

# Boundedness, persistence and stability for classes of forced difference equations arising in population ecology

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## Abstract

Boundedness, persistence and stability properties are considered for a class of nonlinear, possibly infinite-dimensional, forced difference equations which arise in a number of ecological and biological contexts. The inclusion of forcing incorporates the effects of control actions (such as harvesting or breeding programmes), disturbances induced by seasonal or environmental variation, or migration. We provide sufficient conditions under which the states of these models are bounded and persistent uniformly with respect to the forcing terms. Under mild assumptions, the models under consideration naturally admit two equilibria when unforced: the origin and a unique non-zero equilibrium. We present sufficient conditions for the non-zero equilibrium to be stable in a sense which is strongly inspired by the input-to-state stability concept well-known in mathematical control theory. In particular, our stability concept incorporates the impact of potentially persistent forcing. Since the underlying state-space may be infinite-dimensional, our framework enables treatment of so-called integral projection models (IPMs). The theory is applied to a number of examples from population dynamics.

**Keywords.** Absolute stability, density-dependent population models, environmental forcing, forced systems, global asymptotic stability, infinite-dimensional systems, input-to-state stability, integral projection models, Lur'e systems, population persistence.

## 1 Introduction

We consider boundedness, persistence and stability properties of the following class of forced difference equations

$$x^\nabla = Ax + bf(u, c^*x) + v, \quad x(0) = x^0, \quad (1.1)$$

where  $x^\nabla$  denotes the image of  $x$  under the left shift operator, that is,  $x^\nabla(t) = x(t+1)$  for all nonnegative integers  $t$ . The difference equation (1.1) comprises a linear component  $Ax$ , where  $A$  is a bounded linear operator on the state-space  $X$ , assumed to be a Banach space, and a nonlinear component  $bf(u, c^*x)$ . Here  $b \in X$  and  $c^* \in X^*$ , the dual space of  $X$ , and  $f$  is a (typically nonlinear) real-valued function that may depend on a variable  $u$  which, along

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with  $v$ , denotes forcing (which, depending on the context, is interpreted as a control, input or disturbance).

Our motivation for studying (1.1), and particularly the properties of boundedness, persistence and stability, is the potential for applications to population biology and theoretical ecology where models of the form (1.1) often arise. There is clear biological relevance for these three properties depending on the context. Boundedness is a necessary property of a sensible biological model and, moreover, is a key concept when seeking to understand the potential effects of an invasive species or mutant in a novel environment, see, for example, [11]. The notion of persistence relates to the survival of a population (or of certain of its stages) and is relevant, for example, in the context of providing lower bounds for predicted yield in agriculture and horticulture. We comment that several persistence concepts and their properties have been studied in the literature [17, 40, 41, 42, 50]. Informally, boundedness and persistence are opposite properties, concerned with populations becoming neither too big, or too small, respectively. Stability is, of course, a fundamental consideration in all fields where dynamic modelling occurs and pertains to both the qualitative and quantitative long-term behaviour of solutions or equilibria.

Since we seek to model a variety of structured populations, see for instance [5, 8], or ecosystems of several species, the dimension of the state-space  $X$  is not constrained. In fact, the case  $\dim X = \infty$  is included in our development, and therefore, (1.1) can be used to model certain partial-difference and integro-difference equations. The latter, in form of so-called integral projection models, are often employed to describe population models with a continuous structure or stage parameter, in which case the state space  $X$  of (1.1) is naturally a space of functions. Furthermore, in a populations dynamics context, the state variable  $x$  must be nonnegative-valued to be biologically meaningful, corresponding to abundance, concentration or density, for example. Consequently, we impose suitable positivity assumptions on the model data  $A$ ,  $b$ ,  $c^*$  and  $f$  implying that (1.1) is a positive dynamical system, that is, the dynamics leave a positive cone in  $X$  invariant. In this sense, the current paper is embedded in the research field of positive dynamical systems on which there exists a rich literature, see [2, 22, 27, 28, 31], to mention just a few references.

The dynamics of the unforced version of (1.1) (that is,  $f(u, y) = f(y)$  and  $v = 0$ ) have recently been studied by several researchers in a variety of biologically motivated contexts [13, 16, 36, 42, 48]. Under certain assumptions, (1.1) admits a so-called “trichotomy of stability” where precisely one of three situations occurs: zero is globally asymptotically stable; there is a unique non-zero equilibrium which attracts all non-zero solutions; or, all non-zero solutions diverge asymptotically.

In the literature, the study of boundedness, persistence and stability properties of (1.1) does not usually include forcing (denoted by the terms  $u$  and  $v$  in (1.1)), with [17] being an exception. As is well-known, classical (Lyapunov) stability notions are not applicable when exogenous, and potentially persistent, forcing is present, and forcing can have adverse, extreme and unintuitive effects on nonlinear dynamics, see, for example, [46]. Forcing is very natural and important in a biological or ecological context, however, as it allows for the modelling of human interventions, such as management strategies, hunting, poaching, predation or farming, as well as uncontrolled seasonal or demographic variation, or migration. Mathematical systems and control theory provides a toolbox for the study of control and forcing in dynamical systems [23, 45]. Moreover, models of the form (1.1) arise in mathematical control theory in which context they are often called Lur’e systems after the Soviet scientist A. I. Lur’e who made early contributions in the 1940s to their stability properties. The study of the stability properties of Lur’e systems constitutes absolute stability theory which, loosely speaking, seeks to conclude stability of the (unforced) system (1.1) through the interplay of frequency-domain properties of the func-

tion  $c^*(sI - A)^{-1}b$  and boundedness or sector properties of the nonlinearity  $f$ , yielding readily checkable sufficient conditions for global asymptotic and exponential stability of the unforced system (1.1), see [21, 23, 26, 30, 49, 51]. Furthermore, absolute stability is at the heart of [36, 48], where it is used to derive the above mentioned stability trichotomy. Recent work [4, 19, 37, 38] has combined absolute stability ideas with input-to-state stability (ISS) theory to obtain stability criteria which apply to forced Lur'e systems. The ISS concept seeks to generalise the familiar estimate

$$\|x(t)\| \leq M(\gamma^t \|x(0)\| + \max_{0 \leq \tau \leq t-1} \|d(\tau)\|), \quad \forall t \in \mathbb{Z}_+, \quad \text{where } M \geq 1 \text{ and } \gamma \in (0, 1), \quad (1.2)$$

valid for the forced linear system  $x^\nabla = Ax + d$  with exponentially stable  $A$ , to forced nonlinear control systems. Note that (1.2) holds uniformly in  $x(0)$  and  $d$  and that, on the right-hand side of (1.2), the impact of the initial state  $x(0)$  decays over time and the contributions of  $x(0)$  and the forcing  $d$  are separated. ISS was introduced by Sontag [43] in 1989 and has, in the last 30 years, been developed into a mature stability theory of forced nonlinear control systems [9, 44].

In this paper, starting with an ISS result from [19], we derive sufficient conditions for the state  $x$  of (1.1) to exhibit certain boundedness, persistence and stability properties. Our main results are Theorems 4.3 and 5.2, which address boundedness and persistence, and stability, respectively. The persistence notion employed is related to that in [41, 42], see Section 4, and the stability concept we consider is closely related to the above mentioned ISS property, see Section 5. We present conditions under which the unforced system (1.1) admits, in addition to the zero equilibrium, a unique non-zero equilibrium which is both persistent and ISS (in a suitable sense). A consequence of the stability property is the guarantee of asymptotic convergence of the state  $x$  when subject to convergent forcing (see statement (2) of Theorem 5.2 and Corollary 5.5). We remark that the theory developed in this paper is a far reaching generalization of our earlier paper [17]: the state-space is not required to be finite-dimensional as in [17] and the main positivity assumption on the linear system  $(A, b, c^*)$  is less restrictive than that imposed in [17]. Moreover, the approach developed here is more elementary than that in [17] and does not rely on Perron-Frobenius theory and its infinite-dimensional extensions such as (variants of) the Krein-Rutman theorem, see Remark 4.6 for more details. In Section 6 we apply our results to several models from population dynamics. In particular, we provide a detailed discussion of two infinite-dimensional systems both of which involve integral projection models [6, 14, 15, 33, 36].

The paper is organised as follows. In Section 2 we collect a number of mathematical preliminaries, and in Section 3 we provide more details on the the class of models (1.1). Sections 4 and 5 contain the main results pertaining to boundedness and persistence, and stability, respectively. Section 6 contains detailed discussions of both finite and infinite-dimensional examples, and some summarising remarks are made in Section 7. A number of technicalities have been relegated to the Appendix.

## 2 Preliminaries

As usual let  $\mathbb{N}$ ,  $\mathbb{Z}$ ,  $\mathbb{R}$  and  $\mathbb{C}$  denote the positive integers (natural numbers), integers, real numbers and complex numbers, respectively. Furthermore,

$$\mathbb{Z}_+ := \{m \in \mathbb{Z} : m \geq 0\} = \mathbb{N} \cup \{0\} \quad \text{and} \quad \mathbb{R}_+ := \{r \in \mathbb{R} : r \geq 0\}.$$

Let  $Y$  and  $Z$  be normed vector spaces. The space of all bounded linear operators  $Y \rightarrow Z$  is denoted by  $\mathcal{L}(Y, Z)$ . As usual, we set  $\mathcal{L}(Y) := \mathcal{L}(Y, Y)$  and  $Y^* := \mathcal{L}(Y, \mathbb{F})$ , where  $\mathbb{F} = \mathbb{R}$  if  $Y$

is real and  $\mathbb{F} = \mathbb{C}$  if  $Y$  is complex. For  $T \in \mathcal{L}(Y, Z)$ , the adjoint operator  $T^* \in \mathcal{L}(Z^*, Y^*)$  is defined by  $(T^*z^*)(y) := (z^*T)(y)$  for all  $y \in Y$  and  $z^* \in Z^*$ .

The open ball centred at  $y \in Y$  of radius  $\rho > 0$  is defined by

$$\mathbb{B}(y, \rho) := \{x \in Y : \|x - y\| < \rho\}.$$

In this paper, the letters  $X$  and  $C$  will always denote a real Banach space and a cone in  $X$ , respectively. Recall that  $C \subset X$  is a *cone* if  $C$  is closed, convex,  $\rho C \subset C$  for all  $\rho \geq 0$  and  $C \cap (-C) = \{0\}$ , where

$$\rho C := \{\rho x : x \in C\} \quad \text{and} \quad -C := \{-x : x \in C\}.$$

Note that the singleton  $\{0\}$  is a cone and that  $0 \in C$ . If  $C \neq \{0\}$ , then the cone  $C$  is said to be non-trivial. Furthermore, note that  $\{\rho x + \sigma y : x, y \in C, \rho, \sigma \geq 0\} \subset C$ , as follows from convexity and the property that  $\rho C \subset C$  for all  $\rho \geq 0$ . We say that  $C$  is *reproducing* if  $X = C - C$ , where  $C - C := \{x - y : x, y \in C\}$ . If the closure of  $C - C$  is equal to  $X$ , then  $C$  is said to be *total*.

We define a partial order on  $X$  by setting, for  $x, y \in X$ ,

$$x \geq y \quad \text{if} \quad x - y \in C.$$

We write  $x > y$  if  $x \geq y$  and  $x \neq y$ . Furthermore, if  $\text{int } C \neq \emptyset$  and  $x - y \in \text{int } C$ , then  $x > y$  (because otherwise  $0 \in \text{int } C$ , in which case there exists  $\rho > 0$  such that  $\mathbb{B}(0, \rho) \subset C$  and thus  $\mathbb{B}(0, \rho) \subset C \cap (-C)$  which is impossible).

Defining  $C^* \subset X^*$  by

$$C^* := \{x^* \in X^* : x^*(x) \geq 0 \text{ for all } x \in C\},$$

then it is straightforward to verify that  $C^*$  satisfies all the properties of a cone except the condition  $C^* \cap (-C^*) = \{0\}$ . It is well known [10, p. 221] and not difficult to show that  $C^*$  is a cone if, and only if,  $C$  is *total*, in which case  $C^*$  is called *dual cone* of  $C$ .

For the rest of the paper it will always be assumed that the cone  $C$  is total, and so,  $C^*$  is a cone in  $X^*$ .

Note that if  $x, y \in C$ ,  $x^* \in C^*$  and  $x \geq y$ , then  $x^*(x) \geq x^*(y)$ . The partial order on  $X^*$  induced by  $C^*$  will also be denoted by “ $\geq$ ”, that is, for  $x^*, y^* \in X^*$ , we write  $x^* \geq y^*$  if  $x^* - y^* \in C^*$ . It is clear that, for  $x^*, y^* \in X^*$ , we have  $x^* \geq y^*$  if, and only if,  $x^*(x) \geq y^*(x)$  for all  $x \in C$ .

In the following we will be interested in scenarios wherein  $\text{int } C^* \neq \emptyset$ . The next lemma provides a characterization of elements in  $\text{int } C^*$ .

**Lemma 2.1.** *Let  $x^* \in X^*$ .*

(1) *The functional  $x^*$  is in  $\text{int } C^*$  if, and only if,*

$$\inf_{x \in C, \|x\|=1} x^*(x) > 0. \tag{2.1}$$

(2) *If  $x^* \in \text{int } C^*$ ,  $y^* \in C^*$  and  $y^* \geq x^*$ , then  $y^* \in \text{int } C^*$ .*

*Proof.* (1) Assume that  $x^* \in \text{int } C^*$ . Seeking a contradiction, suppose that (2.1) does not hold. Then there exist elements  $x_n \in C$  with  $\|x_n\| = 1$ , where  $n \in \mathbb{N}$ , and such that

$$\varepsilon_n := x^*(x_n) \rightarrow 0 \quad \text{as } n \rightarrow \infty.$$

Assume that there exists  $k \in \mathbb{N}$  such that  $\varepsilon_k = 0$  and choose  $y^* \in X^*$  such that  $y^*(x_k) = 1$  (existence of such a functional is guaranteed by the Hahn-Banach theorem). Then, for every  $\delta > 0$ , the functional  $z_\delta^* := x^* - \delta y^*$  has the property  $z_\delta^*(x_k) = -\delta < 0$ , and so  $z_\delta^* \notin C^*$ , contradicting the hypothesis that  $x^* \in \text{int } C^*$ . Consequently,  $\varepsilon_n > 0$  for all  $n \in \mathbb{N}$ . Invoking again the Hahn-Banach theorem, there exist  $y_n^* \in X^*$  such that  $\|y_n^*\| = 1$  and  $y_n^*(x_n) = 1$  for all  $n \in \mathbb{N}$ . The functionals  $z_n^* := x^* - 2\varepsilon_n y_n^*$  satisfy  $z_n^*(x_n) = -\varepsilon_n < 0$  and thus,  $z_n^* \notin C^*$ . But  $z_n^* \rightarrow x^*$  as  $n \rightarrow \infty$ , contradicting the hypothesis that  $x^* \in \text{int } C^*$ .

Conversely assume that (2.1) holds, in which case

$$\varepsilon := \inf_{x \in C, \|x\|=1} x^*(x) > 0.$$

Let  $y^* \in X^*$  be such that  $\|x^* - y^*\| < \varepsilon/2$ . Then, for all  $x \in C$  with  $\|x\| = 1$ ,

$$y^*(x) = x^*(x) + (y^* - x^*)(x) \geq \varepsilon - \|y^* - x^*\| > \frac{\varepsilon}{2}.$$

Hence,  $y^*(x) \geq (\varepsilon/2)\|x\|$  for all  $x \in C$ , showing that  $y^* \in C^*$ . Consequently,  $\mathbb{B}(x^*, \varepsilon/2) \subset C^*$ , establishing that  $x^* \in \text{int } C^*$ .

(2) Statement (2) is an immediate consequence of statement (1).  $\square$

**Example 2.2.** (1) Let  $X = \mathbb{R}^n$ . Then  $C = \mathbb{R}_+^n$  is a reproducing cone. The dual cone  $C^*$  can be identified with  $C$  and  $\text{int } C^* = \text{int } C = (0, \infty)^n$ .

(2) Let  $\Omega \subset \mathbb{R}^q$  be measurable and  $X = L^r(\Omega, \mathbb{R})$ , where  $1 \leq r \leq \infty$ . Then  $C = L^r(\Omega, \mathbb{R}_+)$  is a reproducing cone, and, for  $r < \infty$ , the dual cone  $C^*$  is given by  $C^* = L^s(\Omega, \mathbb{R}_+)$ , where  $1/r + 1/s = 1$ . Note that  $\text{int } C^* \neq \emptyset$  if, and only if,  $r = 1$ . If  $r = 1$ , then  $C^* = L^\infty(\Omega, \mathbb{R}_+)$  and  $h \in \text{int } C^*$  if, and only if,  $\text{ess inf } h > 0$ .

(3) Let  $X = \mathbb{R}^n$  and  $C = \{x \in \mathbb{R}^n : (x_2^2 + \dots + x_n^2)^{1/2} \leq x_1\}$ . Then  $C$  is a cone, the so-called ‘‘ice cream cone’’ [3]. This cone is reproducing,  $C^* = C$  and  $\text{int } C^* = \text{int } C = \{x \in \mathbb{R}^n : (x_2^2 + \dots + x_n^2)^{1/2} < x_1\}$ .

(4) Let  $\Omega \subset \mathbb{R}$  be compact and  $X = \mathcal{C}(\Omega, \mathbb{R})$ , the space of real-valued continuous functions defined on  $\Omega$ , endowed with the sup norm. Obviously,  $C = \mathcal{C}(\Omega, \mathbb{R}_+)$  is a reproducing cone and  $C^*$  can be identified with the set of finite positive Borel measures on  $\Omega$ . Note that  $\text{int } C^* = \emptyset$ .

(5) Let  $X_1$  and  $X_2$  be real Banach spaces and let  $C_1 \subset X_1$  and  $C_2 \subset X_2$  be cones. Then  $C_1 \times C_2$  is a cone in  $X_1 \times X_2$ . This cone is total (reproducing) if, and only if, both,  $C_1$  and  $C_2$  are total (reproducing). Moreover,  $(C_1 \times C_2)^*$  can be identified with  $C_1^* \times C_2^*$ . The interior of  $(C_1 \times C_2)^*$  is non-empty if, and only if, the interiors of each of  $C_1^*$  and  $C_2^*$  are non-empty.  $\diamond$

An operator  $T \in \mathcal{L}(X)$  is said to be *positive* if  $TC \subset C$ , where  $TC := \{Tx : x \in C\}$ , and in this case we write  $T \geq 0$ . Since

$$(T^*x^*)(x) = x^*(Tx) \quad \forall x \in X, \forall x^* \in X^*,$$

it follows that if  $T$  is positive, then  $T^*$  is positive.

We say that an operator  $T \in \mathcal{L}(X)$  is exponentially stable if there exists  $M \geq 1$  and  $\mu \in (0, 1)$  such that  $\|T^t\| \leq M\mu^t$  for all  $t \in \mathbb{Z}_+$ , or equivalently, if the spectrum of  $T$  is contained in the open unit disc of the complex plane.

Let  $Y$  be a normed vector space. For  $S \subset Y$ , let  $\mathcal{F}(\mathbb{Z}_+, S)$  denote the set of all functions  $\mathbb{Z}_+ \rightarrow S$ . For  $u \in \mathcal{F}(\mathbb{Z}_+, Y)$  and  $t \in \mathbb{Z}_+$ , we set

$$\|u\|_{\ell^\infty(0,t)} := \max \{ \|u(\tau)\| : \tau \in \mathbb{Z}_+, \tau \leq t \}.$$

If  $u \in \mathcal{F}(\mathbb{Z}_+, Y)$  is bounded, then we define  $\|u\|_{\ell^\infty} := \sup\{\|u(t)\| : t \in \mathbb{Z}_+\}$ .

For the proof of the stability theorems in Section 5, we require an input-to-state stability result from control theory. To explain this result, consider the system

$$x^\nabla = Ax + bh(c^*x) + v, \quad x(0) = x^0 \in X, \quad (2.2)$$

where  $x^\nabla$  is the left-shifted version of  $x$ , that is,  $x^\nabla(t) = x(t+1)$ ,  $A \in \mathcal{L}(X)$ ,  $b \in X$  and  $c^* \in X^*$ ,  $h : \mathbb{R} \rightarrow \mathbb{R}$  is a continuous nonlinearity and  $v \in \mathcal{F}(\mathbb{Z}_+, X)$  is a forcing function (input, control). In control theory, systems of the form (2.2) are sometimes referred to as Lur'e systems. Obviously, (2.2) can be thought of as a feedback system obtained by application of the feedback law  $\omega = h(y)$  to the linear controlled and observed system

$$x^\nabla = Ax + b\omega + v, \quad y = c^*x, \quad x(0) = x^0. \quad (2.3)$$

The functions  $\omega$  and  $v$  in (2.3) are interpreted as inputs (controls, disturbances, forcing functions) and  $y$  is called the output (measurement, observation) of (2.3). If  $v = 0$ , then (2.3) reduces to

$$x^\nabla = Ax + b\omega, \quad y = c^*x, \quad x(0) = x^0. \quad (2.4)$$

Associated with (2.4) is the so-called transfer function

$$\mathbf{G}(z) := c_c^*(zI - A_c)^{-1}b,$$

where  $z$  is a complex variable. Here  $A_c$  and  $c_c^*$  denote the canonical complex extensions of  $A$  and  $c^*$ , respectively, to  $X_c$ , the complexification of  $X$ . Applying the  $Z$ -transform (denoted by  $\mathcal{Z}$ ) to (2.4), we obtain

$$(\mathcal{Z}y)(z) = zc_c^*(zI - A_c)^{-1}x^0 + \mathbf{G}(z)(\mathcal{Z}\omega)(z).$$

The above identity shows that, in the frequency domain, the effect of the input on the linear dynamics is described by the product of the transfer function and the  $Z$ -transform of the input.

If  $A$  is exponentially stable, then we set

$$\|\mathbf{G}\|_{H^\infty} := \sup_{|z|=1} |\mathbf{G}(z)| = \sup_{|z| \geq 1} |\mathbf{G}(z)|,$$

where  $H^\infty$  refers to the space of all bounded holomorphic functions defined on the complement of the closed unit disc. Denoting the output of (2.4) corresponding to the initial condition  $x(0) = 0$  by  $y(\omega)$ , we have that

$$\sup\{\|y(\omega)\|_{\ell^2} : \|\omega\|_{\ell^2} = 1\} = \|\mathbf{G}\|_{H^\infty}, \quad \text{where } \|\omega\|_{\ell^2} := \left(\sum_{t=0}^{\infty} |\omega(t)|^2\right)^{1/2}.$$

This identity is well-known in control theory and operator theory and it provides an appealing interpretation of  $\|\mathbf{G}\|_{H^\infty}$  in time-domain terms.

For later purposes, we note that, for every complex number  $\zeta$ ,

$$c_c^*(zI - (A_c + \zeta bc_c^*))^{-1}b = \frac{\mathbf{G}(z)}{1 - \zeta \mathbf{G}(z)}. \quad (2.5)$$

If  $A$  is exponentially stable, then the function on the right-hand side of (2.5) is meromorphic on the complement of the closed unit disc.

The following result is a special case of [19, Corollary 3.3].

**Theorem 2.3.** Consider the system (2.2), denote its solution by  $x(\cdot; x^0, v)$ , and assume that  $h$  is continuous and  $A$  is exponentially stable. If

$$\sup_{y \in \mathbb{R}, y \neq 0} |h(y)/y| < 1/\|\mathbf{G}\|_{H^\infty},$$

where  $1/\|\mathbf{G}\|_{H^\infty} := \infty$  if  $\mathbf{G}(z) \equiv 0$ , then there exist  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $N > 0$  such that

$$\|x(t; x^0, v)\| \leq M\mu^t \|x^0\| + N\|v\|_{\ell^\infty(0,t)} \quad \forall t \in \mathbb{Z}_+, \forall x^0 \in \mathbb{R}^n, \forall v \in \mathcal{F}(\mathbb{Z}_+, X). \quad (2.6)$$

If system (2.2) satisfies (2.6) (for some  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $N > 0$ ), then the zero equilibrium of the unforced ( $v(t) \equiv 0$ ) system  $x^\nabla = Ax + bh(c^*x)$  is said to be exponentially input-to-state stable (ISS). Frequently, it is also said that (2.2) is exponentially ISS. Obviously, exponential ISS implies ISS, and the ISS concept is a standard stability concept in nonlinear control theory. It was defined by Sontag in the 1989 paper [43] in the context of general forced (or controlled) finite-dimensional nonlinear systems, and subsequently, a substantial Lyapunov theoretic ISS framework has been developed in the finite-dimensional setting, see, for example, [9, 25, 44]. Note that (2.6) implies that the zero equilibrium of the unforced system  $x^\nabla = Ax + bh(c^*x)$  is globally exponentially stable (GES).

### 3 Density-dependent population models with forcing

We consider the forced difference equation (1.1). Here  $A \in \mathcal{L}(X)$  is positive,  $b$  and  $c^*$  are non-zero elements in  $C$  and  $C^*$ , respectively, and  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is a continuous nonlinearity, where  $U \subset \mathbb{R}$  is compact. The functions  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  are forcing terms, and we shall always assume that the initial condition belongs to the positive cone,  $x^0 \in C$ . Recall that (1.1) can be thought of as the feedback interconnection of  $\omega = f(u, y)$  and the linear system (2.3).

Typical scenarios for  $f$  are given by:

- $f(w, y) = g(wy)y$ , where  $g : (0, \infty) \rightarrow \mathbb{R}_+$  is continuous and such that  $\lim_{y \rightarrow 0} g(y)y$  exists and is finite;
- $f(w, y) = g(wy)$ , where  $g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is continuous;
- $f(w, y) = wg(y)$ , where  $g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is continuous.

In each of the above cases,  $U$  is a compact subset of  $\mathbb{R}_+$ . We point out that there are interesting and relevant examples of nonlinearities which do not fall into any of the above three scenarios, one such example is given by  $f(w, y) = y/(w + y^\alpha)$ , where  $\alpha > 0$  and  $\alpha \neq 1$ .\*

We impose the following positivity and stability assumptions on the linear system determined by  $A$ ,  $b$  and  $c^*$ .

**(L1)**  $A \in \mathcal{L}(X)$  is positive and exponentially stable.

**(L2)**  $b \in C$ ,  $c^* \in C^*$ ,  $b \neq 0$  and  $c^* \neq 0$ .

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\* Note that if  $\alpha = 1$ , then  $f(w, y) = g(y/w)$ , where  $g(y) = y/(1 + y)$ .

Further assumptions on the nonlinearities  $f$  will be specified in Sections 4 and 5.

The positivity conditions in (L1) and (L2), together with the assumption that the values of  $f$  are non-negative, imply that, for all  $x^0 \in C$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C)$ , the solution  $x$  of (1.1) will stay in the cone  $C$ .

**Proposition 3.1.** *Assume that (L1) and (L2) are satisfied. The following statements hold.*

(1)  $\|\mathbf{G}\|_{H^\infty} = \mathbf{G}(1) \geq 0$  and

$$p := \frac{1}{\mathbf{G}(1)} \in (0, \infty], \quad \text{where } p := \infty \text{ if } \mathbf{G}(1) = 0. \quad (3.1)$$

(2) The operator  $A + \lambda bc^*$  is exponentially stable for all  $\lambda \in [0, p)$ .

(3) If  $p < \infty$ , then  $1 \in \text{spec}(A_c + pbc_c^*)$ , in particular,  $A + pbc^*$  is not exponentially stable.

*Proof.* (1) It follows from (L1) and (L2) that

$$\mathbf{G}(1) = c_c^*(I - A_c)^{-1}b = c^*(I - A)^{-1}b = \sum_{k=0}^{\infty} c^*A^k b \geq 0.$$

Furthermore, a straightforward calculation yields that, for every  $z \in \mathbb{C}$  with  $|z| \geq 1$ ,

$$|\mathbf{G}(z)| = \frac{1}{|z|} |c_c^*(I - (1/z)A_c)^{-1}b| \leq \sum_{k=0}^{\infty} \frac{1}{|z|^{k+1}} c^*A^k b.$$

Combining this with the identity

$$|\mathbf{G}(1)| = \mathbf{G}(1) = c^*(I - A)^{-1}b = \sum_{k=0}^{\infty} c^*A^k b,$$

shows that  $\|\mathbf{G}\|_{H^\infty} = \mathbf{G}(1)$ .

(2) This follows from standard stability radius theory.

(3) By (2.5),

$$c_c^*(zI - (A_c + pbc_c^*))^{-1}b = \frac{\mathbf{G}(z)}{1 - p\mathbf{G}(z)}.$$

The right-hand side of the above identity has a pole at  $z = 1$  and hence  $(zI - (A_c + pbc_c^*))^{-1}$  has a singularity at  $z = 1$ . Consequently,  $1 \in \text{spec}(A_c + pbc_c^*)$ .  $\square$

Note that solutions of (1.1) are also solutions of a difference inclusion of the form

$$x^\nabla - Ax - v \in bF(c^*x), \quad (3.2)$$

where the set-valued function  $F$  is given by

$$F(y) := \{f(w, y) : w \in U\} \quad \forall y \geq 0.$$

It is therefore useful to consider stability properties of the difference inclusion (3.2).



**Proposition 3.2.** *Assume that (L1) and (L2) hold and  $F$  is a set-valued function defined on  $\mathbb{R}_+$ , the values of which are non-empty subsets of  $\mathbb{R}_+$ . If there exist  $\theta \geq 0$  and  $q \in (0, p)$  such that  $\cup_{0 \leq y \leq \theta} F(y)$  is bounded and*

$$\varphi \leq qy \quad \forall \varphi \in F(y), \quad \forall y \geq \theta, \quad (3.3)$$

then there exist  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $N > 0$  such that, for every solution  $x : \mathbb{Z}_+ \rightarrow C$  of (3.2),

$$\|x(t)\| \leq M\mu^t \|x(0)\| + N(\beta_F + \|v\|_{\ell^\infty(0,t)}) \quad \forall t \in \mathbb{Z}_+, \quad \forall v \in \mathcal{F}(\mathbb{Z}_+, C), \quad (3.4)$$

where

$$\beta_F := \sup_{0 \leq y \leq \theta, \varphi \in F(y)} (\varphi - qy) \geq 0.$$

*Proof.* We proceed in two steps.

*Step 1:  $\theta = 0$ .*

Assume that (3.3) holds with  $\theta = 0$  (in which case  $F(0) = \{0\}$ ). If the values of  $F$  are singletons (in which case  $F$  can be identified with a real-valued function), then the claim is an immediate consequence of Theorem 2.3. It is not difficult to see that Theorem 2.3 extends to set-valued nonlinearities and so, in the case wherein  $\theta = 0$ , the estimate (3.4) follows with  $\beta_F = 0$ .

*Step 2:  $\theta > 0$ .*

Note that by the boundedness of the set  $\cup_{0 \leq y \leq \theta} F(y)$ , the constant  $\beta_F$  is finite. Define a set-valued map  $\tilde{F}$  by

$$\tilde{F}(y) := \begin{cases} [0, qy], & 0 \leq y \leq \theta, \\ F(y), & y > \theta. \end{cases}$$

and set  $e(y) := \max(0, \max\{\varphi - qy : \varphi \in F(y)\})$  for  $y \in [0, \theta]$ . It is clear that

$$\varphi \leq qy \quad \forall \varphi \in \tilde{F}(y), \quad \forall y \geq 0,$$

and, moreover,  $\sup_{0 \leq y \leq \theta} e(y) = \beta_F$ . If  $x : \mathbb{Z}_+ \rightarrow C$  is a solution of (3.2), then

$$x^\nabla - Ax - v - bd \in b\tilde{F}(c^*x),$$

where  $d(t) = 0$  if  $c^*x(t) > \theta$  and  $d(t) \in [0, e(c^*x(t))]$  if  $c^*x(t) \leq \theta$ . Consequently, by Step 1, there exist constants  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $L > 0$  such that, for every solution  $x : \mathbb{Z}_+ \rightarrow C$  of (3.2),

$$\|x(t)\| \leq M\mu^t \|x(0)\| + L\|v + bd\|_{\ell^\infty(0,t)} \leq M\mu^t \|x(0)\| + L\|v\|_{\ell^\infty(0,t)} + L\beta_F \|b\| \quad \forall t \in \mathbb{Z}_+,$$

where we have used that  $|d(t)| = d(t) \leq \sup_{0 \leq y \leq \theta} e(y) = \beta_F$ . The claim now follows with  $N := L \max(1, \|b\|)$ .  $\square$

## 4 Boundedness and persistence

In this section we address the first two properties of boundedness and persistence. Assume that (L1) and (L2) hold and let  $U \subset \mathbb{R}$  be compact. Throughout,  $U$  will be the range of permitted values for the scalar forcing term  $u$ . In the special cases we have in mind,  $U \subset \mathbb{R}_+$  with  $0 \notin U$  (see examples further below), but this is not required in the general theory we will develop.

For the rest of the paper, for given  $x^0 \in C$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  we let  $x = x(\cdot; x^0, u, v)$  denote the solution of (1.1). As a matter of convenience, we set

$$C_\rho := C \cap \mathbb{B}(0, \rho), \quad \text{where } \rho > 0.$$

Let  $Y$  be a real normed space and  $T \in \mathcal{L}(X, Y)$ . We say that (1.1) is *ultimately semi-globally  $T$ -persistent* if, for every bounded closed set  $\Gamma \subset C$  with  $0 \notin \Gamma$  and every  $\rho > 0$ , there exist  $\tau \in \mathbb{Z}_+$  and  $\eta > 0$  such that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and all  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ ,

$$\|Tx(t + \tau; x^0, u, v)\| \geq \eta \quad \forall t \in \mathbb{Z}_+.$$

Note that this persistence property is “semi-global” in contrast to the global persistency concepts for unforced systems considered in [41, 42]. On the other hand, the above concept has stronger uniformity properties than those in [41, 42]: the same  $\tau$  “works” for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and all  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ . The relevance of persistence in the context of population dynamics is obvious: its absence is equivalent to extinction. For all practical purposes the semi-global nature of the above persistency concept is sufficient: for any given application context, there exists a bounded closed set  $\Gamma \subset C$  such that every practically relevant initial condition will belong to  $\Gamma$ . In the special case wherein  $Y = X$  and  $T = I$ , we use the term “persistent” rather than “ $I$ -persistent”. If, in the above definition,  $\tau = 0$ , then we simply say that (1.1) is *semi-globally  $T$ -persistent*.

We remark that if, for every  $u \in U$ , the function  $y \mapsto f(u, y)$  is non-decreasing, then, for  $z^* \in C^*$ , the system (1.1) is ultimately semi-globally  $z^*$ -persistent if, and only if, for every bounded closed set  $\Gamma \subset C$ ,  $0 \notin \Gamma$ , there exist  $\tau \in \mathbb{Z}_+$  and  $\eta > 0$  such that  $z^*(x(t + \tau; x^0, u, 0)) \geq \eta$  for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and all  $t \in \mathbb{Z}_+$ , that is, the forcing  $v$  is irrelevant for persistency in this scenario. Moreover, if additionally the norm on  $X$  is monotone, then (1.1) is ultimately semi-globally persistent if, and only if, for every bounded closed set  $\Gamma \subset C$ ,  $0 \notin \Gamma$ , there exist  $\tau \in \mathbb{Z}_+$  and  $\eta > 0$  such that  $\|x(t + \tau; x^0, u, 0)\| \geq \eta$  for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and all  $t \in \mathbb{Z}_+$ .

**Proposition 4.1.** *Assume that (L1) and (L2) hold and  $f(w, 0) = 0$  for all  $w \in U$ . If (1.1) is ultimately semi-globally persistent, then  $c^*(I - A)^{-1}x > 0$  for all  $x \in C$ ,  $x \neq 0$ . In particular,  $\mathbf{G}(1) = c^*(I - A)^{-1}b > 0$ , or, equivalently,  $p < \infty$ , where  $p$  is given by (3.1).*

*Proof.* We prove the claim by contraposition. To this end assume that there exists  $x^0 \in C$ ,  $x^0 \neq 0$ , such that  $c^*(I - A)^{-1}x^0 = 0$ , that is,

$$c^*A^t x^0 = 0 \quad \forall t \in \mathbb{Z}_+.$$

We will show that (1.1) is not ultimately semi-globally persistent. Let  $u \in \mathcal{F}(\mathbb{Z}_+, U)$ , let  $v(t) \equiv 0$  and set  $x(t) := x(t; x^0, u, 0)$ . Then  $f(u(0), c^*x^0) = f(u(0), 0) = 0$  and so,  $x(1) = Ax^0$  and  $c^*x(1) = c^*Ax^0 = 0$ . A trivial induction argument shows that  $x(t) = A^t x^0$  and  $c^*x(t) = 0$  for all  $t \in \mathbb{Z}_+$ . Since, by exponential stability,  $A^t x^0 \rightarrow 0$  as  $t \rightarrow \infty$ , we see that (1.1) is not ultimately semi-globally persistent.  $\square$

Next we introduce suitable assumptions on  $f$  which will enable us to prove boundedness and persistence results for the system (1.1).

**(N1)**  $U \subset \mathbb{R}$  is compact,  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is continuous,  $f(w, y) > 0$  for all  $w \in U$  and  $y > 0$  and

$$\limsup_{y \rightarrow \infty} \frac{\max_{w \in U} f(w, y)}{y} < p, \quad (4.1)$$

where  $p$  is given by (3.1).

(N2) (N1) holds and

$$\liminf_{y \rightarrow 0} \frac{\min_{w \in U} f(w, y)}{y} > p. \quad (4.2)$$

The following result provides classes of examples for which conditions (N1) or (N2) are satisfied.

**Proposition 4.2.** *Let  $U \subset \mathbb{R}_+$  be compact,  $0 \notin U$  and set  $u^- := \min U$  and  $u^+ := \max U$ , in which case  $0 < u^- \leq u^+ < \infty$ .*

(1) *Let  $g : (0, \infty) \rightarrow (0, \infty)$  be continuous and such that  $f_0 := \lim_{y \rightarrow 0} g(y)y$  exists and is finite, and define  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  by*

$$f(w, y) = \begin{cases} g(wy)y, & \text{for } w \in U \text{ and } y > 0 \\ f_0/w, & \text{for } w \in U \text{ and } y = 0. \end{cases}$$

*If  $\limsup_{y \rightarrow \infty} g(y) < p$ , then  $f$  satisfies condition (N1). If additionally,  $\liminf_{y \rightarrow 0} g(y) > p$ , then  $f$  satisfies (N2).*

(2) *Let  $g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  be continuous and such that  $g(y) > 0$  for all  $y > 0$ , and define  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  by  $f(w, y) := g(wy)$  or by  $f(w, y) := wg(y)$  for all  $w \in U$  and  $y \in \mathbb{R}_+$ . If  $\limsup_{y \rightarrow \infty} (g(y)/y) < p/u^+$ , then  $f$  satisfies (N1). If additionally,  $\liminf_{y \rightarrow 0} g(y)/y > p/u^-$ , then  $f$  satisfies (N2).*

*Proof.* The proof of statement (1) is trivial. To prove statement (2), assume that  $g$  is continuous,  $g(y) > 0$  for  $y > 0$  and  $\limsup_{y \rightarrow \infty} (g(y)/y) < p/u^+$ . We focus on the case wherein  $f(w, y) = g(wy)$ . The other case ( $f$  given  $f(w, y) = wg(y)$ ) is straightforward and left to the reader. It is clear that  $f$  is continuous and  $f(w, y) > 0$  for all  $w \in U$  and  $y > 0$ . Moreover, for every  $y > 0$ , there exists  $\xi_y \in [u^-y, u^+y] \subset (0, \infty)$  such that

$$\max_{w \in U} \frac{g(wy)}{wy} = \frac{g(\xi_y)}{\xi_y}.$$

Now, for  $y > 0$ ,

$$\frac{1}{y} \max_{w \in U} f(w, y) \leq \frac{1}{y} \max_{w \in U} \frac{u^+ g(wy)}{w} = u^+ \max_{w \in U} \frac{g(wy)}{wy} = u^+ \frac{g(\xi_y)}{\xi_y},$$

and so, since  $\xi_y \rightarrow \infty$  as  $y \rightarrow \infty$ ,

$$\limsup_{y \rightarrow \infty} \frac{1}{y} \max_{w \in U} f(w, y) \leq u^+ \limsup_{y \rightarrow \infty} \frac{g(\xi_y)}{\xi_y} < p,$$

showing that (N1) holds. Similarly, for every  $y > 0$ , there exists  $\zeta_y \in [u^-y, u^+y] \subset (0, \infty)$  such that

$$\min_{w \in U} \frac{g(wy)}{wy} = \frac{g(\zeta_y)}{\zeta_y}.$$

Thus, for  $y > 0$ ,

$$\frac{1}{y} \min_{w \in U} f(w, y) \geq \frac{1}{y} \min_{w \in U} \frac{u^- g(wy)}{w} = u^- \min_{w \in U} \frac{g(wy)}{wy} = u^- \frac{g(\zeta_y)}{\zeta_y},$$

and consequently, since  $\zeta_y \rightarrow 0$  as  $y \rightarrow 0$ ,

$$\liminf_{y \rightarrow 0} \frac{1}{y} \min_{w \in U} f(w, y) \geq u^- \liminf_{y \rightarrow 0} \frac{g(\zeta_y)}{\zeta_y} > p,$$

establishing that (N2) is satisfied.  $\square$

We remark that, for the stability results in Section 5, the above assumption (N2) will have to be somewhat strengthened. The next result shows that (N1) and (N2), in combination with (L1) and (L2) and a suitable “strict” positivity assumption (see (P1) below), are sufficient to establish semi-global boundedness and persistence properties of (1.1).

**Theorem 4.3.** *Consider the initial-value problem (1.1) and let  $p$  be given by (3.1). Assume that (L1) and (L2) hold and let  $\rho > 0$ . The following statements hold.*

(1) *If (N1) is satisfied and  $\Gamma \subset C$  is bounded, then there exists  $\gamma > 0$  such that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ ,*

$$\|x(t; x^0, u, v)\| \leq \gamma \quad \forall t \in \mathbb{Z}_+.$$

(2) *Assume that (N2) and the following additional condition hold.*

(P1) *There exists  $\tau \in \mathbb{Z}_+$  such that  $c^*(A + bc^*)^\tau \in \text{int } C^*$ .*

*If  $\Gamma \subset C$  is bounded, closed and such that  $0 \notin \Gamma$ , then there exist  $\delta > 0$  and  $\eta > 0$  such that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ ,*

$$\|x(t; x^0, u, v)\| \geq \delta \quad \text{and} \quad c^*x(t + \tau; x^0, u, v) \geq \eta \quad \forall t \in \mathbb{Z}_+.$$

*In particular, (1.1) is semi-globally persistent and ultimately semi-globally  $c^*$ -persistent.*

The above result extends the persistency theory developed in [17] in several directions: the underlying linear system is allowed to be infinite-dimensional, the positivity condition (P1) is less restrictive than the primitivity condition imposed in [17, 48] and the structure of the forced system (1.1) is more general than that considered in [17]. We refer the reader to Remark 4.6 for some further details on the differences between the present paper and [17]. The persistence properties guaranteed by Theorem 4.3 overlap with persistency concepts (for systems without forcing) introduced in [18, 41, 42, 50]. In particular, it follows immediately from statement (2) of Theorem 4.3 that the unforced system (1.1) is strongly  $\|\cdot\|$ -persistent and strongly  $c^*$ -persistent, respectively, in the sense of [41, Definition 3.1].

Note that (P1) implies that  $\text{int } C^* \neq \emptyset$ . We remark that whilst the latter is always satisfied in the finite-dimensional case, it may fail to hold for infinite-dimensional spaces, see Example 2.2. Finally, we point out that the key positivity assumption imposed in [36, Theorem 3.3] is the condition  $c^* \in \text{int } C^*$ , i.e., (P1) with  $\tau = 0$ .

We will show below that (P1) is implied by each of the following conditions.

(P2) *There exists  $\tau \in \mathbb{Z}$  such that  $c^* \sum_{t=0}^{\tau} (A + bc^*)^t \in \text{int } C^*$  and  $c^*b > 0$ .*

(P3) *There exists  $\tau \in \mathbb{N}$  such that  $[(A + bc^*)^*]^\tau$  is strictly positive, that is,  $[(A + bc^*)^*]^\tau x^* \in \text{int } C^*$  for all non-zero  $x^* \in C^*$ .*

The simple example given by  $X = \mathbb{R}^3$ ,  $C = \mathbb{R}_+^3$  and

$$A = \begin{pmatrix} \alpha_1 & 0 & 0 \\ 0 & \alpha_2 & \alpha_3 \\ 0 & 0 & 0 \end{pmatrix}, \quad b = \begin{pmatrix} 0 \\ 0 \\ \beta \end{pmatrix}, \quad c^* = (\gamma_1 \quad \gamma_2 \quad 0), \quad \text{where } \alpha_i, \beta, \gamma_i > 0,$$

shows that (P1) does not imply (P2) or (P3).<sup>†</sup>

To facilitate the proof of Theorem 4.3, we state and prove the following lemma.

**Lemma 4.4.** *Assume that (L1) and (L2) are satisfied. The following statements hold.*

- (1) *If (P1) holds, then  $c^*(A + \lambda bc^*)^\tau \in \text{int } C^*$  for every  $\lambda > 0$ .*
- (2) *If (P1) holds, then  $\mathbf{G}(1) > 0$ , or, equivalently,  $p < \infty$ .*
- (3) *If (P1) holds, then, for every  $\lambda \in [0, p)$ ,*

$$z_\lambda^* := c^*(I - (A + \lambda bc^*))^{-1} \in \text{int } C^* \quad \text{and} \quad z_\lambda^*(A + pbc^*) = z_\lambda^*. \quad (4.3)$$

Furthermore, for  $\lambda, \mu \in [0, p)$ ,

$$z_\lambda^* = \frac{p - \mu}{p - \lambda} z_\mu^*. \quad (4.4)$$

- (4) *If (P2) or (P3) holds, then (P1) is satisfied.*
- (5) *Assume that  $X = \mathbb{R}^n$  and  $C = \mathbb{R}_+^n$ . If  $A + bc^*$  is irreducible and  $c^*b > 0$ , then (P1), (P2) and (P3) hold.*

*Proof.* (1) Let  $\lambda > 0$ . A routine induction argument shows that, for every  $t \in \mathbb{Z}_+$ ,

$$c^*(A + \lambda bc^*)^t \geq c^*(A + bc^*)^t \quad \text{if } \lambda \geq 1,$$

and

$$c^*(A + \lambda bc^*)^t \geq \lambda^t c^*(A + bc^*)^t \quad \text{if } 0 < \lambda < 1.$$

Assume that  $\tau \in \mathbb{Z}_+$  is such that  $c^*(A + bc^*)^\tau \in \text{int } C^*$ . Then the above inequalities yield,

$$c^*(A + \lambda bc^*)^t \geq \min(\lambda^t, 1) c^*(A + bc^*)^t \quad \forall t \in \mathbb{Z}_+, \quad (4.5)$$

and thus, an application of statement (2) of Lemma 2.1 shows that  $c^*(A + \lambda bc^*)^\tau \in \text{int } C^*$ .

(2) We prove the claim by contraposition. To this end assume that  $\mathbf{G}(1) = 0$ . We show that (P1) does not hold. Letting  $\lambda \in (0, p)$ , then, by Proposition 3.1,  $A + \lambda bc^*$  is exponentially stable and, therefore, appealing to (2.5), we conclude that

$$\sum_{t=0}^{\infty} c^*(A + \lambda bc^*)^t b = c^*(I - (A + \lambda bc^*))^{-1} b = \frac{\mathbf{G}(1)}{1 - \lambda \mathbf{G}(1)} = 0.$$

Since  $c^*(A + \lambda bc^*)^t b \geq 0$  for  $t \in \mathbb{Z}_+$ , it follows that  $c^*(A + \lambda bc^*)^t b = 0$  for  $t \in \mathbb{Z}_+$ . By (L2),  $b \neq 0$ , and therefore, for all  $t \in \mathbb{Z}_+$ ,  $c^*(A + \lambda bc^*)^t \notin \text{int } C^*$ . Invoking statement (1), we see that (P1) does not hold.

(3) Let  $\lambda \in [0, p)$ . By Proposition 3.1,  $A + \lambda bc^*$  is exponentially stable, and so  $z_\lambda^*$  is well defined. We show first that  $z_\lambda^*(A + pbc^*) = z_\lambda^*$ . To this end, note that

$$z_\lambda^*(A + pbc^*) = z_\lambda^*(A + \lambda bc^* - I + (p - \lambda)bc^* + I) = -c^* + (p - \lambda)z_\lambda^*bc^* + z_\lambda^*.$$

Using (2.5), we obtain

$$(p - \lambda)z_\lambda^*bc^* = (p - \lambda)c^*(I - (A + \lambda bc^*))^{-1}bc^* = (p - \lambda)\frac{\mathbf{G}(1)}{1 - \lambda \mathbf{G}(1)}c^* = c^*,$$

---

<sup>†</sup>In this example, we have identified a row vector with the linear functional induced by the row vector. We will continue to do so in the rest of the paper in the context of finite-dimensional examples.

and thus,  $z_\lambda^*(A + pbc^*) = z_\lambda^*$ .

Next we derive (4.4). Letting  $\lambda, \mu \in [0, p)$ , we note that, by the second resolvent identity,

$$z_\lambda^* - z_\mu^* = (\lambda - \mu)c^*(I - (A + \lambda bc^*))^{-1}bc^*(I - (A + \mu bc^*))^{-1},$$

and so, using (2.5),

$$z_\lambda^* - z_\mu^* = \frac{(\lambda - \mu)\mathbf{G}(1)}{1 - \lambda\mathbf{G}(1)}z_\mu^*.$$

Consequently,

$$z_\lambda^* = \frac{1 - \mu\mathbf{G}(1)}{1 - \lambda\mathbf{G}(1)}z_\mu^* = \frac{p - \mu}{p - \lambda}z_\mu^*,$$

establishing (4.4). We proceed to show that  $z_\lambda^* \in \text{int } C^*$  for  $\lambda \in (0, p)$ . Since  $A + \lambda bc^*$  is exponentially stable, we have

$$z_\lambda^* = \sum_{t=0}^{\infty} c^*(A + \lambda bc^*)^t \geq c^*(A + \lambda bc^*)^\tau,$$

and it follows from statement (1) and Lemma 2.1 that  $z_\lambda^* \in \text{int } C^*$ . Finally, an application of (4.4) for  $\lambda = 0$  and  $\mu \in (0, p)$  shows that  $z_0^* \in \text{int } C^*$ .

(4) Assume that (P2) holds and let  $\lambda \in (0, 1)$ . Invoking (4.5), we conclude that

$$c^* \sum_{t=0}^{\tau} (A + \lambda bc^*)^t \geq \lambda^\tau c^* \sum_{t=0}^{\tau} (A + bc^*)^t.$$

Hence, setting  $A_\lambda := A + \lambda bc^*$ , it follows from Lemma 2.1 that

$$c^* \sum_{t=0}^{\tau} A_\lambda^t \in \text{int } C^*. \quad (4.6)$$

Now  $c^*(A + bc^*)^\tau = c^*(A_\lambda + (1 - \lambda)bc^*)^\tau$  and a straightforward induction argument shows that

$$c^*(A + bc^*)^\tau \geq c^* \sum_{t=0}^{\tau} [(1 - \lambda)(c^*b)]^{\tau-t} A_\lambda^t \geq \alpha(\tau) c^* \sum_{t=0}^{\tau} A_\lambda^t, \quad (4.7)$$

where

$$\alpha(\tau) := \begin{cases} [(1 - \lambda)(c^*b)]^\tau, & \text{if } (1 - \lambda)c^*b < 1 \\ 1, & \text{if } (1 - \lambda)c^*b \geq 1. \end{cases}$$

By hypothesis,  $\alpha(\tau) > 0$ , and so, invoking (4.6), (4.7) and Lemma 2.1, we obtain that  $c^*(A + bc^*)^\tau \in \text{int } C^*$ , establishing that (P2) implies (P1).

If (P3) holds, then  $c^*(A + bc^*)^\tau = [(A + bc^*)^*]^\tau c^* \in \text{int } C^*$ , showing that (P1) is satisfied.

(5) It is sufficient to show that (P3) holds. Since  $c^*b > 0$ , it is clear that the matrix  $bc^*$  has positive trace and so the trace of  $A + bc^*$  is also positive. It is well known that irreducible non-negative matrices with positive trace are primitive (see, for example, [34, Example 8.3.3]), and consequently, (P3) is satisfied.  $\square$

In the context of making use of (P3), the following lemma is often helpful.

**Lemma 4.5.** *If (P3) holds, then, for every  $\lambda > 0$ , the operator  $[(A + \lambda bc^*)^*]^\tau$  is strictly positive, that is,  $[(A + \lambda bc^*)^*]^\tau x^* \in \text{int } C^*$  for every non-zero  $x^* \in C^*$ .*

The proof of the lemma is similar to that of statement (1) of Lemma 4.4 and is therefore omitted.

**Remark 4.6.** We provide some comments on the differences between the present work and our earlier paper [17]. The theory developed in [17] is restricted to the situation wherein  $X = \mathbb{R}^n$  and  $C = \mathbb{R}_+^n$ , whilst here we consider any total cone satisfying  $\text{int } C^* \neq \emptyset$  and the state space  $X$  may be infinite-dimensional. Another difference is in our argumentation: a key point in both, reference [17] and the present paper, is the formulation of assumptions ensuring the existence of  $z^* \in \text{int } C^*$  such that

$$z^*(A + pbc^*) = z^*, \quad (4.8)$$

that is, guaranteeing the existence of a (strictly) positive left eigenvector of  $A + pbc^*$  corresponding to the eigenvalue 1. In the case wherein  $X = \mathbb{R}^n$  and  $C = \mathbb{R}_+^n$ , if (P3) holds (or, equivalently, if  $A + pbc^*$  is primitive), then Perron-Frobenius theory [3, 34] guarantees the existence of such a (strictly) positive left eigenvector and this is exploited by the authors of the papers [17, 48] in which (P3) rather than (P1) plays a key role. Similarly, in the infinite-dimensional case, (P3) and a variant of the Krein-Rutman theorem [10, Theorem 19.3] can be used to establish the existence of a  $z^* \in \text{int } C^*$  satisfying (4.8) provided that  $A$  is compact. However, as Lemma 4.4 demonstrates, assumption (P1) is sufficient to explicitly construct, from first principles, a functional  $z^* \in \text{int } C^*$  which satisfies (4.8) without assuming compactness of  $A$ . The upshot is that, under weaker hypotheses than in [17, 48] we obtain stronger conclusions (in the sense that they cover the infinite-dimensional case).  $\diamond$

*Proof of Theorem 4.3.* (1) Define a set-valued nonlinearity  $F$  by

$$F(y) := \{f(w, y) : w \in U\} \quad \forall y \in \mathbb{R}_+.$$

By (N1), there exist  $\theta > 0$  and  $q \in (0, p)$  such that

$$0 < \varphi \leq qy \quad \forall y \geq \theta, \quad \forall \varphi \in F(y).$$

It is clear that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and all  $v \in F(\mathbb{Z}_+, C_\rho)$ , the solution  $x(\cdot; x^0, u, v)$  is also a solution of the difference inclusion

$$x^\nabla - Ax - v \in bF(c^*x),$$

and it follows from Proposition 3.2 that there exists  $\gamma > 0$  such that  $\|x(t; x^0, u, v)\| \leq \gamma$  for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$ , all  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$  and all  $t \in \mathbb{Z}_+$ .

(2) Let  $\Gamma \subset C$  be bounded, closed and such that  $0 \notin \Gamma$ , and let  $\rho > 0$ . We proceed in two steps.

*Step 1:* Existence of  $\delta$ .

By (N2), there exists  $y^\sharp > 0$  such that

$$f(w, y) \geq py \quad \forall w \in U, \quad \forall y \in [0, y^\sharp]. \quad (4.9)$$

Let  $\gamma > 0$  be as in statement (1), and set  $y^\dagger := \max\{y^\sharp, \|c^*\|\gamma\}$  and

$$\lambda := \inf\{f(w, y)/y : w \in U, y^\sharp \leq y \leq y^\dagger\} > 0. \quad (4.10)$$

Let  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$ ,  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$  and write

$$x(t) := x(t; x^0, u, v) \quad \text{and} \quad y(t) := c^*x(t; x^0, u, v) \quad \forall t \in \mathbb{Z}_+.$$

For given  $t \in \mathbb{Z}_+$ , we have either  $y(t) \in [0, y^\sharp]$  or  $y(t) > y^\sharp$ .

CASE 1:  $y(t) \in [0, y^\sharp]$ . By (4.9),  $f(u(t), y(t)) \geq py(t)$ , and so

$$x(t+1) \geq (A + pbc^*)x(t).$$

By assumption (P1) and statement (3) of Lemma 4.4 there exists  $z^* \in \text{int } C^*$  such that  $z^*(A + pbc^*) = z^*$ , and consequently,

$$z^*(x(t+1)) \geq z^*(x(t)). \quad (4.11)$$

CASE 2:  $y(t) > y^\sharp$ . By the definition of  $y^\dagger$ ,  $y(t) \leq y^\dagger$  and so, invoking (4.10),

$$f(u(t), y(t)) \geq \lambda y(t) \geq \lambda y^\sharp.$$

As a consequence,  $x(t+1) \geq Ax(t) + \lambda y^\sharp b$ , and so,

$$z^*(x(t+1)) \geq \lambda y^\sharp z^*(b) > 0. \quad (4.12)$$

Combining (4.11) and (4.12) (the outcomes of the considerations in Cases 1 and 2), we conclude that

$$z^*(x(t+1)) \geq \min\{z^*(x(t)), \lambda y^\sharp z^*(b)\} \quad \forall t \in \mathbb{Z}_+,$$

whence

$$z^*(x(t)) \geq \min\{z^*(x^0), \lambda y^\sharp z^*(b)\} \geq \varepsilon \quad \forall t \in \mathbb{Z}_+,$$

where  $\varepsilon > 0$  is the minimum of  $\inf_{\xi \in \Gamma} z^*(\xi)$  and  $\lambda y^\sharp z^*(b)$  (note that the infimum is positive because  $\Gamma$  is bounded, closed and  $0 \notin \Gamma$ ). It follows that there exists  $\delta > 0$  such that  $\|x(t; x^0, u, v)\| \geq \delta$  for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$ , all  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$  and all  $t \in \mathbb{Z}_+$ .

*Step 2: Existence of  $\eta$ .*

Setting  $\mu := \min\{\lambda, p\} > 0$  and appealing to (4.9) and (4.10), we obtain

$$x(t+1) \geq (A + \mu bc^*)x(t) \quad \forall t \in \mathbb{Z}_+,$$

and hence, with  $\tau$  from (P1),

$$c^*x(t+\tau) \geq c^*(A + \mu bc^*)^\tau x(t) \quad \forall t \in \mathbb{Z}_+.$$

By (P1) and statement (1) of Lemma 4.4,  $c^*(A + \mu bc^*)^\tau \in \text{int } C^*$ . Now,  $\|x(t)\| \geq \delta > 0$  for all  $t \in \mathbb{Z}_+$ , and thus, invoking Lemma 2.1, there exists  $\eta > 0$  such that  $c^*x(t+\tau) \geq \eta$  for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$ ,  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$  and all  $t \in \mathbb{Z}_+$ , completing the proof.  $\square$

## 5 Stability

Having established boundedness and persistence results in Section 4 (under suitable assumptions), we are now interested in conditions which will guarantee the existence of a “stable” non-zero equilibrium: the stability notion used here takes into account the forcing terms  $u$  and  $v$  and is reminiscent of the input-to-state stability concept from nonlinear control theory. As has been mentioned already, to derive useful stability results, we need to somewhat strengthen the assumption (N2) on  $f$ .

In the following, let  $p$  be the constant given by (3.1) and let  $u^e \in U$ , where  $U \subset \mathbb{R}$  is compact. The number  $u^e$  will play the role of a target or nominal value for the control variable  $u$ .

The nonlinearity  $f$  appearing in (1.1) is assumed to satisfy the following conditions.



(N3) Condition (N2) holds,

$$|f(u^e, y) - f(u^e, y^e)| = |f(u^e, y) - py^e| < p|y - y^e| \quad \forall y > 0, y \neq y^e, \quad (5.1)$$

where  $y^e$  is the unique positive number such that  $f(u^e, y^e) = py^e$ , and

$$\limsup_{y \rightarrow y^e} \frac{|f(u^e, y) - f(u^e, y^e)|}{|y - y^e|} = \limsup_{y \rightarrow y^e} \frac{|f(u^e, y) - py^e|}{|y - y^e|} < p. \quad (5.2)$$

The existence of  $y^e > 0$  such that  $f(u^e, y^e) = py^e$  follows from the continuity of  $f$ , (4.1) and (4.2), whilst uniqueness of  $y^e$  is a consequence of (5.1).

Note that (5.1) is a sector condition and means that the graph  $F$  of  $y \mapsto f(u^e, y)$  is “sandwiched” between the lines  $L_+ = \{(y, py) : y \geq 0\}$  and  $L_- = \{(y, -py + 2py^e) : y \geq 0\}$ , see Figure 5.1 for an illustration. Obviously, the only points the graph  $F$  has in common with  $L_+$  and  $L_-$  are  $(0, 0)$  and  $(y^e, py^e)$ . Condition (5.2) implies that the intersections of  $F$  with  $L_+$  and  $L_-$  at the point  $(y^e, py^e)$  is non-tangential, whilst (4.2) ensures that  $F$  is non-tangential to  $L_+$  at  $(0, 0)$ . Finally, it follows from the continuity of  $f$  and (4.1), (4.2), (5.1) and (5.2) that, for every  $\eta > 0$ , there exists  $q \in (0, p)$  such that

$$|f(u^e, y) - f(u^e, y^e)| = |f(u^e, y) - py^e| \leq q|y - y^e| \quad \forall y \geq \eta, y \neq y^e. \quad (5.3)$$

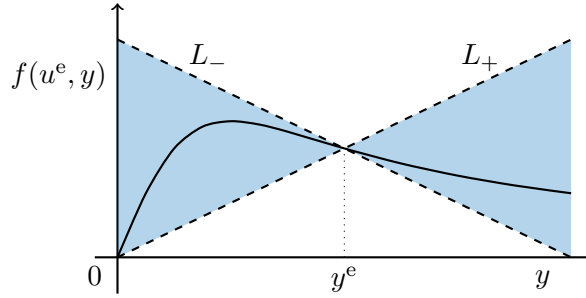


Figure 5.1: Illustration of the sector condition (5.1).

The following lemma shows the existence of a unique non-zero equilibrium of the Lur’e system  $x^\nabla = Ax + bf(u^e, c^*x)$ .

**Lemma 5.1.** *Assume that (L1), (L2) and (N3) hold and set*

$$x^e := (I - A)^{-1}bpy^e. \quad (5.4)$$

*Then  $x^e > 0$ ,  $c^*x^e = y^e$ , and  $x^e$  is the unique non-zero equilibrium of (1.1) with  $u(t) \equiv u^e$  and  $v(t) \equiv 0$ .*

*Furthermore, if (P3) holds, then  $x^*(x^e) > 0$  for all non-zero  $x^* \in C^*$ .*

*Proof.* Since  $x^e = py^e \sum_{k=0}^{\infty} A^k b$ , assumptions (L1) and (L2) imply that  $x^e \geq 0$ . It follows immediately from the definitions of  $x^e$  and  $p$  that  $c^*x^e = y^e$ . Consequently, since  $y^e > 0$ , we conclude that  $x^e \neq 0$ , and so  $x^e > 0$ . To show that  $x^e$  is an equilibrium, note that

$$x^e = (I - A)^{-1}bpy^e = (I - A)^{-1}bf(u^e, y^e) = (I - A)^{-1}bf(u^e, c^*x^e),$$

and so,  $x^e = Ax^e + bf(u^e, c^*x^e)$ . As for uniqueness, let  $x^\dagger$  be another non-zero vector in  $C$  satisfying

$$x^\dagger = Ax^\dagger + bf(u^e, c^*x^\dagger). \quad (5.5)$$

Then  $c^*x^\dagger = \mathbf{G}(1)f(u^e, c^*x^\dagger)$ , and thus,  $f(u^e, c^*x^\dagger) = pc^*x^\dagger$ . Now  $c^*x^\dagger \neq 0$  (otherwise, due to (5.5), 1 would be an eigenvalue of  $A$  which is not possible by (L1)), and so, since  $y^e$  is the unique positive solution of the equation  $f(u^e, y) = py$ , we see that  $c^*x^\dagger = y^e = c^*x^e$ , whence

$$x^\dagger = (I - A)^{-1}bf(u^e, c^*x^\dagger) = (I - A)^{-1}bpy^e = x^e.$$

Let us now additionally assume that (P3) holds. Noting that

$$(A + pbc^*)x^e = x^e + (A - I + pbc^*)x^e = x^e - pby^e + pby^e = x^e,$$

we see that  $(A + pbc^*)^\tau x^e = x^e$ . Consequently, for every  $x^* \in C^*$ ,  $x^* \neq 0$ ,

$$x^*(x^e) = x^*((A + pbc^*)^\tau x^e) = ((A + pbc^*)^*]^\tau x^*)(x^e) > 0.$$

The inequality holds because  $x^e > 0$  and  $[(A + pbc^*)^*]^\tau x^* \in \text{int } C^*$  (as follows from (P3) and Lemma 4.5).  $\square$

We are now in the position to state and prove a stability theorem relating to the non-zero equilibrium of system (1.1).

**Theorem 5.2.** *Let  $U \subset \mathbb{R}$  be compact and  $u^e \in U$ . Assume that (1.1) is ultimately semi-globally  $c^*$ -persistent and (L1), (L2) and (N3) hold. Furthermore, let  $x^e > 0$  be given by (5.4).*

(1) *Let  $\Gamma \subset C$  be bounded, closed and such that  $0 \notin \Gamma$ , and let  $\rho > 0$ . Then there exist  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $N > 0$  such that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ ,*

$$\|x(t; x^0, u, v) - x^e\| \leq M\mu^t \|x^0 - x^e\| + N(\beta(u, t) + \|v\|_{\ell^\infty(0, t)}) \quad \forall t \in \mathbb{Z}_+, \quad (5.6)$$

with

$$\beta(u, t) := \max\{|f(u^e, y) - f(u(s), y)| : s = 0, 1, \dots, t, \ 0 \leq y \leq \gamma\|c^*\|\},$$

where  $\gamma$  is the constant from statement (1) of Theorem 4.3.

(2) *For every  $x^0 \in C$ ,  $x^0 \neq 0$ , every  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and every  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  such that  $u(t) \rightarrow u^e$  and  $v(t) \rightarrow 0$  as  $t \rightarrow \infty$ , we have that  $x(t; x^0, u, v) \rightarrow x^e$  as  $t \rightarrow \infty$ .*

Note that if  $(u_k)_{k \in \mathbb{N}}$  is a sequence in  $\mathcal{F}(\mathbb{Z}_+, U)$  such that  $u_k$  converges to (the constant function)  $u^e$  in the sup-norm as  $k \rightarrow \infty$ , then  $\lim_{k \rightarrow \infty} [\sup_{t \in \mathbb{Z}_+} \beta(u_k, t)] = 0$ .

Before we prove Theorem 5.2, we state the following corollary which is an immediate consequence of Theorem 4.3, statement (4) of Lemma 4.4 and Theorem 5.2.

**Corollary 5.3.** *Assume that (L1), (L2), (N3) and at least one of the conditions (P1)–(P3) is satisfied. Then statements (1) and (2) of Theorem 5.2 hold.*

In the following example, we discuss the stability properties of a simple model for which (P1) holds, but (P3) does not.

**Example 5.4.** Consider the Lur'e system (1.1) with

$$A = \begin{pmatrix} 1/2 & 1/2 & a \\ 1/2 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad b = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}, \quad c^* = (0 \ 1 \ 1), \quad \text{where } a \geq 0,$$

and with the nonlinearity  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ ,  $(w, y) \mapsto 6y/(5 + wy)$ , where  $U \subset \mathbb{R}_+$  is compact and such that  $0 \notin U$  and  $1 \in U$ . The eigenvalues of  $A$  are independent of  $a$  and are given by 0 and  $(1 \pm \sqrt{5})/4$ . Consequently,  $A$  is exponentially stable for all  $a \geq 0$ . In particular, (L1) and (L2) hold for all  $a \geq 0$ . Condition (P3) is satisfied if  $a > 0$ . For  $a = 0$ , (P3) is not satisfied, but (P1) holds. Moreover, we have that  $\mathbf{G}(1) = 1 + 2a$ , showing that, with  $u^e = 1$  and  $y^e = 1 + 12a$ , condition (N3) holds for every  $a \geq 0$ . Hence, the conclusions of Corollary 5.3 apply with

$$x^e = \frac{1 + 12a}{1 + 2a} \begin{pmatrix} 4a \\ 2a \\ 1 \end{pmatrix}.$$

We now discuss the case wherein  $a = 0$ . This case is somewhat degenerate, because for  $a = 0$ , the components  $x_1$  and  $x_2$  are decoupled from  $x_3$  (note the  $A + bc^*$  is reducible) and the dynamics of the  $(x_1, x_2)$ -subsystem are linear and exponentially stable (for  $v = 0$ ). It is therefore clear (without using Corollary 5.3) that the first two components of  $x^e$  are equal to 0 and the third component  $x_3^e$  of  $x^e$  must be the unique positive fixed point of  $f$ , namely  $x_3^e = 1$ . It is interesting that Corollary 5.3 applies to this degenerate situation which is not covered by the results in [17, 48].  $\diamond$

We briefly comment on the papers [36, 42] which consider the uncontrolled version of system (1.1). We note that Theorem 5.2 and Corollary 5.3 are considerable more general than the theory developed in [36] and, in particular, contain [36, Theorem 3.3] as a special case. A comparison of Theorem 5.2 and Corollary 5.3 with results in [42] (see [42, part (b) of Theorem 5.8, part (c) of Theorem 7.1]) is more difficult: whilst there is some overlap, the assumptions imposed and the methods used are quite different and certainly neither set of results contains the other, see also Example 6.2 in this context.

*Proof of Theorem 5.2.* (1) By statement (1) of Theorem 4.3, there exists  $\gamma > 0$  such that, for all  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ ,

$$\|x(t; x^0, u, v)\| \leq \gamma \quad \forall t \in \mathbb{Z}_+.$$

Now let  $x^0 \in \Gamma$ ,  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$  be fixed, but arbitrary, set  $h(y) := f(u^e, y)$ , and write  $x(t) := x(t; x^0, u, v)$ . Then

$$x^\nabla = Ax + b(h(c^*x) + d) + v, \quad \text{where } d := f(u, c^*x) - f(u^e, c^*x).$$

Since  $c^*x^e = y^e$  and  $x^e = Ax^e + bh(y^e)$ , it follows that the function  $\tilde{x}(t) := x(t) - x^e$  satisfies

$$\tilde{x}(t + 1) = A\tilde{x}(t) + b[h(c^*\tilde{x}(t) + y^e) - h(y^e)] + bd(t) + v(t), \quad \forall t \in \mathbb{Z}_+. \quad (5.7)$$

By the hypothesis of ultimate semi-global  $c^*$ -persistence, there exist  $\tau \in \mathbb{Z}_+$  and  $\eta \in (0, y^e)$  such that

$$c^*\tilde{x}(t + \tau) \geq -y^e + \eta \quad \forall t \in \mathbb{Z}_+. \quad (5.8)$$

Defining

$$\tilde{h} : \mathbb{R} \rightarrow \mathbb{R}, \quad y \mapsto \begin{cases} h(y + y^e) - h(y^e), & \text{for } y \geq -y^e + \eta \\ h(\eta) - h(y^e), & \text{for } y < -y^e + \eta, \end{cases}$$

it follows from (5.7) and (5.8) that

$$\tilde{x}(t + 1) = A\tilde{x}(t) + b[\tilde{h}(c^*\tilde{x}(t)) + d(t)] + v(t), \quad \forall t \in \tau + \mathbb{Z}_+. \quad (5.9)$$

By assumption (N3), there exists  $q \in (0, p)$  such that (5.3) holds and consequently,

$$|\tilde{h}(y)| \leq q|y| \quad \forall y \in \mathbb{R}. \quad (5.10)$$

Invoking (L1) and (L2), it follows from Proposition 3.1 that  $\mathbf{G}(1) = \|\mathbf{G}\|_{H^\infty}$ , implying that  $p = 1/\|\mathbf{G}\|_{H^\infty}$ . Combining this with (5.10) and appealing to Theorem 2.3, we conclude that system (5.9) is exponentially ISS (with respect to the forcing  $bd+v$ ). Hence, there exist  $M_0 \geq 1$ ,  $\mu \in (0, 1)$  and  $N_0 > 0$  (depending only on  $A, b, c^*, \rho, U, f$  and  $\Gamma$ ) such that

$$\|\tilde{x}(t + \tau)\| \leq M_0 \mu^t \|\tilde{x}(\tau)\| + N_0 (\|d\|_{\ell^\infty(0,t)} + \|v\|_{\ell^\infty(0,t)}) \quad \forall t \in \mathbb{Z}_+. \quad (5.11)$$

Furthermore, since the function  $y \mapsto h(y+y^e) - h(y^e)$  is linearly bounded on  $[-y^e, \infty)$ , we obtain from (5.7) that

$$\|\tilde{x}(t)\| \leq M_1 \|\tilde{x}(0)\| + N_1 (\|d\|_{\ell^\infty(0,t)} + \|v\|_{\ell^\infty(0,t)}) \quad t = 1, 2, \dots, \tau, \quad (5.12)$$

where the positive constants  $M_1$  and  $N_1$  depend only on  $A, b, c^*$  and  $f$ . Setting  $M := \max(M_0, M_1 \mu^{-\tau})$  and  $N := \max(N_0, N_1)$  and appealing to (5.11) and (5.12), we arrive at

$$\|\tilde{x}(t)\| \leq M \mu^t \|\tilde{x}(0)\| + N (\|d\|_{\ell^\infty(0,t)} + \|v\|_{\ell^\infty(0,t)}) \quad \forall t \in \mathbb{Z}_+.$$

Combining this with

$$\|d\|_{\ell^\infty(0,t)} \leq \max \{ |f(u^e, y) - f(u(s), y)| : s = 0, 1, \dots, t, 0 \leq y \leq \gamma \|c^*\| \} = \beta(u, t),$$

shows that (5.6) holds, completing the proof of statement (1).

(2) Let  $x^0 \in C$  with  $x^0 \neq 0$ , let  $u \in \mathcal{F}(\mathbb{Z}_+, U)$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  be such that  $\lim_{t \rightarrow \infty} u(t) = u^e$  and  $\lim_{t \rightarrow \infty} v(t) = 0$ . Obviously, there exists  $\rho > 0$  such that  $v \in \mathcal{F}(\mathbb{Z}_+, C_\rho)$ , and, by Theorem 4.3, there exists a bounded closed set  $K \subset C$  such that  $0 \notin K$  and  $x(t; x^0, u, v) \in K$  for  $t \in \mathbb{Z}_+$ . By statement (1) (with  $K$  now playing the role of  $\Gamma$ ), there exist  $M \geq 1$ ,  $\mu \in (0, 1)$  and  $N > 0$  such that, for all  $s, t \in \mathbb{Z}_+$ ,

$$\|x(t; x(s; x^0, u, v), u_s, v_s) - x^e\| \leq M \mu^t \|x(s; x^0, u, v) - x^e\| + N (\beta(u_s, t) + \|v_s\|_{\ell^\infty}),$$

where  $u_s(t) = u(t+s)$  and  $v_s(t) = v(t+s)$  for all  $t \in \mathbb{Z}_+$ .

Now  $x(t+s; x^0, u, v) = x(t; x(s; x^0, u, v), u_s, v_s)$  and so, for all  $s, t \in \mathbb{Z}_+$ ,

$$\|x(t+s; x^0, u, v) - x^e\| \leq M \mu^t \|x(s; x^0, u, v) - x^e\| + N (\beta(u_s, t) + \|v_s\|_{\ell^\infty}).$$

Given  $\varepsilon > 0$ , there exists  $\sigma \in \mathbb{Z}_+$  such that  $N (\beta(u_\sigma, t) + \|v_\sigma\|_{\ell^\infty}) \leq \varepsilon/2$  for all  $t \in \mathbb{Z}_+$  (where we have used that  $\sup_{t \in \mathbb{Z}_+} \beta(u_s, t) + \|v_s\|_{\ell^\infty} \rightarrow 0$  as  $s \rightarrow \infty$ ). Moreover, choose  $\theta \in \mathbb{Z}_+$  such that  $M \mu^t \|x(\sigma; x^0, u, v) - x^e\| \leq \varepsilon/2$  for all  $t \geq \theta$ . Consequently,

$$\|x(t; x^0, u, v) - x^e\| \leq \varepsilon \quad \forall t \in (\sigma + \theta) + \mathbb{Z}_+,$$

completing the proof.  $\square$

In the special case that  $f$  is given by  $f(w, y) = g(wy)y$ , statement (2) of Theorem 5.2 can be strengthened.

**Corollary 5.5.** *Let  $g : (0, \infty) \rightarrow (0, \infty)$  be continuous and such that the limit  $\lim_{y \rightarrow 0} g(y)y$  exists,*

$$\liminf_{y \rightarrow 0} g(y) > p \quad \text{and} \quad \limsup_{y \rightarrow \infty} g(y) < p. \quad (5.13)$$

Let  $u^e > 0$  and assume that

$$|g(u^e y)y - g(u^e y^e)y^e| = |g(u^e y)y - p y^e| < p|y - y^e| \quad \forall y > 0, y \neq y^e, \quad (5.14)$$

where  $y^e$  is the unique positive number such that  $g(u^e y^e) = p$ , and

$$\limsup_{y \rightarrow y^e} \frac{|g(u^e y)y - g(u^e y^e)y^e|}{|y - y^e|} = \limsup_{y \rightarrow y^e} \frac{|g(u^e y)y - p y^e|}{|y - y^e|} < p. \quad (5.15)$$

Furthermore, assume that the Lur'e system

$$x^\nabla = Ax + bg(uc^*x)c^*x + v, \quad x(0) = x^0 \in C, \quad (5.16)$$

is ultimately semi-globally  $c^*$ -persistent, (L1) and (L2) hold, and let  $x^e > 0$  be given by (5.4). Then, for every  $x^0 \in C$ ,  $x^0 \neq 0$ , every  $u^\infty > 0$ , every  $u \in \mathcal{F}(\mathbb{Z}_+, (0, \infty))$  and every  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  such that  $u(t) \rightarrow u^\infty$  and  $v(t) \rightarrow 0$  as  $t \rightarrow \infty$ , the solution  $x(t; x^0, u, v)$  of (5.16) converges to the limit  $(u^e/u^\infty)x^e$  as  $t \rightarrow \infty$ .

*Proof.* Let  $x^0 \in C$ ,  $x^0 \neq 0$  and  $u^\infty > 0$ . Consider fixed, but arbitrary elements  $u \in \mathcal{F}(\mathbb{Z}_+, (0, \infty))$  and  $v \in \mathcal{F}(\mathbb{Z}_+, C)$  such that  $u(t) \rightarrow u^\infty$  and  $v(t) \rightarrow 0$  as  $t \rightarrow \infty$ . The strategy is to apply statement (2) of Theorem 5.2. To this end, let  $U$  be any compact set in  $\mathbb{R}_+$  with  $0 \notin U$ ,  $u^e \in U$  and  $(u^e/u^\infty)u(t) \in U$  for all  $t \in \mathbb{Z}_+$ . Setting  $f_0 := \lim_{y \rightarrow 0} g(y)y$  and

$$f(w, y) = \begin{cases} g(wy)y, & \text{for } w \in U \text{ and } y > 0 \\ f_0/w, & \text{for } w \in U \text{ and } y = 0, \end{cases}$$

it follows from (5.13) and Proposition 4.2 that  $f$  satisfies (N2). The conditions (5.14) and (5.15) imply that (5.1) and (5.2) hold for  $f$ . Consequently,  $f$  satisfies (N3). It follows that the hypotheses of Theorem 5.2 hold. Defining, for all  $t \in \mathbb{Z}_+$ ,

$$\tilde{x}(t) := \frac{u^\infty}{u^e} x(t; x^0, u, v), \quad \tilde{u}(t) := \frac{u^e}{u^\infty} u(t), \quad \tilde{v}(t) := \frac{u^\infty}{u^e} v(t),$$

we have that  $\tilde{x}^\nabla = A\tilde{x} + b f(\tilde{u}, c^*\tilde{x}) + \tilde{v}$ . Finally,  $\tilde{u}(t) \rightarrow u^e$  and  $\tilde{v}(t) \rightarrow 0$  as  $t \rightarrow \infty$ , and hence, an application of statement (2) of Theorem 5.2 shows that  $\tilde{x}(t) \rightarrow x^e$  as  $t \rightarrow \infty$  and so,  $x(t; x^0, u, v) \rightarrow (u^e/u^\infty)x^e$  as  $t \rightarrow \infty$ .  $\square$

## 6 Examples from population dynamics

In this section, we use the theory developed in the previous sections in the context of specific examples from population dynamics. We start with two finite-dimensional examples and then proceed to exploit the full power of our results by applying the abstract theory to a class of nonlinear integral projection models.

## 6.1 Finite-dimensional examples

In the first example, we analyse a system which provides a simple model for the dynamics of a population with a refuge.

**Example 6.1.** Consider the following model

$$\left. \begin{aligned} x_1(t+1) &= (1-\varepsilon)g(u(t)x_1(t)) + \varepsilon'(1-\mu)x_2(t) + v_1(t), & x_1(0) &= x_1^0, \\ x_2(t+1) &= (1-\varepsilon')(1-\mu)x_2(t) + \varepsilon g(u(t)x_1(t)) + v_2(t), & x_2(0) &= x_2^0, \end{aligned} \right\} \quad \forall t \in \mathbb{Z}_+, \quad (6.1)$$

where  $x_1(t)$  and  $x_2(t)$  are the density of an active population and its refuge at time-step  $t \in \mathbb{Z}_+$ , respectively; the parameters  $\varepsilon, \varepsilon' \in (0, 1)$  are the respective dispersal rates between the active and refuge populations; the parameter  $\mu \in (0, 1)$  measures the attrition in the refuge; the nonlinearity  $g$  describes density-dependent reproduction of the active population; the forcing  $u(t) \in U := [u^-, u^+] \subseteq (0, \infty)$  models the effect of demographic fluctuations affecting recruitment; and the terms  $v_1(t), v_2(t) \in \mathbb{R}_+$  correspond to immigration. The model (6.1) was proposed in [35], without demographic fluctuations and immigration, as the simplest possible model of an active population coupled to a refuge.

A simplified version of model (6.1) assuming symmetrical dispersal, without immigration, neglecting attrition in the refuge and neglecting demographic fluctuations, that is, with  $\varepsilon = \varepsilon'$ ,  $\mu = 0$ ,  $u = 1$ , and  $v = 0$ , has been considered in [7, 35]. In [35], the simplified model was studied numerically for two nonlinearities known to be able to produce complex dynamics, namely  $g(y) = \lambda y e^{-y}$  and  $g(y) = \lambda y(1 - y)$ . The authors of [7] studied the simplified model analytically with the choice of function  $g(y) = \lambda y/(1 + ky)$ , which is a Beverton-Holt type nonlinearity. They prove persistence and global stability results using specific properties of the Beverton-Holt function, namely that it is strictly increasing and concave. Such an approach would not apply to the unimodal functions originally considered in [35].

We note that (6.1) is a special case of the Lur'e system (1.1) with  $X = \mathbb{R}^2$ ,  $C = \mathbb{R}_+^2$ ,

$$A = \begin{pmatrix} 0 & \varepsilon'(1-\mu) \\ 0 & (1-\varepsilon')(1-\mu) \end{pmatrix}, \quad b = \begin{pmatrix} 1-\varepsilon \\ \varepsilon \end{pmatrix} \quad \text{and} \quad c^* = (1 \ 0),$$

so that assumptions (L1) and (L2) are satisfied. The matrix  $A + bc^*$  is strictly positive (meaning every entry is positive) and consequently (P3) holds, whence (P1) does as well by Lemma 4.4. It is straightforward to compute that

$$\mathbf{G}(1) = \frac{\mu(1-\varepsilon) + \varepsilon'(1-\mu)}{\mu + \varepsilon'(1-\mu)} = \frac{1}{p}.$$

Moreover, fixing  $u^e = 1$  and letting  $g(y) = \lambda y/(1 + ky)$ , condition (N3) holds for the function  $f$  given by  $f(w, y) = g(wy)$  if  $\lambda u^- > 1/\mathbf{G}(1) = p$ . Indeed, [17, Table 5.1] shows that (5.1) is satisfied and a straightforward calculation yields

$$0 < \frac{\partial f}{\partial y}(1, y^e) = \frac{f(1, y^e)}{y^e(1 + ky^e)} = \frac{p}{1 + ky^e} < p, \quad \text{where } y^e = \frac{\lambda - p}{kp},$$

implying that (5.2) holds.

Thus, we can use Corollary 5.3 to obtain a stability result for (6.1). Particularly, if  $\mu = 0$ , we have  $\mathbf{G}(1) = 1$ , thus  $\lambda > 1$  guarantees the existence of a unique positive equilibrium of (6.1) with  $u = 1$  and  $v = 0$  which is stable and attracts every solution with a nonnegative and nonzero

initial condition. Indeed, for each compact subset  $\Gamma \subseteq \mathbb{R}_+^2$  which does not contain zero, the rate of convergence of  $x(t)$  to  $x^e$  is exponential for all  $x^0 \in \Gamma$ , with constants depending on  $\Gamma$  and the model data, but not  $x^0$ . These conclusions extend [7, Theorem 3.1], where symmetrical dispersal was considered in the Beverton-Holt case.

Next, we consider (6.1) with the Ricker-type function  $g(y) = \lambda y e^{-y}$  and assume that

$$\lambda u^+ e^{-2} < p < \lambda u^-. \quad (6.2)$$

Set  $f(w, y) := g(wy)$  and let  $u^e \in [u^-, u^+]$ . The unique positive solution  $y^e$  of  $f(u^e, y) = g(u^e y) = py$  is given by

$$y^e = \frac{\ln(\lambda u^e / p)}{u^e} > 0,$$

and it is not difficult to see that (5.1) is satisfied (cf. [17, Table 5.1]). Furthermore, a routine calculation gives

$$\frac{\partial f}{\partial y}(u^e, y^e) = p(1 - u^e y^e) = p(1 - \ln(\lambda u^e / p)),$$

and it follows from (6.2) that  $|(\partial f / \partial y)(u^e, y^e)| < p$ . Consequently, (5.2) holds and so we have established that, under the assumption (6.2), condition (N3) is satisfied. Thus, we can use Corollary 5.3 to obtain a stability result. By Lemma 5.1, the unique positive equilibrium of (6.1) (for  $u = u^e$  and  $v = 0$ ) is given by

$$x^e := (I - A)^{-1} b p y^e = \frac{\ln(\lambda u^e / p)}{u^e} \begin{pmatrix} 1 \\ \varepsilon(\mu(1 - \varepsilon) + \varepsilon'(1 - \mu))^{-1} \end{pmatrix}. \quad (6.3)$$

For the choice of parameters

$$\lambda = 6, \quad \varepsilon = 0.2, \quad \varepsilon' = 0.3, \quad \mu = 0, \quad u^- = 0.9, \quad u^e = 1, \quad u^+ = 1.1, \quad (6.4)$$

the condition (6.2) holds and so Corollary 5.3 is applicable. Figure 6.1 contains plots of  $\|x(t)\|_1$  and  $\|x(t) - x^e\|_1$  against  $t$  for randomly determined  $u(t) \in [u^-, u^+]$  and  $v_1(t), v_2(t) \in [0, 0.2]$ , and for the two initial conditions

$$x^0 = \begin{pmatrix} 1 \\ 0 \end{pmatrix} \quad \text{and} \quad x^0 = \begin{pmatrix} 0 \\ 2 \end{pmatrix}. \quad (6.5)$$

In particular, Figure 6.1 shows that the impact of the initial vector  $x^0$  on the evolution of  $x(t)$  is dying for large  $t$  as was to be expected by Corollary 5.3. Figure 6.2 contains plots of  $\|x(t)\|_1$  and  $\|x(t) - x^e\|_1$  against  $t$  for

$$u(t) = u^e + (-0.8)^t = 1 + (-0.8)^t \quad \text{and} \quad v(t) = (0.7)^t \begin{pmatrix} 0.2 \\ 0.2 \end{pmatrix} \quad \forall t \in \mathbb{Z}_+, \quad (6.6)$$

and for the two initial conditions in (6.5). Clearly,  $u(t) \rightarrow 1$  and  $v(t) \rightarrow 0$  as  $t \rightarrow \infty$ , and the figures show that  $x(t) \rightarrow x^e$  as  $t \rightarrow \infty$ , illustrating the conclusions of Corollary 5.3.  $\diamond$

**Example 6.2.** We consider a population structured in three groups, namely, juveniles, members of the population who are in a dormant state, which we shall refer to as ‘‘dormants’’, and adults. These stage-classes are denoted by  $x_1$ ,  $x_2$  and  $x_3$ , respectively. We assume that after one time-step the population of juveniles splits between dormants and adults at a fixed rate  $\alpha$ .

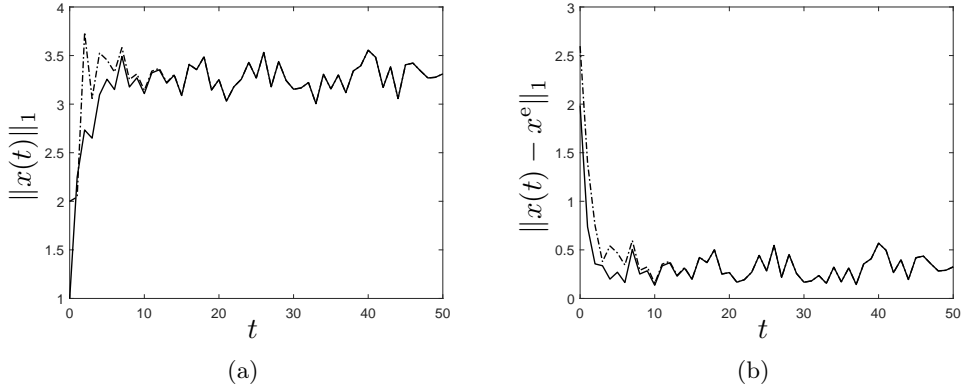


Figure 6.1: Graphs of state  $\|x(t)\|_1$  (a) and state error  $\|x(t) - x^e\|_1$  (b) against  $t$  for the active and refuge population model (6.1) from Example 6.1. The parameter values and initial conditions are as in (6.4) and (6.5), respectively, and  $g(y) = \lambda y e^{-y}$ . The solid and dashed lines correspond to the first and second initial condition in (6.5), respectively.

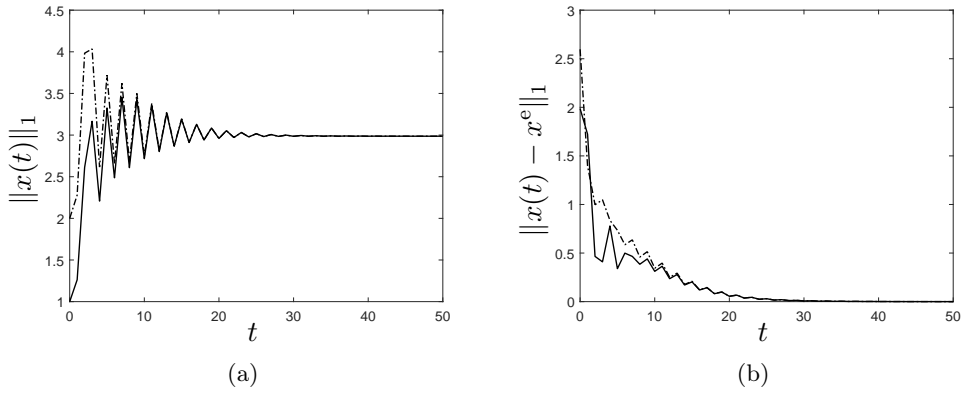


Figure 6.2: Graphs of state  $\|x(t)\|_1$  (a) and state error  $\|x(t) - x^e\|_1$  (b) against  $t$  for the active and refuge population model (6.1) from Example 6.1. The parameter values are as in (6.4) and  $g(y) = \lambda y e^{-y}$ . Here  $u$  and  $v$  are as in (6.6), and the solid and dashed lines correspond to the first and second initial condition in (6.5), respectively.

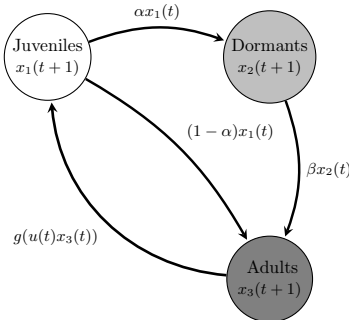


Figure 6.3: Schematic illustration of the population model (6.7).

Dormants remain inactive for one time-step and then they become adults with a fixed rate  $\beta$  or die. Juveniles are produced by adults following a density-dependent reproduction given by a nonlinear function  $g$ .



A schematic representation of the dynamics of the population appears in Figure 6.3. The following system models such a population,

$$\left. \begin{aligned} x_1(t+1) &= g(u(t)x_3(t)) & x_1(0) &= x_1^0, \\ x_2(t+1) &= \alpha x_1(t) & x_2(0) &= x_2^0, \\ x_3(t+1) &= (1-\alpha)x_1(t) + \beta x_2(t) & x_3(0) &= x_3^0, \end{aligned} \right\} \forall t \in \mathbb{Z}_+, \quad (6.7)$$

where  $\alpha, \beta \in (0, 1)$  and, as before, the forcing  $u(t) \in U := [u^-, u^+] \subset (0, \infty)$  models the effect of demographic fluctuations affecting recruitment. The inclusion of dormancy in a population model is natural for several reasons. First, a large number of plants from a wide range of habitats are known to have persistent seed banks, that is, seeds can remain dormant for more than a generation [47]. Second, dormancy is known to affect the stability of the population [32]. Finally, a large fraction of the total population may be present as dormant individuals and therefore ignoring it could give a poor estimate of the size of the population [1].

System (6.7) can be rewritten as the Lur'e system (1.1) with

$$A = \begin{pmatrix} 0 & 0 & 0 \\ \alpha & 0 & 0 \\ 1-\alpha & \beta & 0 \end{pmatrix}, \quad b = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}, \quad c^* = (0 \ 0 \ 1) \quad \text{and} \quad f(w, y) = g(wy).$$

Clearly, conditions (L1) and (L2) hold. Moreover, condition (P1) holds with  $\tau = 3$ . Hence, one can use Theorem 4.3 and Corollary 5.3 to study boundedness, persistence and stability properties of model (6.7). Note that  $c^*b = 0$  and for any

$$z = \begin{pmatrix} 0 \\ 0 \\ z_0^3 \end{pmatrix},$$

with  $z_0^3 \geq 0$  we have  $c^*Az = 0$ . Therefore, the assumptions on  $A$ ,  $b$  and  $c^*$  required in [42, Theorems 4.4, 5.8 (b)] do not hold, and hence, even in the absence of forcing, these results are not applicable to (6.7).  $\diamond$

## 6.2 Infinite-dimensional examples

We conclude the paper with two infinite-dimensional examples to which we apply the theory developed in Sections 4 and 5. The first example considers the class of IPM models and the second provides a numerical illustration of the abstract theory in the context of an IPM coupled to a two-dimensional difference equation.

**Example 6.3.** An exemplar for the infinite-dimensional theory developed in this paper is a class of integro-difference equations, the so-called integral projection models. IPMs were introduced as a tool for ecological modelling in [14], see also [6, 15], and the reader is referred to [33] for a recent review. They are relevant when the population stages are naturally described by a continuous variable, such as size or weight, as opposed to discrete stage-classes, such as insect instars. The purpose of the present example is to interpret the assumptions (L1), (L2), (P1) and (N1)–(N3) in the context of IPMs.

A forced linear IPM typically takes the form

$$\left. \begin{aligned} n(t+1, \xi) &= \int_{\Omega} k(\xi, \zeta)n(t, \zeta) d\zeta + m(t, \xi) & \forall t \in \mathbb{Z}_+, \\ n(0, \xi) &= n^0(\xi), \end{aligned} \right\} \text{almost all } \xi \in \Omega, \quad (6.8)$$

where  $\Omega$  is a measurable subset of  $\mathbb{R}^q$  and  $n(t, \cdot)$  denotes the population distribution at time-step  $t$ , with initial distribution  $n^0$ . Further,  $m$  denotes an additive forcing term which models, say, the effects of migration, breeding or planting schemes. The kernel  $k$  captures survival, growth and recruitment of the population. We refer the reader to [33] for more information on how kernels are constructed and parametrised in practice. In particular, following [36], the kernel  $k$  is often assumed to be of the form  $k = p + r$ , where  $p$  and  $r$  denote a survival and recruitment term, respectively. Specifically,  $p(\xi, \zeta)$  denotes the probability that an individual at stage  $\zeta$  survives or grows to an individual at stage  $\xi$  in one time-step, and so is evidently nonnegative-valued. In applications  $p$  is typically continuous and  $\Omega$  is compact. We shall assume that  $p \in L^\infty(\Omega \times \Omega, \mathbb{R}_+)$ . In the presence of mortality in the population, it typically follows that the assumption

$$\operatorname{ess\,sup}_{\zeta \in \Omega} \int_{\Omega} p(\xi, \zeta) d\xi < 1, \quad (6.9)$$

is satisfied.

To write (6.8) as an infinite-dimensional difference equation, the natural choices for the state space  $X$  and the cone  $C$  are  $X := L^1(\Omega, \mathbb{R})$  and  $C := L^1(\Omega, \mathbb{R}_+)$ . Defining the integral operator  $A : X \rightarrow X$  by

$$(Az)(\cdot) := \int_{\Omega} p(\cdot, \zeta) z(\zeta) d\zeta \quad \forall z \in X, \quad (6.10)$$

it follows from (6.9) that  $A \in \mathcal{L}(X)$  and  $\|A\| < 1$  [29, Theorem 1, Chapter 16], and so  $A$  is exponentially stable. It is clear that  $A$  leaves  $C$  invariant, that is,  $A$  is positive. We have now established that  $A$  satisfies (L1). Assuming that the recruitment term  $r$  can be expressed as

$$r(\xi, \zeta) = b(\xi)\nu c(\zeta), \quad \text{almost all } (\xi, \zeta) \in \Omega \times \Omega,$$

where  $b \in C$  denotes the distribution of new individuals,  $\nu > 0$  is an offspring survival probability over one time-step, and  $c(\zeta)$  denotes the per-capita fecundity of an individual at stage  $\zeta$ , the distribution of offspring in one-step from distribution  $z \in X$  is given by

$$\int_{\Omega} r(\cdot, \zeta) z(\zeta) d\zeta = b(\cdot)\nu \int_{\Omega} c(\zeta) z(\zeta) d\zeta = b(\cdot)\nu c^* z. \quad (6.11)$$

Note that

$$c^* z := \int_{\Omega} c(\zeta) z(\zeta) d\zeta \quad (6.12)$$

is the total number of offspring produced in a single time-step by the distribution  $z \in X$ . Imposing the natural assumption that  $c \in L^\infty(\Omega, \mathbb{R}_+)$ , it follows that  $c^* \in C^*$ . Setting  $x(t) := n(t, \cdot)$ , in light of (6.10)–(6.12), it follows that (6.8) may be expressed as

$$x^\nabla = (A + b\nu c^*)x + v, \quad x(0) = n^0, \quad (6.13)$$

where  $v(t) = m(t, \cdot)$  and we assume that  $m(t, \cdot) \in C$  for every  $t \in \mathbb{Z}_+$ . Since  $b \in C$  and  $c^* \in C^*$ , we have that (L2) is satisfied (provided that  $b \neq 0$  and  $c^* \neq 0$ ).

A nonlinear term arises in (6.13) if the survival probability  $\nu$  depends on the total number of offspring produced in a single time-step, see (6.12). In this case, the linear operator induced by the kernel  $r$  is replaced by the nonlinear operator

$$z \mapsto bg \left( \int_{\Omega} c(\theta) z(\theta) d\theta \right) \int_{\Omega} c(\zeta) z(\zeta) d\zeta = bg(c^* z) c^* z,$$

where  $b$ ,  $c$  and  $c^*$  are as before and  $g$  denotes the probability of survival of new individuals over one time-step. The function  $g$  models density-dependence in recruitment, reflecting competition effects at higher abundance, for instance. Consequently, we obtain

$$x^\nabla = Ax + bg(c^*x)c^*x + v = Ax + bf(c^*x) + v, \quad x(0) = n^0, \quad (6.14)$$

where  $f(y) = g(y)y$  and  $v$  is as before. Evidently, both (6.13) and (6.14) are special cases of (1.1).

The nonlinear assumptions (N1), (N2) and (N3) depend on the interplay between  $f$  in (6.14) and the constant  $p = 1/\mathbf{G}(1)$ . We proceed to discuss the key additional assumption (P1) required for the persistence and stability results in Sections 4 and 5. By part (2) of Example 2.2, (P1) holds with  $\tau = 0$  if, and only if  $\text{ess inf}_{\theta \in \Omega} c(\theta) > 0$ . To discuss the case wherein the integer  $\tau$  is positive, let  $k$  denote the kernel of  $A + bc^*$ , that is,

$$k(\xi, \zeta) = p(\xi, \zeta) + b(\xi)c(\zeta),$$

and, for  $n \in \mathbb{N}$ , define  $k_n$  recursively via  $k_1 := k$  and

$$k_{n+1}(\xi, \zeta) = \int_{\Omega} k(\xi, s)k_n(s, \zeta) ds \quad \forall n \in \mathbb{N}.$$

It is clear that (P1) holds for a non-zero integer  $\tau$  if, and only if,

$$\text{ess inf}_{\zeta \in \Omega} \int_{\Omega} c(s)k_\tau(s, \zeta) ds > 0. \quad (6.15)$$

If  $c$  and  $k$  are continuous, then (6.15) holds if  $\text{supp } c \cap \text{supp } k_\tau(\cdot, \zeta) \neq \emptyset$  for all  $\zeta \in \Omega$  or, equivalently, for every  $\zeta \in \Omega$ , there exists  $s \in \Omega$  such that  $c(s)k_\tau(s, \zeta) > 0$ .

To the best of our knowledge, paper [36] was the first to consider certain nonlinear unforced IPMs, and model them in the abstract infinite-dimensional state-space form (1.1) (with  $f(u, y) = f(y)$  and  $v = 0$ ). Unfortunately, the IPM result [36, Corollary 4.1] is not correct, see Appendix A.  $\diamond$

**Example 6.4.** We consider a model for the Clonal Perennial Herb (*Veratrum album*) from [20]. The model contains an IPM coupled to two-dimensional difference equations, namely

$$\left. \begin{aligned} n(t+1, \xi) &= D(t)p_{\text{sc}}f_{\text{sd}}(\xi) + \int_{m_1}^{m_2} k(\xi, \zeta)n(t, \zeta) d\zeta \\ D(t+1) &= p_{\text{est}}(g_0h^*n(t, \cdot) + g_1S_1(t)) \\ S_1(t+1) &= (1 - g_0)s_0h^*n(t, \cdot) \end{aligned} \right\} \quad \forall t \in \mathbb{Z}_+, \forall \xi \in [m_1, m_2]. \quad (6.16)$$

The variable  $n(t, \xi)$  is the number of plants with (natural logarithm of) shoot diameter equal to  $\xi$  (in mm) at discrete time  $t$ . Following [20], we assume that the variable  $\xi$  takes minimum and maximum values given by  $m_1 = 0$  and  $m_2 = 3.5$  (and so  $e^{m_1} = 1\text{mm}$  and  $e^{m_2} = 33\text{mm}$ ), respectively, and that the time-steps correspond to years. We set  $\Omega := [m_1, m_2]$  and, consequently,  $n(t, \cdot) \in X_0 := L^1(\Omega, \mathbb{R})$  for each  $t \in \mathbb{Z}_+$ . The variables  $D$  and  $S_1$  in (6.16) denote the abundance of the seedling/cotyledon stage-class of *Veratrum*, and the number of one-year old seeds, respectively.<sup>‡</sup> The terms  $g_0$  and  $g_1$  are probabilities of new and one-year old seed germination, respectively, whilst  $s_0$  is the probability of new seed survival. The term  $p_{\text{sc}}$  is the probability of an individual cotyledon growing to the juvenile stage-class in one time-step, and those that do

<sup>‡</sup> Note that [20] uses  $C$  where we use  $D$  here. This is done as to avoid a clash with our standing notation of  $C$  denoting a cone in the state space.

are distributed according to  $f_{\text{sd}} \in C_0$ , where  $C_0 \subset X_0$  is the cone  $C_0 = L^1(\Omega, \mathbb{R}_+)$ . Moreover,  $p_{\text{est}}$  denotes the probability of a seed establishing as a cotyledon.

The kernel  $k$  of the integral operator in (6.16) is given by

$$k(\xi, \zeta) = p(\xi, \zeta) + p_s(\zeta)p_f(\zeta)f_v(\zeta)f_{\text{vd}}(\xi, \zeta) \quad \forall \xi, \zeta \in \Omega, \quad (6.17)$$

where  $p$  is the probability of an individual of size  $\zeta$  surviving to one of size  $\xi$  in a single time-step. It is assumed that  $p$  has the form

$$p(\xi, \zeta) = p_s(\zeta)(1 - p_f(\zeta))g(\xi, \zeta) \quad \forall \xi, \zeta \in \Omega, \quad (6.18)$$

where  $p_s(\zeta)$  and  $p_f(\zeta)$  are the survival probability and flowering probability of an individual of size  $\zeta$ , respectively, and  $g(\xi, \zeta)$  is the probability of an individual of size  $\zeta$  growing to size  $\xi$ , each over one time-step. The term  $1 - p_f$  appears on the right-hand side of (6.18) as flowering is fatal to *Veratrum*, that is, it is monocarpic.

The second summand on the right-hand side of (6.17) captures asexual reproduction of *Veratrum*:  $f_v(\zeta)$  denotes the number of asexual offspring produced by an individual of size  $\zeta$ , where  $f_{\text{vd}}(\xi, \zeta)$  is the probability that an individual of size  $\zeta$  asexually produces an offspring of size  $\xi$  in one time-step.

The functional  $h^*$  in (6.16) is given by

$$h^*z = \int_{\Omega} h(\zeta)z(\zeta) d\zeta \quad \forall z \in X_0, \quad \text{where } h(\zeta) := p_f(\zeta)f_s(\zeta)p_s(\zeta).$$

Here  $f_s(\zeta)$  denotes the expected number of seeds produced by an individual of size  $\zeta$ . Note that  $h^*z$  denotes the total number of seeds produced by the distribution  $z$  in a single time-step.

The functional forms for  $p_s$ ,  $p_f$ ,  $g$ ,  $f_v$ , and  $f_{\text{vd}}$  are as in [20, Table 1]. We use the parameter values

$$\begin{array}{ccccc} a_s = -4.53, & b_s = 5.51, & c_s = 1.04, & a_g = 0.28, & b_g = 0.92, \\ \beta_g = 0.44, & \beta_0 = -7.08, & \beta_s = 1.5, & a_v = -3.2, & b_v = 1.24, \\ a_{\text{vd}} = 1.16, & b_{\text{vd}} = 0.48, & \sigma_{\text{vd}}^2 = 0.18, & g_0 = 0.19, & g_1 = 0.98, \\ s_0 = 0.91, & s_1 = 0.98, & p_{\text{est}} = 0.31. & & \end{array}$$

which are equal to, or within one standard error of, the statistical estimates in [20, Table 1, Pasture environment]. Further,  $f_s(s) = e^{1.5+1.4s}$  (cf. [20, p.202, column 2]) and  $f_{\text{sd}}$  is assumed normally distributed with mean 1.05 and variance 0.72 (cf. [20, p.203, column 1]).<sup>§</sup> In particular, with these choices, the function  $h$  is in  $L^\infty(\Omega, \mathbb{R}_+)$ , and so  $h^* \in C_0^*$ .

The results of the current paper apply to the model (6.16). Since (6.16) is both linear and unforced, however, we proceed to demonstrate how the present results apply to a variation of the above model which includes these extra features. First, we assume that the cotyledon stage-class  $D(t)$  is subject to exogenous forcing  $\nu(t) \geq 0$ , which could be the result of a planting scheme, or dispersal. Second, seeking to capture density-dependent crowding effects which occur at higher abundances, we assume that the constant probability  $p_{\text{sc}}$  which appears in (6.16) is in fact a non-increasing function of  $D$ , and that this probability is subject to some seasonal or

<sup>§</sup>The model in [20] contains an additional stage-class, namely the number of two-year old seeds  $S_2$ . But since the parameter  $g_2 = 0$  (see [20, Table 1]),  $S_2$  does not enter into the other three equations, and so does not play a role in the dynamics and therefore this stage class has been omitted here.

anthropogenic variation  $u(t) > 0$  with nominal value  $u^e = 1$ . Modifying (6.16) in this way, leads to the following system.

$$\left. \begin{aligned} n(t+1, \xi) &= D(t)p_{sc}(u(t)D(t))f_{sd}(\xi) + \int_{m_1}^{m_2} k(\xi, \zeta)n(t, \zeta) d\zeta \\ D(t+1) &= p_{est}(g_0h^*n(t, \cdot) + g_1S_1(t)) + \nu(t) \\ S_1(t+1) &= (1 - g_0)s_0h^*n(t, \cdot) \end{aligned} \right\} \quad \forall t \in \mathbb{Z}_+, \forall \xi \in [m_1, m_2]. \quad (6.19)$$

To write (6.19) in the form (1.1), it is natural to introduce the state space  $X := X_0 \times \mathbb{R}^2$  which is a Banach space when equipped with the norm

$$\left\| \begin{pmatrix} z_0 \\ z_1 \end{pmatrix} \right\|_X := \|z_0\|_{X_0} + \|z_1\|_1 \quad \forall (z_0, z_1) \in X.$$

The dual space of  $X$  can be identified with  $X^* = X_0^* \times \mathbb{R}^2$ . In the given setting, the natural cone  $C \subset X$  to consider is  $C := C_0 \times \mathbb{R}_+^2$ . This cone is reproducing and its dual cone  $C^*$  can be identified with  $C_0^* \times \mathbb{R}_+^2$  and it is clear that the interior of  $C^*$  is non-empty, see Example 2.2.

Defining the integral operator  $A_0 : X_0 \rightarrow X_0$  by

$$(A_0z)(\xi) = \int_{\Omega} k(\xi, \zeta)z(\zeta)d\zeta \quad \forall z \in X_0,$$

the assumptions on  $k$  ensure that  $k$  is continuous and non-negative, and therefore  $A_0$  is a bounded positive operator [29, Theorem 1, Chapter 16]. We proceed to introduce the linear system  $(A, b, c^*)$  which underlies the abstract formulation of (6.16). To this end, we define a positive bounded linear operator  $A : X \rightarrow X$  by

$$Az := \begin{pmatrix} A_0 & 0 & 0 \\ p_{est}g_0h^* & 0 & p_{est}g_1 \\ (1 - g_0)s_0h^* & 0 & 0 \end{pmatrix} z, \quad \forall z \in X, \quad (6.20)$$

and set

$$b := \begin{pmatrix} f_{sd} \\ 0 \\ 0 \end{pmatrix}, \quad c^*z := (0 \ 1 \ 0)z, \quad \forall z \in C. \quad (6.21)$$

It is clear that  $b \in C$  and  $c^* \in C^*$ , and so (L2) is satisfied. The forced nonlinear system (6.16) may be written as

$$x^\nabla = Ax + bp_{sc}(uc^*x)c^*x + v, \quad x(0) = x^0 \in C, \quad (6.22)$$

where

$$x(t) := \begin{pmatrix} n(t, \cdot) \\ D(t) \\ S(t) \end{pmatrix}, \quad v(t) := \begin{pmatrix} 0 \\ \nu(t) \\ 0 \end{pmatrix}; \quad \forall t \in \mathbb{Z}_+.$$

Clearly, (6.22) is a special case of (1.1) with  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  given by  $f(u, y) := p_{sc}(uy)y$ .

From the block structure of  $A$ , we have that the spectral radii  $r(A)$  of  $A$  and  $r(A_0)$  of  $A_0$  coincide. With the given parameter values, we compute numerically that  $r(A) = r(A_0) \approx 0.9413$ , and so  $A$  is exponentially stable and (L1) holds. Ecologically, this means that asexual reproduction alone is not sufficient to maintain the population of *Veratum* asymptotically. For asymptotic population stasis or growth, a contribution from seed production and germination is required.

To show that assumption (P1) is satisfied, we compute that

$$c^*(A + bc^*)^3 = p_{\text{est}} \text{row} \begin{pmatrix} h^*(g_0 A_0^2 + g_0^2 p_{\text{est}} h^*(f_{\text{sd}})I + g_1(1 - g_0)s_0 A_0) \\ h^*((g_0 A_0 + g_1(1 - g_0)s_0 I)f_{\text{sd}}) \\ p_{\text{est}} g_0 g_1 h^*(f_{\text{sd}}) \end{pmatrix},$$

We note that (P1) cannot hold for  $\tau < 3$ , as there exist  $z_\tau \in C$  with  $z_\tau \neq 0$ , such that  $c^*(A + bc^*)^\tau z_\tau = 0$  for  $\tau \in \{0, 1, 2\}$ . By the choice of  $p_f$ ,  $p_s$  and  $f_s$ , we have that  $\text{ess inf } h > 0$ , and thus,  $h^* \in \text{int } C_0^*$ . Hence,

$$c^*(A + bc^*)^3 \geq p_{\text{est}} \begin{pmatrix} g_0^2 p_{\text{est}} h^*(f_{\text{sd}}) h^* & g_1(1 - g_0)s_0 h^*(f_{\text{sd}}) & p_{\text{est}} g_0 g_1 h^*(f_{\text{sd}}) \end{pmatrix} \in \text{int } C^*,$$

and so, by Lemma 2.1,  $c^*(A + bc^*)^3 \in \text{int } C^*$ .

For the purpose of numerical simulations, we approximate (6.22) by using a finite-element method, the details of which are given in Appendix B. We numerically compute that  $\mathbf{G}(1) \approx 87.8$ , and so  $p \approx 0.0114$ . We assume that

$$p_{\text{sc}}(y) = \frac{q_{\text{sc}}}{1 + 3y} \quad \forall y \geq 0, \quad (6.23)$$

where  $q_{\text{sc}} = 0.52$ . Since  $q_{\text{sc}} > p$ , the function  $f : U \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  given by  $f(w, y) = p_{\text{sc}}(wy)y$  satisfies (5.1), see [17, Example 4.1, Table 5.1], where  $U \subset (0, \infty)$  is an arbitrary compact set such that  $1 \in U$ . Moreover, the unique positive solution  $y^e$  of  $f(1, y) = py$  is given by  $y^e = (q_{\text{sc}} - p)/(3p) \approx 3.52$ . Finally,

$$\frac{\partial f}{\partial y}(1, y^e) = \frac{p}{1 + 3y^e} \in (0, p),$$

whence (5.2) holds, and we conclude that the condition (N3) is satisfied. Consequently, the hypotheses of Corollary 5.3 are satisfied. The simulations shown below illustrate the conclusions of Corollary 5.3 in the context of the system under consideration.

Figure 6.4 illustrates the semi-global exponential stability of  $x^e$  — the state error  $\|x(t) - x^e\|_X$  is plotted against  $t$  for three randomly chosen non-zero initial conditions, in the absence of forcing ( $u = 1, v = 0$ ). Figures 6.5(a)–(b) give an illustration of the ISS property of  $x^e$  — it shows plots of the state errors against  $t$  for two different initial states (0 and  $x^e$ ),  $u = 1$  and three different additive forcing terms  $v_k$  with

$$v_k(t) = 4k + \rho(t), \quad \forall t \in \mathbb{Z}_+, \quad k \in \{1, 2, 3\}, \quad (6.24)$$

where  $\rho$  is “small” random noise. Observe in Figure 6.5(a) that the contribution to  $\|x(t) - x^e\|_X$  from the initial error  $x(0) - x^e = x^e$  decays over time.

Figures 6.6(a)–(c) show plots of the state errors against  $t$  for three different initial conditions, zero additive forcing ( $v = 0$ ), and three periodic multiplicative forcing terms  $u_k$  given by

$$u_k(t) = \frac{k}{2}(1 + 0.8 \sin t), \quad \forall t \in \mathbb{Z}_+, \quad k \in \{1, 2, 3\}. \quad (6.25)$$

Whilst Figures 6.4–6.6 illustrate different facets of our main stability result Theorem 5.2 and its Corollary 5.3, Figures 6.7(a)–(c) provide an illustration of Corollary 5.5 by showing the convergence of  $x(t)$  to  $x^e/u^\infty$  for  $u^\infty = 0.8$ , when subject to three pairs of forcing functions  $(u_k, v_k)$  given by

$$u_1(t) = u^\infty, \quad u_2 = u^\infty(1 + (-0.8)^t \cos t), \quad u_3 = u^\infty(1 + (0.9)^t), \quad v_k(t) = k\rho(t)(0.9)^t \quad (6.26)$$

where  $k \in \{1, 2, 3\}$  and  $\rho(t)$  is randomly drawn from  $[0, 1]$ . Evidently, for very  $k \in \{1, 2, 3\}$ ,  $u_k(t)$  and  $v_k(t)$  converge to  $u^\infty$  and 0, respectively, as  $t \rightarrow \infty$ .  $\diamond$

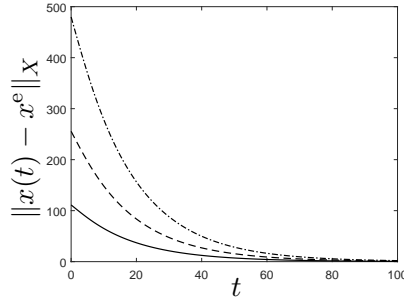


Figure 6.4: Graph of  $\|x(t) - x^e\|_X$  against  $t$  for the *Veratrum* model of Example 6.4. The simulations use three random initial conditions  $x^0$  of increasing norm and forcing is absent ( $u = 1, v = 0$ ).

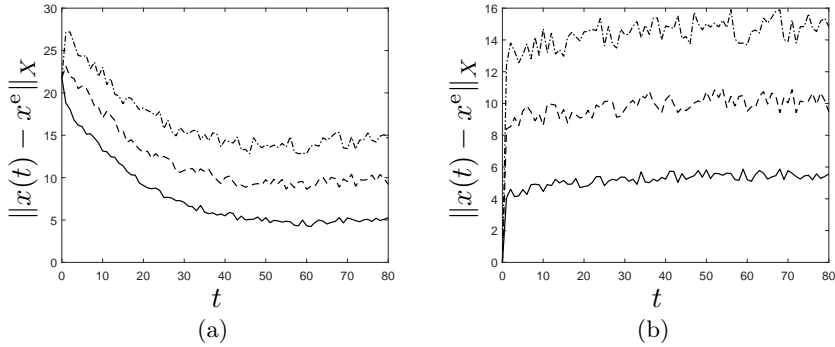


Figure 6.5: Graph of state errors against  $t$  for the *Veratrum* model of Example 6.4. The simulations in both panels use additive forcing  $\nu_k$  from (6.24), with solid, dashed, and dashed-dotted lines corresponding to  $k = 1, 2, 3$ , respectively. Multiplicative forcing is absent ( $u = 1$ ) in these simulations and the initial conditions in panels (a) and (b) are 0 and  $x^e$ , respectively.

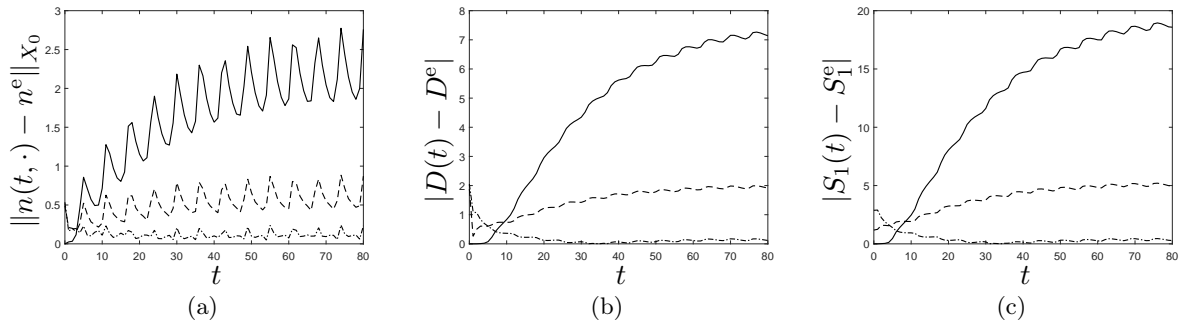


Figure 6.6: Graph of state errors against  $t$  for the *Veratrum* model of Example 6.4. The simulations use three initial conditions, zero additive forcing ( $v = 0$ ) and three periodic forcing  $u_k$  given by (6.25), with solid, dashed, and dashed-dotted lines corresponding to  $k = 1, 2, 3$ , respectively. The solid line uses  $x(0) = x^e$  and the other two lines are randomly chosen non-zero initial conditions.

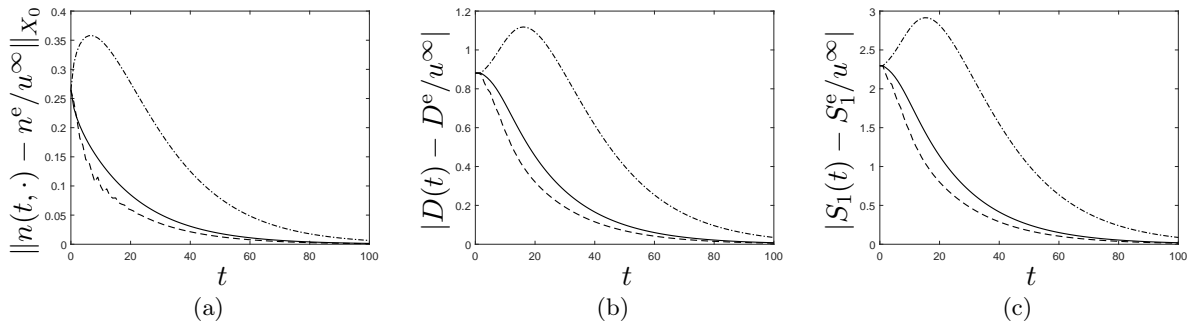


Figure 6.7: Graph of state errors against  $t$  for the *Veratrum* model of Example 6.4. The simulations all use initial condition  $x^e$ , and three different pairs of forcing functions  $(u_k(t), v_k(t))$  from (6.26), with solid, dashed, and dashed-dotted lines corresponding to  $k = 1, 2, 3$ , respectively.

## 7 Summary

We have presented boundedness, persistence and stability results for the class of nonlinear, forced difference equations (1.1) which arise frequently in population biology and theoretical ecology. Our treatment permits the situation wherein the state-space is infinite-dimensional, enabling the modelling of structured populations with a finite number of stages as well as populations with a continuum of stages (the latter are frequently described in terms of integro-difference equations, such as IPMs). The system (1.1) has both a linear and a nonlinear component, corresponding to a mixture of density-independent and density-dependent dynamical scenarios. A key feature of these models is that they are instances of positive systems, and so the state is constrained to lie in a positive cone. Under natural conditions these models admit two equilibria in the absence of forcing: zero and a non-zero steady state. The inclusion of forcing facilitates the modelling of a number of exogenous processes, including disturbances, environmental variation, or control or intervention strategies, all of which are relevant in a number of application scenarios, from conservation and community ecology, to pest management.

Our main result for boundedness and persistence is Theorem 4.3, and our main stability results are Theorem 5.2, Corollary 5.3 and Corollary 5.5. To accommodate the contribution from potentially persistent forcing terms, our stability results are inspired by the concept of input-to-state stability from nonlinear control theory, which we discussed briefly in Section 2. Informally, we establish our results by examining the interplay between the underlying linear system (2.4), particularly its transfer function “gain”  $\mathbf{G}(1) = 1/p$  (see Proposition 3.1), and the nonlinear term  $f$ . This interplay is captured in the nonlinear and sector type assumptions (N1), (N2) and (N3). The persistence and stability results very much rely on the positivity property (P1) imposed on the linear system  $(A, b, c^*)$  which ensures that the origin of the nonlinear system (1.1) is repelling in a suitable sense. Section 6 contains detailed discussions of four examples from population ecology demonstrating how the theory applies in both finite- and infinite-dimensional settings.

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## Appendix

### A An example relating to [36, Corollary 4.1]

Here we show, by providing a counter example, that the IPM result [36, Corollary 4.1] is not correct. To see this, assume that, in the notation of [36],  $\Omega = [0, 1]$  and the functions  $c : [0, 1] \rightarrow \mathbb{R}_+$  and  $p : [0, 1] \times [0, 1] \rightarrow \mathbb{R}_+$  are continuous and satisfy

$$c(\xi) = 0 \quad \forall \xi \in [1/2, 1] \quad \text{and} \quad \|c\|_{L^\infty} > 0,$$

and

$$p(x, \xi) = 0 \quad \forall (x, \xi) \in [0, 1/2] \times [1/2, 1] \quad \text{and} \quad \max_{0 \leq \xi \leq 1} \int_0^1 p(x, \xi) dx < 1.$$

Then, with  $n(\xi, 0) = 0$  for  $\xi \in [0, 1/2]$  and  $\|n(\cdot, 0)\|_{L^1} > 0$ , we have that

$$c^T n(\cdot, 0) = \int_0^1 c(\xi) n(\xi, 0) d\xi = 0,$$

and

$$\int_0^1 p(x, \xi) n(\xi, 0) d\xi = \int_{1/2}^1 p(x, \xi) n(\xi, 0) d\xi = 0 \quad \forall x \in [0, 1/2].$$

Now

$$n(x, 1) = \int_0^1 p(x, \xi) n(\xi, 0) d\xi + b(x) f(c^T n(\cdot, 0)) = \int_0^1 p(x, \xi) n(\xi, 0) d\xi = 0 \quad \forall x \in [0, 1/2],$$

where we have assumed that  $f(0) = 0$ . By repeated application of the above argument, it follows that

$$y(t) = c^T n(\cdot, t) = 0 \quad \forall t \in \mathbb{Z}_+. \tag{A.1}$$

Choosing continuous  $b : [0, 1] \rightarrow \mathbb{R}_+$  such that  $c^T b = \int_0^1 c(\xi) b(\xi) d\xi > 0$ , it is clear that  $c^T (I - A)^{-1} b > 0$ , and so for any non-decreasing concave function  $f$  with  $f(0) = 0$ ,  $\lim_{y \rightarrow 0} f(y)/y > p_e^*$  and  $\lim_{y \rightarrow \infty} f(y)/y < p_e^*$ , the assumptions of [36, Corollary 4.1] are satisfied, where  $1/p_e^* = c^T (I - A)^{-1} b$ . But if [36, Corollary 4.1] was correct, then  $\lim_{t \rightarrow \infty} y(t) > 0$ , in contradiction to (A.1).

Finally, denoting the integral operator

$$L^1(0, 1) \rightarrow L^1(0, 1), \quad \zeta \mapsto \int_0^1 p(\cdot, \xi) \zeta(\xi) d\xi$$

by  $A$ , an inspection of the above argument shows that  $\ker c^T$  has an  $A$ -invariant subspace  $S \subset L^1(0, 1)$  containing strictly positive elements.

### B Example 6.4: further details

We provide some details on the numerical approximation scheme. For notational convenience in this section we set  $\underline{N} := \{1, 2, \dots, N\}$  for each  $N \in \mathbb{N}$ .

To derive a numerical approximation of the forced nonlinear IPM (6.22), we discretise the state variable  $n$  via finite elements. To this end, we consider  $n(t+1, \xi)$ , multiply by  $\psi \in L^1(\Omega) := L^1(\Omega, \mathbb{R})$  and integrate over  $\Omega$  to obtain

$$\begin{aligned} \int_{\Omega} \psi(\xi) n(t+1, \xi) d\xi &= \int_{\Omega} \psi(\xi) \left[ (A_0 n(t, \cdot))(\xi) + p_{\text{sc}}(u(t)D(t))D(t) f_{\text{sd}}(\xi) \right] d\xi \\ &= \int_{\Omega} \psi(\xi) \left( \int_{\zeta \in \Omega} k(\xi, \zeta) n(t, \zeta) d\zeta \right) d\xi \\ &\quad + \left( \int_{\Omega} \psi(\xi) f_{\text{sd}}(\xi) d\xi \right) p_{\text{sc}}(u(t)D(t))D(t). \end{aligned} \quad (\text{B.1})$$

We seek an approximate solution to (B.1) of the form

$$n_N(t, \xi) = \sum_{j=1}^N a_j(t) \phi_j(\xi), \quad \forall t \in \mathbb{Z}_+, \quad \forall \xi \in \Omega, \quad (\text{B.2})$$

where  $N \in \mathbb{N}$ ,  $\phi_j$  are given functions in  $L^1(\Omega)$  and  $a_j$  are to-be-determined scalar coefficients. Substituting (B.2) into (B.1), and testing against  $\psi = \phi_i$  for each  $i \in \underline{N}$  gives

$$\begin{aligned} \sum_{j=0}^N \left( \int_{\Omega} \phi_i(\xi) \phi_j(\xi) d\xi \right) a_j(t+1) &= \sum_{j=0}^N \left( \int_{\Omega} \phi_i(\xi) \int_{\zeta \in \Omega} k(\xi, \zeta) \phi_j(\xi) d\zeta d\xi \right) a_j(t) \\ &\quad + \left( \int_{\Omega} \phi_i(\xi) f_{\text{sd}}(\xi) d\xi \right) p_{\text{sc}}(u(t)D(t))D(t). \end{aligned} \quad (\text{B.3})$$

Setting

$$z(t) := (a_1(t) \quad \dots \quad a_N(t))^T \in \mathbb{R}^N \quad \forall t \in \mathbb{Z}_+,$$

we see that (B.3) may be expressed in matrix form as

$$Ez^\nabla = Fz + Gf(u, D). \quad (\text{B.4})$$

Here  $(E, F, G) \in \mathbb{R}^{N \times N} \times \mathbb{R}^{N \times N} \times \mathbb{R}^N$  are given entrywise by

$$E_{ij} := \int_{\Omega} \phi_i(\xi) \phi_j(\xi) d\xi, \quad F_{ij} := \int_{\Omega} \phi_i(\xi) \left( \int_{\Omega} k(\xi, \zeta) \phi_j(\zeta) d\zeta \right) d\xi, \quad \forall i, j \in \underline{N}, \quad (\text{B.5})$$

and

$$G_i := \int_{\Omega} \phi_i(\xi) f_{\text{sd}}(\xi) d\xi, \quad \forall i \in \underline{N}. \quad (\text{B.6})$$

Since we are seeking to approximate the  $L^1(\Omega)$  functions  $n(t, \cdot)$  in  $L^1(\Omega)$  (that is, we are not approximating any derivatives), we choose as finite-dimensional approximation spaces the linear span of  $N$  piecewise constant functions. Specifically, for fixed  $N \in \mathbb{N}$ , we define  $\xi_j := m_1 + j(m_2 - m_1)/N$  for  $j \in \{0, 1, \dots, N\}$ ,  $\Delta := (m_2 - m_1)/N$  and

$$\phi_i : \Omega \rightarrow \mathbb{R}_+, \quad \phi_i(\xi) := \begin{cases} \frac{1}{\sqrt{\Delta}} & \xi_{i-1} \leq \xi \leq \xi_i \\ 0 & \text{else,} \end{cases} \quad \forall i \in \underline{N}.$$

An advantage of such a choice is that, as readily seen,  $E = I$ , because  $E_{ij} = 0$  if  $i \neq j$  and

$$E_{ii} = \int_{m_1}^{m_2} \phi_i^2(\xi) d\xi = \frac{1}{\Delta} \int_{\xi_{i-1}}^{\xi_i} d\xi = 1, \quad \forall i \in \underline{N}.$$

Moreover, by inspection of (B.5) and (B.6), it follows that with the above choice of piecewise constant  $\phi_j$ ,  $F$  and  $G$  in (B.6) have nonnegative entries.

Noting that

$$\begin{aligned} h^* n_N(t, \cdot) &= \sum_{j=0}^N \left( \int_{\Omega} p_f(\xi) f_s(\xi) p_s(\xi) \phi_j(\xi) d\xi \right) a_j(t) \\ &= H^T z(t), \quad \forall t \in \mathbb{Z}_+, \end{aligned}$$

where the entries of  $H \in \mathbb{R}^N$  are given by

$$H_j := \int_{\Omega} p_f(\xi) f_s(\xi) p_s(\xi) \phi_j(\xi) d\xi, \quad \forall j \in \underline{N},$$

we arrive at the finite-dimensional approximation to (6.22) given by

$$x_N^\nabla = \begin{pmatrix} z^\nabla \\ D^\nabla \\ S_1^\nabla \end{pmatrix} = \begin{pmatrix} F & 0 & 0 \\ p_{\text{est}} g_0 H^T & 0 & p_{\text{est}} g_1 \\ (1 - g_0) s_0 H^T & 0 & 0 \end{pmatrix} \begin{pmatrix} z \\ D \\ S_1 \end{pmatrix} + \begin{pmatrix} G \\ 0 \\ 0 \end{pmatrix} p_{\text{sc}}(uD)D + v. \quad (\text{B.7})$$

Note that  $F$ ,  $G$  and  $H$  have nonnegative entries. The numerical simulations for Example 6.4 have been generated via (B.7) with  $N = 30$ .

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