Electronic Journal of Qualitative Theory of Differential Equations
2018, No. **49**, 1–15; https://doi.org/10.14232/ejqtde.2018.1.49 www.math.u-szeged.hu/ejqtde/

Permanence for a class of non-autonomous delay differential systems

Dedicated to Professor László Hatvani on the occasion of his 75th birthday

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Received 29 December 2017, appeared 26 June 2018
Communicated by Gergely Röst

Abstract. We are concerned with 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 delay differential equations. Sufficient conditions for the exponential asymptotic stability of the linear system are established. By using this stability, the permanence of the perturbed nonlinear system is studied. Under more restrictive constraints on the coefficients, the system has a cooperative type behaviour, in which case explicit uniform lower and upper bounds for the solutions are obtained. As an illustration, the asymptotic behaviour of a non-autonomous Nicholson system with distributed delays is analysed.

Keywords: delay differential equations, persistence, permanence, stability.

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

1 Introduction

This paper concerns the study of permanence for some families of non-autonomous delay differential equations (DDEs) which have significant applications in population dynamics.

For $\tau \geq 0$, consider the Banach space $C := C([-\tau, 0]; \mathbb{R}^n)$ endowed with the norm $\|\phi\| = \max_{\theta\in[-\tau,0]} |\phi(\theta)|$, where $|\cdot|$ is a fixed norm in $\mathbb{R}^n$. We consider DDEs expressed in a general abstract form as

$$x'(t) = L(t)x_t + F(t, x_t), \qquad t \geq 0, \tag{1.1}$$

where $x_t \in C$ denotes the segment of the solution $x(t)$ given by $x_t(\theta) = x(t + \theta)$, $-\tau \leq \theta \leq 0$, $L(t) : C \to \mathbb{R}^n$ is linear bounded and continuous on t and the nonlinearities are given by continuous functions $F : [0, \infty) \times C \to \mathbb{R}^n$. As usual in mathematical biology models, we

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assume the existence of a linear instantaneous negative feedback term in each equation of (1.1). To be more precise, writing $L = (L_1, \dots, L_n)$ and $F = (F_1, \dots, F_n)$, we further assume:

$$\begin{aligned} L_i(t)\phi &= \sum_{j=1}^{n} L_{ij}(t)\phi_j, \qquad t \ge 0,\ \phi = (\phi_1, \dots, \phi_n) \in C \\ L_{ii}(t)\phi_i &= -d_i(t)\phi_i(0) + L_{ii,0}(t)\phi_i, \qquad i = 1, \dots, n, \end{aligned} \tag{1.2}$$

where $d_i(t) > 0$ and $L_{ii,0}(t)$ is non-atomic at zero (see [10] for a definition); each component F_i of the nonlinearity F depends only on t and on the ith component of the solution, so that

$$F(t, \phi) = (F_1(t, \phi_1), \dots, F_n(t, \phi_n)) \quad \text{for } t \ge 0, \phi = (\phi_1, \dots, \phi_n) \in C. \tag{1.3}$$

This family encompasses a significant number of delayed systems of differential equations used in structured population dynamics, epidemiology and other fields. For the last decade, systems of differential equations with time delays and patch structure have been extensively studied, since they have been proposed as quite realistic models to account for situations where several populations or variables are distributed over n different classes or patches, according to a variety of relevant aspects for the model, with transitions among the patches.

As a subfamily, we may restrict our attention to non-autonomous differential equations with multiple time-varying delays of the form

$$\begin{aligned} x_i'(t) = &-d_i(t)x_i(t) + \sum_{j=1}^{n} a_{ij}(t)x_j(t - \sigma_{ij}(t)) \\ &- g_i(t, x_i(t)) + f_i(t, x_i(t - \tau_{i1}(t)), \dots, x_i(t - \tau_{im}(t))), \end{aligned} \tag{1.4}$$

for $i = 1, \dots, n$, where all the coefficients and delay functions are continuous and nonnegative.

Here, we pursue the investigation in [8], where the stability and permanence of systems

$$\begin{aligned} x_i'(t) = &-d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t)h_{ik}(t, x_i(t - \tau_{ik}(t))), \qquad i = 1, \dots, n,\ t \ge 0, \end{aligned} \tag{1.5}$$

was studied. Note that (1.5) is a particular case of (1.4). Moreover, (1.5) is obtained by adding a delayed nonlinear perturbation to a linear ordinary differential equations (ODEs) of type $x'(t) = A(t)x(t)$, while in (1.4) delays are included in the linear terms.

The purpose of this paper is twofold. First, in Section 2 we generalize the setting in (1.5), by considering systems (1.1) with distributed delays in both the linear and nonlinear terms. Then, extending some ideas in [8], we give conditions for the global exponential stability of linear systems $x'(t) = L(t)x_t$. This stability and the monotone character of the linear system is exploited to further establish sufficient conditions for the permanence of (1.1). Secondly, by restricting the type of dependence on time in the nonlinearities $F(t, x_t)$ in (1.3), and taking advantage of the permanence previously established, explicit estimates for uniform lower and upper bounds of all solutions are obtained. This is the subject of Section 3. The results will be illustrated with applications to systems inspired in well-known population dynamics models.

2 Stability and permanence

In this section, we give some results on stability and permanence. We start by introducing some notation.

By C^+ we denote the cone of nonnegative functions in C, $C^+ = C([-\tau,0];[0,\infty)^n)$, and by $\operatorname{int} C^+$ its interior. Let $\le$ be the usual partial order generated by C^+: $\phi \le \psi$ if and only if $\psi - \phi \in C^+$; by $\phi \ll \psi$, we mean that $\psi - \phi \in \operatorname{int} C^+$. The relations $\ge$ and $\gg$ are defined in the obvious way; thus, we write $\psi \ge 0$ for $\psi \in C^+$ and $\psi \gg 0$ for $\psi \in \operatorname{int} C^+$. A vector $v \in \mathbb{R}^n$ is identified in C with the constant function $\psi(s) = v$ for $-\tau \le s \le 0$. For $\tau = 0$, we take $C = \mathbb{R}^n, C^+ = [0,\infty)^n$, and the induced order $\le$ is the usual partial order in $\mathbb{R}^n$.

Unless otherwise stated, we consider the maximum norm in $\mathbb{R}^n$. For a positive vector $v = (v_1,\dots,v_n)$ we denote by v^{-1} the vector $v^{-1} = (v_1^{-1},\dots,v_n^{-1})$ and by $|\cdot|_v$ the norm defined by $|x|_v = \max_{1\le i\le n}(v_i|x_i|)$ for $x = (x_1,\dots,x_n) \in \mathbb{R}^n$; the associated norm for $\phi \in C$ is $\|\phi\|_v = \max_{\theta\in[-\tau,0]} |\phi(\theta)|_v$. Hereafter, we use $\mathbf{1} = (1,\dots,1)$.

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

$$x'(t) = f(t,x_t), \quad t \in I, \tag{2.1}$$

where $I = [0,\infty)$ and $f : I \times D \to \mathbb{R}^n$ is continuous. Of course, any other choice of $I = \mathbb{R}$ or $I = [t_0,\infty)$ with $t_0 \in \mathbb{R}$ is possible. Suppose that f is sufficiently regular, 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.

Now, suppose that $[0,\infty)$ is the maximal interval of existence for any solution $x(t,0,\phi)$ of (2.1) with initial condition $x_0 = \phi \in D$, and write $f = (f_1,\dots,f_n)$. The DDE (2.1) is said to be *cooperative* if it satisfies Smith's quasimonotone condition given by

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

Similarly to what happens for ODEs, there is a comparison result between solutions for two distinct DDEs $x'(t) = f(t,x_t)$ and $x'(t) = g(t,x_t)$, if $f \le g$ and at least one of the functions f or g is cooperative. See Smith's monograph [15], for further definitions and relevant properties of cooperative systems.

Consider a non-autonomous linear differential equation with distributed delays

$$x'(t) = L(t)x_t \tag{2.2}$$

with $L(t)$ as in (1.2). We further write (2.2) in the form

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1}^n \int_{-\tau}^0 x_j(t+s)d_s\nu_{ij}(t,s), \qquad i = 1,\dots,n,\ t \ge 0, \tag{2.3}$$

for which the following assumptions will be imposed:

(L1) the functions $d_i : [0,\infty) \to (0,\infty)$ are continuous; the measurable functions $\nu_{ij}(t,s)$ are bounded, nondecreasing in $s \in [-\tau,0]$, with the total variation $\operatorname{Var}_{[-\tau,0]} \nu_{ij}(t,\cdot)$ of $\nu_{ij}(t,\cdot)$ on $[-\tau,0]$, given by

$$a_{ij}(t) := \int_{-\tau}^0 d_s\nu_{ij}(t,s) = \nu_{ij}(t,0) - \nu_{ij}(t,-\tau), \tag{2.4}$$

a continuous function on $t \ge 0$, for $i,j \in \{1,\dots,n\}$;

(L2) there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $T \geq 0$ such that $d_i(t)v_i - \sum_{j=1}^n a_{ij}(t)v_j \geq 0$ for all $t \geq T$, $i = 1, \dots, n$.

A stronger version of (L2) will be often considered:

(L2*) there exist a vector $v = (v_1, \dots, v_n) \gg 0$ and $T \geq 0$, $\delta > 0$ such that $d_i(t)v_i - \sum_{j=1}^n a_{ij}(t)v_j \geq \delta$ for all $t \geq T$, $i = 1, \dots, n$.

Define the $n \times n$ matrix-valued functions

$$D(t) = \operatorname{diag}(d_1(t), \dots, d_n(t)), \quad A(t) = [a_{ij}(t)] \quad \text{for } t \in [0, \infty).$$

Assumptions (L2), respectively (L2*), are thus simply written as: there exist a vector $v \gg 0$ and $T \geq 0$ such that $[D(t) - A(t)]v \geq 0$, respectively $[D(t) - A(t)]v \geq \delta \mathbf{1}$ for some $\delta > 0$, for all $t \geq T$.

Observe that the particular case of (2.3) with time-varying discrete delays given by

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1}^n a_{ij}(t)x_j(t - \sigma_{ij}(t)), \qquad i = 1, \dots, n, \tag{2.5}$$

is obtained with $\nu_{ij}(t,s) = a_{ij}(t)H_{-\sigma_{ij}(t)}(s)$, where $H_t(s)$ is the Heaviside function $H_t(s) = 0$ if $s \leq t$, $H_t(s) = 1$ if $s > t$, the delay functions $\sigma_{ij}(t)$ are continuous and satisfy $0 \leq \sigma_{ij}(t) \leq \tau$.

The theorem below addresses the asymptotic behaviour of the linear DDE (2.3), as well as the dissipativeness for systems obtained by adding a bounded perturbation $f(t, x_t)$ to (2.3).

Theorem 2.1. *Consider the non-autonomous linear equation* (2.3).

(i) If (L1) is satisfied, (2.3) *is cooperative and the cone C^+ is positively invariant.*

(ii) If (L1), (L2) are satisfied, (2.3) *is uniformly stable. Moreover, for v and T as in (L2), $|x(t, t_0, \varphi)|_{v^{-1}} \leq \|\varphi\|_{v^{-1}}$, $t \geq t_0 \geq T, \varphi \in C$.*

(iii) If (L1), (L2) are satisfied and $a_{ij}(t)$ are bounded functions for all i, j,* (2.3) *is globally exponentially stable on $[0, \infty)$; in other words, there exist $k, \alpha > 0$ such that $|x(t, t_0, \varphi)| \leq ke^{-\alpha(t - t_0)}\|\varphi\|$ for all $t \geq t_0 \geq 0$ and $\varphi \in C$.*

(iv) If (L1), (L2) are satisfied, and $f \colon [0, \infty) \times C \to \mathbb{R}^n$ is continuous and bounded, $f = (f_1, \dots, f_n)$, then all solutions of the DDE*

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1}^n \int_{-\tau}^0 x_j(t+s)d_s\nu_{ij}(t,s) + f_i(t, x_t), \qquad t \geq 0,\ i = 1, \dots, n, \tag{2.6}$$

are defined on $[0, \infty)$ and (2.6) *is dissipative, i.e., there exists $M > 0$ such that $\limsup_{t \to \infty} |x(t)| \leq M$ for any solution $x(t)$ of* (2.6).

Proof. (i) Write (2.3) in the form (2.2), where $L(t) = (L_1(t), \dots, L_n(t)) : C \to \mathbb{R}^n$ is linear bounded for $t \geq 0$. From hypothesis (L1), $\nu_{ij}(t,s)$ are nondecreasing, thus $a_{ij}(t) \geq 0$, and L satisfies (Q). Clearly, the linearity of L also implies that $L_i(t)\phi \geq 0$ for all $i = 1, \dots, n, t \geq 0$ whenever $\phi \in C^+$ and $\phi_i(0) = 0$. Thus, the set C^+ is positively invariant for (2.3) [15, p. 82].

(ii) Rescaling the variables by $\hat{x}_i(t) = v_i^{-1}x_i(t)$ $(1 \leq i \leq n)$, where $v = (v_1, \dots, v_n) \gg 0$ is a vector as in (L2), we obtain a new linear DDE $\hat{x}'(t) = \hat{L}(t)\hat{x}_t$, where the corresponding matrices $\hat{D}(t) = \operatorname{diag}(\hat{d}_1(t), \dots, \hat{d}_n(t))$ and $\hat{A}(t) = [\hat{a}_{ij}(t)]$ have entries $\hat{d}_i(t) = d_i(t)$ and

$\hat{a}_{ij}(t) = v_i^{-1} a_{ij}(t) v_j$. In this way, and after dropping the hats for simplicity, we may consider (2.3) where $v = \mathbf{1} := (1, \dots, 1)$ is the positive vector in (L2) and $|x|_{v^{-1}} = \max_{1 \le i \le n} |x_i|$. We now adapt some argument in [8].

Let $x(t) \neq 0$ be a solution of (2.3). To prove the claim, we show that $\|x_t\| \le \|x_{t_0}\|$ on each fixed interval $J = [t_0, t_1]$, $T \le t_0 < t_1$. Define $u_j = \max_{[t_0 - \tau, t_1]} |x_j(t)|$, and let $u_i = \max_{1 \le j \le n} u_j$, with $u_i = |x_i(t_*)|$ for some $t_* \in [t_0 - \tau, t_1]$. If $t_* \in [t_0 - \tau, t_0]$, then $\|x_t\| \le \|x_{t_0}\|$ for $t \in J$. If $t_* \in J$, it suffices to show that $|x_i(t)|$ is non-increasing on J, or, in other words, 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 $D_i(t) = \int_{t_0}^t d_i(s)\, ds$, from (L2) and the definition of $a_{ij}(t)$, we derive $x_i'(t) + d_i(t) x_i(t) \le d_i(t) u_i$ for $t \in J$. Hence

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

For $t = t_*$, we obtain $u_i e^{-D_i(t_*)} \le x_i(t_0) e^{-D_i(t_*)}$, which implies $u_i = x_i(t_0)$.

(iii) Without loss of generality, take $v = \mathbf{1}$ and $T, \delta > 0$ in (L2*), and let $M > 0$ be such that $\sum_j a_{ij}(t) \le M$, for all $t \ge T$, $i = 1, \dots, n$. Effect the change of variables $y(t) = e^{\varepsilon t} x(t)$ for a small $\varepsilon > 0$ to be determined later. The linear DDE (2.3) is transformed into

$$y_i'(t) = -\tilde{d}_i(t) y_i(t) + \sum_{j=1}^n \int_{-\tau}^0 e^{-\varepsilon s} y_j(t+s) d_s \nu_{ij}(t,s), \qquad i = 1, \dots, n,\ t \ge 0,$$

or equivalently,

$$y_i'(t) = -\tilde{d}_i(t) y_i(t) + \sum_{j=1}^n \tilde{L}_{ij}(t)(y_{j,t}), \qquad i = 1, \dots, n,\ t \ge 0,$$

where $\tilde{d}_i(t) = d_i(t) - \varepsilon$ and

$$\tilde{L}_{ij}(t)\phi_j = \int_{-\tau}^0 e^{-\varepsilon s} \phi_j(s) d_s \nu_{ij}(t,s).$$

We have $\|\tilde{L}_{ij}(t)\| \le e^{\varepsilon\tau} a_{ij}(t)$. Next, we observe that, for $\varepsilon > 0$ sufficiently small, this transformed system satisfies (L2):

$$\begin{aligned}
\tilde{d}_i(t) - \sum_j e^{\varepsilon\tau} a_{ij}(t) &= d_i(t) - \varepsilon - e^{\varepsilon\tau} \sum_j a_{ij}(t) \\
&\ge (1 - e^{\varepsilon\tau}) \sum_j a_{ij}(t) - \varepsilon + \delta \\
&\ge (1 - e^{\varepsilon\tau}) M - \varepsilon + \delta \to \delta > 0 \quad \text{as } \varepsilon \to 0^+.
\end{aligned}$$

From (ii), it follows that $|y(t, t_0, \varphi)| \le \|\varphi\|$ for $t \ge t_0 \ge T$, thus $|x(t, t_0, \varphi)| \le e^{-\varepsilon t} \|\varphi\|$ for all $t \ge t_0 \ge T$ and $\varphi \in C$.

(iv) Let $T(t, \sigma)$ be the solution operator and $X(t, \sigma)$ the fundamental matrix solution for (2.3). See Chapter 6 of [10] for definitions and results. From (iii), (2.3) is globally exponentially stable on $[0, \infty)$, and [10, Lemma 6.5.3] implies that there are positive constants k, K, α such that $\|T(t, \sigma)\| \le k e^{-\alpha(t-\sigma)}$, $\|X(t, \sigma)\| \le K e^{-\alpha(t-\sigma)}$, $t \ge \sigma$. The solutions $x(t) = x(t, \sigma, \varphi)$ of (2.6) are given by the variation of constants formula [10, p. 173] as

$$x_t(\sigma, \varphi)(\theta) = T(t, \sigma)\varphi(\theta) + \int_\sigma^{t+\theta} X(t+\theta, s) f(s, x_s(\sigma, \varphi))\, ds.$$

With $|f|$ uniformly bounded by $m > 0$ on $[0, \infty) \times C$, this leads to $\limsup_{t \to \infty} |x(t, \sigma, \varphi)| \le mK/\alpha$.

□

Remark 2.2. The criterion for the exponential stability of the linear system (2.3) in Theorem 2.1(iii) does not require that the functions $d_i(t)$ are either bounded above or below by positive constants, however the coefficients $a_{ij}(t)$ must be bounded.

Remark 2.3. In a recent paper, Hatvani [12] studied a scalar linear equation of the form

$$x'(t) = -a(t)x(t) + b(t)\int_{t-\tau}^{t} \lambda(s)x(s)\,ds, \qquad t \ge 0, \tag{2.7}$$

with $a, b : [0,\infty) \to [0,\infty), \lambda : [-\tau,\infty) \to \mathbb{R}$ piecewise continuous continuous, for which sufficient conditions for its asymptotic stability and uniform asymptotic stability were given. The approach used by Hatvani in [12] is quite different from our techniques, since it relies on the method of Lyapunov functionals and the annulus argument, see also [3, 11]. Moreover, the elaborate, powerful criteria established in [12] do not require the boundedness of the coefficients functions $a(t), b(t)$.

We now add a perturbation $F(t, x_t)$ to (2.3), where F satisfies (1.3). In order to include a broad class of systems, we write the new system as

$$\begin{aligned} x_i'(t) =& -d_i(t)x_i(t) + \sum_{j=1}^{n}\int_{-\tau}^{0} x_j(t+s)d_s\nu_{ij}(t,s) \\ & - \kappa_i(t)x_i^p(t) + \sum_{k=1}^{m}\beta_{ik}(t)\int_{t-\tau_{ik}(t)}^{t} h_{ik}(s, x_i(s))\,d_s\eta_{ik}(t,s), \qquad i = 1,\dots,n, \end{aligned} \tag{2.8}$$

where $p > 1$, the delays are bounded and, without loss of generality, $\max_{i,k}\sup_{t\ge 0}\tau_{ik}(t) \le \tau$. Assume also:

(F1) $\tau_{ik}, \kappa_i, \beta_{ik} : \mathbb{R} \to [0,\infty)$ are continuous and bounded, 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

$$\beta_i(t) := \sum_{k=1}^{m}\beta_{ik}(t)\int_{t-\tau_{ik}(t)}^{t} d_s\eta_{ik}(t,s) > 0, \qquad t \in \mathbb{R}, \tag{2.9}$$

for $i \in \{1,\dots,n\},\ k \in \{1,\dots,m\}$.

Besides the previous matrices $D(t), A(t)$, define the $n \times n$ matrix-valued functions

$$\begin{aligned} &B(t) = \operatorname{diag}(\beta_1(t),\dots,\beta_n(t)) \\ &M(t) = B(t) + A(t) - D(t), \qquad t \ge 0. \end{aligned} \tag{2.10}$$

System (2.8) can be used to model the growth of n populations structured into n classes or patches, with migration among them. For a biological interpretation of such models, see [5, 8, 13]. Clearly, the case of multiple discrete time dependent delays of the form

$$\begin{aligned} x_i'(t) =& -d_i(t)x_i(t) + \sum_{j=1}^{n}\sum_{k=1}^{m} a_{ijk}(t)x_j(t-\sigma_{ijk}(t)) \\ & - \kappa_i(t)x_i^2(t) + \sum_{k=1}^{m}\beta_{ik}(t)h_{ik}(t, x_i(t-\tau_{ik}(t))), \qquad i = 1,\dots,n,\ t \ge 0, \end{aligned} \tag{2.11}$$

is included in our setting.

For the definitions of persistence and permanence given below, see e.g. [13].

Definition 2.1. Fix
$$C_0 = \{\phi \in C : \phi \geq 0, \phi(0) > 0\}$$
as the set of admissible initial conditions. A DDE $x'(t) = f(t, x_t)$ is said to be **uniformly persistent** (in C_0) if all solutions $x(t, 0, \phi)$ with $\phi \in C_0$ are defined on $[0, \infty)$ and there is $m > 0$ such that $\liminf_{t\to\infty} x_i(t, 0, \phi) \geq m$ for all $1 \leq i \leq n, \phi \in C_0$. The system is said to be **permanent** (in C_0) if it is dissipative and uniformly persistent; in other words, all solutions $x(t, 0, \phi), \phi \in C_0$, are defined on $[0, \infty)$ and there are positive constants m, M such that, given any $\phi \in C_0$, there exists $t_0 = t_0(\phi)$ for which
$$m \leq x_i(t, 0, \phi) \leq M, \qquad 1 \leq i \leq n,\ t \geq t_0.$$

The following criterion for permanence of (2.8) relies on the dissipativeness of the system.

Theorem 2.4. *Let $a_{ij}(t), \beta_i(t)$ be defined by (2.4), (2.9). Assume (L1), (L2*), (F1), and suppose that:*

(F2) $h_{ik} : [0, \infty) \times [0, \infty) \to [0, \infty)$ are bounded, continuous, locally Lipschitzian in the second variable, with $h_{ik}(t, 0) = 0$ for $t \geq 0$ and
$$h_{ik}(t, x) \geq h_i^-(x), \qquad t \geq 0,\ x \geq 0,\ k = 1, \dots, m,$$
where $h_i^- : [0, \infty) \to [0, \infty)$ is continuous on $[0, \infty)$, continuously differentiable in a right neighbourhood of 0, with $h_i^-(0) = 0, (h_i^-)'(0) = 1$ and $h_i^-(x) > 0$ for $x > 0$, $i \in \{1, \dots, n\}$.

(F3) there exist vectors $u = (u_1, \dots, u_n) \gg 0$ and $\eta = (\eta_1, \dots, \eta_n) \gg 0$ such that
$$M(t)u \geq \eta \quad \text{for large } t > 0. \tag{2.12}$$

Then (2.8) is permanent.

Proof. Write (2.8) in the form (1.1) and observe that $x_i'(t) \geq L_i(t)x_t - \kappa_i(t)x_i(t)^p$ with $L_i(t)\phi \geq -d_i(t)\phi_i(0)$ for $\phi \in C^+$. We first compare solutions of (2.8) with solutions of the decoupled system of ODEs
$$y_i'(t) = -d_i(t)y_i(t) - \kappa_i(t)y_i(t)^p, \qquad i = 1, \dots, n, \tag{2.13}$$
which obviously satisfies (Q). We deduce that solutions $x(t) = x(t, 0, \phi)$ of (2.8) with initial conditions $x_0 = \phi$ ($\phi \in C_0$) satisfy $x_i(t) \geq y_i(t)$ for $t \geq 0, i = 1, \dots, n$, where $y(t) = (y_1(t), \dots, y_n(t))$ is the solution of (2.13) with initial condition $y(0) = (\phi_1(0), \dots, \phi_n(0)) > 0$. Hence $x(t) > 0$ for $t > 0$.

On the other hand, we compare solutions of (2.8) with the solutions of the auxiliary cooperative system
$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1}^{n} \int_{-\tau}^{0} x_j(t+s)d_s\nu_{ij}(t, s) + M_i, \qquad i = 1, \dots, n, \tag{2.14}$$
where $M_i > 0$ are such that
$$\beta_i(t) \max_k \sup_{t,x\geq 0} h_{ik}(t, x) \leq M_i, \qquad i = 1, \dots, n.$$
Theorem 2.1 implies that system (2.14) is dissipative. By comparison, each solution $x(t, \sigma, \varphi)$ of (2.8) is bounded from above by the solution of (2.14) with the same initial condition $\varphi \in C_0$, thus (2.8) is dissipative as well.

Once the dissipativeness is observed, the result of uniform persistence follows by comparison of solutions with solutions of a second auxiliary system, which here is taken as

$$\begin{aligned} x_i'(t) = &- d_i(t)x_i(t) + \sum_{j=1}^{n} \int_{-\tau}^{0} x_j(t+s)d_s\nu_{ij}(t,s) \\ &- \kappa_i(t)x_i^p(t) + \sum_{k=1}^{m} \beta_{ik}(t) \int_{t-\tau_{ik}(t)}^{t} H_i(x_i(s))\, d_s\eta_{ik}(t,s), \qquad i = 1,\dots,n, \end{aligned} \tag{2.15}$$

where $H_i(x) = h_i^-(x)$ for $0 \le x \le \varepsilon$, $H_i(x) = h_i^-(\varepsilon)$, and ε is chosen sufficiently small so that H_i is non-decreasing (in this way (2.15) is cooperative) and $h_{ik}(t,x) \ge H_i(x)$ for all $t \ge 0, x \ge 0$. One can check that the arguments for the proof of Theorem 3.3 in [8] can be carefully adapted to the present situation, in order to deal with the distributed delays, thus as in [8] one concludes that (2.15) is uniformly persistent. Details are omitted. Since solutions of (2.8) are bounded from below by solutions of (2.15), it follows that it is also uniformly persistent. This ends the proof. □

Remark 2.5. The arguments above show that in (2.8) the terms $-\kappa_i(t)x_i^p(t)$ $(p > 1)$ can actually be replaced by instantaneous nonlinearities of the form $-\kappa_i(t)g_i(x_i(t))$, with $k_i(t)$ as above and $g_i : [0,\infty) \to [0,\infty)$ continuous and $g_i(x) = o(x)$ as $x \to 0^+$.

Hypothesis (F2) depends solely on the type of nonlinearity added to (2.3), while (F3) depends also on the linear coefficients. To test whether there are positive vectors satisfying hypotheses (L2*) and (F3), the following lemma is useful.

Lemma 2.6. *Suppose that* $\liminf_{t\to\infty} \beta_i(t) > 0$, $i = 1,\dots,n$, *and that there exist a vector* $v = (v_1,\dots,v_n) \gg 0, T_0 \ge 0$ *and positive constants* α_i, γ_i *such that*

$$1 < \alpha_i \le \frac{\beta_i(t)v_i}{d_i(t)v_i - \sum_{j=1}^{n} a_{ij}(t)v_j} \le \gamma_i \quad \text{for } t \ge T_0,\ i = 1,\dots,n. \tag{2.16}$$

Then assumptions (L2) and (F3) are satisfied.*

Proof. Let $\beta_i(t) \ge \beta_i^- > 0$ for $t \ge T_1$, with $T_1 \ge T_0$. From (2.16), we have $d_i(t)v_i - \sum_{j=1}^{n} a_{ij}(t)v_j \ge \gamma_i^{-1}\beta_i^- v_i$ and $\beta_i(t)v_i - d_i(t)v_i + \sum_{j=1}^{n} a_{ij}(t)v_j \ge (\alpha_i - 1)\big(d_i(t)v_i - \sum_{j=1}^{n} a_{ij}(t)v_j\big) \ge (\alpha_i - 1)\gamma_i^{-1}\beta_i^- v_i$ for all $t \ge 0$ and $i \in \{1,\dots,n\}$, thus (L2*) and (F3) hold for a common vector $v = u$ as in (2.16). □

Example 2.7. Consider the system:

$$\begin{aligned} x_i'(t) = &\sum_{k=1}^{m_i} \frac{\beta_{ik}(t)x_i(t-\tau_{ik}(t))}{1 + c_{ik}(t)x_i^{\alpha}(t-\tau_{ik}(t))} + \sum_{j=1}^{n} a_{ij}(t)x_j(t-\sigma_{ij}(t)) \\ &- d_i(t)x_i(t) - \kappa_i(t)x_i^2(t), \qquad t \ge 0,\ i = 1,\dots,n, \end{aligned} \tag{2.17}$$

where $\alpha \ge 1$, all the coefficients $\beta_{ik}(t), c_{ik}(t), a_{ij}(t), d_i(t), \kappa_i(t)$ and delays $\tau_{ik}(t), \sigma_{ij}(t)$ are non-negative, continuous and bounded functions in $t \in [0,\infty)$, $k = 1,\dots,m_i$, $i,j = 1,\dots,n$; the functions $c_{ik}(t)$ are assumed to be bounded below from zero.

System (2.17) can be interpreted as a model for n populations of one or multiple species, distributed over n different classes with dispersal terms among them, with Beverton–Holt nonlinearities $h_{ik}(t,x) = \frac{x}{1+c_{ik}(t)x^{\alpha}}$ $(\alpha \ge 1)$. The coefficients $a_{ij}(t)$ stand for the migration rates of populations moving from class j to class i, and $\sigma_{ij}(t)$ for the time-delays during dispersion.

The instantaneous loss term $-d_i(t)x_i(t)$ incorporates the death rate for the ith-population, as we all as the terms $-d_{ji}(t)x_i(t)$, to account for the individuals that leave class i to move to different classes $j \neq i$. (It is thus natural to consider $d_{ii}(t) \equiv 0$ for each $i \in \{1, \dots, n\}$, but this assumption is not relevant here).

With $\alpha = 1$, (2.17) can be seen as a modified delayed logistic equation for n populations of one or multiple species, distributed over n different classes with dispersal terms among them. See [1] for the deduction of the model in the case $n = 1$ as well as for a biological interpretation, and [2,7] for more results. With $\kappa_i \equiv 0$, we obtain a generalization of Mackey–Glass equation for n populations with patch structure and migration among the patches.

System (2.17) has the form (2.11) with $h_{ik}(t,x) = \frac{x}{1+c_{ik}(t)x^\alpha}$ for $t, x \geq 0$. If $\alpha = 1$, $h_{ik}(t,x)$ are increasing in the second variable, hence (2.17) is cooperative. Since $c_{ik}(t)$ are bounded above and below by positive constants, let $0 < \underline{c_i} \leq c_{ik}(t) \leq \overline{c_i}$. One obtains $h_i^-(x) \leq h_{ik}(t,x) \leq \underline{c_i}^{-1}$, with $h_i^-(x) = \frac{x}{1+\overline{c_i}x}$. If $\alpha > 1$, the functions $x \mapsto h_{ik}(t,x)$ are not monotone, but they are bounded, unimodal and satisfy $h_{ik}(t,x) \geq \frac{x}{1+\overline{c_i}x^\alpha}$ for $t, x \geq 0$. Hence, (F1), (F2) are satisfied. As an application of Theorem 2.4, we deduce that if there exist $\delta > 0, T > 0$ and positive vectors v, u such that

$$[D(t) - A(t)]v \geq \delta \mathbf{1}, \quad M(t)u \geq \delta \mathbf{1}, \quad \text{for } t \geq T, \tag{2.18}$$

then (2.17) is permanent (in the set of solutions with initial conditions in C_0).

Example 2.8. Consider the following non-autonomous Nicholson system with patch structure and multiple time-dependent discrete delays (see e.g. [8,9,14]):

$$\begin{aligned} x_i'(t) = &-d_i(t)x_i(t) + \sum_{j=1, j\neq i}^{n} a_{ij}(t)x_j(t) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t)x_i(t-\tau_{ik}(t))e^{-c_i(t)x_i(t-\tau_{ik}(t))}, \qquad i = 1, \dots, n, \end{aligned} \tag{2.19}$$

which has the form (2.11) with nonlinearities $h_{ik} = h_i$ given by $h_i(t,x) = xe^{-c_i(t)x}$ for all i, k. Here, the coefficient and delay functions are supposed to satisfy (L1), (F1), with $c_i(t) > 0$ continuous and bounded. Clearly, (F2) is satisfied, hence if conditions (2.18) hold the system is permanent.

Generalizations of (2.19) will be presented in Example 3.2. Other useful population models can be written in the form (2.8) (see e.g. [5]). Among them, instead of the Ricker-type terms as in (2.19), one could consider modified exponentials $h_{ik}(t,x) = xe^{-c_{ik}(t)x^\alpha}$ $(\alpha > 0)$.

3 Uniform lower and upper bounds for models with cooperative behaviour

If $\kappa_i \equiv 0$ and the nonlinearities h_{ik} are autonomous and identical in each equation i, system (2.8) becomes

$$\begin{aligned} x_i'(t) = &-d_i(t)x_i(t) + \sum_{j=1}^{n} \int_{-\tau}^{0} x_j(t-s)d_s\nu_{ij}(t,s) \\ &+ \sum_{k=1}^{m} \beta_{ik}(t) \int_{t-\tau_{ik}(t)}^{t} h_i(x_i(s))\, d_s\eta_{ik}(t,s), \ i = 1, \dots, n, \end{aligned} \tag{3.1}$$

and (F2) simply reads as

(F2*) $h_i : [0,\infty) \to [0,\infty)$ are locally Lipschitz continuous, bounded, and differentiable on a vicinity of 0^+, with $h_i(0) = 0, h_i'(0) = 1$, $h_i(x) > 0$ for $x > 0$, $i \in \{1, \dots, n\}$.

In some concrete applications, the a priori knowledge of permanence of (2.8) can be used to deduce explicit upper and lower bounds for the asymptotic behaviour of solutions. This technique was used in [2,6] for cooperative scalar equations, and in [7] for multi-dimensional cooperative DDEs. Although in general (2.8) is non-monotone, here the method is illustrated with the situation of autonomous functions $h_i(x)$ as in (3.1), if constraints are imposed in order to force (3.1) to have a cooperative type behaviour.

For functions h_i satisfying $h_i(0) = 0, h_i'(0) = 1$ as in (F2*), we may write $h_i(x) = xg_i(x)$, where g_i is continuous and $g_i(0) = 1$. We now impose an additional hypothesis:

(F4) there exists $\max_{x\geq 0} h_i(x) = h_i(c_i^*)$; with c_i^* the first point of absolute maximum of $h_i(x)$, $h_i(x)$ is increasing on $[0, c_i^*]$ and $h_i(x)/x$ is decreasing on $(0, c_i^*]$, where , $i = 1, \dots, n$.

Theorem 3.1. *Assume (L1), (F1), (F2*) and (F4). In addition, suppose that:*

(i) $\liminf_{t\to\infty} \beta_i(t) > 0,\ i = 1, \dots, n$;

(ii) there exists $v = (v_1, \dots, v_n) \gg 0$ *such that*

$$\begin{aligned} &\liminf_{t\to\infty} \frac{\beta_i(t)v_i}{d_i(t)v_i - \sum_j a_{ij}(t)v_j} > 1, \\ &\limsup_{t\to\infty} \frac{\beta_i(t)v_i}{d_i(t)v_i - \sum_j a_{ij}(t)v_j} < (h_i(c_i^*))^{-1} v_i \min_{1\leq j\leq n} (v_j^{-1} c_j^*), \qquad i = 1, \dots, n. \end{aligned} \tag{3.2}$$

Then all solutions $x(t) = x(t, 0, \phi)$ *of* (3.1) *with* $\phi \in C_0$ *satisfy the estimates*

$$\limsup_{t\to\infty} x_i(t) < c_i^*, \qquad i = 1, \dots, n$$

and

$$m \leq \liminf_{t\to\infty} (x_i(t)/v_i) \leq \limsup_{t\to\infty} (x_i(t)/v_i) \leq M, \qquad i = 1, \dots, n, \tag{3.3}$$

with explicit uniform lower and upper bounds

$$\begin{aligned} M &= \max_{1\leq i\leq n} \frac{1}{v_i} g_i^{-1} \left(\liminf_{t\to\infty} \frac{d_i(t)v_i - \sum_j a_{ij}(t)v_j}{\beta_i(t)v_i} \right) \\ m &= \min_{1\leq i\leq n} \frac{1}{v_i} g_i^{-1} \left(\limsup_{t\to\infty} \frac{d_i(t)v_i - \sum_j a_{ij}(t)v_j}{\beta_i(t)v_i} \right), \end{aligned} \tag{3.4}$$

where the functions g_i *are defined by* $g_i(x) = h_i(x)/x$ *for* $x > 0$ *and* $i = 1, \dots, n$.

Proof. From (3.2), there exist $T_0 \geq 0$ and constants α_i, γ_i such that

$$\alpha_i \leq \frac{\beta_i(t)v_i}{d_i(t)v_i - \sum_j a_{ij}(t)v_j} \leq \gamma_i, \qquad t \geq T_0,\ i = 1, \dots, n, \tag{3.5}$$

with

$$\alpha_i > 1 \quad \text{and} \quad \gamma_i < (h_i(c_i^*))^{-1} v_i \min_{1\leq j\leq n} (v_j^{-1} c_j^*), \qquad i = 1, \dots, n.$$

Since $\beta_i(t)$ are bounded, the above estimates also imply that $d_i(t), a_{ij}(t)$ are bounded on $[0,\infty)$, for all i,j. From Theorem 2.4 and Lemma 2.6, the imposed assumptions imply that (3.1) is permanent.

Rescaling the variables as $y_j(t) = x_j(t)/v_j$, (3.1) is transformed into

$$\begin{aligned} y_i'(t) = &-d_i(t)y_i(t) + \sum_{j=1}^n v_i^{-1}v_j \int_{-\tau}^0 y_j(t-s)d_s\nu_{ij}(t,s) \\ &+ \sum_{k=1}^m \beta_{ik}(t)\int_{t-\tau_{ik}(t)}^t \hat h_i(y_i(s))\,d_s\eta_{ik}(t,s), \qquad i=1,\dots,n,\ t\ge 0, \end{aligned} \tag{3.6}$$

where $\hat h_i(x) := v_i^{-1}h_i(v_i x), x \ge 0$. For (3.6), $\hat a_{ij}(t) := v_i^{-1}a_{ij}(t)v_j$ replaces $a_{ij}(t)$ in formula (2.4), for all i,j. In what follows, we keep the hats in (3.6) in order to avoid misinterpretations. System (3.6) satisfies the hypotheses (L1), (F1), (F2*) and (3.2) with $v = \mathbf{1}$.

For any solution $x(t) := x(t,0,\phi)$ of (3.1), set $\underline{x}_j := \liminf_{t\to\infty} x_j(t), \overline{x}_j := \limsup_{t\to\infty} x_j(t)$, $1 \le j \le n$. From Theorem 2.4, $0 < \underline{x}_j \le \overline{x}_j < \infty$ for all j. Next, consider the corresponding solution $y(t)$ of (3.6), and $\underline{y}_j := \liminf_{t\to\infty} y_j(t)$, $\overline{y}_j := \limsup_{t\to\infty} y_j(t)$, $1 \le j \le n$, not forgetting however that $\underline{y_j} = \underline{x}_j/v_j$ and $\overline{y_j} = \overline{x}_j/v_j$, so the weights v_j must be taken into consideration in the final estimates.

For (3.6), each one of the functions $\hat h_i$ attains its absolute maximum at $v_i^{-1}c_i^*$ and $\hat h_i(x) < \hat h_i(v_i^{-1}c_i^*) = v_i^{-1}h_i(c_i^*)$ for $0 \le x < v_i^{-1}c_i^*$. Together with (3.6), we consider the auxiliary system

$$\begin{aligned} u_i'(t) = &-d_i(t)u_i(t) + \sum_{j=1}^n v_i^{-1}v_j \int_{-\tau}^0 u_j(t-s)d_s\nu_{ij}(t,s) \\ &+ \sum_{k=1}^m \beta_{ik}(t)\int_{t-\tau_{ik}(t)}^t \hat H_i(u_i(s))\,d_s\eta_{ik}(t,s), \qquad i=1,\dots,n,\ t\ge 0, \end{aligned} \tag{3.7}$$

where $\hat H_i(x) = \hat h_i(x)$ if $0 \le x \le v_i^{-1}c_i^*$, $\hat H_i(x) = v_i^{-1}h_i(c_i^*)$ if $x \ge v_i^{-1}c_i^*$. It is apparent that (3.7) satisfies the quasimonotone condition (Q).

From Theorem 2.1, all the positive solutions $u(t)$ of (3.7) are bounded, thus $\overline{u}_j := \limsup_{t\to\infty} u_j(t)$ are finite, $1 \le j \le n$. Consider an i such that $\overline{u}_i = \max_{1\le j\le n} \overline{u}_j$.

By the fluctuation lemma, take a sequence (t_k) with $t_k \to \infty$, $u_i'(t_k) \to 0$ and $u_i(t_k) \to \overline{u}_i$. For any $\varepsilon > 0$ small and k sufficiently large, we have $0 < u_j(s) \le \overline{u}_i + \varepsilon$ for $s \ge t_k - \tau$ and all j. Recalling that all the coefficient functions are bounded on $[0,\infty)$, for sufficiently large k, from (3.5) and (2.9) we derive

$$\begin{aligned} u_i'(t_k) \le &-d_i(t_k)(\overline{u}_i - \varepsilon) + (\overline{u}_i + \varepsilon)\Big(\sum_j \hat a_{ij}(t_k)\Big) + \beta_i(t_k)v_i^{-1}h_i(c_i^*) \\ = &\Big(d_i(t_k) - \sum_j \hat a_{ij}(t_k)\Big)\left[-\overline{u}_i + \frac{\beta_i(t_k)}{d_i(t_k) - \sum_j \hat a_{ij}(t_k)} v_i^{-1}h_i(c_i^*)\right] + O(\varepsilon) \\ \le &\Big(d_i(t_k) - \sum_j \hat a_{ij}(t_k)\Big)\left[-\overline{u}_i + \gamma_i v_i^{-1}h_i(c_i^*)\right] + O(\varepsilon). \end{aligned}$$

Taking limits $k \to \infty, \varepsilon \to 0^+$, this leads to $0 \le \overline{d}_i[-\overline{u}_i + \gamma_i v_i^{-1}h_i(c_i^*)]$, where $\overline{d}_i = \sup_{t\ge 0} d_i(t)$. Thus,

$$\overline{u}_i \le \gamma_i v_i^{-1}h_i(c_i^*) < \min_{1\le j\le n}(v_j^{-1}c_j^*) \le v_i^{-1}c_i^*$$

and, for any other j,

$$\overline{u}_j \le \overline{u}_i < \min_{1\le \ell\le n}(v_\ell^{-1}c_\ell^*) \le v_j^{-1}c_j^*.$$

Since (3.7) is cooperative and $\hat{h}_j(x) \le \hat{H}_j(x)$ for all j, we derive that $y(t) \le u(t)$ for solutions $y(t), u(t)$ of (3.6), (3.7), respectively, with the same initial conditions [15]. This yields that $\overline{y}_j \le \overline{u}_j < v_j^{-1}c_j^*$ for all $j \in \{1,\dots,n\}$, and hence, for $t > 0$ sufficiently large, $y(t)$ is also a solution of (3.7).

Returning to the original (after scaling) system (3.6), in a similar way we fix i such that $\overline{y}_i = \max_{1\le j\le n} \overline{y}_j$, and choose a sequence (t_k) with $t_k \to \infty$, $y_i'(t_k) \to 0$ and $y_i(t_k) \to \overline{y}_i$. For any $\varepsilon > 0$ such that $\overline{y}_i + \varepsilon < v_i^{-1}c_i^*$ and k sufficiently large, we have

$$\begin{aligned} y_i'(t_k) \le & -d_i(t_k)(\overline{y}_i - \varepsilon) + (\overline{y}_i + \varepsilon)\Big(\sum_j \hat{a}_{ij}(t_k)\Big) + \beta_i(t_k)\hat{h}_i(\overline{y}_i + \varepsilon) \\ &= \Big(d_i(t_k) - \sum_j \hat{a}_{ij}(t_k)\Big)\left[-\overline{y}_i + \frac{\beta_i(t_k)}{d_i(t_k) - \sum_j \hat{a}_{ij}(t_k)}\hat{h}_i(\overline{y}_i + \varepsilon)\right] + O(\varepsilon) \\ &= \Big(d_i(t_k) - \sum_j \hat{a}_{ij}(t_k)\Big)\overline{y}_i\left[-1 + \frac{\beta_i(t_k)}{d_i(t_k) - \sum_j \hat{a}_{ij}(t_k)}\,\frac{h_i(v_i(\overline{y}_i + \varepsilon))}{v_i\overline{y}_i}\right] + O(\varepsilon). \end{aligned}$$

Taking limits $k \to \infty, \varepsilon \to 0^+$, this estimate yields

$$1 \le \limsup_{t\to\infty}\left[\frac{\beta_i(t)}{d_i(t) - \sum_j \hat{a}_{ij}(t)}\right] g_i(v_i\overline{y}_i).$$

In other words,

$$g_i(v_i\overline{y}_i) \ge \liminf_{t\to\infty} \frac{d_i(t) - \sum_j \hat{a}_{ij}(t)}{\beta_i(t)},$$

or equivalently

$$\overline{y}_i \le \frac{1}{v_i} g_i^{-1}\left(\liminf_{t\to\infty} \frac{d_i(t) - \sum_j \hat{a}_{ij}(t)}{\beta_i(t)}\right)$$

from which we derive $\overline{x}_j/v_j \le \overline{x}_i/v_i \le M, j = 1,\dots,n$, for M as in (3.4).

For the lower estimate we use arguments similar to the ones above, by considering $\underline{y}_i = \min_{1\le j\le n} \underline{y}_j$ and a sequence (t_k) with $t_k \to \infty$, $y_i'(t_k) \to 0$ and $y_i(t_k) \to \underline{y}_i$, so details are omitted. It is however important to notice that $d_i(t)v_i - \sum_j a_{ij}(t)v_j \ge \gamma_i^{-1}\beta_i(t)v_i$ where γ_i is as in (3.5), thus from (i) we deduce that $d_i(t)v_i - \sum_j a_{ij}(t)v_j$ is bounded away from zero by a positive constant. □

Example 3.2. Consider a Nicholson system with distributed delays

$$\begin{aligned} x_i'(t) = & -d_i(t)x_i(t) + \sum_{j=1,j\ne i}^{n} \alpha_{ij}(t)\int_{t-\sigma_{ij}(t)}^{t} \lambda_{ij}(s)x_j(s)\,ds \\ & + \sum_{k=1}^{m} \beta_{ik}(t)\int_{t-\tau_{ik}(t)}^{t} \gamma_{ik}(s)x_i(s)e^{-c_ix_i(s)}\,ds, \qquad i = 1,\dots,n, \end{aligned} \tag{3.8}$$

where $c_i > 0$, $d_i(t) > 0, \alpha_{ij}(t), \lambda_{ij}(t), \beta_{ik}(t), \gamma_{ik}(t), \sigma_{ij}(t), \tau_{ik}(t)$ are continuous, bounded and nonnegative for $t \ge 0$, for all i, j, k. According to the biological explanation of the model, $\alpha_{ij}(t)$ are the dispersal rates of the population in class j moving to class i, so one may incorporate a delay in the migration terms, to account for the time the species take to move among different patches (see e.g. [16]). Clearly the nonlinearities $h_i(x) = xe^{-c_ix}, x \ge 0$, satisfy (F2*), (F4), with $c_i^* = c_i^{-1}$, $h_i(x) = xg_i(x)$ where $g_i(x) = e^{-c_ix}$ and $h_i(c_i^*)^{-1} = c_ie$. Thus (3.8) has a cooperative type behaviour when each component $x_i(t)$ of any positive solutions $x(t)$ has values in the interval $(0, c_i^{-1})$ where h_i is strictly increasing. As an immediate consequence of the Theorem 3.1, we get the explicit uniform lower and upper bounds given in the following theorem:

Theorem 3.3. *Consider (3.8), define*

$$a_{ij}(t) := \alpha_{ij}(t) \int_{t-\sigma_{ij}(t)}^{t} \lambda_{ij}(s)\, ds, \qquad \beta_i(t) := \sum_{k=1}^{m} \beta_{ik}(t) \int_{t-\tau_{ik}(t)}^{t} \gamma_{ik}(s)\, ds$$

for $1 \le i, j \le n, i \ne j, t \ge 0$, *and suppose that:*

(i) $\liminf_{t\to\infty} \beta_i(t) > 0,\ 1, \dots, n$;

(ii) there exist $v = (v_1, \dots, v_n) \gg 0$, $T_0 \ge 0$ *and constants* α_i, γ_i *such that (3.5) is satisfied with*

$$\alpha_i > 1 \quad \text{and} \quad \gamma_i < e \frac{v_i c_i}{\max\limits_{1\le j\le n} (v_j c_j)}, \qquad i = 1, \dots, n.$$

Then, all the solutions $x(t) = x(t, 0, \phi)$ *with* $\phi \in C_0$ *satisfy the estimates (3.3) with explicit uniform lower and upper bounds* m, M *given by*

$$\begin{aligned} M &= \max_{1\le i\le n} \frac{1}{v_i c_i} \log\left(\limsup_{t\to\infty} \frac{\beta_i(t) v_i}{d_i(t) v_i - \sum_{j\ne i} a_{ij}(t) v_j} \right) \\ m &= \min_{1\le i\le n} \frac{1}{v_i c_i} \log\left(\liminf_{t\to\infty} \frac{\beta_i(t) v_i}{d_i(t) v_i - \sum_{j\ne i} a_{ij}(t) v_j} \right). \end{aligned} \tag{3.9}$$

If (3.2) holds with $v = \mathbf{1}$ and $c_i = c$ for all i, a better criterion is obtained. This is illustrated here with a situation with discrete delays.

Corollary 3.4. *Consider the system*

$$x_i'(t) = -d_i(t)x_i(t) + \sum_{j=1, j\ne i}^{n} a_{ij}(t) x_j(t - \sigma_{ij}(t)) + \sum_{k=1}^{m} \beta_{ik}(t) x_i(t - \tau_{ik}(t)) e^{-c x_i(t-\tau_{ik}(t))}, \tag{3.10}$$

where all the coefficients and delays are continuous and bounded, $c > 0$, $d_i(t) > 0$ *and* $a_{ij}(t)$ $(j \ne i), \beta_{ik}(t), \sigma_{ij}(t), \tau_{ik}(t)$ *are nonnegative, with* $\beta_i(t) := \sum_{k=1}^{m} \beta_{ik}(t) \ge \delta > 0$, *for* $t \ge 0$ *and all* i, j, k. *Assume that*

$$\alpha_i := \liminf_{t\to\infty} \frac{\beta_i(t)}{d_i(t) - \sum_j a_{ij}(t)} > 1, \qquad \gamma_i := \limsup_{t\to\infty} \frac{\beta_i(t)}{d_i(t) - \sum_j a_{ij}(t)} < e, \qquad i = 1, \dots, n.$$

Then, all positive solutions $x(t) = (x_1(t), \dots, x_n(t))$ *of (3.10) satisfy the estimates*

$$c^{-1} \min_{1\le i\le n} \log(\alpha_i) \le \liminf_{t\to\infty} x_j(t) \le \limsup_{t\to\infty} x_j(t) \le c^{-1} \max_{1\le i\le n} \log(\gamma_i), \qquad 1 \le j \le n. \tag{3.11}$$

For the scalar case of (3.8), we obtain the next corollary:

Corollary 3.5. *Consider the non-autonomous Nicholson's equation given by*

$$x'(t) = -d(t)x(t) + \sum_{k=1}^{m} \tilde{\beta}_k(t) \int_{t-\tau_k(t)}^{t} \gamma_k(s)x(s)e^{-cx(s)}\, ds \tag{3.12}$$

where $c > 0$, $d(t) > 0, \tilde{\beta}_k(t), \gamma_k(t) \geq 0, \tau_k(t) > 0$ *are continuous and bounded functions on* $[0,\infty)$. *Suppose that* $\liminf_{t\to\infty} \sum_{k=1}^{m} \beta_k(t) > 0$, *where* $\beta_k(t) = \tilde{\beta}_k(t) \int_{t-\tau_k(t)}^{t} \gamma_k(s)\, ds > 0$, *and*

$$1 < \liminf_{t\to\infty} \left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t) \right), \qquad \limsup_{t\to\infty} \left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t) \right) < e. \tag{3.13}$$

Then, all the solutions $x(t) = x(t, 0, \phi)$ *with* $\phi \in C_0$ *satisfy the estimates*

$$\begin{aligned} \liminf_{t\to\infty} \log \left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t) \right) &\leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \\ &\leq \limsup_{t\to\infty} \log \left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t) \right). \end{aligned} \tag{3.14}$$

In particular, for the non-autonomous Nicholson's equation with time-varying discrete delays given by

$$x'(t) = -d(t)x(t) + \sum_{k=1}^{m} \beta_k(t)x(t-\tau_k(t))e^{-cx(t-\tau_k(t))}, \qquad t \geq 0, \tag{3.15}$$

condition (3.13) *implies that all solutions* $x(t) = x(t, 0, \phi)$ *with* $\phi \in C_0$ *satisfy* (3.14).

Remark 3.6. For the case (3.15), the above corollary recovers Theorem 3.3 in [6] under slightly weaker hypotheses. See also [4] and references therein, for the stability and global attractivity of a positive equilibrium analyses for n-dimensional Nicholson systems with constant coefficients and multiple time-varying delays of the form

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

Acknowledgements

This work was partially supported by Fundação para a Ciência e a Tecnologia (Portugal) under project UID/MAT/04561/2013.

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