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Global attractivity and extinction for Lotka–Volterra systems with infinite delay and feedback controls

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The paper deals with a multiple species Lotka–Volterra model with infinite distributed delays and feedback controls, for which we assume a weak form of diagonal dominance of the instantaneous negative intra-specific terms over the infinite delay effect in both the population variables and controls. General sufficient conditions for the existence and attractivity of a saturated equilibrium are established. When the saturated equilibrium is on the boundary of $\mathbb{R}^n_+$, sharper criteria for the extinction of all or part of the populations are given. While the literature usually treats the case of competitive systems only, here no restrictions on the signs of the intra- and inter-specific delayed terms are imposed. Moreover, our technique does not require the construction of Lyapunov functionals.

1. Introduction

After several decades of intensive study and use of functional differential equations (FDEs) in population dynamics, it is now very well understood that the introduction of delays in differential equations leads, in general, to more realistic population models, and much more complex and rich dynamics. Nevertheless, delays are not harmless and often create instability and oscillations unless they are either small or neutralized by instantaneous terms. When the delays are infinite it is not clear how to surpass the effect of the infinite past of the system so, in order to obtain stability results, some form of instantaneous dominance is expected. On the other hand, the consideration of FDEs with infinite delay is relevant in accounting for systems with 'infinite memory', and goes back to the works of Volterra. In fact, for Lotka–Volterra systems or other general population models, whether the global stability may persist under large or even infinite delays without strictly dominating instantaneous negative feedbacks is a question that has attracted the interest of many researchers, and had partial positive answers (see, for example, Kuang [16], Xu *et al*. [27], Faria [5] and references therein).

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Recently, the study of population models with delays and controls, in particular Lotka–Volterra models, has received some attention (see, for example, [3, 9, 17, 21, 22, 25, 28] and references therein). In this paper, we consider the following n-species Lotka–Volterra system with feedback controls and infinite delays:

$$\left.\begin{aligned} x_i'(t) &= x_i(t)\biggl(b_i - \mu_i x_i(t) \\ &\qquad - \sum_{j=1}^{n} a_{ij}\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s \\ &\qquad\qquad - c_i\int_0^\infty G_i(s)u_i(t-s)\,\mathrm{d}s\biggr), \\ u_i'(t) &= -e_i u_i(t) + d_i x_i(t), \end{aligned}\right\} \quad i = 1, 2, \dots, n, \tag{1.1}$$

where μ_i, c_i, d_i, e_i are positive constants, $b_i, a_{ij} \in \mathbb{R}$ and the kernels

$$K_{ij}, G_i \colon [0, \infty) \to [0, \infty)$$

are L^1-functions, normalized so that

$$\int_0^\infty K_{ij}(s)\,\mathrm{d}s = 1, \qquad \int_0^\infty G_i(s)\,\mathrm{d}s = 1$$

for $i, j = 1, 2, \dots, n$. Without loss of generality, we assume that, for all i, the linear operators defined by $L_{ii}(\varphi) = \int_0^\infty K_{ii}(s)\varphi(-s)\,\mathrm{d}s$, for bounded continuous functions $\varphi\colon (-\infty, 0] \to \mathbb{R}$, are non-atomic at 0, which amounts to having $K_{ii}(0) = K_{ii}(0^+)$.

In biological terms, $x_i(t)$ denotes the density of the population i with Malthusian growth rate b_i and instantaneous self-limitation coefficient $\mu_i > 0$, and a_{ii} and a_{ij} $(i \neq j)$ are, respectively, the intra- and inter-specific delayed acting coefficients; $u_i(t)$ denotes a feedback control variable, $i, j = 1, 2, \dots, n$. Due to the biological interpretation of (1.1), we are only interested in positive (or non-negative) solutions. We therefore consider solutions of (1.1) with *admissible* initial conditions, i.e.

$$\left.\begin{gathered} x_i(\theta) = \varphi_i(\theta) \geqslant 0, \quad u_i(\theta) = \psi_i(\theta) \geqslant 0, \quad \theta \in (-\infty, 0), \\ \varphi_i(0) > 0, \quad \psi_i(0) > 0, \end{gathered}\right\} \tag{1.2}$$

with φ_i, ψ_i *bounded* continuous functions on $(-\infty, 0]$, $i = 1, 2, \dots, n$.

In order to have an effective feedback control, it is natural to impose that each G_i $(1 \leqslant i \leqslant n)$ satisfies

$$\int_0^\infty G_i(s)\varphi(-s)\,\mathrm{d}s > 0 \tag{1.3}$$

for any positive bounded continuous function φ defined on $(-\infty, 0]$ with $\varphi(0) > 0$. In particular, (1.3) holds if G_i is continuous at 0 with $G_i(0) > 0$, or if G_i has a jump discontinuity at 0 with $G_i(0) - G_i(0^+) > 0$.

For simplicity of exposition, we consider (1.1), but our study applies to more general systems of the form

$$\left.\begin{aligned} x_i'(t) &= x_i(t)\biggl(b_i - \mu_i x_i(t) \\ &\qquad - \sum_{j=1}^{n} a_{ij}\int_0^\infty x_j(t-s)\,\mathrm{d}\eta_{ij}(s) \\ &\qquad\qquad - c_i\int_0^\infty u_i(t-s)\,\mathrm{d}\nu_i(s)\biggr), \\ u_i'(t) &= -e_i u_i(t) + d_i x_i(t), \end{aligned}\right\} \quad i = 1, 2, \dots, n, \tag{1.4}$$

where all the coefficients are as in (1.1), $\eta_{ij}, \nu_i \colon [0, \infty) \to \mathbb{R}$ are bounded variation functions that are supposed to be normalized such that their total variation is 1 and the ν_i are non-decreasing on $[0, \infty)$. Note that, in (1.1), we supposed that $K_{ij}(t) \geqslant 0$ on $[0, \infty)$, but the above scenario does not impose this restriction. Some of our general results, however, require that the kernels K_{ij} in (1.1) are non-negative, or that the functions η_{ij} in (1.4) are non-decreasing, although they can easily be adapted to deal with systems without such constraints.

Our study was strongly motivated by some previous work of the authors. The uncontrolled Lotka–Volterra system with infinite distributed delays was studied by Faria [5], and questions of partial survival and extinction of species in non-autonomous delayed Lotka–Volterra systems were addressed by Muroya in [20] (see also [19]). The works of Gopalsamy and Weng [9], and Li *et al*. [17], where special cases of two-dimensional competitive Lotka–Volterra systems with controls and no diagonal delays were studied, were an important source of inspiration for the present paper. Here, the investigation refers to controlled Lotka–Volterra models of any dimension n. While the literature usually only deals with the case of competitive systems (i.e. systems with $a_{ij} \geqslant 0$ for $j \neq i$) with $b_i > 0$, here no restrictions on the signs of a_{ij} and b_i will be imposed. Moreover, infinite delays are incorporated in the control terms (see also [22] for a competitive model). Another novelty is that our method does not require the construction of a specific Lyapunov functional.

Clearly, the introduction of controls in a delayed Lotka–Volterra system might change the existence, position and stability of equilibria. The main goal of the present paper is to address the global asymptotic dynamics of solutions to the system (1.1), (1.2), in what is concerned with the establishment of sufficient conditions for the existence and attractivity of a (not necessarily positive) *saturated equilibrium* (see [15, 16] and § 3 for a definition). As in previous works [5, 9, 17, 22], we assume that (1.1) satisfies some form of diagonal dominance of the instantaneous negative terms $\mu_i x_i(t)$ over the infinite delay terms (these involving both the population variables and the controls) so that the usual instability caused by the introduction of the delays is cancelled. For some of our stability results, another prerequisite is that the uncontrolled Lotka–Volterra system ((1.1) with $c_i = 0$ $(1 \leqslant i \leqslant n)$) already possesses a globally attractive saturated equilibrium. These assumptions, although they seem restrictive, are quite natural; moreover, here the main goal is to use the controls to change the position of the saturated equilibrium while keeping its stability, as emphasized by some examples. For a biological interpretation of the use of controls, see, for example, [9, 25, 28] and references therein.

We now briefly describe the contents of the paper. From a theoretical perspective, dealing with FDEs with infinite delays requires a careful choice of a suitable Banach phase space (usually called an *admissible space*), in order to recover classical results of well-posedness of the initial-value problem, existence and uniqueness of solutions, continuation of solutions, etc. For this reason, in § 2 we set some basic notation for FDEs with infinite delay, and insert (1.1) into such a framework. In § 3, after studying the existence of a unique saturated equilibrium (x^*, u^*) and the boundedness of positive solutions to (1.1), theorem 3.8 provides a general criterion for the global attractivity of (x^*, u^*). Also, a sufficient condition for the dissipativeness of (1.1) is given. In § 4, sharper criteria are established for the global attractivity of a saturated equilibrium (x^*, u^*) that is not strictly positive. In this situation, this means the extinction of all or part of the populations. Our results turn out to be particularly powerful for predator–prey models. We also emphasize that, for the uncontrolled system, we derive better results for partial (or total) extinction than the ones in [5]. Our techniques also allow us to obtain a perturbation result for non-autonomous Lotka–Volterra systems with a limiting model of the form (1.1) or (1.4) as $t \to \infty$. The particular case of a two-dimensional Lotka–Volterra system is covered in § 5. In §§ 4 and 5, some examples illustrate our results.

2. An abstract formulation

Since (1.1) has unbounded delays, we must carefully formulate the problem by defining an appropriate Banach phase space where the problem is well posed.

Let g be a function satisfying the following properties.

(g1) $g\colon (-\infty, 0] \to [1, \infty)$ is a non-increasing continuous function and $g(0) = 1$.

(g2)

$$\lim_{u \to 0^-} \frac{g(s+u)}{g(s)} = 1 \quad \text{uniformly on} \quad (-\infty, 0].$$

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

For $n \in \mathbb{N}$, define the Banach space $\mathrm{UC}_g = \mathrm{UC}_g(\mathbb{R}^n)$, where 'UC' stands for 'uniformly continuous',

$$\mathrm{UC}_g := \biggl\{\phi \in C((-\infty, 0]; \mathbb{R}^n)\colon \sup_{s \leqslant 0} \frac{|\phi(s)|}{g(s)} < \infty, \\ \frac{\phi(s)}{g(s)} \text{ is uniformly continuous on } (-\infty, 0]\biggr\},$$

with the norm

$$\|\phi\|_g = \sup_{s \leqslant 0} \frac{|\phi(s)|}{g(s)},$$

where $|\cdot|$ is a chosen norm in $\mathbb{R}^n$. Consider also the space $\mathrm{BC} = \mathrm{BC}(\mathbb{R}^n)$ of bounded continuous (BC) functions $\phi\colon (-\infty, 0] \to \mathbb{R}^n$. It is clear that $\mathrm{BC} \subset \mathrm{UC}_g$, with $\|\phi\|_g \leqslant \|\phi\|_\infty$ for $\phi \in \mathrm{BC}$ and $\|\cdot\|_\infty$ the supremum norm in BC. Here, BC will be considered as a subspace of UC_g, so BC is endowed with the norm of UC_g.

The space UC_g is an admissible phase space for n-dimensional FDEs with infinite delay (see [13, 14]) written in the abstract form

$$\dot{x}(t) = f(t, x_t), \tag{2.1}$$

where $f\colon D \subset \mathbb{R} \times \mathrm{UC}_g \to \mathbb{R}^n$ is continuous and, as usual, segments of solutions in the phase space UC_g are denoted by x_t, $x_t(s) = x(t+s)$, $s \leqslant 0$, with components $x_{t,i}$. The standard results, therefore, on existence and uniqueness of solutions for the Cauchy problem $\dot{x}(t) = f(t, x_t)$, $x_0 = \varphi$ hold when f is regular enough and $\varphi \in \mathrm{UC}_g$. Moreover, for initial conditions $\varphi \in \mathrm{BC}$, bounded positive orbits are precompact in UC_g [10].

We now set an appropriate formulation for problem (1.1), (1.2). From [11] and [7, lemma 4.1], for any $\delta > 0$ there is a continuous function g satisfying (g1)–(g3) and such that

$$\int_0^\infty g(-s)K_{ij}(s)\,\mathrm{d}s < 1 + \delta, \quad \int_0^\infty g(-s)G_i(s)\,\mathrm{d}s < 1 + \delta, \quad i, j = 1, \dots, n. \tag{2.2}$$

When dealing with (1.4), where the more general linearities are given by bounded variation functions $\eta_{ij}(s)$, $\nu_i(s)$ with total variation 1 and $\nu_i(s)$ non-decreasing, (2.2) should be replaced by

$$\int_0^\infty g(-s)\,\mathrm{d}|\eta_{ij}(s)| < 1 + \delta, \quad \int_0^\infty g(-s)\,\mathrm{d}\nu_i(s) < 1 + \delta, \quad i, j = 1, \dots, n. \tag{2.3}$$

Whenever an abstract setting is required, in what follows we shall always assume that (1.1) takes the abstract form (2.1) in the phase space $\mathrm{UC}_g = \mathrm{UC}_g(\mathbb{R}^{2n})$ for some fixed $\delta > 0$ and function g satisfying (g1)–(g3) and (2.2), and consider solutions with initial conditions

$$x_0 = \varphi, \quad u(0) = \psi, \tag{2.4}$$

where $(\varphi, \psi) \in \mathrm{BC}(\mathbb{R}^{2n})$. The system (1.1) has a unique solution $(x(t), u(t)) = (x(t; \varphi, \psi), u(t; \varphi, \psi))$ satisfying (2.4). Moreover, since only positive or non-negative solutions of (1.1) are biologically meaningful, we restrict our framework to positive or non-negative initial conditions. A vector $x \in \mathbb{R}^n$ is said to be *positive*, or *non-negative*, if all its components are positive, or non-negative, respectively, and we write $x > 0$, $x \geqslant 0$, respectively. We define and denote in a similar way *positive* and *non-negative functions* in BC, and *positive* and *non-negative matrices* as well. As usual, we use the notation $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n \colon x \geqslant 0\}$. In the space UC_g, a vector c is identified with the constant function $\psi(s) = c$ for $s \leqslant 0$.

Consider the positive cone $\mathrm{BC}^+ = \mathrm{BC}^+(\mathbb{R}^{2n}) = \{(\varphi, \psi) \in \mathrm{BC} \colon \varphi(s),\ \psi(s) \geqslant 0$ for all $s \leqslant 0\}$. As a set of admissible initial conditions for (1.1), we take the subset BC^+_0 of BC^+, $\mathrm{BC}^+_0 = \{(\varphi, \psi) \in \mathrm{BC}^+ \colon \varphi(0) > 0,\ \psi(0) > 0\}$. It is easy to see that all the coordinates of solutions with initial conditions in BC^+ (respectively, BC^+_0) remain non-negative (respectively, positive) for all $t \geqslant 0$, whenever they are defined.

In the following, we shall consider norms $|\cdot|_d$ in $\mathbb{R}^N$ ($N = n$ or $N = 2n$) given by $|(x_1, \dots, x_N)|_d = \max_{1 \leqslant i \leqslant N} d_i|x_i|$, for some $d = (d_1, \dots, d_N) > 0$. For such norms in $\mathbb{R}^N$, in order to be more explicit, we denote the norm in UC_g by $\|\cdot\|_{g,d}$,

$$\|\psi\|_{g,d} = \sup_{s\leqslant 0} \frac{|\psi(s)|_d}{g(s)}.$$

3. Existence and global attractivity of a saturated equilibrium

In the absence of controls, the Lotka–Volterra system reads as

$$x_i'(t) = x_i(t)\biggl(b_i - \mu_i x_i(t) - \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) x_j(t-s)\,\mathrm{d}s\biggr), \tag{3.1}$$

for which

$$M_0 = N + A, \quad \text{where } N = \mathrm{diag}(\mu_1, \dots, \mu_n),\ A = [a_{ij}], \tag{3.2}$$

is designated as the interaction *community matrix*. As for ordinary differential equations (ODEs), the algebraic properties of M_0 determine many features of the asymptotic behaviour of solutions to (3.1) (see, for example, [5, 6, 15]). Clearly, the introduction of controls might change the dynamics of (3.1). Here, the main aim is to use the controls to change the position of a globally attractive equilibrium and give general criteria for its attractivity.

For (1.1), we define the *controlled community matrix* as

$$M = N + A + C, \quad \text{where } C = \mathrm{diag}\left(\frac{c_1 d_1}{e_1}, \dots, \frac{c_n d_n}{e_n}\right). \tag{3.3}$$

We also consider the matrices

$$\hat{M}_0 = N - |A|, \quad \hat{M} = N - |A| - C, \quad \text{where } |A| = [|a_{ij}|]. \tag{3.4}$$

Note that $(x^*, u^*) = (x_1^*, \dots, x_n^*, u_1^*, \dots, u_n^*) \in \mathbb{R}^n \times \mathbb{R}^n$ is an equilibrium of (1.1) if and only if

$$x_i^* = 0 \text{ or } (Mx^*)_i = b_i, \quad \text{and} \quad u_i^* = \frac{d_i}{e_i} x_i^*, \quad i = 1, \dots, n,$$

where x_i is the ith coordinate of the vector $\boldsymbol{x}$.

Throughout the paper, we shall use the definition of a *saturated equilibrium*.

Definition 3.1. Let $(x^*, u^*) = (x_1^*, \dots, x_n^*, u_1^*, \dots, u_n^*)$ be an equilibrium of (1.1). We say that (x^*, u^*) is a *saturated equilibrium* if (x^*, u^*) is non-negative and

$$(Mx^*)_i \geqslant b_i \quad \text{whenever } x_i^* = 0,\ i = 1, \dots, n.$$

Remark 3.2. We observe that if $(x^*, u^*) \geqslant 0$ is an equilibrium of (1.1) on the border of the positive cone $\mathbb{R}_+^n \times \mathbb{R}_+^n$, i.e. $x_i^* = u_i^* = 0$ for some i, and (x^*, u^*) is not saturated, then (x^*, u^*) is unstable. In fact, (1.1) and the ODE system in $\mathbb{R}_+^n \times \mathbb{R}_+^n$,

$$\left.\begin{aligned} x_i'(t) &= x_i(t)\biggl(b_i - \mu_i x_i(t) - \sum_{j=1}^{n} a_{ij} x_j(t) - c_i u_i(t)\biggr), \\ u_i'(t) &= -e_i u_i(t) + d_i x_i(t), \end{aligned}\right\} \quad i = 1, 2, \dots, n, \tag{3.5}$$

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share the same equilibria. Since $\mathbb{R}^n_+ \times \mathbb{R}^n_+$ is forward invariant for (3.5), if $(x^*, u^*) \geqslant 0$ is an equilibrium of (3.5) and (x^*, u^*) is not saturated, then (x^*, u^*) is unstable, since the characteristic equation for the linearized equation about (x^*, u^*) has an eigenvalue with positive real part (see, for example, [15]).

When analysing (1.1), our concepts of attractivity and stability always refer to the set of *admissible solutions*, i.e. to solutions $(x(t), u(t)) = (x(t; \varphi, \psi), u(t; \varphi, \psi))$ with (φ, ψ) in the set of admissible initial conditions. In particular, an equilibrium (x^*, u^*) of (1.1) is *globally attractive* if all solutions $(x(t), u(t))$ of (1.1), with initial conditions $(x_0, u_0) = (\varphi, \psi) \in \mathrm{BC}_0^+$, satisfy $\lim_{t\to\infty} x(t) = x^*, \lim_{t\to\infty} u(t) = u^*$. It is *globally asymptotically stable* (GAS) if it is stable and globally attractive.

We recall some concepts from matrix theory, which will be used in the next sections.

Definition 3.3. Let $B = [b_{ij}]$ be an $n \times n$ matrix. We say that B is an *M-matrix* (respectively, *non-singular M-matrix*) if $b_{ij} \leqslant 0$ for $i \neq j$ and all its eigenvalues have non-negative (respectively positive) real parts. The matrix B is said to be a *P-matrix* if all its principal minors are positive.

Remark 3.4. It is well known that there are several equivalent ways of defining M-matrices, non-singular M-matrices and P-matrices; in [8], these matrices are also designated by *matrices of classes* K_0, K and P, respectively (see [1,8,15] for further properties of these matrices). In particular, we recall that a square matrix with non-positive off-diagonal entries is an M-matrix (respectively, a non-singular M-matrix) if and only if all of its principal minors are non-negative (respectively, positive); so any non-singular M-matrix is a P-matrix. A related concept is the notion of a *Volterra–Lyapunov stable* (*VL-stable*) matrix, i.e. an $n\times n$ matrix $B = [b_{ij}]$ for which there exists a positive vector $d = (d_1, \dots, d_n)$ such that $\sum_{i,j=1}^n x_i d_i b_{ij} x_j < 0$ for all $x = (x_1, \dots, x_n) \neq 0$. If $-B$ is VL-stable, then B is also a P-matrix; the converse is true for the particular case of a 2×2 matrix, but not for higher dimensions. For Lotka–Volterra ODE systems of the form $x_i' = x_i[b_i - \sum_{j=1}^n a_{ij} x_j]$, $1 \leqslant i \leqslant n$, it is known that if $-[a_{ij}]$ is VL-stable, then there is one globally stable saturated equilibrium [15, p. 199].

Consider both the original and the controlled community matrices M_0, M, as well as the matrices $\hat{M}_0$, $\hat{M}$ (see (3.2)–(3.4)). For the uncontrolled system (3.1), it was shown [5, corollary 4.1] that if $\hat{M}_0$ is a non-singular M-matrix, then there is a unique saturated equilibrium of (3.1) that is a global attractor of all solutions with initial conditions $x_0 = \varphi \in \mathrm{BC}_0^+(\mathbb{R}^n)$. The idea now is to prove a similar result for (1.1). We start by studying the existence of a saturated equilibrium and the boundedness of solutions to (1.1).

Theorem 3.5. *Assume that M is a P-matrix, where M is the controlled community matrix in (3.3). There is then a unique saturated equilibrium (x^*, u^*) of (1.1).*

Proof. If M is a P-matrix, then for each vector $b = (b_1, \dots, b_n) \in \mathbb{R}^n$ there is a unique non-negative vector x^* such that $Mx^* \geqslant b$ and $(Mx^*)_i = b_i$ if $x_i^* > 0$ [1, p. 274]. With $u^* = (u_1^*, \dots, u_n^*)$, where $u_i^* = (d_i/e_i)x_i^*$, this means that (x^*, u^*) is the unique saturated equilibrium of (1.1). □

If all coefficients in (1.1) are positive, then clearly all positive solutions are bounded, since the inequalities $x_i'(t) \leqslant x_i(t)(b_i - \mu_i x_i(t))$ hold, and positive solutions of the logistic ODEs $y'(t) = y(t)(b_i - \mu_i y(t))$ are bounded. This is not the case, however, if we allow some of the coefficients a_{ij} to be negative, unless further constraints on M_0 are imposed.

Lemma 3.6. *Assume that the matrix $\hat{M}_0$ in (3.4) is a non-singular M-matrix. Then, all solutions of (1.1) with initial conditions (1.2) are defined and bounded on $[0, \infty)$.*

Proof. Solutions of (1.1) with initial conditions (1.2) are positive whenever they are defined. For (1.1) written in the abstract form $X'(t) = F(X_t)$, the function F transforms bounded sets of $\mathrm{UC}_g(\mathbb{R}^{2n})$ into bounded sets of $\mathbb{R}^{2n}$, and hence solutions are defined on compact intervals $[0, \alpha]$ for all $\alpha > 0$, and therefore on $[0, \infty)$.

Since $\hat{M}_0$ is a non-singular M-matrix, there is a positive vector $\eta = (\eta_1, \dots, \eta_n)$ such that $\hat{M}_0 \eta > 0$ [8], i.e.

$$\mu_i \eta_i > \sum_{j=1}^{n} |a_{ij}| \eta_j, \quad i = 1, \dots, n.$$

Choose an arbitrarily small $\delta > 0$ such that

$$\mu_i - (1 + \delta) \sum_{j=1}^{n} |a_{ij}| \frac{\eta_j}{\eta_i} > 0, \quad i = 1, \dots, n, \tag{3.6}$$

and a function g for which (g1)–(g3) and (2.2) hold.

For $\bar{\eta} = (\eta_1^{-1}, \dots, \eta_n^{-1}, e_1(d_1\eta_1)^{-1}, \dots, e_n(d_n\eta_n)^{-1})$, we furthermore consider $\mathbb{R}^{2n}$ equipped with the norm $|\cdot|_{\bar{\eta}}$ given by

$$|(x_1, \dots, x_n, u_1, \dots, u_n)|_{\bar{\eta}} = \max\left\{ \max_i \left(\frac{1}{\eta_i} |x_i| \right), \max_i \left(\frac{e_i}{\eta_i d_i} |u_i| \right) \right\}.$$

Let $(x(t), u(t)) = (x_1(t), \dots, x_n(t), u_1(t), \dots, u_n(t))$ be a positive solution of (1.1). We claim that

$$\sup_{t \geqslant 0} |(x(t), u(t))|_{\bar{\eta}} < \infty. \tag{3.7}$$

For the sake of contradiction, assume that (3.7) fails. Then, for any $K > 0$, there exists $T > 0$ such that

$$\left. \begin{aligned} |(x(T), u(T))|_{\bar{\eta}} &\geqslant |(K, \dots, K)|_{\bar{\eta}}, \\ |(x(T), u(T))|_{\bar{\eta}} &\geqslant |(x(t), u(t))|_{\bar{\eta}}, \end{aligned} \right\} \quad 0 \leqslant t \leqslant T. \tag{3.8}$$

Consider (3.8) with K such that

$$|(K, \dots, K)|_{\bar{\eta}} > \|(x_0, u_0)\|_{g, \bar{\eta}} = \sup_{s \leqslant 0} \frac{|(x(s), u(s))|_{\bar{\eta}}}{g(s)},$$

and sufficiently large, to be specified later.

If $|(x(T),u(T))|_{\bar\eta} = (e_i/\eta_i d_i)u_i(T) > (1/\eta_i)x_i(T)$ for some $i \in \{1,\dots,n\}$, then from (1.1) we obtain

$$u_i'(T) < -e_i u_i(T) + d_i \frac{e_i}{d_i} u_i(T) \leqslant 0,$$

which is not possible since the definition of T implies that $u_i'(T) \geqslant 0$. Thus, $|(x(T),u(T))|_{\bar\eta} = (1/\eta_i)x_i(T)$ for some $i \in \{1,\dots,n\}$. Clearly, $x_i'(T) \geqslant 0$.

Let $0 \leqslant t \leqslant T$ and let $s \geqslant 0$. Note that

$$\frac{1}{\eta_j}\frac{x_j(t-s)}{g(-s)} \leqslant \frac{1}{\eta_j}\frac{x_j(t-s)}{g(t-s)} < \frac{1}{\eta_j}K \leqslant \frac{1}{\eta_i}x_i(T) \quad \text{if } t-s \leqslant 0,$$

and

$$\frac{1}{\eta_j}\frac{x_j(t-s)}{g(-s)} \leqslant \frac{1}{\eta_i}x_i(T) \quad \text{if } 0 \leqslant t-s \leqslant T.$$

Hence,

$$\begin{aligned} \eta_j^{-1}\left|a_{ij}\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s\right| &\leqslant \eta_j^{-1}|a_{ij}|\int_0^\infty g(-s)K_{ij}(s)\frac{x_j(t-s)}{g(-s)}\,\mathrm{d}s \\ &< (1+\delta)\eta_i^{-1}|a_{ij}|x_i(T), \quad j=1,\dots,n. \end{aligned} \tag{3.9}$$

From (1.1) and (3.9), we obtain

$$0 \leqslant x_i'(T) \leqslant x_i(T)\left[b_i - \left(\mu_i - (1+\delta)\sum_{j=1}^n |a_{ij}|\frac{\eta_j}{\eta_i}\right)x_i(T)\right].$$

By (3.6), this is a contradiction if K is chosen such that

$$K > b_i\left(\mu_i - (1+\delta)\sum_{j=1}^n |a_{ij}|\frac{\eta_j}{\eta_i}\right)^{-1}.$$

□

In fact, a better criterion for the uniform boundedness of all positive solutions of (1.1) will be given later (see theorem 3.10).

Note that $\hat M_0 = \hat M + C$, where C is a positive diagonal matrix. By [8, theorem 5.1.1], it follows that if $\hat M$ is an M-matrix, then $\hat M_0$ is a non-singular M-matrix. Now, if $\hat M_0$ is a non-singular M-matrix, then there is a positive vector $\eta = (\eta_1,\dots,\eta_n)$ such that $\hat M_0\eta > 0$, i.e. $\mu_i\eta_i > \sum_{j=1}^n |a_{ij}|\eta_j$ for $1 \leqslant i \leqslant n$ (see [8]); in particular, this implies a 'diagonal dominance' of M_0 in the sense that $(\mu_i + a_{ii})\eta_i > \sum_{j\neq i}|a_{ij}|\eta_j$ for $1 \leqslant i \leqslant n$. From [15, p. 201], it follows that if $\hat M_0$ is a non-singular M-matrix, then $-M_0$ (and hence $-M$ as well) is VL-stable, and therefore a P-matrix.

Lemma 3.7. *Assume that the matrix $\hat M$ in (3.4) is a non-singular M-matrix and that the unique saturated equilibrium (x^*,u^*) of (1.1) is positive. Then (x^*,u^*) is locally asymptotically stable.*

Proof. As observed, if $\hat M$ is an M-matrix, then M is a P-matrix and there is a unique saturated equilibrium (x^*,u^*). The linearization of (1.1) about (x^*,u^*) is

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given by

$$\begin{bmatrix} y'(t) \\ v'(t) \end{bmatrix} = -\left(B \begin{bmatrix} y(t) \\ v(t) \end{bmatrix} + \mathcal{L} \begin{bmatrix} y_t \\ v_t \end{bmatrix} \right), \tag{3.10}$$

with $y(t), v(t) \in \mathbb{R}^n$, and the linear operator $\mathcal{L}\colon \mathrm{BC}_g(\mathbb{R}^{2n}) \subset \mathrm{UC}_g(\mathbb{R}^{2n}) \to \mathbb{R}^{2n}$ and the $(2n) \times (2n)$ matrix B defined as

$$\mathcal{L} = (\mathcal{L}_1, \dots, \mathcal{L}_{2n}), \qquad B = \mathrm{diag}(\alpha_1, \dots, \alpha_n, e_1, \dots, e_n),$$

where

$$\alpha_i = \begin{cases} \mu_i x_i^* & \text{if } x_i^* > 0, \\ \displaystyle\sum_{j=1}^n a_{ij} x_j^* - b_i & \text{if } x_i^* = 0, \end{cases}$$

and

$$\left. \begin{aligned} \mathcal{L}_i(\varphi, \psi) &= x_i^* \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s) \varphi_j(-s)\, \mathrm{d}s \\ &\qquad\qquad + x_i^* c_i \int_0^\infty G_i(s) \psi_i(-s)\, \mathrm{d}s, \\ \mathcal{L}_{n+i}(\varphi, \psi) &= -d_i \varphi_i(0), \end{aligned} \right\} \quad i = 1, \dots, n,$$

for $(\varphi, \psi) = (\varphi_1, \dots, \varphi_n, \psi_1, \dots, \psi_n)$. Note that $\alpha_i \geqslant 0$ for $1 \leqslant i \leqslant n$.

For $(\boldsymbol{e}_1, \dots, \boldsymbol{e}_{2n})$, the canonical basis of $\mathbb{R}^{2n}$, define $L\colon = B + [\mathcal{L}_i(\boldsymbol{e}_j)]_{i,j}$ and $\hat{L} := B - [|\mathcal{L}_i(\boldsymbol{e}_j)|]_{i,j}$ $(1 \leqslant i,\ j \leqslant 2n)$. We have

$$[\mathcal{L}_i(\boldsymbol{e}_j)]_{i,j=1}^{2n} = \begin{bmatrix} A(x^*) & C(x^*) \\ -D & 0 \end{bmatrix},$$

with $A(x^*) = [x_i^* a_{ij}]_{i,j}$ $(1 \leqslant i,\ j \leqslant n)$, $C(x^*) = \mathrm{diag}(x_1^* c_1, \dots, x_n^* c_n)$ and $D = \mathrm{diag}(d_1, \dots, d_n)$. Now, suppose that $x^* > 0$. It is easy to see that the matrices L and $\hat{L}$ are equivalent to, respectively,

$$\begin{bmatrix} M(x^*) & C(x^*) \\ 0 & E \end{bmatrix}, \qquad \begin{bmatrix} \hat{M}(x^*) & -C(x^*) \\ 0 & E \end{bmatrix},$$

where

$$\begin{aligned} E &= \mathrm{diag}(e_1, \dots, e_n), \\ N(x^*) &= \mathrm{diag}(\mu_1 x_1^*, \dots, \mu_n x_n^*), \\ \tilde{C}(x^*) &= \mathrm{diag}\left(x_1^* \frac{c_1 d_1}{e_1}, \dots, x_n^* \frac{c_n d_n}{e_n} \right), \\ M(x^*) &= N(x^*) + A(x^*) + \tilde{C}(x^*), \\ \hat{M}(x^*) &= N(x^*) - A(x^*) - \tilde{C}(x^*). \end{aligned}$$

Note that $M(x^*)$ and $\hat{M}(x^*)$ are obtained from M and $\hat{M}$, respectively, by multiplying each line i by x_i^*. Hence, it follows that $\det L \neq 0$ and that $\hat{L}$ is a non-singular

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M-matrix as well. From [5], we derive that the linear system (3.10) is asymptotically stable. □

We remark that if $x_i^* = 0$, then the ith line of the above matrix $[\mathcal{L}_i(\boldsymbol{e}_j)]$ is 0. Hence, a saturated equilibrium (x^*, u^*) of (1.1) on the boundary of the positive cone is not necessarily asymptotically stable. Thus, although its linearization (3.10) is stable, one cannot deduce that (x^*, u^*) is stable as a solution of (1.1).

Our main general result on the global attractivity of the saturated equilibrium is given below.

THEOREM 3.8. *Assume that the matrix $\hat{M}$ in (3.4) is an M-matrix. There is then a unique saturated equilibrium (x^*, u^*) of (1.1) that is a global attractor of all solutions with initial conditions (1.2). Moreover, if in addition $x^* > 0$ and $\hat{M}$ is non-singular, then (x^*, u^*) is GAS.*

Proof. Since $\hat{M}$ is an M-matrix, from theorem 3.5 and lemma 3.6 we conclude that there is a unique saturated equilibrium (x^*, u^*) of (1.1) and that all positive solutions are defined and bounded on $[0, \infty)$. Lemma 3.7 shows that (x^*, u^*) is stable if it is a positive equilibrium. We now need to show that (x^*, u^*) is a global attractor of all positive solutions of (1.1).

Denote by I_n the $n \times n$ identity matrix. If $\hat{M}$ is an M-matrix, then for any $\delta_0 > 0$ the matrix $\delta_0 I_n + \hat{M}$ is a non-singular M-matrix. Fix any $\delta_0 > 0$ and a positive vector $\eta = (\eta_1, \dots, \eta_n)$ such that $(\delta_0 I_n + \hat{M})\eta > 0$, i.e.

$$\left(\delta_0 + \mu_i - c_i \frac{d_i}{e_i}\right)\eta_i > \sum_{j=1}^{n} |a_{ij}|\eta_j, \quad i = 1, \dots, n.$$

Choose $\delta > 0$ such that

$$\left(\delta_0 + \mu_i - c_i \frac{d_i}{e_i}\right)\eta_i - (1+\delta)\sum_{j=1}^{n} |a_{ij}|\eta_j > 0, \quad 1 \leqslant i \leqslant n, \tag{3.11}$$

and a function g for which conditions (g1)–(g3) and (2.2) are fulfilled. We abuse the notation, and denote norms in both $\mathbb{R}^{2n}$ and in $\mathbb{R}^n$ by $|\cdot|_{\bar{\eta}}$, where

$$|(x_1, \dots, x_n, u_1, \dots, u_n)|_{\bar{\eta}} := \max_{1 \leqslant i \leqslant n} \left\{ \max\left(\frac{1}{\eta_i}|x_i|, \frac{e_i}{\eta_i d_i}|u_i|\right)\right\} \quad \text{in } \mathbb{R}^{2n},$$
$$|x|_{\bar{\eta}} := \max_{1 \leqslant i \leqslant n} \frac{1}{\eta_i}|x_i| \quad \text{in } \mathbb{R}^n,$$

and consider $\mathrm{UC}_g(\mathbb{R}^{2n})$ and $\mathrm{UC}_g(\mathbb{R}^n)$ equipped with the norms $\|\cdot\|_{g,\bar{\eta}}$.

Let $(x(t), u(t))$ be a positive solution of (1.1). With the change of variables

$$\left.\begin{aligned} y_i(t) &= x_i(t) - x_i^*, \\ v_i(t) &= u_i(t) - u_i^*, \end{aligned}\right\} \quad i = 1, \dots, n,$$

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the system (1.1), together with definition 3.1, lead to

$$y_i'(t) = -(y_i(t) + x_i^*)\biggl(\mu_i y_i(t) + \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s\biggr) \quad \text{if } x_i^* > 0, \tag{3.12}$$

$$y_i'(t) \leqslant -y_i(t)\biggl(\mu_i y_i(t) + \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s\biggr) \quad \text{if } x_i^* = 0, \tag{3.13}$$

$$v_i'(t) = -e_i v_i(t) + d_i y_i(t), \tag{3.14}$$

$i = 1, 2, \dots, n$. Define

$$\liminf_{t\to\infty} y_i(t) = -l_i, \quad \limsup_{t\to\infty} y_i(t) = L_i, \quad i = 1, \dots, n, \tag{3.15}$$

and set

$$l = \max_{1\leqslant i\leqslant n} \frac{l_i}{\eta_i}, \qquad L = \max_{1\leqslant i\leqslant n} \frac{L_i}{\eta_i}, \qquad U = \max(l, L).$$

Integrating (3.14), we get

$$v_i(t) = v_i(0)\mathrm{e}^{-e_i t} + d_i \mathrm{e}^{-e_i t} \int_0^t \mathrm{e}^{e_i s} y_i(s)\,\mathrm{d}s, \quad t \geqslant 0, \tag{3.16}$$

and therefore

$$-x_i^* \leqslant -l_i \leqslant \frac{e_i}{d_i} \liminf_{t\to\infty} v_i(t) \leqslant \frac{e_i}{d_i} \limsup_{t\to\infty} v_i(t) \leqslant L_i < \infty. \tag{3.17}$$

Since $U \geqslant 0$, it is enough to prove that $U = 0$. In order to get a contradiction, assume that $U > 0$.

Define $I = \{1, \dots, n\}$, $I_1 = \{i \in I : \eta_i^{-1} L_i = U\}$ and $I_2 = \{i \in I : \eta_i^{-1} l_i = U\}$. The assumption $U > 0$ implies that $x_i^* > 0$ if $i \in I_2$; otherwise, with $x_i^* = 0$, we get $\liminf_{t\to\infty} x_i(t) = \liminf_{t\to\infty} y_i(t) = -l_i = -\eta_i U \geqslant 0$, and thus $U = 0$.

The coordinates $y_j(t)$, $v_j(t)$ are uniformly bounded for $t \geqslant 0$, and thus, as remarked in § 2, the positive orbit $\{(y_t, v_t) : t \geqslant 0\}$ is precompact in $\mathrm{UC}_g(\mathbb{R}^{2n})$.

Take any sequence (t_k) with $t_k \to \infty$. Thus, there is a subsequence of (y_{t_k}, v_{t_k}), still denoted by (y_{t_k}, v_{t_k}), converging to some (ϕ, ψ) in $\mathrm{UC}_g(\mathbb{R}^{2n})$. Let ϕ_j, ψ_j $(1 \leqslant j \leqslant n)$ be the components of ϕ, ψ, respectively. Take any $\varepsilon > 0$ and let $t^* > 0$ be such that $\eta_j^{-1}|y_j(t)| \leqslant U + \varepsilon$ for $t \geqslant t^*$, $1 \leqslant j \leqslant n$. For any $s \geqslant 0$, if k is large so that $t_k - s \geqslant t^*$, then

$$\eta_j^{-1} \frac{|y_{t_k,j}(-s)|}{g(-s)} = \eta_j^{-1} \frac{|y_j(t_k - s)|}{g(-s)} \leqslant \eta_j^{-1} |y_j(t_k - s)| \leqslant U + \varepsilon,$$

and therefore we get $\eta_j^{-1}\|\phi_j\|_g \leqslant U + \varepsilon$. In a similar way, we obtain

$$\eta_j^{-1}\biggl(\frac{e_i}{d_i}\biggr)\|\psi_j\|_g \leqslant U + \varepsilon.$$

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Hence, we conclude that $\|(\phi,\psi)\|_{g,\bar\eta} \leqslant U$. Moreover, if $i \in I_1 \cup I_2$ and (t_k) is chosen in such a way that $\eta_i^{-1}|y_i(t_k)| \to U$, we furthermore deduce that $\|\phi\|_{g,\bar\eta} = \eta_i^{-1}|\phi_i(0)| = U$ and that $y_{t_k,j}$, $v_{t_k,j}$ converge uniformly to ϕ_j, ψ_j, respectively, on each compact set of $[0,\infty)$.

Fix $i \in I_1 \cup I_2$. By the fluctuation lemma, take a sequence (t_k) with $t_k \to \infty$, $y_i'(t_k) \to 0$ and

$$\eta_i^{-1} y_i(t_k) \to \begin{cases} U & \text{if } i \in I_1, \\ -U & \text{if } i \in I_2. \end{cases}$$

As above, we may assume that $(y_{t_k}, v_{t_k}) \to (\phi,\psi) \in \mathrm{UC}_g(\mathbb{R}^{2n})$ for the norm $\|\cdot\|_{g,\bar\eta}$.

First, we consider the case $i \in I_1$, and thus $\eta_i^{-1} y_i(t_k) \to U$.

Since the linear operator $\psi \mapsto \int_0^\infty G_i(s)\psi(-s)\,\mathrm{d}s$, defined for $\psi \in \mathrm{BC}(\mathbb{R}) \subset \mathrm{UC}_g(\mathbb{R})$, is bounded, there exists

$$\nu := \lim_{k\to\infty} \int_0^\infty G_i(s) v_i(t_k - s)\,\mathrm{d}s = \int_0^\infty G_i(s)\psi_i(-s)\,\mathrm{d}s.$$

From (3.17), we have

$$|\psi_i(-s)| \leqslant \eta_i \left(\frac{d_i}{e_i}\right) U \quad \text{for any } s \geqslant 0,$$

and thus $\nu \geqslant -\eta_i(d_i/e_i)U$. From (1.3), the equality $\nu = -\eta_i(d_i/e_i)U$ implies that $\psi_i(0) = -\eta_i(d_i/e_i)U$. But, from (3.16), we have

$$v_i(t_k) = v_i(0)\mathrm{e}^{-e_i t_k} + d_i \int_0^{t_k} \mathrm{e}^{-e_i u} y_{t_k,i}(-u)\,\mathrm{d}u,$$

and from Lebesgue's dominated convergence theorem it follows that

$$\lim_{k\to\infty} v_i(t_k) = \psi_i(0) = d_i \int_0^\infty \mathrm{e}^{-e_i u}\phi_i(-u)\,\mathrm{d}u.$$

Since ϕ_i is a continuous function with $\eta_i^{-1}|\phi_i(-s)| \leqslant U$ for $s > 0$ and $\eta_i^{-1}\phi_i(0) = U$, then $\eta_i^{-1}\int_0^\infty \mathrm{e}^{-e_i s}\phi_i(-s)\,\mathrm{d}s > -U/e_i$. We conclude, therefore, that

$$\eta_i^{-1}\nu > -\frac{d_i}{e_i}U. \tag{3.18}$$

Moreover, despite the use of a specific vector $\eta = \eta(\delta_0)$ and norm $\|\cdot\|_{g,\bar\eta}$ in $\mathrm{UC}_g(\mathbb{R}^n)$, obviously the limit ν does not depend on the chosen norm $|\cdot|_{\bar\eta}$ in $\mathbb{R}^n$.

Next, define

$$H_i(t) = \mu_i y_i(t) + \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s. \tag{3.19}$$

From (3.12) and (3.13), we obtain

$$y_i'(t_k) \leqslant -(y_i(t_k) + x_i^*) H_i(t_k).$$

From (2.2), we have (see (3.9))

$$\left|a_{ij}\int_0^\infty K_{ij}(s)y_j(t_k-s)\,\mathrm{d}s\right| \leqslant |a_{ij}|\int_0^\infty g(-s)K_{ij}(s)\frac{|y_j(t_k-s)|}{g(-s)}\,\mathrm{d}s \leqslant (1+\delta)|a_{ij}|\|y_{t_k,j}\|_g, \tag{3.20}$$

and this leads to

$$\begin{aligned} H_i(t_k) &\geqslant \mu_i y_i(t_k) - (1+\delta)\sum_{j=1}^n |a_{ij}|\|y_{t_k,j}\|_{g,\bar\eta} + c_i\int_0^\infty G_i(s)v_i(t_k-s)\,\mathrm{d}s \\ &\geqslant \mu_i y_i(t_k) - (1+\delta)\sum_{j=1}^n |a_{ij}|\eta_j\|y_{t_k}\|_{g,\bar\eta} + c_i\int_0^\infty G_i(s)v_i(t_k-s)\,\mathrm{d}s. \end{aligned} \tag{3.21}$$

By letting $k\to\infty$, from (3.11) and (3.21) we have

$$0 \geqslant \left(\mu_i\eta_i - (1+\delta)\sum_{j=1}^n |a_{ij}|\eta_j\right)U + c_i\nu \geqslant \left(c_i\frac{d_i}{e_i} - \delta_0\right)\eta_i U + c_i\nu. \tag{3.22}$$

Since $\delta_0>0$ is arbitrarily small, this yields $\nu \leqslant -(d_i/e_i)\eta_i U$, which is not possible in view of (3.18).

Now, consider the case $i\in I_2$. Then, $\eta_i^{-1}y_i(t_k)\to -U$ and (3.12) holds.

If $y_i(t)$ is eventually monotone, then $y_i(t)\to -\eta_i U$ and $v_i(t)\to -(d_i/e_i)\eta_i U$. Using arguments similar to the ones above, we obtain

$$\begin{aligned} H_i(t_k) &\leqslant \mu_i y_i(t_k) + (1+\delta)\sum_{j=1}^n |a_{ij}|\eta_j\|y_{t_k}\|_{g,\bar\eta} + c_i\int_0^\infty G_i(s)v_i(t_k-s)\,\mathrm{d}s \\ &\to \left[-\left(\mu_i + c_i\frac{d_i}{e_i}\right)\eta_i + (1+\delta)\sum_{j=1}^n |a_{ij}|\eta_j\right]U < 0. \end{aligned} \tag{3.23}$$

Since $y_i'(t_k) = -(y_i(t_k)+x_i^*)H_i(t_k)$, using the above estimate we obtain

$$0 \geqslant (-\eta_i U + x_i^*)\left[\left(\mu_i + c_i\frac{d_i}{e_i}\right)\eta_i - (1+\delta)\sum_{j=1}^n |a_{ij}|\eta_j\right]U,$$

and thus $y_i(t)\to -x_i^* = -\eta_i U$ as $t\to\infty$. Since $y_i(t) > -x_i^*$ for $t>0$, this is only possible if $y_i'(t)\leqslant 0$ for t large, so that $\eta_i^{-1}y_i(t)\searrow -U$. But in this case, from (3.12), it follows that $H_i(t)\geqslant 0$ for t large, which contradicts (3.23).

If $y_i(t)$ is not eventually monotone, then we can assume that $y_i(t_k)$ is a sequence of minima, so that $H_i(t_k)=0$, and this case is treated as the case $i\in I_1$. These arguments show that $U=0$, and the proof is complete. □

Remark 3.9. As referred to in the introduction, clearly the above proof applies to systems (1.4). In fact, with the terms

$$a_{ij}\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s \quad \text{and} \quad c_i\int_0^\infty G_i(s)u_i(t-s)\,\mathrm{d}s$$

replaced, respectively, by the more general linearities

$$a_{ij}\int_0^\infty x_j(t-s)\,\mathrm{d}\eta_{ij}(s) \quad \text{and} \quad c_i\int_0^\infty u_i(t-s)\,\mathrm{d}\nu_i(s),$$

where η_{ij}, ν_i are normalized bounded variation functions and ν_i are non-decreasing, we use (2.3) instead of (2.2), the estimates (3.20) are replaced by

$$\begin{aligned}\left|a_{ij}\int_0^\infty y_j(t_k-s)\,\mathrm{d}\eta_{ij}(s)\right| &\leqslant |a_{ij}|\int_0^\infty g(-s)\frac{|y_j(t_k-s)|}{g(-s)}\,\mathrm{d}|\eta_{ij}(s)| \\ &\leqslant (1+\delta)|a_{ij}|\|y_{t_k,j}\|_g, \quad i,j=1,\dots,n,\end{aligned}$$

the limit ν is now given by $\nu=\int_0^\infty \psi_i(-s)\,\mathrm{d}\nu_i(s)$, and all the other arguments are valid.

With the usual notation of

$$a_{ij}=a_{ij}^+-a_{ij}^-, \quad \text{where } a_{ij}^+=\max\{a_{ij},0\} \text{ and } a_{ij}^-=\max\{-a_{ij},0\},$$

we define

$$M_0^-=\operatorname{diag}(\mu_1,\dots,\mu_n)-A^-, \quad \text{where } A^-=[a_{ij}^-]. \tag{3.24}$$

Note that $M_0^-\geqslant\hat{M}_0$, and hence, in general, imposing that M_0^- is a non-singular M-matrix is weaker than requiring that $\hat{M}_0$ is a non-singular M-matrix. We now give sufficient conditions for the dissipativeness of (1.1), improving lemma 3.6

THEOREM 3.10. *If M_0^- is a non-singular M-matrix, then (1.1) is dissipative, that is, there exists $K>0$ such that $\limsup_{t\to\infty} x_i(t)\leqslant K$, $\limsup_{t\to\infty} u_i(t)\leqslant K$, $1\leqslant i\leqslant n$, for all solutions $(x(t),u(t))$ of (1.1) with initial conditions (1.2).*

Proof. A solution $(x(t),u(t))$ of (1.1) with initial condition $(x_0,u_0)=(\varphi,\psi)\in \mathrm{BC}_0^+$ satisfies

$$\left.\begin{aligned} x_i'(t)&\leqslant x_i(t)\biggl(b_i-\mu_i x_i(t)+\sum_{j=1}^n a_{ij}^-\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s\biggr),\\ u_i'(t)&=-e_iu_i(t)+d_ix_i(t),\end{aligned}\right\} \quad i=1,2,\dots,n.$$

Let $(X(t),U(t))$ be the solution of the system

$$\left.\begin{aligned} X_i'(t)&=X_i(t)\biggl(b_i-\mu_iX_i(t)\\ &\qquad+\sum_{j=1}^n a_{ij}^-\int_0^\infty K_{ij}(s)X_j(t-s)\,\mathrm{d}s\biggr),\\ U_i'(t)&=-e_iU_i(t)+d_iX_i(t),\end{aligned}\right\} \quad i=1,2,\dots,n, \tag{3.25}$$

with the initial conditions $X_0=\varphi$ and $U(0)=\psi(0)$. Since (3.25) is cooperative or, in other words, it satisfies the quasi-monotonicity condition in [23, ch. 5], by comparison results, it follows that $x(t)\leqslant X(t)$, $u(t)\leqslant U(t)$. From [5, corollary 4.1], $(X(t),U(t))\to(X^*,U^*)$ as $t\to\infty$, where (X^*,U^*) is the saturated equilibrium of (3.25). Thus, the solutions $(x(t),u(t))$ of the initial-value problems (1.1), (1.2) satisfy $\limsup_{t\to\infty} x_i(t)\leqslant X_i^*$, $\limsup_{t\to\infty} u_i(t)\leqslant U_i^*, 1\leqslant i\leqslant n$. □

Our setting contemplates all the possibilities for the signs of the coefficients b_i, a_{ij} in (3.1). In biological terms, the most interesting cases are, however, (i) $a_{ij} \geqslant 0$ for $i \neq j$ (competitive systems), (ii) $a_{ij} \leqslant 0$ for $i \neq j$ (cooperative systems), (iii) $a_{ij} > 0$, $a_{ji} < 0$ (predator–prey systems) if species i is a prey for the predator species j, $i \neq j$. On the other hand, the existence of a positive equilibrium depends heavily on the coefficients b_i and can be studied in more detail by using Cramer's rule. Nevertheless, a criterion for cooperative systems is given here.

THEOREM 3.11. *Consider (1.1) with $b_i > 0$ and $a_{ij} \leqslant 0$ for all $i \neq j$. If M is a non-singular M-matrix, then there exists a unique positive equilibrium of (1.1).*

Proof. Define $b = (b_1, \dots, b_n)$. Since M is a non-singular M-matrix, $M^{-1} \geqslant 0$ [1]. This implies that $(M^{-1}b)_i = 0$ if and only if the ith line of M^{-1} is 0, which is not possible. Therefore, $x^* := M^{-1}b$ is a positive vector and (x^*, u^*), with $u_i^* = (d_i/e_i)x_i^*$, $1 \leqslant i \leqslant n$, is a positive equilibrium of (1.1). □

4. Extinction and stability

For the results in this section, it is important to consider (1.1) with K_{ij} non-negative, or the more general system (1.4) with η_{ij} non-decreasing, $i, j = 1, \dots, n$. Straightforward generalizations for the situation of K_{ij} in (1.1) changing signs or η_{ij} non-monotone on $[0, \infty)$ can, however, be derived (see [5] for the case of uncontrolled Lotka–Volterra models).

We now seek better sufficient conditions for extinction for either all or part of the populations. Together with the controlled Lotka–Volterra system (1.1), consider the ODE (3.5), and write (3.5) in the form

$$X'(t) = F(X(t))$$

for $X(t) = (x_1(t), \dots, x_n(t), u_1(t), \dots, u_n(t))$.

Define $\lambda_i = \mu_i + (c_i d_i/e_i)$. If $X^* = (x^*, u^*) = (x_1^*, \dots, x_n^*, u_1^*, \dots, u_n^*)$ is an equilibrium of (3.5), then

$$DF(X^*) = \begin{bmatrix} Df(x^*) & -C(x^*) \\ D & -E \end{bmatrix},$$

where $C(x^*) = \operatorname{diag}(c_1 x_1^*, \dots, c_n x_n^*), D = \operatorname{diag}(d_1, \dots, d_n), E = \operatorname{diag}(e_1, \dots, e_n)$, and

$$\frac{\partial f_i}{\partial x_i}(x^*) = b_i - \lambda_i x_i^* - \sum_{j=1}^{n} a_{ij} x_j^* - (\mu_i + a_{ii}) x_i^*,$$

$$\frac{\partial f_i}{\partial x_j}(x^*) = -a_{ij} x_i^* \quad \text{if } i \neq j.$$

Note that $(\partial f_i/\partial x_i)(x^*) = -(\mu_i + a_{ii})x_i^*$ if $x_i^* > 0$, otherwise $(\partial f_i/\partial x_i)(x^*) = b_i - \sum_{j \neq i} a_{ij} x_j^* \leqslant 0$ for a saturated equilibrium X^* with $x_i^* = 0$.

For the trivial equilibrium, we have $C(0) = 0$, and hence, the spectrum of $DF(0)$ is $\sigma(DF(0)) = \{b_1, \dots, b_n, -e_1, \dots, -e_n\}$. We conclude, therefore, that 0 is a stable equilibrium for the linearization of (3.5) at 0 (which is also the linearization of (1.1))

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if and only if $b_i \leqslant 0$, $1 \leqslant i \leqslant n$, and the introduction of the controls does not change its stability.

Let M be a P-matrix. If $b_i \leqslant 0$, $1 \leqslant i \leqslant n$, then 0 is the saturated equilibrium. Conversely, if $b_i > 0$ for some i, then $DF(0)$ is unstable and 0 is not the saturated equilibrium. In the latter case, we have seen that (1.1) is dissipative if M_0^- is a non-singular M-matrix; there then exists a compact global attractor [12, theorem 3.4.8], which, however, need not be the saturated equilibrium. When 0 is saturated, rather than using theorem 3.8, the next result provides a better criterion for extinction of all populations.

THEOREM 4.1. *Assume that M is a P-matrix. The equilibrium 0 is the saturated equilibrium of (1.1) if and only if $b_i \leqslant 0$ for $1 \leqslant i \leqslant n$. In this case, if M_0^- is an M-matrix, where M_0^- is defined as in (3.24), then the equilibrium 0 of (1.1) is globally attractive.*

Proof. Since M_0^- is an M-matrix, for any arbitrarily small $\delta_0 > 0$ consider a positive vector $\eta = (\eta_1, \dots, \eta_n)$ such that $(M_0^- + \delta_0 I_n)\eta > 0$ [8]. Let $(x(t), u(t))$ be a solution of (1.1). After a scaling $x_i \mapsto \bar{x}_i = \eta_i^{-1} x_i$, $u_i \mapsto \bar{u}_i = \eta_i^{-1} u_i$, $1 \leqslant i \leqslant n$, and dropping the bars for the sake of simplicity, we may suppose that $(x(t), u(t))$ is a solution of (1.1) and that $(M_0^- + \delta_0 I_n)\eta > 0$ with $\eta = (1, \dots, 1)$. Next, choose $\delta > 0$ small and g satisfying (g1)–(g3) and (2.2), with

$$\delta_0 + \mu_i - (1+\delta)\sum_{j=1}^{n} a_{ij}^- > 0, \quad 1 \leqslant i \leqslant n. \tag{4.1}$$

Define $L_i = \limsup_{t\to\infty} x_i(t)$ and $U = \max_{1\leqslant i\leqslant n} L_i$. For the sake of contradiction, assume that $U > 0$ and choose $i \in \{1, \dots, n\}$ such that $L_i = U$. Consider a sequence (t_k) with $t_k \to \infty$, $x_i'(t_k) \to 0$, $x_i(t_k) \to U$ as $k \to \infty$. We now argue as in the proof of theorem 3.8, omitting some of the details. For some subsequence of (x_{t_k}, u_{t_k}), still denoted by (x_{t_k}, u_{t_k}), there is $(\phi, \psi) \in \mathrm{BC}^+(\mathbb{R}^{2n}) \subset \mathrm{UC}_g(\mathbb{R}^{2n})$ such that $x_{t_k} \to \phi$, $u_{t_k} \to \psi$ and $\|\phi\|_g = U = \phi_i(0)$. Next, from (1.3) and the fact that $\psi_i(0) = d_i \int_0^\infty \mathrm{e}^{-e_i u}\phi_i(-u)\,\mathrm{d}u > 0$, we obtain

$$\nu := \lim_{k\to\infty} \int_0^\infty G_i(s) u_i(t_k - s)\,\mathrm{d}s = \int_0^\infty G_i(s)\psi_i(-s)\,\mathrm{d}s > 0.$$

Choose $\delta_0 > 0$ small and k large so that $c_i \int_0^\infty G_i(s) u_i(t_k - s)\,\mathrm{d}s > \delta_0 U$. Since $b_i \leqslant 0$, for k large estimates as in (3.9) yield

$$\begin{aligned} x_i'(t_k) &\leqslant x_i(t_k)\biggl(b_i - \mu_i x_i(t_k) + \sum_{j=1}^{n} a_{ij}^- \int_0^\infty K_{ij}(s) x_j(t_k - s)\,\mathrm{d}s \\ &\qquad\qquad - c_i \int_0^\infty G_i(s) u_i(t_k - s)\,\mathrm{d}s\biggr) \\ &\leqslant -x_i(t_k)\biggl(\mu_i x_i(t_k) - \sum_{j=1}^{n} a_{ij}^- \|x_{t_k,j}\|_g \int_0^\infty g(-s) K_{ij}(s)\,\mathrm{d}s + \delta_0 U\biggr) \\ &\leqslant -x_i(t_k)\biggl(\mu_i x_i(t_k) - (1+\delta)\sum_{j=1}^{n} a_{ij}^- \|x_{t_k,j}\|_g + \delta_0 U\biggr). \end{aligned}$$

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By letting $k \to \infty$ we obtain

$$0 \geqslant \left[\delta_0 + \mu_i - (1+\delta)\sum_{j=1}^{n} a_{ij}^-\right] U,$$

which contradicts (4.1). Hence $U = 0$, and the proof is complete. □

Consider now the case of a saturated equilibrium $(x^*, u^*) \neq 0$ of (1.1) with $x^* \in \partial(\mathbb{R}^n_+)$. By reordering the variables, write $x^* = (x_1^*, \dots, x_p^*, 0, \dots, 0)$ with $x_i^* > 0$ for $1 \leqslant i \leqslant p$, where $1 < p < n$. Here, the attractivity of (x^*, u^*) means the extinction of the populations $x_i(t)$, $p+1 \leqslant j \leqslant n$, while the first p populations $x_i(t)$ stabilize with time at the 'saturated' value x_i^*. For this situation, the next result improves theorem 3.8. Its statement includes theorems 3.8 and 4.1 as particular cases.

Theorem 4.2. *Assume that M is a P-matrix, let (x^*, u^*) be the saturated equilibrium of (1.1) and suppose that $x^* = (x_1^*, \dots, x_p^*, 0, \dots, 0)$ $(0 \leqslant p \leqslant n)$. Write $n_1 = p$, $n_2 = n - p$ and the matrices $A = [a_{ij}]$, $|A| = [|a_{ij}|]$ and $A^- = [a_{ij}^-]$ in the form*

$$A = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}, \qquad |A| = \begin{bmatrix} |A_{11}| & |A_{12}| \\ |A_{21}| & |A_{22}| \end{bmatrix}, \qquad A^- = \begin{bmatrix} A_{11}^- & A_{12}^- \\ A_{21}^- & A_{22}^- \end{bmatrix},$$

where A_{kl}, $|A_{kl}|$, A_{kl}^- are $n_k \times n_l$ matrices for $k, l = 1, 2$. Define also

$$\hat{\mathcal{M}}_{11} = \operatorname{diag}\left(\mu_1 - c_1\frac{d_1}{e_1}, \dots, \mu_p - c_p\frac{d_p}{e_p}\right) - |A_{11}|,$$
$$\mathcal{M}_{22}^- = \operatorname{diag}(\mu_{p+1}, \dots, \mu_n) - A_{22}^-.$$

If the matrix

$$\hat{\mathcal{M}} := \begin{bmatrix} \hat{\mathcal{M}}_{11} & -|A_{12}| \\ -|A_{21}| & \mathcal{M}_{22}^- \end{bmatrix} \tag{4.2}$$

is an M-matrix, then (x^*, u^*) is a global attractor for the solutions $(x(t), u(t))$ of (1.1), (1.2).

Proof. The cases $p = n$ and $p = 0$ were treated in theorems 3.8 and 4.1, respectively. Now, consider $0 < p < n$. Again, the proof follows along the lines of the proof of theorem 3.8, so some details are omitted.

Assume that $\hat{\mathcal{M}}$ is an M-matrix. Choose an arbitrarily small $\delta_0 > 0$. Since $\delta_0 I_n + \hat{\mathcal{M}}$ is a non-singular M-matrix, there is a positive vector η such that $(\delta_0 I_n + \hat{\mathcal{M}})\eta > 0$. After a scaling $x_i \mapsto \bar{x}_i = \eta_i^{-1} x_i$, $u_i \mapsto \bar{u}_i = \eta_i^{-1} u_i$, $1 \leqslant i \leqslant n$, and dropping the bars for the sake of simplicity, we may suppose that $\eta = (1, \dots, 1)$. Choose $\delta > 0$ small and g satisfying (g1)–(g3) and (2.2), with

$$\delta_0 + \mu_i - c_i\frac{d_i}{e_i} > (1+\delta)\sum_{j=1}^{n} |a_{ij}|, \quad 1 \leqslant i \leqslant n_1, \tag{4.3}$$

$$\delta_0 + \mu_i > (1+\delta)\left(\sum_{j=1}^{n_1} |a_{ij}| + \sum_{j=n_1+1}^{n} a_{ij}^-\right), \quad n_1 + 1 \leqslant i \leqslant n. \tag{4.4}$$

For $i > n_1$, let $\alpha_i \geqslant 0$ be such that $b_i + \alpha_i = \sum_{j=1}^{n_1} a_{ij}x_j^*$ and define $\alpha_i = 0$ for $1 \leqslant i \leqslant n_1$. We now effect the changes $y_i(t) = x_i(t) - x_i^*$, $v_i(t) = u_i(t) - u_i^*$ for $1 \leqslant i \leqslant n$, so we keep $y_i(t) = x_i(t)$, $v_i(t) = u_i(t)$ for $n_1 + 1 \leqslant i \leqslant n$. Together with (3.14), we obtain

$$y_i'(t) = -(y_i(t) + x_i^*)H_i(t), \quad 1 \leqslant i \leqslant n,$$

where now

$$\begin{aligned} H_i(t) = \alpha_i + \mu_i y_i(t) + \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \\ + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s, \quad 1 \leqslant i \leqslant n. \end{aligned} \tag{4.5}$$

Define l_i and L_i as in (3.15) and recall that $0 \leqslant -l_i \leqslant L_i$ for $i > n_1$. Set $l = \max_{1\leqslant i\leqslant n_1} l_i$, $L = \max_{1\leqslant i\leqslant n} L_i$. We need to prove that $U := \max(l, L) = 0$.

For any $\varepsilon > 0$ small, if $t > 0$ is sufficiently large, we have

$$\begin{aligned} \left| a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \right| &\leqslant |a_{ij}|(\max(l_j, L_j) + \varepsilon), \quad 1 \leqslant i,\ j \leqslant n, \\ \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s &\geqslant -a_{ij}^-(L_j + \varepsilon), \qquad\qquad n_1 + 1 \leqslant j \leqslant n. \end{aligned}$$

Suppose that $U > 0$. If $U = L_i$ or $U = l_i$ for some $i \in \{1, \dots, n_1\}$, we choose a sequence $t_k \to \infty$ with $y_i'(t_k) \to 0$, $y_i(t_k) \to L_i$, respectively $y_i(t_k) \to -l_i$, and $(y_{t_k}, v_{t_k}) \to (\phi, \psi) \in \mathrm{BC} \subset \mathrm{UC}_g$ as $k \to \infty$. If $U = l_i > 0$ for some $i \in \{1, \dots, n_1\}$ and $y_i(t)$ is eventually monotone, we proceed as in the proof of theorem 3.8 and easily get a contradiction. Otherwise, (t_k) may be chosen such that $H_i(t_k) = 0$. We argue as in the proof of theorem 3.8 and obtain the estimates (3.21), respectively (3.23) (where now we suppose that $\eta_j = 1$ for all j). As in (3.18), we obtain $\nu := \lim_{k\to\infty} \int_0^\infty G_i(s) v_i(t_k - s)\,\mathrm{d}s > -d_i L_i/e_i$ if $y_i(t_k) \to L_i$, and $\nu < d_i l_i/e_i$ if $y_i(t_k) \to -l_i$, so we may suppose that $\delta_0 > 0$ in (4.3) and (4.4) was chosen such that $c_i\nu/L_i > -c_i d_i/e_i + \delta_0$, respectively $c_i\nu/l_i < c_i d_i/e_i - \delta_0$. By taking limits $k \to \infty$, $\varepsilon_0 \to 0^+$, we derive

$$0 \geqslant \left(\mu_i - (1+\delta)\sum_{j=1}^{n} |a_{ij}|\right) U + c_i\nu,$$

in contradiction to (4.3).

If $U = L_i$ for some $i \in \{n_1 + 1, \dots, n\}$, we choose a sequence $t_k \to \infty$ with $y_i(t_k) \to L_i$, $y_i'(t_k) \to 0$, proceed as above and obtain

$$0 \geqslant \left(\alpha_i + \mu_i - (1+\delta)\sum_{j=1}^{n_1} |a_{ij}| - (1+\delta)\sum_{j=n_1+1}^{n} a_{ij}^-\right) U + c_i\nu, \tag{4.6}$$

where now $0 \leqslant \phi_i(-s) \leqslant U$, $\phi_i(0) = U > 0$, and thus $d_i\int_0^\infty \mathrm{e}^{-e_i s}\phi_i(-s)\,\mathrm{d}s > 0$, which implies that $\nu := \lim_{k\to\infty} \int_0^\infty G_i(s) v_i(t_k - s)\,\mathrm{d}s > 0$. The above estimate, therefore, contradicts (4.4). □

For equilibria on the boundary of $\mathbb{R}^n_+$, and depending on the sizes and signs of coefficients b_i, one might be able to slightly improve the conditions in theorem 4.2.

THEOREM 4.3. *Assume that M is a P-matrix, let (x^*, u^*) be the saturated equilibrium of (1.1), and suppose that $x^* = (x_1^*, \dots, x_p^*, 0, \dots, 0)$ $(1 \leqslant p < n)$. As well as the notation in the statement of theorem 4.2, we further define $\mathcal{A}_{21} = [\tilde{a}_{ij}]$, where*

$$\tilde{a}_{ij} = \begin{cases} a_{ij}^- & \text{if } b_i + \sum_{j=1}^{p} a_{ij}^- x_j^* \leqslant 0, \\ |a_{ij}| & \text{if } b_i + \sum_{j=1}^{p} a_{ij}^- x_j^* > 0, \end{cases} \qquad i = p+1, \dots, n, \ j = 1, \dots, p. \tag{4.7}$$

If

$$\hat{\mathcal{M}} := \begin{bmatrix} \hat{\mathcal{M}}_{11} & -|A_{12}| \\ -\mathcal{A}_{21} & \mathcal{M}_{22}^- \end{bmatrix} \tag{4.8}$$

is an M-matrix, then (x^*, u^*) is a global attractor for the solutions $(x(t), u(t))$ of (1.1), (1.2). In particular, if $A_{21} \geqslant 0$, $b_i \leqslant 0$ for $p < i \leqslant n$, and $\hat{\mathcal{M}}_{11}$ and $\mathcal{M}_{22}^-$ are M-matrices, then (x^*, u^*) is globally attractive.

Proof. Set $p = n_1$, $n - p = n_2$, $y_i(t) = x_i(t) - x_i^*$, $v_i(t) = u_i(t) - u_i^*$ for $1 \leqslant i \leqslant n$. For each $i > n_1$, the function $H_i(t)$ in (4.5) is given by

$$\begin{aligned} H_i(t) &= \alpha_i + \mu_i y_i(t) + \sum_{j=1}^{n_1} a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \\ &\quad + \sum_{j=n_1+1}^{n} a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s \\ &\geqslant \alpha_i - \sum_{i=1}^{n_1} a_{ij}^+ x_j^* + \mu_i y_i(t) - \sum_{j=1}^{n} a_{ij}^- \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \\ &\quad + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s \\ &= -\biggl(b_i + \sum_{j=1}^{n_1} a_{ij}^- x_j^*\biggr) + \mu_i y_i(t) - \sum_{j=1}^{n} a_{ij}^- \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \\ &\quad + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s. \end{aligned} \tag{4.9}$$

For each $i > n_1$, we can use the arguments in the above proof with the right-hand side of (4.5) replaced by the above estimate if $(b_i + \sum_{j=1}^{n_1} a_{ij}^- x_j^*) \leqslant 0$.

Now, if $A_{21} \geqslant 0$ and $b_i \leqslant 0$ for $p < i \leqslant n$, the matrix in (4.8) becomes

$$\hat{\mathcal{M}} = \begin{bmatrix} \hat{\mathcal{M}}_{11} & -|A_{12}| \\ 0 & \mathcal{M}_{22}^- \end{bmatrix},$$

which is an M-matrix if and only if $\hat{\mathcal{M}}_{11}$ and $\mathcal{M}_{22}^-$ are M-matrices. □

In applications, the following corollary is also useful.

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Corollary 4.4. *Assume that M is a P-matrix, let (x^*, u^*) be the unique saturated equilibrium of (1.1), and let $h_i\colon [0,\infty) \to \mathbb{R}$ be continuous functions with $h_i(t) \to 0$ as $t \to \infty$ $(1 \leqslant i \leqslant n)$. Under the assumptions of theorems 3.8, 4.2 or 4.3, all solutions $(x(t), u(t))$ of*

$$\left.\begin{aligned} x_i'(t) = x_i(t)\biggl(b_i - \mu_i x_i(t) \\ - \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) x_j(t-s)\,\mathrm{d}s \\ - c_i \int_0^\infty G_i(s) u_i(t-s)\,\mathrm{d}s - h_i(t)\biggr), \\ u_i'(t) = -e_i u_i(t) + d_i x_i(t), \end{aligned}\right\} \quad i = 1, 2, \ldots, n \tag{4.10}$$

with initial conditions (1.2) satisfy $(x(t), u(t)) \to (x^*, u^*)$ as $t \to \infty$.

Proof. The result follows by repeating the above proofs with $H_i(t)$ in (3.19), (4.5) or (4.9) replaced by $\mathcal{H}_i(t) := H_i(t) + h_i(t)$, $i = 1, \ldots, n$. □

Example 4.5. We introduce a delayed control in the single population model proposed by Volterra and studied by Miller [18]:

$$\left.\begin{aligned} x'(t) &= x(t)\biggl(a - bx(t) - \int_c^t f(t-s)x(s)\,\mathrm{d}s - \int_c^t g(t-s)u(s)\,\mathrm{d}s\biggr), \\ u'(t) &= -eu(t) + dx(t), \end{aligned}\right\} \tag{4.11}$$

where $c = 0$ or $c = -\infty$, $a, b, d, e > 0$, the memory functions $f\colon [0,\infty) \to \mathbb{R}$, $g\colon [0,\infty) \to [0,\infty)$ are continuous and in $L^1[0,\infty)$ and $g(0) > 0$. For $c = -\infty$, (4.11) is the autonomous system

$$\begin{aligned} x'(t) &= x(t)\biggl(a - bx(t) - \int_0^\infty f(s)x(t-s)\,\mathrm{d}s - \int_0^\infty g(s)u(t-s)\,\mathrm{d}s\biggr), \\ u'(t) &= -eu(t) + dx(t), \end{aligned}$$

whereas for $c = 0$ (4.11) takes the form

$$\begin{aligned} x'(t) &= x(t)\biggl(a - bx(t) - \int_0^t f(s)x(t-s)\,\mathrm{d}s - \int_0^t g(s)u(t-s)\,\mathrm{d}s\biggr), \\ u'(t) &= -eu(t) + dx(t). \end{aligned}$$

From theorem 3.8 (see also remark 3.9) and corollary 4.4, if $b \geqslant (d/e)\int_0^\infty g(s)\,\mathrm{d}s + \int_0^\infty |f(s)|\,\mathrm{d}s$, then, for any positive solution $(x(t), u(t))$ of (4.11) with either $c = 0$ or $c = -\infty$, we have $x(t) \to x^* = a[b + (d/e)\int_0^\infty g(s)\,\mathrm{d}s + \int_0^\infty f(s)\,\mathrm{d}s]^{-1}$ as $t \to \infty$.

When a predator–prey system of the form (1.1) is considered, the next result provides less restrictive sufficient conditions for the extinction of all the predator populations.

Theorem 4.6. *Assume that M is a P-matrix, let (x^*, u^*) be the saturated equilibrium of (1.1), and suppose that $x^* = (x_1^*, \ldots, x_p^*, 0, \ldots, 0)$ $(1 \leqslant p < n)$. With*

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the notation of theorem 4.2, assume that $A_{12} \geqslant 0$, $A_{21} \leqslant 0$. *If* $\hat{\mathcal{M}}_{11}$, $\mathcal{M}_{22}^-$ *are M-matrices, then* (x^*, u^*) *is a global attractor for the solutions* $(x(t), u(t))$ *of system (1.1), (1.2).*

Proof. Write $n_1 = p$, $n_2 = n - p$. Let $(x(t), u(t))$ be a positive solution of (1.1), and set $y_i(t) = x_i(t) - x_i^*$, $v_i(t) = u_i(t) - u_i^*$ for $1 \leqslant i \leqslant n_1$, and $y_i(t) = x_i(t)$, $v_i(t) = u_i(t)$ for $n_1 + 1 \leqslant i \leqslant n$.

Claim 4.7. $\limsup_{t\to\infty} x_i(t) \leqslant x_i^*$ *for* $i = 1, \dots, n_1$.

With $A_{12} \geqslant 0$, together with (3.14), we get

$$y_i'(t) \leqslant -(y_i(t) + x_i^*)\biggl(\mu_i y_i(t) - \sum_{j=1}^{n_1} |a_{ij}| \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s + c_i \int_0^\infty G_i(s) v_i(t-s)\,\mathrm{d}s\biggr)$$

for $i = 1, 2, \dots, n_1$. Fix any $\delta_0 > 0$ small. With $\hat{\mathcal{M}}_{11}$ an M-matrix, and after a scaling of the variables, we may suppose that $(\delta_0 I_{n_1} + \hat{\mathcal{M}}_{11})\eta > 0$ for the positive vector $\eta = (1, \dots, 1) \in \mathbb{R}^{n_1}$. Define $L_i = \limsup_{t\to\infty} y_i(t)$, $U = \max_{1\leqslant i\leqslant n_1} L_i$. We need to prove that $U \leqslant 0$.

Suppose that $U > 0$. As for the estimate (3.20), for any $\varepsilon > 0$ the definition of U implies that $\int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \leqslant (U + \varepsilon)$ for $t > 0$ large and $j = 1, \dots, n_1$. Applying the proof of theorem 3.8, it is clear that we shall get a contradiction, as in (3.22).

Claim 4.8. $\limsup_{t\to\infty} \int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \leqslant 0$ *for* $j = 1, \dots, n_1$, $i = 1, \dots, n$.

Fix $j \in \{1, \dots, n_1\}$, $i \in \{1, \dots, n\}$ and $\delta > 0$. Since $y_j(t)$ is uniformly bounded in $\mathbb{R}$, there is $T_1 > 0$ such that $\int_{T_1}^\infty K_{ij}(s)|y_j(t-s)|\,\mathrm{d}s \leqslant \delta/2$. From claim 4.7, $\limsup_{t\to\infty} y_j(t) \leqslant 0$, and hence there is $T_2 \geqslant T_1$ such that $y_j(t) < \delta/2$ for each $t \geqslant T_2$. Thus, for $t \geqslant 2T_2$, we have

$$\int_0^\infty K_{ij}(s) y_j(t-s)\,\mathrm{d}s \leqslant \int_0^{T_2} K_{ij}(s) y_j(t-s)\,\mathrm{d}s + \delta/2 < \delta.$$

This proves claim 4.8

Claim 4.9. $\lim_{t\to\infty} x_i(t) = 0$ *for* $i = n_1 + 1, \dots, n$.

For each $i \in \{n_1 + 1, \dots, n\}$, we only need to prove that $\limsup_{t\to\infty} x_i(t) \leqslant 0$. Together with the equations $u_i'(t) = -e_i x_i(t) + d_i u_i(t)$, we now obtain

$$x_i'(t) = x_i(t)\biggl(b_i - \mu_i x_i(t) - \sum_{j=1}^{n} a_{ij} \int_0^\infty K_{ij}(s) x_j(t-s)\,\mathrm{d}s - c_i \int_0^\infty G_i(s) u_i(t-s)\,\mathrm{d}s\biggr)$$

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$$\leqslant x_i(t)\biggl(\beta_i - \mu_i x_i(t) - \sum_{j=n_1+1}^{n} a_{ij}\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s \\ - c_i\int_0^\infty G_i(s)u_i(t-s)\,\mathrm{d}s - h_i(t)\biggr),$$

where $\beta_i := b_i - \sum_{j=1}^{n_1} a_{ij}x_j^* \leqslant 0$ (by the definition of a saturated equilibrium) and

$$h_i(t) = \sum_{j=1}^{n_1} a_{ij}\int_0^\infty K_{ij}(s)y_j(t-s)\,\mathrm{d}s, \quad i = n_1+1,\dots,n.$$

From claim 4.8, and since $A_{21} \leqslant 0$, we have $\limsup_{t\to\infty}(-h_i(t)) \leqslant 0$ for $i = n_1+1,\dots,n$. From corollary 4.4 (see also the proof of theorem 4.2), the hypothesis that $\mathcal{M}_{22}^-$ is an M-matrix implies claim 4.9.

Claim 4.10. *$\lim_{t\to\infty} x_i(t) = x_i^*$, $\lim_{t\to\infty} u_i(t) = u_i^*$ for $i = 1,\dots,n_1$.*

We write

$$\left.\begin{aligned} y_i'(t) &= -(y_i(t)+x_i^*)\biggl(\mu_i y_i(t) + \sum_{j=1}^{n_1} a_{ij}\int_0^\infty K_{ij}(s)y_j(t-s)\,\mathrm{d}s \\ &\qquad + c_i\int_0^\infty G_i(s)v_i(t-s)\,\mathrm{d}s + h_i(t)\biggr), \\ v_i'(t) &= -e_i v_i(t) + d_i y_i(t), \end{aligned}\right\} \quad i = 1,2,\dots,n_1,$$

where now

$$h_i(t) = \sum_{j=n_1+1}^{n} a_{ij}\int_0^\infty K_{ij}(s)x_j(t-s)\,\mathrm{d}s, \quad i = 1,\dots,n_1.$$

Applying the same arguments as those used in the proof of claim 4.8, where now we use claim 4.9 instead of claim 4.7, we get $\lim_{t\to\infty} h_i(t) = 0$, $1 \leqslant i \leqslant n_1$. Claim 4.10 again follows from corollary 4.4. □

It is straightforward to apply the above results to uncontrolled systems (3.1), which, in the case of saturated equilibria on $\partial(\mathbb{R}_+^n)$, lead to better criteria than the ones in [5], as stated below.

Corollary 4.11. *Assume that M_0 is a P-matrix, let x^* be the saturated equilibrium of (3.1), and suppose that $x^* = (x_1^*,\dots,x_p^*,0,\dots,0)$ $(1 \leqslant p < n)$. With the same notation as that used in the statement of theorem 4.2, define also*

$$\hat{\mathcal{M}}_0 := \begin{bmatrix} \hat{\mathcal{M}}_{0,11} & -|A_{12}| \\ -\mathcal{A}_{21} & \mathcal{M}_{0,22}^- \end{bmatrix},$$

where

$$\hat{\mathcal{M}}_{0,11} = \mathrm{diag}(\mu_1,\dots,\mu_p) - |A_{11}|, \quad \mathcal{M}_{0,22}^- = \mathrm{diag}(\mu_{p+1},\dots,\mu_n) - A_{22}^-$$

and $\mathcal{A}_{21} = [\tilde{a}_{ij}]$ is given by (4.7). If $\hat{\mathcal{M}}_0$ is a non-singular M-matrix, then x^* is a global attractor for all positive solutions $x(t)$ of (3.1). Moreover, if either (i) $A_{21} \geqslant$

0, $b_i \leqslant 0$ for $p < i \leqslant n$, or (ii) $A_{12} \geqslant 0$, $A_{21} \leqslant 0$, and $\hat{\mathcal{M}}_{0,11}$ and $\mathcal{M}^-_{0,22}$ are non-singular M-matrices, then x^* is a global attractor for the positive solutions of (3.1).

5. The two-species Lotka–Volterra system

As an application of the results in the previous sections, we now analyse with some attention the dynamics for a planar controlled Lotka–Volterra system with delays, without any special constraints on the signs of the Malthusian coefficients b_i and intra- and inter-specific coefficients a_{ij}. For the sake of simplicity, we consider a planar system (1.1) with discrete delays, but the analysis below can be performed for infinite distributed delays as well.

Consider the system

$$\left.\begin{aligned} x_1'(t) &= x_1(t)(b_1 - \mu_1 x_1(t) - a_{11}x_1(t-\tau_{11}) - a_{12}x_2(t-\tau_{12}) - c_1^0 u_1(t) \\ &\qquad - c_1^1 u_1(t-\sigma_1)), \\ u_1'(t) &= -e_1 u_1(t) + d_1 x_1(t), \\ x_2'(t) &= x_2(t)(b_2 - \mu_2 x_2(t) - a_{21}x_1(t-\tau_{21}) - a_{22}x_2(t-\tau_{22}) - c_2^0 u_2(t) \\ &\qquad - c_2^1 u_2(t-\sigma_2)), \\ u_2'(t) &= -e_2 u_2(t) + d_2 x_2(t), \end{aligned}\right\} \tag{5.1}$$

where μ_i, c_i^0, d_i, e_i are positive constants, $c_i^1 \geqslant 0$, $b_i, a_{ij} \in \mathbb{R}$, $\tau_{ij}, \sigma_i \geqslant 0$, $i, j = 1, 2$. Define $c_i = c_i^0 + c_i^1$, $i = 1, 2$. With the above notation, the community matrix is

$$M = \begin{bmatrix} \lambda_1 + a_{11} & a_{12} \\ a_{21} & \lambda_2 + a_{22} \end{bmatrix}, \quad \text{where } \lambda_i = \mu_i + \frac{c_i d_i}{e_i},\ i = 1, 2.$$

In what follows, we suppose, in addition, that M is a P-matrix, i.e.

$$\det M > 0 \quad \text{and} \quad \lambda_i + a_{ii} > 0,\ i = 1, 2. \tag{5.2}$$

There are three possible equilibria on the boundary of $\mathbb{R}^4_+$: the trivial equilibrium $E_0 = (0, 0, 0, 0)$, $E_1 = (b_1/(\lambda_1 + a_{11}), b_1 d_1/((\lambda_1 + a_{11})e_1), 0, 0)$ if $b_1 > 0$, and $E_2 = (0, 0, b_2/(\lambda_2 + a_{22}), b_2 d_2/((\lambda_2 + a_{22})e_2))$ if $b_2 > 0$. There is a positive equilibrium $E^* = (x_1^*, u_1^*, x_2^*, u_2^*)$, where

$$x_1^* = \frac{b_1(\lambda_2 + a_{22}) - a_{12}b_2}{\det M}, \qquad x_2^* = \frac{b_2(\lambda_1 + a_{11}) - a_{21}b_1}{\det M},$$
$$u_i^* = \frac{d_i}{e_1} x_i^*, \quad i = 1, 2,$$

if and only if

$$b_1(\lambda_2 + a_{22}) > a_{12}b_2, \qquad b_2(\lambda_1 + a_{11}) > a_{21}b_1. \tag{5.3}$$

As already observed, the trivial equilibrium is saturated if and only if $b_1, b_2 \leqslant 0$. In this case, 0 is globally attractive if $\mu_i - a_{ii}^- \geqslant 0$ ($i = 1, 2$) and $(\mu_1 - a_{11}^-)(\mu_2 - a_{22}^-) \geqslant a_{12}^- a_{21}^-$. If $b_i > 0$, then E_i is an equilibrium on the boundary of the positive cone, $i = 1, 2$.

Next we give a detailed analysis of the absolute stability, and lack of it, for the case of b_1, b_2 positive. The case $b_2 \leqslant 0 < b_1$ will be studied afterwards.

Let $b_1, b_2 > 0$, so that the equilibria E_0, E_1, E_2 always exist, with E_0 unstable. At least one of the conditions in (5.3) is satisfied; otherwise, we get $a_{12}b_2 \geqslant b_1(\lambda_2 + a_{22}) > 0$, $a_{21}b_1 \geqslant b_2(\lambda_1 + a_{11}) > 0$ and $[(\lambda_1 + a_{11})(\lambda_2 + a_{22}) - a_{12}a_{21}]b_1 b_2 = b_1 b_2 \det M \leqslant 0$, which is not possible.

We now study the stability of E_1. Clearly, a similar analysis can be performed for E_2. The characteristic equation for the linearized equation about the equilibrium $E_1 = (X_1, (d_1/e_1)X_1, 0, 0)$ is given by

$$\det \Delta(\lambda) = 0 \quad \text{for } \Delta(\lambda) = \lambda I_4 + \begin{bmatrix} N(\lambda) & E(\lambda) \\ 0 & C \end{bmatrix} \tag{5.4}$$

(I_n is the $n \times n$ identity matrix), where $X_1 = b_1/(\lambda_1 + a_{11})$ and

$$N(\lambda) = \begin{bmatrix} X_1(\mu_1 + a_{11}e^{-\lambda\tau_{11}}) & X_1(c_1^0 + c_1^1 e^{-\lambda\sigma_1}) \\ -d_1 & e_1 \end{bmatrix}, \qquad E(\lambda) = \begin{bmatrix} X_1 a_{12} e^{-\lambda\tau_{12}} & 0 \\ 0 & 0 \end{bmatrix},$$

$$C = \begin{bmatrix} -(b_2 - a_{21}X_1) & 0 \\ -d_2 & e_2 \end{bmatrix}.$$

If $b_2(\lambda_1 + a_{11}) > a_{21}b_1$, then $b_2 - a_{21}X_1 > 0$ and E_1 is unstable. If $b_2(\lambda_1 + a_{11}) \leqslant a_{21}b_1$, the matrix $-C$ is stable, and therefore E_1 is the unique saturated equilibrium. In fact, in this situation, there is no positive equilibrium, but, as already observed, the condition $b_1(\lambda_2 + a_{22}) > a_{12}b_2$ must hold, and from a dual analysis we would conclude that E_2 is unstable.

When E_1 is the unique saturated equilibrium, conditions (5.2) are not, however, sufficient to conclude that E_1 is a global attractor of all positive solutions for all sizes of the delays τ_{11}, σ_1. In fact, the characteristic roots of (5.4) are $\lambda = -e_2 < 0$, $\lambda = b_2 - a_{21}X_1 \leqslant 0$ and the solutions of $h(\lambda) = 0$, where

$$h(\lambda) = P(\lambda) + e^{-\lambda\tau_{11}}Q(\lambda) + X_1 d_1 c_1^1 e^{-\lambda\sigma_1} \tag{5.5}$$

with $P(\lambda) = \lambda^2 + \lambda(e_1 + X_1\mu_1) + X_1(\mu_1 e_1 + d_1 c_1^0)$, $Q(\lambda) = a_{11}X_1(\lambda + e_1)$. The equation $h(\lambda) = 0$ is the characteristic equation for the system

$$\left.\begin{aligned} x'(t) &= -X_1[\mu_1 x(t) + a_{11}x(t - \tau_{11}) + c_1^0 u(t) + c_1^1 u(t - \sigma_1)], \\ u'(t) &= -[e_1 u(t) - d_1 x(t)]. \end{aligned}\right\} \tag{5.6}$$

With $\tau_{11}, \sigma_1 = 0$, the solutions λ of $h(\lambda)$ are the eigenvalues of the matrix

$$-N(0) = -\begin{bmatrix} X_1(\mu_1 + a_{11}) & X_1 c_1 \\ -d_1 & e_1 \end{bmatrix},$$

which has $\det(-N(0)) = X_1(\lambda_1 + a_{11})e_1 > 0$ (from (5.2)) and trace $T_0 := -X_1(\mu_1 + a_{11}) - e_1$. If $T_0 \leqslant 0$, then E_1 is stable as an equilibrium of (5.6) with $\tau_{11}, \sigma_1 = 0$, otherwise, E_1 is unstable. It is particularly difficult to study a second-order characteristic equation with two delays such as (5.5) (see, for example, [2,26] and references therein). For instance, fixing $\sigma_1 = 0$, the following situations are possible: either (5.6) is stable for all $\tau \geqslant 0$, or its stability changes once or at most a finite number

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of times as τ_{11} increases and it eventually becomes unstable [4]. In the latter case, there is $\tau^* > 0$ such that, for $\tau_{11} > \tau^*$, although E_1 is saturated, it also becomes unstable as a solution to (5.1). Now, assume that $\mu_1 - |a_{11}| - c_1(d_1/e_1) \geqslant 0$. The trace T_0 of $-N(0)$, then, is always negative, and hence E_1 is asymptotically stable for (5.6) with $\tau_{11}, \sigma_1 = 0$. Moreover, the matrix

$$\hat{N}(0) = \begin{bmatrix} X_1(\mu_1 - |a_{11}|) & -X_1c_1 \\ -d_1 & e_1 \end{bmatrix}$$

has $\det \hat{N}(0) = X_1e_1(\mu_1 - |a_{11}| - c_1(d_1/e_1)) \geqslant 0$ and has trace $\hat{T}_0 = X_1(\mu_1 - |a_{11}|) + e_1 > 0$, and hence $\hat{N}(0)$ is an M-matrix [8]. By [6], it follows that (5.6) is exponentially stable for all delays $\tau_{11}, \sigma_1 > 0$. By theorem 4.2, E_1 is the global attractor of all positive solutions of (5.1) if

$$\hat{\mathcal{M}} = \begin{bmatrix} \mu_1 - |a_{11}| - c_1\dfrac{d_1}{e_1} & -|a_{12}| \\ -a_{21} & \mu_2 - a_{22}^- \end{bmatrix}$$

is an M-matrix, or, in other words,

$$\left.\begin{aligned} \mu_1 - |a_{11}| - c_1\frac{d_1}{e_1} \geqslant 0, \qquad \mu_2 - a_{22}^- \geqslant 0, \\ \left(\mu_1 - |a_{11}| - c_1\frac{d_1}{e_1}\right)(\mu_2 - a_{22}^-) \geqslant |a_{12}|a_{21}. \end{aligned}\right\} \tag{5.7}$$

Assume now that (5.3) holds, so that the positive equilibrium E^* exists. For the linearized equation about E^*, written as

$$X'(t) = -[DX(t) + L(X_t)],$$

where $D = \operatorname{diag}(x_1^*\mu_1, e_1, x_2^*\mu_2, e_2)$, the characteristic equation is given by

$$\det \Delta(\lambda) := \lambda I_4 + D + L(\mathrm{e}^{\lambda\cdot} I_4) = 0,$$

and similar computations to the ones above lead to

$$D + L(\mathrm{e}^{\lambda\cdot} I_4) = \begin{bmatrix} N_1(\lambda) & E_1(\lambda) \\ E_2(\lambda) & N_2(\lambda) \end{bmatrix}, \tag{5.8}$$

where

$$\left.\begin{aligned} N_i(\lambda) &= \begin{bmatrix} x_i^*(\mu_i + a_{ii}\mathrm{e}^{-\lambda\tau_{ii}}) & x_i^*(c_i^0 + c_i^1\mathrm{e}^{-\lambda\sigma_i}) \\ -d_i & e_i \end{bmatrix}, \\ E_i(\lambda) &= \begin{bmatrix} x_i^* a_{ij}\mathrm{e}^{-\lambda\tau_{ij}} & 0 \\ 0 & 0 \end{bmatrix}, \end{aligned}\right\} \quad i, j = 1, 2,\ j \neq i.$$

One can easily check that $\det \Delta(0) = \det(D + L(I_4)) = x_1^*x_2^*e_1e_2 \det M$, and thus $\det \Delta(0) > 0$ since M is a P-matrix. As for the study of the stability of E_1, even if E^* is asymptotically stable for the corresponding ODE system obtained by taking all the delays equal to 0 in (5.1), the positive equilibrium E^* of (5.1) might become unstable as the delays increase. In fact, by letting $c_1, c_2 \to 0^+$, from (5.8) we obtain $\det \Delta(\lambda) \to (\lambda + e_1)(\lambda + e_2)h(\lambda)$, where now

$$h(\lambda) = \begin{vmatrix} \lambda + x_1^*(\mu_1 + a_{11}\mathrm{e}^{-\lambda\tau_{11}}) & x_1^* a_{12}\mathrm{e}^{-\lambda\tau_{12}} \\ x_2^* a_{21}\mathrm{e}^{-\lambda\tau_{21}} & \lambda + x_2^*(\mu_2 + a_{22}\mathrm{e}^{-\lambda\tau_{22}}) \end{vmatrix}.$$

Choosing, for example, $\tau_{ii} = 0$ $(i = 1, 2)$ and $a_{12} = 1$, $a_{21} = -1$, one can see that it is possible to choose the other coefficients in such a way that $(\mu_1 + a_{11})x_1^* = (\mu_2 + a_{22})x_2^* =: b$ and $x_1^* x_2^* =: c > b^2$. Then, $h(\lambda) = (\lambda + b)^2 + c\mathrm{e}^{-\lambda(\tau_{12}+\tau_{21})}$, which has roots $\pm \mathrm{i}\sqrt{c - b^2}$ if $\tau := \tau_{12} + \tau_{21} = \tau_n$, where

$$\tau_n \in (0, \pi) + 2n\pi, \quad \tan(\tau_n \sqrt{c - b^2}) = \frac{2b\sqrt{c - b^2}}{c - 2b^2}, \quad n = 0, 1, 2, \dots.$$

In particular, for $\tau > \tau_0$ and close to τ_0, there is a pair of characteristic roots with positive real parts, and thus the equilibrium becomes unstable. Moreover, (5.1) has a sequence of Hopf bifurcations at $\tau = \tau_n$, $n = 0, 1, 2, \dots$ [24]. However, if

$$\hat{M} = \begin{bmatrix} \mu_1 - |a_{11}| - c_1 \dfrac{d_1}{e_1} & -|a_{12}| \\ -|a_{21}| & \mu_2 - |a_{22}| - c_2 \dfrac{d_2}{e_2} \end{bmatrix}$$

is an M-matrix, we have the conditions

$$\left.\begin{aligned} \left(\mu_1 - |a_{11}| - c_1 \frac{d_1}{e_1}\right)\left(\mu_2 - |a_{22}| - c_2 \frac{d_2}{e_2}\right) \geqslant |a_{12}a_{21}|, \\ \mu_i - |a_{ii}| - c_i d_i e_i \geqslant 0, \quad i = 1, 2, \end{aligned}\right\} \tag{5.9}$$

and from theorem 3.8 we conclude that the positive equilibrium E^* is globally attractive for all sizes of delays τ_{ij}, σ_i.

As an application of the use of the controls, in the example below we change the position of the globally attractive equilibrium from the boundary to the interior of $\mathbb{R}^2_+$, recovering one of the species otherwise condemned to extinction.

Example 5.1. Consider the following uncontrolled system with $n = 2$ and, for example, $b_1 = 1$, $b_2 = \frac{1}{3}$, $\mu_1 = \mu_2 = 1$, $a_{11} = a_{22} = a_{21} = \frac{1}{2}$, $a_{12} = \frac{1}{8}$:

$$\begin{aligned} x_1'(t) &= x_1(t)(1 - x_1(t) - \tfrac{1}{2}x_1(t - \tau_{11}) - \tfrac{1}{8}x_2(t - \tau_{12})), \\ x_2'(t) &= x_2(t)(\tfrac{1}{3} - x_2(t) - \tfrac{1}{2}x_1(t - \tau_{21}) - \tfrac{1}{2}x_2(t - \tau_{22})). \end{aligned}$$

With the above notation, we have

$$M_0 = \begin{bmatrix} \frac{3}{2} & \frac{1}{8} \\ \frac{1}{2} & \frac{3}{2} \end{bmatrix}, \qquad \hat{M}_0 = \begin{bmatrix} \frac{1}{2} & -\frac{1}{8} \\ -\frac{1}{2} & \frac{1}{2} \end{bmatrix}.$$

The saturated equilibrium is $(X_1, 0) = (\frac{2}{3}, 0)$. Furthermore, $\det M_0 > 0$ and $\hat{M}_0$ is a non-singular M-matrix, hence, from [5], we derive that $(X_1, 0)$ is GAS. We now introduce the controls in order to recover the $x_2(t)$ population that otherwise would become extinct with time. Clearly, for any choice of positive coefficients c_i, d_i, e_i,

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$i = 1, 2$, conditions (5.3) hold, and therefore the controlled system (5.1) with the above coefficients has a positive equilibrium E^*. Now, if we choose, for example, $\alpha_i := c_i(d_i/e_i) \leqslant \frac{1}{4}$, $i = 1, 2$, we have that

$$\hat{M} = \begin{bmatrix} \frac{1}{2} - \alpha_1 & -\frac{1}{8} \\ -\frac{1}{2} & \frac{1}{2} - \alpha_2 \end{bmatrix}$$

is an M-matrix. Invoking theorem 3.8, we get that E^* is a global attractor of all positive solutions.

Now, suppose that $b_2 \leqslant 0 < b_1$ and $a_{21} \geqslant 0$. Clearly, (5.3) fails to be true, E_1 is the saturated equilibrium, and, by theorem 4.3, E_1 is a global attractor of all positive solutions of (5.1) if

$$\mu_1 - |a_{11}| - c_1 \frac{d_1}{e_1} \geqslant 0, \qquad \mu_2 - a_{22}^- \geqslant 0. \tag{5.10}$$

Next, consider a typical predator–prey system such as (5.1), where $b_2 < 0 < b_1$ and $a_{12} > 0$, $a_{21} < 0$. In the absence of the positive equilibrium, which amounts to having $b_2(\lambda_1 + a_{11}) \leqslant a_{21}b_1$, E_1 is the saturated equilibrium. Now, using theorem 4.6, if (5.10) is satisfied, then again E_1 is a global attractor. In this framework, we again illustrate how the controls can be used to change the position of a globally attractive saturated equilibrium.

Example 5.2. For the particular case of $b_1 = 1$, $b_2 = -\frac{5}{4}$, $\mu_1 = \mu_2 = 1$, $a_{11} = a_{22} = \frac{1}{2}$, $a_{12} = \frac{1}{8}$, $a_{21} = -2$, we obtain the predator–prey system without controls

$$\begin{aligned} x_1'(t) &= x_1(t)(1 - x_1(t) - \tfrac{1}{2}x_1(t - \tau_{11}) - \tfrac{1}{8}x_2(t - \tau_{12})), \\ x_2'(t) &= x_2(t)(-\tfrac{5}{4} - x_2(t) + 2x_1(t - \tau_{21}) - \tfrac{1}{2}x_2(t - \tau_{22})), \end{aligned}$$

with community matrix

$$M_0 = \begin{bmatrix} \frac{3}{2} & \frac{1}{8} \\ -2 & \frac{3}{2} \end{bmatrix}.$$

For this system, $(x_1^*, x_2^*) = (\frac{53}{80}, \frac{1}{20})$ is the positive equilibrium. Moreover, since $\det M_0 > 0$ and

$$\hat{M}_0 = \begin{bmatrix} \frac{1}{2} & -\frac{1}{8} \\ -2 & \frac{1}{2} \end{bmatrix}$$

is an M-matrix, from [5] it follows that (x_1^*, x_2^*) is globally attractive. We now introduce the controls, in order to drive the predators to extinction. For the above chosen coefficients, $b_2(\mu_1 + a_{11} + c_1(d_1/e_1)) \leqslant a_{21}b_1$ if and only if $c_1(d_1/e_1) \geqslant \frac{1}{10}$, in which case $E_1 = (1/(\frac{3}{2} + c_1(d_1/e_1)), d_1e_1/(\frac{3}{2}e_1 + c_1d_1), 0, 0)$ is the saturated equilibrium. If we now choose $\frac{1}{10} \leqslant c_1(d_1/e_1) \leqslant \frac{1}{2}$, theorem 4.6 yields that $\mu_1 - |a_{11}| - c_1(d_1/e_1) \geqslant 0$, and thus E_1 is a global attractor of all positive solutions.

We summarize the above global asymptotic behaviour results as follows.

Proposition 5.3. *Consider the system (5.1) and assume that (5.2) holds.*

(i) *If* $b_1, b_2 \leqslant 0$, *then* 0 *is the saturated equilibrium; in this case,* 0 *is globally attractive if* $\mu_i - a_{ii}^- \geqslant 0$ $(i = 1, 2)$ *and* $(\mu_1 - a_{11}^-)(\mu_2 - a_{22}^-) \geqslant a_{12}^- a_{21}^-$.

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(ii) *If (5.3) holds, there exists a positive equilibrium that is GAS under the additional conditions (5.9).*

(iii) *If* $b_1, b_2 > 0$ *and* $b_2(\lambda_1 + a_{11}) \leqslant a_{21}b_1$*, then* E_1 *is the saturated equilibrium; in this case,* E_1 *is a global attractor of all positive solutions if conditions (5.7) are satisfied.*

(iv) *If* $b_2 \leqslant 0 < b_1$ *and either (a)* $a_{21} \geqslant 0$ *or (b)* $a_{12} > 0$*,* $a_{21} < 0$*,* $b_2(\lambda_1 + a_{11}) \leqslant a_{21}b_1$*, then* E_1 *is the saturated equilibrium; in this case,* E_1 *is a global attractor of all positive solutions if conditions (5.10) are satisfied.*

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