R}^n$. We now consider DDEs obtained by adding a bounded delayed perturbation $f(t, x_t)$ to systems (2.1), where, as before, $x_t \in C$ is given by $x_t(\theta) = x(t + \theta), -\tau \leq \theta \leq 0$. For simplicity, in what follows we take $\alpha = 0$, but any $\alpha \in \mathbb{R}$ could be considered.

From Theorem 2.2, one obtains:

Theorem 2.3. *Consider an $n \times n$ matrix $A(t) = [a_{ij}(t)]$ of bounded functions satisfying (a1), (a3) on $[0, \infty)$, and a function $f : [0, \infty) \times C \to \mathbb{R}^n$ continuous and bounded. Then, all solutions of the DDE*

$$x'(t) = A(t)x(t) + f(t, x_t), \quad t \geq 0, \tag{2.2}$$

are defined on $[0, \infty)$ and (2.2) is dissipative, i.e., there exists $M > 0$ such that $\limsup_{t\to\infty} |x(t)| \leq M$ for any solution $x(t)$ of (2.2).

Proof. Let $|f(t, \varphi)| \leq L$ for $t \geq 0, \varphi \in C$. From Theorem 2.2, there are $K > 0, \alpha > 0$ such that $|X(t)X^{-1}(t_0)| \leq Ke^{-\alpha(t-t_0)}$, $t \geq t_0 \geq 0$, where $X(t)$ is a fundamental solution matrix for (2.1). By the variation of constants formula, the solutions $x(t)$ of (2.2) satisfy

$$x(t) = X(t)X^{-1}(t_0)x(t_0) + X(t)\Big(\int_{t_0}^{t} X^{-1}(s)f(s, x_s)\, ds \Big) \quad (t, t_0 \geq 0), \tag{2.3}$$

so that $|x(t)| \leq Ke^{-\alpha(t-t_0)}|x(t_0)| + \frac{KL}{\alpha}(1 - e^{-\alpha(t-t_0)}) \to \frac{KL}{\alpha}$ as $t \to \infty$. □

We now set some further notation. Let C^+ be the cone of nonnegative functions in C, $C^+ = C([-\tau, 0]; [0, \infty)^n)$, and $int\, C^+$ its interior. Hereafter, $\leq$ also denotes the usual partial order generated by C^+: $\phi \leq \psi$ if and only if $\psi - \phi \in C^+$; by $\phi \ll \psi$, we mean that $\psi - \phi \in int\, C^+$. The definition of the relations $\geq$ and $\gg$ are then clear; thus, we write $\psi \geq 0$ for $\psi \in C^+$ and $\psi \gg 0$ for $\psi \in int\, C^+$. A vector $v \in \mathbb{R}^n$ is identified in C with the constant function $\psi(s) = v$ for $-\tau \leq s \leq 0$.

Let $D \subset C([-\tau, 0]; \mathbb{R}^n)$ $(\tau \geq 0)$ be open, and consider a non-autonomous DDE written as

$$x'(t) = f(t, x_t), \quad t \geq 0, \tag{2.4}$$

where $f : [0, \infty) \times D \to \mathbb{R}^n$ is continuous and regular enough so that the initial value problem is well-posed, in the sense that for each $(\sigma, \phi) \in [0, \infty) \times D$ there exists a unique solution of the problem $x'(t) = f(t, x_t), x_\sigma = \phi$, defined on a maximal interval of existence. This solution will be denoted by $x(t, \sigma, \phi)$ in $\mathbb{R}^n$ or $x_t(\sigma, \phi)$ in C. When considering more than one DDE $x'(t) = f(t, x_t)$, the notation $x(t, \sigma, \phi, f)$ where the argument f is made explicit will be used to clarify which DDE is being considered.

To simplify the terminology, we say that (2.4) is *cooperative* if it satisfies Smith's *quasi-monotone condition* (Q), given by (see [24])

(Q) for $\phi, \psi \in D, \phi \le \psi$ and $\phi_i(0) = \psi_i(0)$, then $f_i(t, \phi) \le f_i(t, \psi),\ i = 1, \dots, n, t \ge 0$.

It is well-known that (Q) guarantees monotonocity of solutions relative to initial data and allows comparison of solutions between two related DDEs, $x'(t) = f(t, x_t), x'(t) = g(t, x_t)$ with $f \le g$: if at least one of them is cooperative, then $x(t, \sigma, \phi, f) \le x(t, \sigma, \psi, g)$ for $t \ge \sigma$ if $\phi \le \psi$ ([24]). These and other properties of cooperative ODEs and DDEs will turn out to be very useful in the next sections. The lemma below will be often applied, see p. 82 of [24].

Lemma 2.3. *[24] Consider* (2.4) *in* $D \subset C([-\tau, 0]; \mathbb{R}^n)$*, and let* $v = (v_1, \dots, v_n) \in \mathbb{R}^n$*.*

(i) If $f_i(t, \phi) \le 0$ *for all* $i = 1, \dots, n, t \ge 0$ *whenever* $\phi \in D, \phi \le v$ *and* $\phi_i(0) = v_i$*, then the set* $\{\phi \in D : \phi \le v\}$ *is positively invariant for* (2.4)*.*

(ii) If $f_i(t, \phi) \ge 0$ *for all* $i = 1, \dots, n, t \ge 0$ *whenever* $\phi \in D, \phi \ge v$ *and* $\phi_i(0) = v_i$*, then the set* $\{\phi \in D : \phi \ge v\}$ *is positively invariant for* (2.4)*.*

Remark 2.2. Clearly, if (a1) is satisfied, then (2.1) is a cooperative system and the nonnegative cone $[0, \infty)^n$ is forward invariant. If in addition (a2) is satisfied and $v = (v_1, \dots, v_n) \gg 0$ is as in (a2), for $x \in \mathbb{R}^n$ such that $x \le v$ and $x_i = v_i$, then $(A(t)x)_i \le 0$. This implies that the interval $[0, v] := [0, v_1] \times \cdots \times [0, v_n]$ is forward invariant as well.

3 Global behaviour for a class of non-monotone and non-autonomous DDEs

In this section, we consider n-dimensional delayed structured models (1.1), where the linear ODE system (2.1) is globally exponentially stable, f is continuous, bounded, and, in general, non-monotone. Although some generalizations are possible, we restrict our framework to perturbations $f(t, x_t) = (f_1(t, x_{1,t}), \dots, f_n(t, x_{n,t}))$, with each component $f_i(t, \phi_i)$ of the form $f_i(t, \phi_i) = \sum_{k=1}^m n_{ik}(t, \phi_i(-\tau_{ik}(t)))$, for $t \ge 0, \phi = (\phi_1, \dots, \phi_n) \in C$. Moreover, we suppose that $n_{ik}(t, 0) = 0$ for $t \ge 0$ and have partial derivative with respect to the second variable at $x = 0^+$ given by $\frac{\partial n_{ik}}{\partial x}(t, 0) = \beta_{ik}(t) \ge 0$; thus $n_{ik}(t, x)$ is written as $n_{ik}(t, x) = \beta_{ik}(t) h_{ik}(t, x)$ with $h_{ik}(t, 0) = 0, \frac{\partial h_{ik}}{\partial x}(t, 0) = 1, t \ge 0$. Below, some additional assumptions on $n_{ik}(t, x)$ will be imposed. This leads to a non-autonomous system with multiple discrete time-dependent delays of the form

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1, j\ne i}^{n} a_{ij}(t)x_j(t) + \sum_{k=1}^{m} \beta_{ik}(t) h_{ik}(t, x_i(t - \tau_{ik}(t))),\ i = 1, \dots, n,\ t \ge 0. \quad (3.1)$$

Throughout the remainder of this paper, either the whole or a part of the following set of hypotheses will be imposed:

(h1) the functions $d_i, a_{ij}\,(j \neq i)$ are continuous and bounded, with $a_{ij}(t) \geq 0, i \neq j, d_i(t) > 0$ for $t \geq 0$ and $i, j \in \{1, \dots, n\}$

(h2) there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $\delta > 0, T_0 \geq 0$ such that $d_i(t)v_i \geq \sum_{j=1,j\neq i}^n a_{ij}(t)v_j + \delta$ for $t \geq T_0, i \in \{1, \dots, n\}$;

(h3) τ_{ik}, β_{ik} are continuous and bounded, with $\tau_{ik}(t) \geq 0, \beta_{ik}(t) \geq 0$ and

$$\beta_i(t) := \sum_{k=1}^m \beta_{ik}(t) > 0$$

for $t \in [0, \infty)$, $i \in \{1, \dots, n\}, k \in \{1, \dots, m\}$;

(h4) $h_{ik} : [0, \infty) \times [0, \infty) \to [0, \infty)$ are bounded, continuous, $h_{ik}(t, x)$ are locally Lipschitzian in x, with

$$h_i^-(x) \leq h_{ik}(t, x) \leq h_i^+(x), \qquad t, x \geq 0, k = 1, \dots, m,$$

where $h_i^\pm : [0, \infty) \to [0, \infty)$ are continuous on $[0, \infty)$ and continuously differentiable in a vicinity of 0^+, with $h_i^\pm(0) = 0, (h_i^\pm)'(0) = 1$ and $h_i^-(x) > 0$ for $x > 0$, $i \in \{1, \dots, n\}$.

For simplicity, here we only treat non-autonomous systems with discrete non-autonomous delays, but our framework applies with straightforward adjustments to the more general case of systems with multiple distributed time-varying delays of the form

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1,j\neq i}^n a_{ij}(t)x_j(t) + f_i(t, x_{i,t}),\ i = 1, \dots, n, \tag{3.2}$$

with $f_i(t, x_{i,t})$ given by

$$f_i(t, x_{i,t}) = \sum_{k=1}^m \beta_{ik}(t)h_{ik}\big(t, L_{ik}(t, x_{i,t})\big) \text{ or } f_i(t, x_{i,t}) = \sum_{k=1}^m \beta_{ik}(t)L_{ik}\big(t, h_{ik}(\cdot, x_{i,t}(\cdot))\big), \tag{3.3}$$

where

$$L_{ik}(t, \phi) = \int_{-\tau}^0 \phi(s)\, d_s\eta_{ik}(t, s) \quad \text{for } t \geq 0,\ \phi \in C([-\tau, 0], \mathbb{R}),$$

$\tau > 0$, the measurable functions $\eta_{ik} : [0, \infty) \times [-\tau, 0] \to \mathbb{R}$ are continuous on t, with $\eta_{ik}(t, \cdot)$ non-decreasing and normalized so that $\int_{-\tau}^0 d_s\eta_{ik}(t, s) = 1,\ i = 1, \dots, n, k = 1, \dots, m, t \geq 0$, and for which (h3), (h4) hold. Besides (3.3), and under some natural conditions, other forms of dependence on distributed delays can be incorporated in (3.2).

In what follows, we refer to the $n \times n$ matrix-valued functions defined on $[0, \infty)$ by

$$\begin{aligned} &D(t) = diag\,(d_1(t), \dots, d_n(t)), \quad A(t) = [a_{ij}(t)] \\ &B(t) = diag\,(\beta_1(t), \dots, \beta_n(t)), \quad M(t) = B(t) + A(t) - D(t), \qquad t \geq 0, \end{aligned} \tag{3.4}$$

where $a_{ii}(t) \equiv 0$. The matrix $M(t)$ is often designated as the *community matrix* of the population system (3.1).

Remark 3.1. We stress that under (h1), (h2) the linear homogeneous ODE $x'(t) = -[D(t) - A(t)]x(t)$ possesses two important features: it is cooperative and globally exponentially stable. Of course, if $A(t)$ is periodic or almost periodic, Theorem 2.1 allows us to replace (h2) by the weaker condition $[D(t) - A(t)]v \geq 0$ for $t \in \mathbb{R}$ and $[D(t_0) - A(t_0)]v \gg 0$ for some $t_0 \in \mathbb{R}$ and $v \gg 0$.

System (3.1) can be interpreted as a model for n populations structured into n classes or patches, with migration among them: $x_i(t)$ denotes the density of the ith population; $a_{ij}(t)$ is the migration rate of the population in class j moving to class i; $d_i(t)$ is the coefficient of instantaneous loss for class i, which incorporates both the death rate and the emigration rates of the population that leaves class i to move to other classes; the birth contribution for each population is given by the nonlinear terms $\sum_k \beta_{ik}(t)h_{ik}(t, x_i(t - \tau_{ik}(t)))$.

With this interpretation, $d_i(t) = m_i(t) + \sum_{j\neq i} a_{ji}(t)$, where $m_i(t)$ is the death rate for the ith population, so it is natural to impose $a_{ij}(t) \geq 0$ and $d_i(t) > \sum_{j\neq i} a_{ji}(t)$ for all i, j, i.e., $D(t) - A(t)^T$ is uniformly diagonally dominant for $t \geq 0$. It is also natural to assume that $a_{ij}(t) = \varepsilon_{ij}(t)a_{ji}(t)$ for $i \neq j$ and $t \geq 0$, with $\varepsilon_{ij}(t) \in (0, 1]$, to account for some loss of the populations, when moving to different patches (see [27]), thus $[D(t) - A(t)]\mathbf{1} \gg 0$ for $t \geq 0$. If the mortality rates $m_i(t)$ are bounded below by a positive constant m_0, then $[D(t) - A(t)]\mathbf{1} \geq m_0\mathbf{1}$ for $t \geq 0$. To some degree, these comments justify assumption (h2) from a biological point of view.

Following the general approach in the literature, here multiple (time-varying) discrete delays have been introduced in the birth function. In biological terms, most situations do not require the consideration of more than one delay, either a discrete or a distributed delay, but occasionally multiple delays should be incorporated in each equation. For examples of such situations, we refer to generalizations of the classic Mackey-Glass model for the production of red blood cells in [1] and to [25] for other references.

As an important example of application, we have in mind the following non-autonomous Nicholson system with patch structure and multiple time-dependent discrete delays:

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) + \sum_{k=1}^{m} \beta_{ik}(t)x_i(t - \tau_{ik}(t))e^{-c_{ik}(t)x_i(t-\tau_{ik}(t))}, \qquad (3.5)$$

for $i = 1, \dots, n,\ t \geq 0$. For (3.5), we shall always assume that the coefficient and delay functions satisfy (h1), (h3) and that $c_{ik}(t) \geq c_i > 0$ are continuous and bounded. With nonlinearities given by $h_{ik}(t, x) = xe^{-c_{ik}(t)x}$ for all i, k, (h4) is obviously satisfied.

The *autonomous* version of (3.5) with $n = 1$ and $m = 1$ is the famous *Nicholson's blowfly equation*, given by $N'(t) = -dN(t) + \beta N(t - \tau)e^{-aN(t-\tau)}$ $(d, \beta, a, \tau > 0)$. A large-scale literature on the scalar Nicholson's blowflies equation, on a number of generalizations and on related models has been produced since its introduction by Gurney et al. [13], and real world applications implemented. Nevertheless, a number of problems regarding scalar Nicholson-type equation still remain unsolved, see [2, 3] and references therein. On the other hand, results concerning multi-dimensional versions of such models are still quite limited. Not only is the literature on Nicholson systems very sparse, but also most authors have only treated *autonomous* Nicholson systems, and only recently have non-autonomous Nicholson systems been considered. See [4, 7, 10, 15, 16, 17, 28, 29, 31], also for biological details of the models and additional references.

Besides Ricker-type nonlinearities as in the non-autonomous Nicholson system (3.5), other useful population models can be written in the form (3.1). Among them, are models with Mackey-Glass type nonlinearities of the form (see [19])

$$h_{ik}(t,x) = xe^{-c_{ik}(t)x^{\alpha}} \quad (\alpha > 0) \quad \text{or} \quad h_{ik}(t,x) = \frac{x}{1 + c_{ik}(t)x^{\alpha}} \quad (\alpha \geq 1),$$

which satisfy (h4) if $c_{ik}(t)$ are continuous and bounded below and above by positive constants.

System (3.1) is considered as a DDE in $C = C([-\tau, 0]; \mathbb{R}^n)$, where $\tau = \max_{i,k} \sup_{t \geq 0} \tau_{ik}(t)$. Unless specifically mentioned, $\|\phi\| = \max_{\theta \in [-\tau,0]} |\phi(\theta)|$ for $\phi \in C$, where $|\cdot|$ is the maximum norm in $\mathbb{R}^n$. Motivated by the applications to mathematical biology, only nonnegative solutions of (3.1) are meaningful. For this reason, initial conditions are taken in either C^+ or C_0, where

$$C_0 = \{\varphi \in C^+ : \varphi(0) \gg 0\}.$$

Together with (3.1), we also consider its linearization at the origin:

$$y_i'(t) = -d_i(t)y_i(t) + \sum_{j=1, j \neq i}^{n} a_{ij}(t)y_j(t) + \sum_{k=1}^{m} \beta_{ik}(t)y_i(t - \tau_{ik}(t)), \quad i = 1, \dots, n. \tag{3.6}$$

Write (3.1), (3.6) as $x'(t) = f(t, x_t), y'(t) = g(t, y_t)$ respectively, where $f = (f_1, \dots, f_n), g = (g_1, \dots, g_n)$ and

$$f_i(t, \phi) = -d_i(t)\phi_i(0) + \sum_{j=1, j \neq i}^{n} a_{ij}(t)\phi_j(0) + \sum_{k=1}^{m} \beta_{ik}(t)h_{ik}(t, \phi_i(-\tau_{ik}(t)))$$

and

$$g_i(t, \phi) = -d_i(t)\phi_i(0) + \sum_{j=1, j \neq i}^{n} a_{ij}(t)\phi_j(0) + \sum_{k=1}^{m} \beta_{ik}(t)\phi_i(-\tau_{ik}(t)).$$

Assume (h1), (h3), (h4). For $t \geq 0$ and $\phi \geq 0, \phi_i(0) = 0$, then $f_i(t, \phi) \geq 0$ and $g_i(t, \phi) \geq 0$, which implies that $x(t) := x(t, 0, \phi, f) \geq 0$ and $y(t) := y(t, 0, \phi, g) \geq 0$ for $t \geq 0$. Moreover, $x_i'(t) \geq -d_i(t)x_i(t)$ and $y_i'(t) \geq -d_i(t)y_i(t)$ for $t \geq 0$ and $1 \leq i \leq n$. Hence both C^+ and C_0 are positively invariant for (3.1) and (3.6). The next result is a consequence of Theorem 2.3.

Theorem 3.1. *Under the assumptions (h1)-(h4), all solutions of* (3.1) *with initial conditions in* C_0 *are defined and strictly positive on* $[0, \infty)$*; moreover, there exists* $L > 0$ *such that, for any* $\phi \in C_0$*, there is* $T = T(\phi) > 0$ *such that*

$$0 < x_i(t, 0, \phi) < L \quad \text{for} \quad t \geq T, \ i = 1, \dots, n. \tag{3.7}$$

We now introduce a notation often used for DDEs (cf. [24], p. 82): if there is no possibility of misinterpretation with intervals of $\mathbb{R}$ or $\mathbb{R}^n$, for $v \in \mathbb{R}^n$ we also denote $[0, v]$ and $[v, \infty)$ as the subsets of C given by $[0, v] = \{v \in C^+ : \varphi \leq v\}$ and $[v, \infty) = \{v \in C : \varphi \geq v\}$.

Lemma 3.1. *Under (h1), (h3), system* (3.6) *is cooperative, and the following holds:*

(i) If there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $T_0 \geq 0$ such that $M(t)v \leq 0$ for $t \geq T_0$, then the sets $[0, cv] \cap C_0$ (where $c > 0$) are invariant for (3.6) *with $t \geq T_0$; in particular, the solutions of* (3.6) *are uniformly stable.*

(ii) If there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $T_0 \geq 0$ such that $M(t)v \geq 0$ for $t \geq T_0$, then the sets $[cv, \infty) \cap C_0$ (where $c > 0$) are invariant for (3.6) *with $t \geq T_0$.*

Proof. Since g satisfies (Q), (3.6) is cooperative. Let $M(t)v \leq 0$ for $t \geq T_0$, for some strictly positive vector $v = (v_1, \dots, v_n) \in \mathbb{R}^n$ and some $T_0 \geq 0$. For $\phi \in C^+$ with $\phi \leq v$, if $\phi_i(0) = v_i$ for some i, then $g_i(t, \phi) \leq \big(M(t)v\big)_i \leq 0$ for $t \geq T_0$, proving that $[0, v] \cap C_0$ is positively invariant (see Lemma 2.3); since the system is linear, for any positive constant c the set $[0, cv] \cap C_0$ is positively invariant as well. From the monotonicity, it follows that the solution $y = 0$ of (3.6) is uniformly stable. The proof of (ii) is similar. □

Definition 3.1. *The trivial solution $x \equiv 0$ of* (3.1) *is said to be* **stable** *if for any $\varepsilon > 0$ there is $\delta = \delta(\varepsilon) > 0$ such that $\|x_t(0, \phi)\| < \varepsilon$ for all $\phi \in C_0$ with $\|\phi\| < \delta$ and $t \geq 0$; 0 is said to be* **globally attractive** *(in C_0) if $x(t, 0, \phi) \to 0$ as $t \to \infty$, for all solutions of* (3.1) *with initial conditions $x_0 = \phi \in C_0$; 0 is* **globally asymptotically stable (GAS)** *if it is stable and globally attractive.*

The next result gives sufficient conditions for the stability and global attractivity of the trivial equilibrium. When (3.1) refers to a population model, the global attractivity of 0 means the extinction of the populations in all patches.

Theorem 3.2. *Assume (h1), (h3) and (h4) with $0 < h_i^+(x) < x$, $x > 0, 1 \leq i \leq n$. Further suppose that:*

(i) there exist $v = (v_1, \dots, v_n) \gg 0$ and $T_0 \geq 0$ such that $M(t)v \leq 0$ for $t \geq T_0$;

(ii) either $\liminf_{t \to \infty} \beta_i(t) > 0$ or $\limsup_{t \to \infty} (M(t)v)_i < 0$, for all $i = 1, \dots, n$.

Then the trivial solution of (3.1) *is GAS in C_0.*

Proof. From (ii), for each $i = 1, \dots, n$, either $\beta_i(t) \geq \underline{\beta}_i > 0$ for t large or $(M(t)v)_i \leq -\lambda_i < 0$ for t large. In particular, together with (h3), conditions (i) and (ii) imply (h2).

For $\phi \in C_0, t_0 \geq 0$ and $i \in \{1, \dots, n\}$, it holds $f_i(t, \phi) \leq g_i(t, \phi)$. In this way, the solutions of (3.1) and (3.6) satisfy $x(t, t_0, \phi, f) \leq y(t, t_0, \phi, g), t \geq t_0$. From Lemma 3.1, the zero solution of (3.1) is stable. Now, we show that it attracts all solutions with initial conditions in C_0.

With $\hat{x}_j(t) = x_j(t)/v_j$, system (3.1) reads as

$$\hat{x}_i'(t) = -d_i(t)\hat{x}_i(t) + \sum_{j=1, j \neq i}^{n} \hat{a}_{ij}(t)\hat{x}_j(t) + \sum_{k=1}^{m} \beta_{ik}(t)\hat{h}_{ik}(t, \hat{x}_i(t - \tau_{ik}(t))), \ i = 1, \dots, n, \ t \geq 0, \quad (3.8)$$

where $\hat{a}_{ij}(t) = v_i^{-1} a_{ij}(t) v_j, j \neq i$, and $\hat{h}_{ik}(t, x) = v_i^{-1} h_{ik}(t, v_i x)$ satisfy (h4). Hence, without loss of generality we consider the original system (3.1) and take $v = \mathbf{1}$ in (i), (ii).

The solutions $x(t) = x(t, t_0, \phi, f)$ are bounded, so define $u_j = \limsup_{t \to \infty} x_j(t)$ and let $u_i = \max_{1 \leq j \leq n} u_j$. If $u_i > 0$, by the fluctuation lemma take a sequence (t_k) with $t_k \to \infty$, $x_i(t_k) \to$

$u_i, x_i'(t_k) \to 0$. For any small $\varepsilon > 0$ with $u_i - \varepsilon > 0$, for k large we get $t_k \geq T_0 + \tau$, $u_j - \varepsilon \leq x_j(t) \leq u_j + \varepsilon$ and $h_{ik}(t, x_i(t)) \leq \max_{x \in [0, u_i+\varepsilon]} h_i^+(x)$, for $t \in [t_k - \tau, t_k]$. Thus,

$$\begin{aligned} x_i'(t_k) &\leq -d_i(t_k)(u_i - \varepsilon) + \sum_{j \neq i} a_{ij}(t_k)(u_j + \varepsilon) + \sum_p \beta_{ip}(t_k) h_i^+(x_i(t_k - \tau_{ip}(t_k))) \\ &\leq -u_i\Big(d_i(t_k) - \sum_{j \neq i} a_{ij}(t_k)\Big) + \beta_i(t_k) \max_{x \in [0, u_i + \varepsilon]} h_i^+(x) + O(\varepsilon). \end{aligned}$$

Taking limits $k \to \infty, \varepsilon \to 0^+$, we derive that

$$0 \leq \limsup_{t \to \infty} u_i\Big(\beta_i(t) - d_i(t) + \sum_{j \neq i} a_{ij}(t)\Big) + (\max_{x \in [0, u_i]} h_i^+(x) - u_i) \liminf_{t \to \infty} \beta_i(t).$$

Since $\max_{x \in [0, u_i]} h_i^+(x) < u_i$ and one of the conditions in (ii) is satisfied, this is not possible. Therefore $u_i = 0$, and the proof is complete. □

For the definitions of persistence and permanence given below, see e.g. [26].

Definition 3.2. *A set $S \subset C^+$ is an admissible set of initial conditions for $x'(t) = f(t, x_t)$ if any solution $x(t, 0, \phi)$ with initial condition $x_0 = \phi \in S$ satisfies $x_t \in S$ for $t \geq 0$, whenever it is defined. A DDE $x'(t) = f(t, x_t)$ is said to be* **persistent** *in S, for S an admissible set of initial conditions, if all solutions $x(t, 0, \phi)$ with $\phi \in S$ are defined and bounded below away from zero on $[0, \infty)$, i.e., $\liminf_{t \to \infty} x_i(t, 0, \phi) > 0$ for all $1 \leq i \leq n, \phi \in S$; and $x'(t) = f(t, x_t)$ is* **uniformly persistent** *in S if there is $m > 0$ such that $\liminf_{t \to \infty} x_i(t, 0, \phi) \geq m$ for all $1 \leq i \leq n, \phi \in S$. The system is said to be* **permanent** *in S if it is dissipative and uniformly persistent; in other words, all solutions $x(t, 0, \phi), \phi \in S$, are defined on $[0, \infty)$ and there are positive constants m, M such that, given any $\phi \in S$, there exists $t_0 = t_0(\phi)$ for which*

$$m \leq x_i(t, 0, \phi) \leq M, \quad 1 \leq i \leq n, \, t \geq t_0.$$

Hereafter, unless otherwise stated, the notions of persistence, uniform persistence and permanence always refer to the choice of $S = C_0$ as the set of admissible initial conditions.

Observe that a *linear homogeneous* DDE system is uniformly persistent (in C_0) if and only if all components of all solutions with initial conditions in C_0 tend to ∞ as $t \to \infty$. The next result concerns the uniform persistence of (3.6).

Proposition 3.1. *Assume (h1), (h3), and that there exist vectors $v \gg 0, \eta \gg 0$ such that*

$$M(t)v \geq \eta \quad \text{for large} \quad t > 0. \tag{3.9}$$

Then all solutions $y(t)$ of (3.6) *with initial conditions in C_0 satisfy* $\lim_{t \to \infty} y_i(t) = \infty$, $i = 1, \dots, n$.

Proof. For $\phi \in C_0, t_0 \geq \tau$, we have $y_t = y_t(t_0, \phi) \in int\, C^+$ for $t \geq t_0$, thus $y_\tau \geq cv$ for some small $c > 0$. System (3.6) is linear and cooperative, with $[v, \infty)$ forward invariant for t on the interval $[T_0, \infty)$ if $M(t)v \geq 0$ for $t \geq T_0$. To simplify the exposition, as before we take $v = \mathbf{1}$. We only need to show that all components $u_i(t)$ of the solution $u(t) := y(t, T_0, \mathbf{1})$ satisfy $\lim_{t \to \infty} u_i(t) = \infty$.

For $j \in \{1, \dots, n\}$, let $c_j = \liminf_{t\to\infty} x_j(t) \in [1, \infty]$. Suppose that $c_j < \infty$ for some $j \in \{1, \dots, n\}$, and take $c_i = \min_j c_j$, for the natural ordering in $(0, \infty]$. Then, there is a sequence $t_k \to \infty$ such that $u_i(t_k) \to c_i, u_i'(t_k) \to 0$. On the other hand, from (3.9) there are $\eta_i, T_1 > 0$ such that $\beta_i(t) - d_i(t) + \sum_{j\neq i} a_{ij}(t) \geq \eta_i > 0, t \geq T_1$. For any small $\varepsilon > 0$ and k sufficiently large, we obtain

$$\begin{aligned} u_i'(t_k) &\geq -d_i(t_k)u_i(t_k) + (c_i - \varepsilon)\Big(\sum_{j\neq i} a_{ij}(t_k) + \beta_i(t_k)\Big) \\ &\geq d_i(t_k)[-u_i(t_k) + (c_i - \varepsilon)] + (c_i - \varepsilon)\eta_i, \end{aligned}$$

and therefore $0 \geq c_i\eta_i > 0$, which is not possible. This ends the proof. □

For dissipative systems (3.1) with nonlinearities satisfying (h4), the above criterion for the uniform persistence of the linearization at zero also provides a criterion for its uniform persistence. This is stated in the main theorem of this section, given below. For a relevant extension, see Theorem 3.4.

Theorem 3.3. *Assume (h1)-(h4), and suppose that there exist $v \gg 0, \eta \gg 0$ such that (3.9) is satisfied. Then (3.1) is uniformly persistent, and thus permanent.*

Proof. After effecting a scaling of the variables, we take $v = (1, \dots, 1) = \mathbf{1}$ in condition (3.9), thus there exist constants $\eta_i > 0\,(i = 1, \dots, n)$ such that, for some T_0,

$$\beta_i(t) \geq d_i(t) - \sum_{j\neq i} a_{ij}(t) + \eta_i, \quad t \geq T_0.$$

On the other hand, $d_i(t) - \sum_{j\neq i} a_{ij}(t) \leq \overline{d}_i := \sup_{t\geq T_0} d_i(t)$, and with $1 < \alpha_i < 1 + \eta_i/\overline{d}_i$ we obtain

$$\alpha_i^{-1}\beta_i(t) - d_i(t) + \sum_{j\neq i} a_{ij}(t) > 0, \quad \text{for} \quad t \geq T_0, i = 1, \dots, n. \tag{3.10}$$

For h_i^- as in (h4), we can choose $L > m > 0$ such that the uniform estimate (3.7) holds, $h_i^-(m) = \min_{x\in[m,L]} h_i^-(x)$, with $(h_i^-)'(x) > 0$ and $\alpha_i^{-1}x < h_i^-(x)$ for $x \in (0, m]$ and all i.

Consider the auxiliary *cooperative* system

$$\begin{aligned} x_i'(t) &= -d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) + \sum_{k=1}^{m} \beta_{ik}(t)H_i(x_i(t - \tau_{ik}(t))) \\ &=: F_i(t, x_t), \quad i = 1, \dots, n,\ t \geq 0, \end{aligned} \tag{3.11}$$

where $H_i(x) = h_i^-(x)$ if $0 \leq x \leq m$, $H_i(x) = h_i^-(m)$ if $x \geq m$.

For $x(t)$ a positive solution of (3.1), for $t > 0$ sufficiently large and $1 \leq i \leq n$, we have $x_i(t) \leq L$ and $h_{ik}(t, x_i(t - \tau_{ik}(t))) \geq H_i(x_i(t - \tau_{ik}(t)))$. Therefore, if (3.11) is uniformly persistent, then (3.1) is uniformly persistent as well.

Now, we consider any solution $x(t) = x(t, T_0, \phi, F)$ of (3.11) with $x_{T_0} = \phi \in C_0$ (where T_0 is as in (3.10)), and claim that

$$\liminf_{t\to\infty} x_i(t) \geq m, \quad 1 \leq i \leq n.$$

In fact, we shall show that there exists $T \geq 0$ such that

$$x_i(t) \geq m \quad \text{for} \quad t \geq T, 1 \leq i \leq n. \tag{3.12}$$

The proof, inspired by some arguments in [10], is divided into several steps.

Step 1. We prove that if $\min\{x_j(t) : 1 \leq j \leq n, t \in [T, T+\tau]\} \geq m$ for some $T \geq T_0$, then $x_j(t) \geq m$ for all $t \geq T$ and $j = 1, \dots, n$.

Assume that $x_j(t) \geq m$ for $t \in [T, T+\tau]$ and $j = 1, \dots, n$. Let $t_0 \in [T+\tau, T+2\tau]$ and $i \in \{1, \dots, n\}$ such that $x_i(t_0) = \min\{x_j(t) : 1 \leq j \leq n, t \in [T+\tau, T+2\tau]\}$.

If $x_i(t_0) < m$, we have

$$0 \geq x_i'(t_0) = -d_i(t_0)x_i(t_0) + \sum_{j=1, j\neq i}^{n} a_{ij}(t_0)x_j(t_0) + \sum_{k=1}^{m} \beta_{ik}(t) H_i(x_i(t_0 - \tau_{ik}(t_0))).$$

Note that $x_i(t_0 - \tau_{ik}(t_0)) \geq m$ if $t_0 - \tau_{ik}(t_0) \in [T, T+\tau]$ and $x_i(t_0 - \tau_{ik}(t_0)) \geq x_i(t_0)$ if $t_0 - \tau_{ik}(t_0) \in [T+\tau, t_0]$, hence $H_i(x_i(t_0 - \tau_{ik}(t_0))) \geq H_i(x_i(t_0))$. From (3.10) and the definition of m we obtain

$$\begin{aligned} 0 &\geq \left(-d_i(t_0) + \sum_{j=1}^{n} a_{ij}(t_0) \right) x_i(t_0) + \beta_i(t_0) H_i(x_i(t_0)) \\ &\geq \left(-d_i(t_0) + \sum_{j=1}^{n} a_{ij}(t_0) + \alpha_i^{-1}\beta_i(t_0) \right) x_i(t_0) > 0, \end{aligned} \tag{3.13}$$

which is not possible. Thus, $x_i(t_0) \geq m$. By iteration, this proves Step 1.

Step 2. Next, for any T_0 as in (3.10) and $s_0 := \min\{x_j(t) : 1 \leq j \leq n, t \in [T_0, T_0+\tau]\}$, we shall show the estimate

$$\min_j \min_{t \in [T_0+\tau, T_0+2\tau]} x_j(t) \geq s_1,$$

where

$$s_1 := \min\left\{ m, \min_j \left(\alpha_j H_j(s_0) \right) \right\}.$$

To simplify the exposition, take $T_0 = 0$. In this way, we denote $s_0 := \min\{x_j(t) : 1 \leq j \leq n, t \in [0, \tau]\} > 0$. If $s_0 \geq m$, from Step 1 the proof is complete. Now, consider the case $s_0 < m$. By the definition of m, $h_j^-(s_0)\alpha_j = H_j(s_0)\alpha_j > s_0$ for all j, thus $s_1 > s_0$. We claim that

$$\min_j \min_{t \in [\tau, 2\tau]} x_j(t) \geq s_1. \tag{3.14}$$

Otherwise, there are $t_1 \in [\tau, 2\tau]$ and $i \in \{1, \dots, n\}$ such that $x_i(t_1) < s_1$ and $x_j(t) \geq x_i(t_1)$ for all $t \in [\tau, t_1]$ and $j \in \{1, \dots, n\}$.

Since $x_i(t_1 - \tau_{ik}(t_1)) \geq \min\{s_0, x_i(t_1)\}$, we have $H_i(x_i(t_1 - \tau_{ik}(t_1))) \geq \min\{H_i(s_0), H_i(x_i(t_1))\}$. We now consider two cases separately.

If $s_0 \geq x_i(t_1)$, then $H_i(s_0) \geq H_i(x_i(t_1))$ and we get (3.13) with t_0 replaced by t_1, thus a contradiction.

If $s_0 < x_i(t_1)$, then $H_i(s_0) < H_i(x_i(t_1))$. Since $x_i(t_1) < s_1 \leq \alpha_i H_i(s_0)$, we derive

$$0 \geq x_i'(t_1) \geq \left(-d_i(t_1) + \sum_{j=1}^{n} a_{ij}(t_1) \right) x_i(t_1) + \beta_i(t_1) H_i(s_0)$$
$$> \left(-d_i(t_1) + \sum_{j=1}^{n} a_{ij}(t_1) + \beta_i(t_1)\alpha_i^{-1} \right) x_i(t_1) > 0,$$

which is again a contradiction. This proves the estimate (3.14).

Step 3. Now, we define by recurrence the sequence

$$s_{k+1} = \min \left\{ m, \min_j \left(\alpha_j H_j(s_k) \right) \right\}, \quad k \in \mathbb{N}_0.$$

If $s_k = m$ for some $k \in \mathbb{N}$, (3.12) follows by Steps 1 and 2. In this case, $\alpha_j H_j(s_k) > m$, hence $s_p = m$ for all $p > k$. If $s_k < m$ for all k, (s_k) is strictly increasing, because

$$s_{k+1} = \min_j \left(\alpha_j H_j(s_k) \right) > s_k.$$

For $s^* = \lim s_k$, from the definition of m we derive

$$0 < s^* \leq m \quad \text{and} \quad s^* \geq \min_j \alpha_j H_j(s^*) > s^*,$$

which is not possible. The proof is complete. □

Remark 3.2. We observe that assumptions (h2) and (3.9) are satisfied if $\liminf_{t\to\infty} \beta_i(t) > 0$ and

$$\gamma_i \geq \frac{\beta_i(t) v_i}{d_i(t) v_i - \sum_{j \neq i} a_{ij}(t) v_j} \geq \alpha_i > 1, \quad \text{for} \quad t \geq T_0,\ i = 1, \dots, n, \tag{3.15}$$

for some vector $v = (v_1, \dots, v_n) \gg 0$ and constants α_i, γ_i.

Example 3.1. Consider the system

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t) x_j(t) + \beta_i(t) \frac{x_i(t - \tau_i(t)))}{1 + c_i(t) x_i^{\alpha_i}(t - \tau_i(t))},\ i = 1, \dots, n,\ t \geq 0, \tag{3.16}$$

where $\alpha_i \geq 1$, $d_i(t) > 0, a_{ij}(t) \geq 0, c_i(t), \beta_i(t), \tau_i(t) \geq 0$ are continuous and bounded and $0 < c_i^- \leq c_i(t) \leq c_i^+, \beta_i(t) \geq \beta_i^- > 0$, $t \geq 0, i = 1, \dots, n$. For $h_i(t, x) = x(1 + c_i(t)x^{\alpha_i})^{-1}, h_i^{\pm}(x) = x(1 + c_i^{\mp} x^{\alpha_i})^{-1}$, we have $h_i^-(x) \leq h_i(t, x) \leq h_i^+(x)$, $h_i^{\pm}(0) = 0, (h_i^{\pm})'(0) = 1$ and $0 < h_i^-(x) \leq h_i^+(x) < x$ for $x > 0$. For each vector $v = (v_1, \dots, v_n) \gg 0$, define

$$l_i(v) = \liminf_{t\to\infty} \frac{\beta_i(t) v_i}{d_i(t) v_i - \sum_{j \neq i} a_{ij}(t) v_j},\ L_i(v) = \limsup_{t\to\infty} \frac{\beta_i(t) v_i}{d_i(t) v_i - \sum_{j \neq i} a_{ij}(t) v_j}, \quad i = 1, \dots, n.$$

From Theorem 3.2 and Remark 3.2, the zero solution of (3.16) is GAS if there exists $v \gg 0$ such that $L_i(v) < 1$ for all i, whereas (3.16) is permanent if there exists $v \gg 0$ such that $1 < l_i(v), L_i(v) < \infty$ for all i.

A careful reading of the proof above leads to several generalizations. First, it is clear that, in the statement of Theorem 3.3, hypothesis (h2) can actually be replaced by the dissipativeness of the system. Having this in mind, one also sees that the same arguments apply to dissipative systems more general than (3.1), where, in each equation i, the instantaneous terms $a_{ij}(t)x_j(t)$ are replaced by linear delayed terms and the nonlinear terms are as in (3.3). This is expressed in the next theorem.

Theorem 3.4. *Consider a non-autonomous system of one of the forms*

$$\begin{aligned} x_i'(t) = -d_i(t)x_i(t) &+ \sum_{j=1, j\neq i}^{n} a_{ij}(t) \int_{-\tau}^{0} x_j(t+s)\, d_s\nu_{ij}(t,s) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t) \int_{-\tau}^{0} h_{ik}(s, x_i(t+s))\, d_s\eta_{ik}(t,s),\ \ i=1,\dots,n,\ \ t\geq 0, \end{aligned} \tag{3.17}$$

$$\begin{aligned} x_i'(t) = -d_i(t)x_i(t) &+ \sum_{j=1, j\neq i}^{n} a_{ij}(t) \int_{-\tau}^{0} x_j(t+s)\, d_s\nu_{ij}(t,s) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t) h_{ik}\left(t, \int_{-\tau}^{0} x_i(t+s)\, d_s\eta_{ik}(t,s)\right),\ \ i=1,\dots,n,\ \ t\geq 0, \end{aligned} \tag{3.18}$$

where: $d_i(t), a_{ij}(t), \beta_{ik}(t), h_{ik}(t,x)$ satisfy (h1), (h3) and (h4); the measurable functions ν_{ij}, η_{ik} : $[0,\infty)\times[-\tau,0]\to\mathbb{R}$ are continuous from the left in s, $\nu_{ij}(t,\cdot), \eta_{ik}(t,\cdot)$ are non-decreasing and normalized so that

$$\int_{-\tau}^{0} d_s\nu_{ij}(t,s) = \int_{-\tau}^{0} d_s\eta_{ik}(t,s) = 1, \quad i,j=1,\dots,n, k=1,\dots,m, t\geq 0.$$

Assume also that (3.17)*, or* (3.18)*, is dissipative and that* (3.9) *is satisfied for some $v, \eta \gg 0$. Then, the system is uniformly persistent.*

We now apply the previous theorems to the Nicholson system (3.5).

Theorem 3.5. *Consider system* (3.5)*, where $d_i, a_{ij}, \beta_{ik}, c_{ik}, \tau_{ik} : [0,\infty)\to[0,\infty)$ are continuous and bounded, with $d_i(t), \beta_i(t) = \sum_{k=1}^{m}\beta_{ik}(t)$ strictly positive and $c_{ik}(t)\geq c_i > 0$ on $[0,\infty)$, for all i,j,k. With the notation in* (3.4)*, assume that there exist a vector $u \gg 0$ and $\delta > 0, T_0 \geq 0$ such that $[D(t)-A(t)]u \geq \delta\mathbf{1}$ for $t\geq T_0$. Then:*

(i) Eq. (3.5) *is dissipative.*

(ii) If there exist a vector $v \gg 0$ and $T_0 \geq 0$ such that $M(t)v \leq 0$ for $t \geq T_0$ and either $\liminf_{t\to\infty}\beta_i(t) \gg 0$ or $\limsup_{t\to\infty}(M(t)v)_i \ll 0\, (1\leq i\leq n)$, the zero solution of (3.5) *is GAS.*

(iii) If there exist vectors $v \gg 0, \eta \gg 0$ such that $M(t)v \geq \eta$ for $t\geq T_0$, then (3.5) *is permanent.*

Example 3.2. Consider the planar system

$$\begin{aligned} x_1'(t) &= -(1+\cos^2 t)x_1(t) + \gamma_1(1+\sin^2 t)x_2(t) + \sum_{j=1}^{m}(\beta_{1j}+f_{1j}(t))x_1(t-\tau_{1j}(t))e^{-c_{1j}(t)x_1(t-\tau_{1j}(t))}, \\ x_2'(t) &= -(1+\sin^2 t)x_2(t) + \gamma_2(1+\cos^2 t)x_1(t) + \sum_{j=1}^{m}(\beta_{2j}+f_{2j}(t))x_2(t-\tau_{2j}(t))e^{-c_{2j}(t)x_2(t-\tau_{2j}(t))}, \end{aligned} \tag{3.19}$$

where $\gamma_i > 0, \beta_{ij} \geq 0$ with $\beta_i := \sum_{j=1}^m \beta_{ij} > 0$, all the functions $f_{ij}(t), c_{ij}(t), \tau_{ij}(t)$ are continuous, nonnegative and bounded on $[0,\infty)$, with $c_{ij}(t)$ bounded below by positive constants, for $t \geq 0, i = 1,2, j = 1,\dots,m$. Write $f_i(t) := \sum_{j=1}^m f_{ij}(t)$, let f_i^-, f_i^+ be such that $0 \leq f_i^- \leq f_i(t) \leq f_i^+$ for $t \geq 0$ and denote $\beta_i^- = \beta_i + f_i^-, \beta_i^+ = \beta_i + f_i^+$, $i = 1,2$. With the notation in (3.4), we have

$$D(t) - A(t) = \begin{bmatrix} 1+\cos^2 t & -\gamma_1(1+\sin^2 t) \\ -\gamma_2(1+\cos^2 t) & 1+\sin^2 t \end{bmatrix},$$
$$M(t) = \begin{bmatrix} \beta_1 + f_1(t) - (1+\cos^2 t) & \gamma_1(1+\sin^2 t) \\ \gamma_2(1+\cos^2 t) & \beta_2 + f_2(t) - (1+\sin^2 t) \end{bmatrix}.$$

Consider a vector $u = (1, u_2)$ with $u_2 > 0$, and write $[D(t) - A(t)]u = \begin{bmatrix} \delta_1(t) \\ \delta_2(t) \end{bmatrix}$. Since $\min \delta_1(t) = 1 - 2u_2\gamma_1, \min \delta_2(t) = u_2 - 2\gamma_2$, if

$$4\gamma_1\gamma_2 \leq 1 \tag{3.20}$$

we can find u_2 such that $2\gamma_2 \leq u_2 \leq (2\gamma_1)^{-1}$, implying that $[D(t) - A(t)]u \geq 0$ for $t \in \mathbb{R}$. On the other hand, $\delta_1(\frac{\pi}{4}) = \frac{3}{2}(1 - u_2\gamma_1) > 0, \delta_2(\frac{\pi}{4}) = \frac{3}{2}(-\gamma_2 + u_2) > 0$. By Theorem 2.1, we conclude that the ODE $x' = -[D(t) - A(t)]x$ is globally exponentially stable.

We now look for a vector $v = (1, v_2) \gg 0$ such that $M(t)v \geq \eta \gg 0$. Write $M(t)v = \begin{bmatrix} m_1(t) \\ m_2(t) \end{bmatrix}$ and observe that $m_1(t) \geq \eta_1 := \beta_1^- - 2 + v_2\gamma_1$, $m_2(t) \geq \eta_2 := v_2(\beta_2^- - 2) + \gamma_2$, $t \geq 0$. Now assume that:

$$\text{either} \quad \beta_1^- \geq 2 \quad \text{or} \quad \beta_2^- \geq 2 \quad \text{or} \quad (2 - \beta_1^-)(2 - \beta_2^-) < \gamma_1\gamma_2. \tag{3.21}$$

One easily verifies that: (i) if either $\beta_1^- \geq 2$ or $\beta_2^- \geq 2$, one can find $v_2 > 0$ such that $\eta_1 > 0, \eta_2 > 0$; (ii) if $\beta_i^- < 2$ for $i = 1,2$, and $(2 - \beta_1^-)(2 - \beta_2^-) < \gamma_1\gamma_2$, for any v_2 such that $(2 - \beta_1)\gamma_1^{-1} < v_2 < \gamma_2(2 - \beta_2)^{-1}$ we have $M(t)v \geq \eta = (\eta_1, \eta_2) \gg 0$. From Theorem 3.5.(iii), conditions (3.20)-(3.21) imply that (3.19) is permanent.

As an illustration, with $m = 1$ and $\beta_1 = 2, \gamma_1 = 1 = 4\gamma_2, f_1(t) = f_2(t) = 0$, we conclude that

$$\begin{aligned} x_1'(t) &= -(1+\cos^2 t)x_1(t) + (1+\sin^2 t)x_2(t) + 2x_1(t - \tau_{1j}(t))e^{-c_{1j}(t)x_1(t-\tau_{1j}(t))} \\ x_2'(t) &= -(1+\sin^2 t)x_2(t) + \frac{1}{4}(1+\cos^2 t)x_1(t) + \beta_2 x_2(t - \tau_{2j}(t))e^{-c_{2j}(t)x_2(t-\tau_{2j}(t))} \end{aligned} \tag{3.22}$$

is permanent for any $\beta_2 > 0$.

On reverse, if $\beta_i^+ < 1$, $i = 1,2$, for a positive vector $v = (1, v_2)$ we obtain $M(t)v = \begin{bmatrix} m_1(t) \\ m_2(t) \end{bmatrix}$ with $m_1(t) \leq \eta_1 := \beta_1^+ - 1 + 2v_2\gamma_1,\ m_2(t) \leq \eta_2 := v_2(\beta_2^+ - 1) + 2\gamma_2,\ t \geq 0$. At this point, assume

$$\beta_i^+ < 1,\ i = 1,2 \quad \text{and} \quad 4\gamma_1\gamma_2 \leq (1 - \beta_1^+)(1 - \beta_2^+). \tag{3.23}$$

Thus, choosing v_2 such that $2\gamma_2(1 - \beta_2^+)^{-1} \leq v_2 \leq (2\gamma_1)^{-1}(1 - \beta_1^+)$ we obtain $M(t)v \leq 0$ for all $t \geq 0$. From Theorem 3.5.(ii), conditions (3.23) imply that the trivial solution of (3.19) is GAS. In particular, this is the case of the zero solution of

$$\begin{aligned} x_1'(t) &= -(1+\cos^2 t)x_1(t) + \frac{1}{4}(1+\sin^2 t)x_2(t) + \frac{1}{2}x_1(t - \tau_{1j}(t))e^{-c_{1j}(t)x_1(t-\tau_{1j}(t))} \\ x_2'(t) &= -(1+\sin^2 t)x_2(t) + \frac{1}{4}(1+\cos^2 t)x_1(t) + \beta_2 x_2(t - \tau_{2j}(t))e^{-c_{2j}(t)x_2(t-\tau_{2j}(t))} \end{aligned} \tag{3.24}$$

for any $0 < \beta_2 \leq \frac{1}{2}$.

Remark 3.3. In recent years, some attention has been given to Nicholson's blowflies equations and systems with *harvesting*. For the n-dimensional case, such systems are obtained by adding linear harvesting terms with delays to (3.5), so that it becomes:

$$\begin{aligned} x_i'(t) =& -d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t)x_i(t-\tau_{ik}(t))e^{-c_{ik}(t)x_i(t-\tau_{ik}(t))} - H_i(t)x_i(t-\sigma_i(t)), \quad i = 1, \dots, n, \end{aligned} \tag{3.25}$$

where the new coefficients $H_i(t)$ and delays $\sigma_i(t)$ are continuous, nonnegative and bounded. For the scalar case of (3.25), Liu [18] studied both the global exponential stability of the zero solution and the permanence. The almost periodic scalar case of (3.25) was studied in [30], and the n-dimensional case in [28], where the authors established criteria for the existence and global exponential stability of a positive almost periodic solution by using properties of almost periodic functions and Lyapunov functionals. See also [31] for a periodic system (3.25) with $n = 2$. From the proof of Theorem 3.2, we deduce that Theorem 3.5.(ii), on the global asymptotic stability of the zero solution, applies to (3.5) replaced by (3.25), without any changes. However, the result on permanence in Theorem 3.5.(iii) does not carry over to (3.25). An interesting open problem is to generalize our results, and find sufficient conditions for the permanence of (3.25).

Remark 3.4. In [9], Faria studied the persistence and permanence of a class of *cooperative* DDEs with possible *infinite* delay of the form $x_i'(t) = F_i(x_t) - x_i(t)G_i(x_t)$, $1 \leq i \leq n$. By using properties of cooperative systems, it was shown that, under some additional conditions, all positive solutions are bounded below and above by positive equilibria, which in particular proves the permanence. The persistence and permanence for the non-autonomous system $x_i'(t) = F_i(t, x_t) - x_i(t)G_i(t, x_t)$, $1 \leq i \leq n$, was also addressed in [9] by comparing it above and below with autonomous cooperative systems. Although the basic idea is similar (comparison of solutions with solutions of cooperative systems), the results and techniques in [9] do not apply to the study of systems (3.1): not only does (3.1) not have the above form, but the nonlinearities $h_{ik}(t, x)$ are in general non-monotone on the second variable. On the other hand, this remark raises another interesting open problem: how to extend the results about permanence in this paper to systems with *infinite delay*, since it is clear that the proof of Theorem 3.3 does not work for the infinite delay case.

4 Sharp criteria for systems with autonomous coefficients

The case of an autonomous system (3.1), or of (3.1) with constant coefficients but time-varying delays, is particularly important in applications. For these situations, the matrices A, B, D, M in (3.4) are autonomous, and their properties play an important role in the analysis of the asymptotic behaviour of solutions. For the sake of completeness and convenience of the reader, some elements from matrix theory will be recalled here. We start with some definitions.

Definition 4.1. *Let $N = [n_{ij}]$ be a square matrix. The matrix N is said to be* **reducible** *if there is a simultaneous permutation of rows and columns that brings N to the form*

$$\begin{bmatrix} N_{11} & 0 \\ N_{21} & N_{22} \end{bmatrix},$$

with N_{11} and N_{22} square matrices; N is an **irreducible matrix** *if it is not reducible. For N with nonpositive off-diagonal entries (i.e., $n_{ij} \leq 0$ for $i \neq j$), N is said to be a* **non-singular M-matrix** *if all its eigenvalues have positive real parts. We say that N is a* **cooperative matrix** *if it has nonnegative off-diagonal entries (i.e., $n_{ij} \geq 0$ for $i \neq j$).*

The reader should be aware that many authors use the term *M-matrix* with the above meaning of the term *non-singular M-matrix*. For alternative definitions and properties of M-matrices, see [11]. Namely, it is important to remark that, for a square matrix N with nonpositive off-diagonal entries, N is a non-singular M-matrix if and only if there exists a vector $u \gg 0$ such that $Nu \gg 0$.

System (3.1) with constant coefficients becomes

$$x_i'(t) = -d_i x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij} x_j(t) + \sum_{k=1}^{m} \beta_{ik} h_{ik}(x_i(t - \tau_{ik}(t))), \; i = 1, \dots, n, \; t \geq 0, \tag{4.1}$$

and hypothesis (h4) translates simply as

(h4*) $h_{ik} : [0, \infty) \to [0, \infty)$ are bounded, locally Lipschitzian and continuously differentiable on a vicinity of 0^+, with $h_{ik}(0) = 0, h_{ik}'(0) = 1$ and $h_{ik}(x) > 0$ for $x > 0$, $i \in \{1, \dots, n\}, k \in \{1, \dots, m\}$.

For (4.1), the results in the previous section are summed up in the following theorem:

Theorem 4.1. *Consider system* (4.1)*, where $d_i > 0$, $a_{ij} \geq 0, \beta_{ik} \geq 0$ with $\beta_i := \sum_{k=1}^{m} \beta_{ik} > 0$, $h_{ik}, \tau_{ik} : [0, \infty) \to [0, \infty)$ are continuous, with $\tau_{ik}(t)$ uniformly bounded from above by some $\tau > 0$, $i, j = 1, \dots, n, k = 1, \dots, m$, and suppose that (h4*) is satisfied. Define the $n \times n$ matrices*

$$A = [a_{ij}], \; B = diag\,(\beta_1, \dots, \beta_n), \; D = diag\,(d_1, \dots, d_n), \; M = B - D + A, \tag{4.2}$$

where $a_{ii} := 0$ $(1 \leq i \leq n)$, and assume that $D - A$ is a non-singular M-matrix. Then:

(i) (4.1) *is dissipative;*

(ii) If in addition $h_i^+(x) := \max_{1 \leq k \leq m} h_{ik}(x) < x$ for $x > 0, i = 1, \dots, n$, and there exists a vector $v \gg 0$ such that $Mv \leq 0$, the trivial solution of (4.1) *is GAS;*

(iii) If there exists a vector $v \gg 0$ such that $Mv \gg 0$, (4.1) *is permanent.*

For an $n \times n$ matrix N, the *spectral bound* or *stability modulus* $s(N)$ is defined by

$$s(N) = \{Re\,\lambda : \lambda \in \sigma(N)\},$$

where $\sigma(N)$ denotes the spectrum of N. For a cooperative and irreducible matrix N, it is well-known that the spectral bound $s(N)$ is a (simple) eigenvalue, with a strictly positive associated eigenvector, see Appendix A.5 of [26]; moreover, $s(N) > 0$ if and only if there exists a strictly positive vector $v \in \mathbb{R}^n$ with $Nv \gg 0$ [10]. Thus, a threshold criterion of permanence versus extinction is obtained from Theorem 4.1 when A is an irreducible matrix.

Corollary 4.1. *Assume all the general hypotheses of Theorem 4.1 (including (h4*) and that $D - A$ is a non-singular M-matrix) are satisfied. Further assume that A is irreducible and $h_i^+(x) < x$ for $x > 0, i = 1, \ldots, n$. Then: (i) if $s(M) \leq 0$, the trivial solution of* (4.1) *is GAS; (ii) if $s(M) > 0$,* (4.1) *is permanent.*

This threshold criterion is not valid, in general, when A (and therefore M as well) is reducible. Our next task is to replace the assumptions in Theorem 4.1 by sharp conditions for extinction versus permanence when M is reducible. We emphasize that usually the case of a reducible community matrix M is not treated in the literature.

By an adequate simultaneous permutation of rows and columns, which amounts to a permutation of the variables in the original system (4.1), we may suppose that the $n \times n$-matrix A has been transformed into the triangular form

$$A = \begin{bmatrix} A_{11} & 0 & \ldots & 0 \\ A_{21} & A_{22} & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ A_{k1} & A_{k2} & \ldots & A_{kk} \end{bmatrix}, \tag{4.3}$$

where the diagonal blocks $A_{11}, \ldots, A_{kk}$ are square matrices of size $n_1, \ldots, n_k$ respectively, $n_1 + \cdots + n_k = n$, and are irreducible. Clearly, $k = 1$ if A is irreducible. Observe that a square $n \times n$-matrix $A = [a_{ij}]$ is *irreducible* if and only if for any nonempty proper subset $I \subset \{1, \ldots, n\}$ there are $i \in I$ and $j \in \{1, \ldots, n\} \setminus I$ such that $a_{ij} \neq 0$.

The next result extends Corollary 4.1 and gives necessary and sufficient conditions for both the uniform persistence and the global asymptotic stability of the zero solution of (4.1), in the case of a reducible matrix A. The result for uniform persistence was inspired by [21].

Theorem 4.2. *Consider system* (4.1) *where $d_i > 0$, $a_{ij} \geq 0$, $\beta_{ik} \geq 0$ with $\beta_i := \sum_{k=1}^m \beta_{ik} > 0$, $\tau_{ik} : [0, \infty) \to [0, \infty)$ are continuous and bounded, the functions h_{ik} satisfy (h4*) with $h_i^+(x) := \max_{1 \leq k \leq m} h_{ik}(x) < x$ for any $x > 0$, for $i, j = 1, \ldots, n$, $k = 1, \ldots, m$. Let A, B, D, M be the matrices defined in* (4.2)*. Assume that $D - A$ is a non-singular M-matrix. Without loss of generality, further assume that A has the block lower triangular structure as in* (4.3)*, with irreducible diagonal blocks $A_{11}, \ldots, A_{kk}$, and denote by M_{jj} the associated blocks in the matrix M, that is, $M_{jj} = B_j - D_j + A_{jj}$, with $B_j = diag(\beta_i)_{i \in I_j}$ and $D_j = diag(d_i)_{i \in I_j}$, where I_j is the set formed by the n_j indexes corresponding to the rows of the block A_{jj}, for each $j = 1, \ldots, k$; and $M_{ij} = A_{ij}$ for $1 \leq j < i \leq k$. Then:*

(i) System (4.1) *is uniformly persistent if and only if $s(M_{jj}) > 0$ for every index $j \in \{1, \ldots, k\}$ such that, except for the diagonal block M_{jj}, all the other blocks on the row are null.*

(ii) The null solution of system (4.1) *is GAS if and only if $s(M) \leq 0$.*

Proof. In the case of A irreducible, the results are given in Corollary 4.1. From now on, A is assumed to be a reducible matrix with the triangular form (4.3) with $k > 1$. We make a few remarks beforehand.

First, observe that the property of $D - A$ being a non-singular M-matrix is preserved under a simultaneous permutation of rows and columns (so that $D - A$ becomes $P(D - A)P^T$ for some orthogonal matrix P), therefore system (4.1) is dissipative, and thus the uniform persistence in (i) can actually be replaced by the permanence. Secondly, for each $j = 1, \dots, k$, we consider the lower dimensional system associated with the irreducible block M_{jj}, formed by the n_j equations

$$x_i'(t) = -d_i\, x_i(t) + \sum_{p\in I_j, p\neq i} a_{ip}\, x_p(t) + \sum_{q=1}^{m} \beta_{iq}\, h_{iq}(x_i(t-\tau_{iq}(t)))\,,\ i \in I_j\,,\ t \geq 0\,, \qquad (4.4)$$

and observe that it satisfies all the hypotheses in Corollary 4.1, as $D_j - A_{jj}$ is a non-singular M-matrix as well. Finally, for any vector v in $\mathbb{R}^n$ or any map v taking values in $\mathbb{R}^n$, we introduce the notation $v^j = (v_i)_{i\in I_j}$ for each $j = 1, \dots, k$, so that $v = (v^1, \dots, v^k)$.

(i) To simplify the writing, we may assume without loss of generality that the diagonal blocks in (4.3) with all null blocks to their left (if any) are placed in the first rows. In other words, we assume that $\{A_{11}, \dots, A_{ll}\}$ are exactly the diagonal blocks with all other blocks on their row null, for some $1 \leq l \leq k$. In this way, for $1 \leq j \leq l$, system (4.4) is just a lower dimensional decoupled subsystem of system (4.1).

Now, suppose that system (4.1) is uniformly persistent. Then, for each $j = 1, \dots, l$, system (4.4) naturally inherits the property of uniform persistence from the total system, and Corollary 4.1 implies that $s(M_{jj}) > 0$ for any $j = 1, \dots, l$, so this is a necessary condition.

Conversely, assume that $s(M_{jj}) > 0$ for any $j = 1, \dots, l$. Applying once more Corollary 4.1, we deduce that systems (4.4) are uniformly persistent for any $j = 1, \dots, l$. Therefore, there exists $m_0 > 0$ such that for any $\phi \in C_0$, $\liminf_{t\to\infty} x_i(t, 0, \phi) \geq m_0$ for all $i \in I_1 \cup \ldots \cup I_l$. At this point, if $l = k$ the proof is complete, whereas if $l < k$ we have to deal with the remaining components of the solution.

We now consider the case $l < k$ and look at the components $x_i(t, 0, \phi)$ for $i \in I_{l+1}$. The method here is twofold: first, since there is at least a non-null block to the left of $M_{l+1,l+1}$, we will show that one component $x_{i_1}(t, 0, \phi)$ ($i_1 \in I_{l+1}$) of the solution eventually stays bounded away from 0. Secondly, once we have raised one component in I_{l+1}, we recursively raise the rest of them, one by one, by applying the irreducible character of $M_{l+1,l+1}$.

More precisely, as there is at least one non-null block to the left of $M_{l+1,l+1}$, there are indexes $i_1 \in I_{l+1}$ and $j_1 \in I_j$ for some $1 \leq j \leq l$ such that $a_{i_1 j_1} > 0$. Now, for an initial condition $\phi \in C_0$, there exists a $t_0 = t_0(\phi)$ such that $x_i(t, 0, \phi) \geq m_0$ for all $t \geq t_0$ and for all $i \in I_1 \cup \ldots \cup I_l$. Therefore, for $t \geq t_0$, $x_{i_1}'(t, 0, \phi) \geq -d_{i_1}\, x_{i_1}(t, 0, \phi) + a_{i_1 j_1}\, m_0$. Now, we consider the scalar cooperative ODE

$$y'(t) = -d_{i_1}\, y(t) + a_{i_1 j_1}\, m_0\,,\ t \geq 0\,,$$

whose solution, for the previous time $t_0 \geq 0$, is written as

$$y(t, t_0, y(t_0)) = y(t_0)\, e^{-d_{i_1}(t-t_0)} + \frac{a_{i_1 j_1}\, m_0}{d_{i_1}}(1 - e^{-d_{i_1}(t-t_0)})\,,$$

so that there exist $m_1 > 0$ and $t_1 \geq t_0$ such that $y(t, t_0, y(t_0)) \geq m_1$ for any $t \geq t_1$, provided that $y(t_0) \geq 0$. The application of a standard argument of comparison of solutions permits to conclude that $x_{i_1}(t, 0, \phi) \geq m_1$ for any $t \geq t_1$.

If $I_{l+1} = \{i_1\}$, we are done with this block. If not, as $A_{l+1,l+1}$ is irreducible, there exists an index $i_2 \in I_{l+1} \setminus \{i_1\}$ such that $a_{i_2 i_1} > 0$. As before, we consider the scalar ODE

$$y'(t) = -d_{i_2}\, y(t) + a_{i_2 i_1}\, m_1\,,\ t \geq 0\,,$$

for which we find a constant $m_2 > 0$ and a time $t_2 \geq t_1$ such that if $t \geq t_2$, $y(t, 0, y(t_1)) \geq m_2$ for any $t \geq t_2$, independently of the value $y(t_1) \geq 0$. In a similar way, we conclude that the i_2th component of the solution of (4.1) satisfies $x'_{i_2}(t, 0, \phi) \geq -d_{i_2} \, x_{i_2}(t, 0, \phi) + a_{i_2 i_1} \, m_1$ for any $t \geq t_1$, and once more, by comparing solutions, we have $x_{i_2}(t, 0, \phi) \geq m_2$ for any $t \geq t_2$.

At this point, if $I_{l+1} = \{i_1, i_2\}$ we are finished with this block; if not, as $A_{l+1,l+1}$ is irreducible, considering $\{i_1, i_2\}$ and its complement $I_{l+1} \setminus \{i_1, i_2\}$, we may affirm that there exist indexes $i_3 \in I_{l+1} \setminus \{i_1, i_2\}$ and $j \in \{i_1, i_2\}$ such that $a_{i_3 j} > 0$; now, the argument to lift the component $x_{i_3}(t, 0, \phi)$ is just the same as the one for $x_{i_2}(t, 0, \phi)$.

Iterating this procedure inside the irreducible block $A_{l+1,l+1}$, we conclude that there is a constant $m'_0 = \min\{m_0, m_1, \ldots, m_{n_{l+1}}\} > 0$ such that for any $\phi \in C_0$, there exists a $t'_0 = t'_0(\phi)$ such that $x_i(t, 0, \phi) \geq m'_0$ for all $t \geq t'_0$ and for all $i \in I_1 \cup \ldots \cup I_l \cup I_{l+1}$.

To finish, note that the procedure for the remaining components of the solution, if any, is identical to the one just developed for the set of indexes I_{l+1}.

(ii) Note that $s(M) = \max\{s(M_{11}), \ldots, s(M_{kk})\}$, so that $s(M) \leq 0$ if and only if $s(M_{jj}) \leq 0$ for $j = 1, \ldots, k$. Because of the triangular structure of A in (4.3), and with the previous notation for $\phi = (\phi^1, \ldots, \phi^k)$, it is apparent that, for $j = 2, \ldots, k$, the "faces"

$$F_j = \{\phi = (\phi^1, \ldots, \phi^k) \in C^+ \mid \phi^1 = \ldots = \phi^{j-1} = 0\}$$

of the nonnegative cone C^+ are positively invariant. In this way, for an initial condition $\phi \in F_j$ ($2 \leq j \leq k$), the solution remains in F_j, thus the component $x^j(t, 0, \phi)$ is a solution of the system (4.4).

We first assume that the null solution of (4.1) is GAS in the nonnegative cone C^+. For any $j = 1, \ldots, k$ fixed, we now show that any solution $y(t, 0, \phi^j)$ of system (4.4) with initial condition $\phi^j \in C^+([-\tau, 0]; \mathbb{R}^{n_j})$ has $\lim_{t\to\infty} y(t, 0, \phi^j) = 0$. This is clear for $j = 1$, as system (4.4) is a decoupled subsystem of system (4.1). For $j > 1$, just consider $\widetilde{\phi} \in C^+([-\tau, 0]; \mathbb{R}^n)$ with $\widetilde{\phi}^j = \phi^j$ and $\widetilde{\phi}^i = 0$ for any $i < j$, so that $\widetilde{\phi} \in F_j$. Then, $x^j(t, 0, \widetilde{\phi})$ is a solution of system (4.4), thus $y(t, 0, \phi^j) = x^j(t, 0, \widetilde{\phi}) \to 0$ as $t \to \infty$, as we wanted. With this behaviour for each j, the persistent case in Corollary 4.1 is precluded, and then it must be $s(M_{jj}) \leq 0$.

Conversely, assume that $s(M_{jj}) \leq 0$, so that there exist vectors $v^j \in \mathbb{R}^{n_j}$, $v_j \gg 0$ such that $M_{jj} \, v^j \leq 0$ for $j = 1, \ldots, k$. Without loss of generality, we suppose that $k = 2$, so that M has the form

$$M = B - D + \begin{bmatrix} A_{11} & 0 \\ A_{21} & A_{22} \end{bmatrix}, \tag{4.5}$$

where A_{ii} are $n_i \times n_i$ irreducible blocks ($i = 1, 2$). The general case of k blocks follows by iterating the procedure below.

With M given by (4.5), (4.1) is equivalent to

$$\begin{aligned} x'_i(t) &= -d_i \, x_i(t) + \sum_{p \in I_1, p \neq i} a_{ip} \, x_p(t) + \sum_{k=1}^{m} \beta_{ik} \, h_{ik}(x_i(t - \tau_{ik}(t))), \;\; i \in I_1, \, t \geq 0 \\ x'_i(t) &= -d_i \, x_i(t) + \sum_{p \in I_2, p \neq i} a_{ip} \, x_p(t) + \sum_{k=1}^{m} \beta_{ik} \, h_{ik}(x_i(t - \tau_{ik}(t))) + \sum_{p \in I_1} a_{ip} x_p(t), \;\; i \in I_2, \, t \geq 0 \, . \end{aligned} \tag{4.6}$$

We first claim that the trivial solution of (4.1) is globally attractive. Let $\phi \in C^+$, and write $x(t,0,\phi) = (x^1(t,0,\phi^1), x^2(t,0,\phi))$. (Recall that $x^1(t,0,\phi)$ is just the solution of system (4.4) for $j=1$ with initial condition ϕ^1.) Corollary 4.1 implies that $\lim_{t\to\infty} x^1(t,0,\phi^1) = 0$. In particular, in (4.6) we have $q_i(t) := \sum_{p\in I_1} a_{ip} x_p(t,0,\phi^1) \to 0$ as $t \to \infty$ for any $i \in I_2$. At this point, the proof of $\lim_{t\to\infty} x^2(t,0,\phi) = 0$ is obtained by simply repeating the argument used in the proof of Theorem 3.2 applied to the second system in (4.6). Details are omitted.

It remains to prove the stability of the null solution of (4.6). For a given $\phi = (\phi^1, \phi^2) \in C^+$, as before we denote the solution of (4.1) by $x(t,0,\phi) = (x^1(t,0,\phi^1), x^2(t,0,\phi))$.

From the assumptions on h_{ik}, for $i \in I_2$, we construct maps $\widetilde{h}_i : [0,\infty) \to [0,\infty)$ satisfying the following conditions: $\widetilde{h}_i$ are continuous, bounded, nondecreasing, equal to h_i^+ on a right neighbourhood of 0, and such that $h_i^+(x) \le \widetilde{h}_i(x) < x$ for all $x > 0$. Now, we consider an n-dimensional system, whose first n_1 equations are given by (4.4) with $j = 1$ (as in (4.6)) and the last equations given by the n_2-dimensional system

$$y_i'(t) = -d_i\, y_i(t) + \sum_{p\in I_2, p\neq i} a_{ip}\, y_p(t) + \sum_{k=1}^{m} \beta_{ik}\, \widetilde{h}_i(y_i(t-\tau_{ik}(t))) + \sum_{p\in I_1} a_{ip}\, x_p(t),\ i \in I_2, t \ge 0, \tag{4.7}$$

written for short as $y_i'(t) = \widetilde{f}_i(t, y_t)$. Since (4.7) is cooperative, a comparison of solutions leads to $x^2(t,0,\phi) \le y(t,0,\phi,\widetilde{f})$ for $t \ge 0$.

Fix any $\varepsilon > 0$. Let $\widetilde{\varepsilon} > 0$ be sufficiently small so that $\beta_i(\varepsilon v_i^2 - \widetilde{h}_i(\varepsilon v_i^2)) \ge \widetilde{\varepsilon}\, v_i^2,\ i \in I_2$. Of course, Corollary 4.1 (or Theorem 3.2) yields the stability of the null solution for the first system in (4.6), thus there is $\delta_1 = \delta_1(\varepsilon) > 0$ such that $0 \le x^1(t,0,\phi^1) \le \varepsilon v^1$ for $t \ge 0$ whenever $0 \le \phi^1 \le \delta_1 v^1$. Moreover, we find $\widetilde{\delta}_1 = \widetilde{\delta}_1(\widetilde{\varepsilon}) = \widetilde{\delta}_1(\varepsilon) > 0$ such that if $0 \le \phi^1 \le \widetilde{\delta}_1 v^1$, then $0 \le A_{21} x^1(t,0,\phi^1) \le \widetilde{\varepsilon} v^2$ for $t \ge 0$.

Take $\delta = \min(\delta_1, \widetilde{\delta}_1)$, and consider an initial condition $\phi \in C^+$ with $0 \le \phi^1 \le \delta v^1$ and $0 \le \phi^2 \le \varepsilon v^2$. We first solve the decoupled n_1-dimensional system, and replace in (4.7) the terms $\sum_{p\in I_1} a_{ip}\, x_p(t)$ by $\sum_{p\in I_1} a_{ip}\, x_p(t,0,\phi^1)$. The crucial point is to check that εv^2 is an "upper" solution for this new cooperative system, or in other words, that $\widetilde{f}(t, \varepsilon v^2) \le 0$ for any $t \ge 0$; this allows concluding that the set $[0, \varepsilon v^2] \subset C([-\tau, 0]; \mathbb{R}^{n_2})$ is positively invariant for (4.7) (see Lemma 2.3). For each $i \in I_2$, we have

$$\begin{aligned}\widetilde{f}_i(t, \varepsilon v^2) &= -d_i\, \varepsilon v_i^2 + \sum_{j\in I_2, j\neq i} a_{ij}\, \varepsilon v_j^2 + \beta_i\, \widetilde{h}_i(\varepsilon v_i^2) + \sum_{j\in I_1} a_{ij}\, x_j^1(t,0,\phi^1)\\ &= -d_i\, \varepsilon v_i^2 + \sum_{j\in I_2, j\neq i} a_{ij}\, \varepsilon v_j^2 + \beta_i \varepsilon v_i^2 + \beta_i(\widetilde{h}_i(\varepsilon v_i^2) - \varepsilon v_i^2) + \sum_{j\in I_1} a_{ij}\, x_j^1(t,0,\phi^1)\,,\end{aligned}$$

hence,

$$\widetilde{f}(t, \varepsilon v^2) \le \varepsilon M_{22}\, v^2 - \widetilde{\varepsilon}\, v^2 + \widetilde{\varepsilon}\, v^2 \le 0.$$

As a consequence, and summarizing, we deduce that, whenever $0 \le \phi^1 \le \delta v^1$ and $0 \le \phi^2 \le \varepsilon v^2$ then $0 \le x^1(t,0,\phi^1) \le \varepsilon v^1$ and $0 \le x^2(t,0,\phi^1,\phi^2) \le y(t,0,\phi^1,\phi^2) \le \varepsilon v^2$ for $t \ge 0$. This ends the proof. □

Theorem 4.2 also provides conditions for partial extinction and partial persistence. As an illustration, we summarise the results for a Nicholson system.

Example 4.1. Consider the Nicholson system with autonomous coefficients and time-dependent delays given by

$$x_i'(t) = -d_i x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij} x_j(t) + \sum_{k=1}^{m} \beta_{ik} x_i(t-\tau_{ik}(t)) e^{-c_{ik} x_i(t-\tau_{ik}(t))}, \ i = 1, \dots, n, \ t \geq 0, \quad (4.8)$$

where $d_i > 0, c_{ik} > 0, a_{ij} \geq 0, \beta_{ik} \geq 0$ with $\beta_i := \sum_{k=1}^{m} \beta_{ik} > 0$, $\tau_{ik} : [0, \infty) \to [0, \tau]$ $(\tau > 0)$ are continuous, for all i, j, k, and $D - A$ is a non-singular M-matrix. By applying Theorem 4.2 to this model, we obtain:

(i) if $s(M) \leq 0$, 0 is GAS;

(ii) if M is written in the triangular form (for some $k \in \{1, \dots, n\}$ and some $l \in \{1, \dots, k\}$)

$$M = \begin{bmatrix} M_{11} & \dots & 0 & 0 & \dots & 0 \\ \vdots & \ddots & \vdots & \vdots & & \vdots \\ 0 & \dots & M_{ll} & 0 & \dots & 0 \\ M_{l+1,1} & \dots & M_{l+1,l} & M_{l+1,l+1} & \dots & 0 \\ \vdots & & \vdots & \vdots & \ddots & \vdots \\ M_{k1} & \dots & M_{k,l} & M_{k,l+1} & \dots & M_{kk} \end{bmatrix}, \quad (4.9)$$

with M_{jj} $(1 \leq j \leq k)$ irreducible blocks and $M_{jp} \neq 0$ for some $p < j$ and $j = l+1, \dots k$, then (4.8) is permanent if and only if $s(M_{jj}) > 0$ for $j = 1, \dots, l$;

(iii) moreover, for M written in the triangular form (4.9), if $l > 1$ and there exist $p, j \in \{1, \dots, l\}$ such that $s(M_{pp}) \leq 0$ and $s(M_{jj}) > 0$, then the n_p populations $x_i(t)$ with $i \in I_p$ become extinct, whereas the n_j populations $x_i(t)$ with $i \in I_j$ uniformly persist.

Remark 4.1. In this way, we have recovered and extended all the results regarding extinction and uniform persistence established in [7, 10] for the particular case of (4.8) with constant delays τ_{ik} and $c_{ik} = 1$ for all i, k. For such autonomous systems, the sharp criterion for extinction of all populations, $s(M) \leq 0$, was proven in [10] by using the unimodal shape of the specific Ricker nonlinearity $h(x) = xe^{-x}$. However, as shown in the proof of Theorem 4.2, the techniques presented in Section 3, based on comparison of solutions with solutions for auxiliary cooperative systems, allow us to carry out the arguments for the more general model (4.1). Also, the permanence of Nicholson autonomous systems in [10] was proven under the stronger requirement of $Mv \gg 0$ for some $v \gg 0$ (and $D - A$ a non-singular M-matrix).

Acknowledgements

This work was partially supported by Fundação para a Ciência e a Tecnologia under project UID/MAT/-04561/2013 (T. Faria) and by Ministerio de Economía y Competitividad under project MTM2015-66330, and the European Commission under project H2020-MSCA-ITN-2014 (R. Obaya and A. M. Sanz).
The authors are very grateful to the referee, whose careful reading and valuable comments led to significant improvements of the manuscript.

References

[1] Bélair, J., Mackey, M., Mahaffy, J.: Age-structured and two-delays models for erythropoiesis, Math. Biosci. **241**, 109–119 (2006).

[2] Berezansky, L., Braverman, E.: Boundedness and persistence of delay differential equations with mixed nonlinearity, Appl. Math. Comput. **279**, 154–169 (2016).

[3] Berezansky, L., Braverman, E., Idels, L.: Nicholson's blowflies differential equations revisited: main results and open problems, Appl. Math. Model. **34**, 1405–1417 (2010).

[4] Berezansky, L., Idels, L., Troib, L.: Global dynamics of Nicholson-type delay systems with applications, Nonlinear Anal. RWA **12**, 436–445 (2011).

[5] Coppel, W.A.: Dichotomies in Stability Theory, Lecture Notes in Mathematics, Vol. 629, Springer-Verlag, Berlin-New York (1978).

[6] Cushing, J.M.: An Introduction to Structured Population Dynamics, Conference Series in Applied Mathematics Vol 71, SIAM, Philadelphia (1998).

[7] Faria, T.: Global asymptotic behaviour for a Nicholson model with patch structure and multiple delays, Nonlinear Anal. **74**, 7033–7046 (2011).

[8] Faria, T.: Global dynamics for Lotka-Volterra systems with infinite delay and patch structure, Appl. Math. Comput. **245**, 575–590 (2014) .

[9] Faria, T.: Persistence and permanence for a class of functional differential equations with infinite delay, J. Dyn. Diff. Equ. **28**, 1163–1186 (2016).

[10] Faria, T., Röst, G.: Persistence, permanence and global stability of an n-dimensional Nicholson system, J. Dyn. Diff. Equ. **26**, 723–744 (2014).

[11] Fiedler, M.: Special Matrices and Their Applications in Numerical Mathematics, Martinus Nijhoff Publ. (Kluwer), Dordrechit (1986).

[12] Fink, A.M.: Almost Periodic Differential Equations, Lecture Notes in Math. 377, Springer- Verlag, Berlin (1974).

[13] Gurney, W.S.C., Blythe, S.P., Nisbet, R.M.: Nicholson's blowflies revisited, Nature **287**, 17–21 (1980).

[14] Hale, J. K.: Ordinary Differential Equations, John Wiley & Sons, Inc., New York (1969).

[15] Liu, B.: Global stability of a class of delay differential equations, J. Comput. Appl. Math. **233**, 217–223 (2009).

[16] Liu, B.: Global stability of a class of Nicholson's blowflies model with patch structure and multiple time-varying delays, Nonlinear Anal. RWA **11**, 2557–2562 (2010).

[17] Liu, B.: The existence and uniqueness of positive periodic solutions of Nicholson-type delay systems, Nonlinear Anal. RWA **12**, 3145–3451 (2011).

[18] Liu, B.: Global dynamic behaviors for a delayed Nicholson's blowflies model with a linear harvesting term, Electron. J. Qual. Theory Differ. Equ. 2013 No. 45, 1–13 (2013).

[19] Mackey, M.C., Glass, L.: Oscillations and chaos in physiological control systems, Science **197**, no.4300, 287–289 (1997).

[20] Metz, J.A.J., Diekmann, O.: The Dynamics of Physiologically Structured Populations, Lecture Notes in Biomath. **68**, Springer-Verlag (1986).

[21] Novo, S., Obaya, R., Sanz, A.M.: Uniform persistence and upper Lyapunov exponents for monotone skew-product semiflows, Nonlinearity **26**, 1–32 (2013).

[22] Obaya, R., Sanz, A.M.: Uniform and strict persistence in monotone skew-product semiflows with applications to non-autonomous Nicholson systems, J. Differential Equations **261**, 4135– 4163 (2016).

[23] Sacker, R.J., Sell, G.R.: A spectral theory for linear differential systems, J. Differential Equations **27**, 320–358 (1978).

[24] Smith, H.L.: Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems, Mathematical Surveys and Monographs, Amer. Math. Soc., Providence, RI (1995).

[25] Smith, H.L.: An Introduction to Delay Differential Equations with Applications to Life Sciences, Texts in Applied Mathematics Vol. 57, Springer, Berlin (2011).

[26] Smith, H.L., Thieme, H.R.: Dynamical Systems and Population Persistence, Amer. Math. Soc., Providence, RI (2011).

[27] Takeuchi, Y., Cui, J., Miyazaki, R., Saito, Y.: Permanence of delayed population model with dispersal loss, Math. Biosci. **201**, 143–156 (2006).

[28] Wang, L.: Almost periodic solution for Nicholson's blowflies model with patch structure and linear harvesting terms, Appl. Math. Model. **37**, 2153–2165 (2013).

[29] Wang, W., Wang, L., Chen, W.: Existence and exponential stability of positive almost periodic solution for Nicholson-type delay systems, Nonlinear Analysis RWA **12**, 1938–1949 (2011).

[30] Zhang, A.: New results on almost periodic solutions for a Nicholson's blowflies model with a linear harvesting term, Electron. J. Qual. Theory Differ. Equ. 2014, No. 37, 1–14 (2014).

[31] Zhou, Q.: The positive periodic solution for Nicholson-type delay system with linear harvesting terms, Appl. Math. Model. **37** 5581–5590 (2013).