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Global stability of an age-structured population model

Daniel Franco[a,b], Hartmut Logemann[b], Juan Perán[a]

[a] *Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED), c/ Juan del Rosal 12, 28040, Madrid, Spain*
[b] *Department of Mathematical Sciences, University of Bath, Bath BA2 7AY, UK*

Abstract

We consider a nonlinear discrete-time population model for the dynamics of an age-structured species. This model has the form of a Lure feedback system (well-known in control theory) and is a particular case of the system studied by Townley et al. in [1]. The main objective is to show that, in this case, the range of nonlinearities for which the existence of globally asymptotically stable non-zero equilibrium can be guaranteed is considerably larger than in the main result in [1]. We illustrate our results with several biologically meaningful examples.

Keywords: Age-structured species, Feedback systems, Global stability, Lure systems, Population dynamics

1. Introduction

Leslie matrix models have been widely employed to understand the dynamics of populations structured into age classes [2]. The model can be written as follows

$$x_{t+1} = P(x_t)x_t. \tag{1}$$

Here $x_t \in \mathbb{R}^n_+$ is the class distribution vector (where $\mathbb{R}_+ = [0, \infty)$) at discrete time $t \in \mathbb{N}$ and

$$P(x) = \begin{pmatrix} \rho + \phi_1(x) & \phi_2(x) & \phi_3(x) & \cdots & \phi_n(x) \\ \tau_1(x) & 0 & 0 & \cdots & 0 \\ 0 & \tau_2(x) & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & \tau_{n-1}(x) & 0 \end{pmatrix},$$

with $0 < \tau_i \leq 1$ and $0 \leq \phi_i$. The subdiagonal elements, τ_i, capture the demographic transitions between age-categories, whilst in the elements in the first row, ϕ_i, correspond to the newborns and ρ is the fraction of individuals in the first age class who remain in this class after one time unit (for example, because they do not mature in one time step).

In this paper, we consider the following system

$$x_{t+1} = Ax_t + bf(c^T x_t), \tag{2}$$

where A is an asymptotically stable non-negative matrix in $\mathbb{R}^{n\times n}$, $b, c \in \mathbb{R}^n_+ \setminus \{0\}$ and $f\colon \mathbb{R}_+ \to \mathbb{R}_+$ is a continuous map with $f(0) = 0$ and $f(y) > 0$ for $y \in \mathbb{R}_+ \setminus \{0\}$. Systems of the form (2) are known in systems & control theory as Lure systems, the stability properties of which have been studied in the context of so-called absolute stability theory (mainly in a continuous-time setting), see, for example [3, 4]. Introducing the linear controlled and observed system

$$x_{t+1} = Ax_t + bu_t, \quad y_t = c^T x_t, \tag{3}$$

the Lure system (2) can be thought of as the closed-loop system obtained by applying nonlinear feedback of the form $u_t = f(y_t)$ to the linear system (3).

We note that if A and b satisfy

$$A = \begin{pmatrix} 1-\delta & 0 & 0 & \cdots & 0 \\ a_1 & 0 & 0 & \cdots & 0 \\ 0 & a_2 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & a_{n-1} & 0 \end{pmatrix}, \quad b = \begin{pmatrix} b_1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \tag{4}$$

where $0 < \delta \leq 1$, and $a_i, b_1 > 0$,

then system (2) is a particular case of system (1) in which a constant proportion of the individuals in each age-category, from 1 to $n-1$, at time-step t reaches the next age class in the time-step $t+1$, i.e., the functions $\tau_i(x) = a_i$ are constant; moreover, $\rho = 1-\delta$ and $\phi_i(x) = b_1 f(c^T x)/\|x\|_1$ for all i, where where $\|\cdot\|_1$ is the 1-norm in $\mathbb{R}^n$, that is, $\|x\|_1 = \sum_{i=1}^n |x_i|$, where x_i denotes the i-th component of x.

The global dynamics of (2) have been recently considered in [1], where it is shown that (under certain conditions) system (2) satisfies a trichotomy of stability, which is characterised by the relationship between the graph of f and the line with slope

$$p := \frac{1}{c^T(I-A)^{-1}b}.$$

We emphasize that the results in [1] are not restricted to the special case given in (4). Nevertheless, in [1], those results are illustrated by a model for *Chinook Salmon* (*Oncorhynchus tshawytscha*) which satisfies (4).

In [1], the following sector property for f is crucial for the proof of the existence of a positive global attractor for system (2):

(C) There exists a unique $y^* > 0$ so that $f(y^*) = py^*$ and

$$|f(y) - py^*| < p|y - y^*|, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\}. \tag{5}$$

Actually, in [1], the stronger assumption that there exists $m \in (0, p)$ such that

$$|f(y) - py^*| \leq m|y - y^*|, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\} \tag{6}$$

was imposed. Although not explicitly stated in [1], (6) guarantees global exponential stability, whilst (5) is sufficient for global asymptotic stability.

Defining $f_p : \mathbb{R}_+ \to \mathbb{R}_+$ by

$$f_p(y) = f(y)/p, \quad y \in \mathbb{R}_+,$$

we remark that the sector condition (C) implies that y^* is a global attractor for the scalar difference equation

$$z_{t+1} = f_p(z_t), \tag{7}$$

where by global we mean that for all positive y, the orbit $f^n(y)$ of y converges to y^* as $n \to \infty$. Condition (C) is satisfied, for example, by the Beverton-Holt map ($f(y) = \lambda y/(K + y)$, $\lambda, K > 0$) and the Ricker map ($f(y) = y \exp(-\lambda y)$, $\lambda > 0$), whenever $|f'(y^*)| < p$, i.e. when the fixed point y^* of the map f_p is

locally asymptotically stable: the proof for the Beverton-Holt map is straightforward and the reader can find the Ricker map case discussed in [1]. However, as Figure 1 illustrates, for other important maps, the condition $|f'(y^*)| < p$ is not sufficient for (C) to hold. For example, this happens in the case of the generalized Beverton-Holt map [5],

$$f(y) = \frac{\lambda y}{1 + (y/K)^\beta}, \quad K > 0,\ \lambda > 0,\ \beta > 0,$$

or the Hassel map [6],

$$f(y) = \frac{\lambda y}{(1 + y/K)^\beta}, \quad K > 0,\ \lambda > 0,\ \beta > 0.$$

Generalized Beverton-Holt (also called Maynard-Smith) and Hassel maps have been extensively employed in ecological modelling. Moreover, the corresponding dynamics are well known. Interestingly, these maps have the very desirable property, as have many others density dependences, that the corresponding global dynamics can be characterised by the local dynamics [7], i.e. local stability guarantees global stability. This naturally raises the question of whether or not condition (C) can be relaxed.

In this paper, we show that the sector condition (C) is not necessary to establish the existence of a positive global attractor for system (2) when A and b are given by (4). We prove that, in this case, it is sufficient that the scalar difference equation (7) has a positive global attractor y^*. This will allow us to use well-known sufficient conditions for global stability for maps to formulate easily verifiable conditions for the existence of a positive global attractor for system (2) with A and b as in (4). We illustrate this idea with two different conditions which involve Schwarzian derivatives and envelopments by linear fractional functions.

Our approach is different from that in [1] which is essentially based on arguments of small-gain type. Indeed, small-gain and absolute stability arguments do not apply to the nonlinearities considered in this paper. Instead, we exploit that, in our particular case, system (2) can be reduced to a n-th order scalar difference equation with dynamics dominated by those of a first-order difference

equation (see [8, 9] and references therein).

2. Preliminaries

We start with some definitions. For a continuous map $F\colon \mathbb{R}_+^n \to \mathbb{R}_+^n$, consider the difference equation

$$x_{t+1} = F(x_t), \quad t \geq 0, \tag{8}$$

with initial condition $x_0 \in \mathbb{R}_+^n$. We say that a non-zero equilibrium $x^* \in \mathbb{R}_+^n$ of the equation (8) is a *global attractor* if, for every $x_0 \in \mathbb{R}_+^n \setminus \{0\}$,

$$\lim_{k\to\infty} F^k(x_0) = x^*,$$

where, as usual, F^k denotes the k-fold composition of F with itself.

Similarly, for a continuous map $G\colon \mathbb{R}_+^n \to \mathbb{R}_+$, consider the n-th order difference equation

$$y_{t+1} = G(y_t, y_{t-1} \ldots, y_{t-n+1}), \quad t \geq 0, \tag{9}$$

with initial conditions $y_0, \ldots, y_{1-n} \in \mathbb{R}_+$. We say that $y^* \in \mathbb{R}_+$ is an *equilibrium* of the equation (9) if $y^* = G(y^*, \ldots, y^*)$, and we say that such a non-zero equilibrium is a *global attractor* if

$$\lim_{k\to\infty} y_k = y^*,$$

for every solution $\{y_k\}_{k\geq 1-n}$ of equation (9) with initial conditions such that $(y_0, \ldots, y_{1-n}) \in \mathbb{R}_+^n \setminus \{0\}$.

For both equations (8) and (9), we say that a non-zero equilibrium is a *global stable attractor* if it is a global attractor and it is stable.

Whilst we are mainly interested in studying the case in which A and b are of the form (4), in this section we deal with system (2) under more general conditions. We do this because we think that Lemma 3 is of independent interest and will be useful in future work. We consider the following conditions for A, b and c in system (2):

(A1) A is a non-negative $n \times n$-matrix with spectral radius $r(A) < 1$;

(A2) $b, c \in \mathbb{R}^n_+ \setminus \{0\}$;

(A3) $A + bc^T$ is primitive, i.e. there exists $k \in \mathbb{N}$ such that all entries of $(A + bc^T)^k$ are positive.

The following result is contained in lemmata 3.1 and 3.2 in [1].

Lemma 1. *Assume that* (A1)-(A3) *hold. Then,* $p \in (0, \infty)$. *Moreover,* $r(A + pbc^T) = 1$.

We note that in the particular case of A and b satisfying (4) condition (A1) trivially holds. Moreover, in this case (A3) is not necessary to guarantee that $p^{-1} = c^T(I - A)^{-1}b > 0$ (and hence $0 < p < \infty$). Indeed, the first column of $(I - A)^{-1}$ is given by

$$\begin{pmatrix} \frac{1}{\delta} & \frac{a_1}{\delta} & \frac{a_1 a_2}{\delta} & \dots & \frac{\prod_{j=1}^{n-1} a_j}{\delta} \end{pmatrix}^T.$$

Therefore, denoting the components of c by $c_1, \dots, c_n$,

$$p^{-1} = c^T(I - A)^{-1}b = \frac{b_1}{\delta}\left(c_1 + \sum_{j=2}^{n}\left(c_j \prod_{k=1}^{j-1} a_k\right)\right), \tag{10}$$

which is positive even when $A + bc^T$ is not primitive (for example, if $\delta = 1$, $c_n > 0$ and $c_i = 0$ for $i \neq n$).

Whilst, in the particular case (4), (A3) is not necessary to guarantee that $p^{-1} > 0$, (A3) is nevertheless a crucial assumption and we therefore provide a necessary and sufficient condition for (A3) to be satisfied.

Lemma 2. *Assume that* A *and* b *are as in* (4) *and* $c = (c_1, \dots, c_n)^T \in \mathbb{R}^n_+$. *Define* $C := \{i : c_i > 0\} \subset \mathbb{N}$.

The matrix $A + bc^T$ *is primitive if, and only if,* $c_n > 0$ *and one of the following conditions holds:* (i) $0 < \delta < 1$ *or* (ii) $\gcd C = 1$.

Proof. It is well-known that a non-negative matrix is primitive if, and only if, its di-graph is strongly connected and the lengths of its cycles are relatively prime, see [10]. The claim follows from a straightforward application of this result. □

The next result gives a sufficient condition for every solution of system (2) with non-trivial initial condition to be bounded away from zero.

Lemma 3. *Assume that* (A1)-(A3) *hold and that there exists a positive* y^* *such that*

$$(f_p(y) - y)(y - y^*) < 0, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\}. \tag{11}$$

If a solution of system (2) *with* $x_0 \in \mathbb{R}^n_+ \setminus \{0\}$ *is bounded, then it is also bounded away from zero.*

Proof. Let $\{x_t\}_{t\geq 0}$ be a bounded solution of system (2) with $x_0 \in \mathbb{R}^n_+ \setminus \{0\}$. We are going to show that $\inf_{t\geq 0} \|x_t\|_1 > 0$.

Clearly, the sequence of real numbers $\{c^T x_t\}_{t\geq 0}$ is also bounded. We define

$$\mu := \sup_{t\geq 0}\{c^T x_t\} \geq 0,$$

$y^{**} := \max\{y^*, \mu\} \geq y^* > 0$ and

$$\eta := \min_{y\in[y^*, y^{**}]} f(y) > 0.$$

The primitivity assumption (A3) guarantees that $A + pbc^T$ is also primitive because the di-graph of $A + qbc^T$ is the same as that of $A + bc^T$ for all positive q. Therefore, Lemma 1 and the Perron-Frobenius theorem guarantee that 1 is an eigenvalue of $A + pbc^T$ with an associated positive left eigenvector v^T.

If $c^T x_t \in [y^*, y^{**}]$, then we have

$$v^T x_{t+1} \geq v^T A x_t + v^T b\eta \geq v^T b\eta > 0.$$

If $c^T x_t \in [0, y^*)$, then, by condition (11), $f(c^T x_t) \geq pc^T x_t$, and, as a consequence, we obtain

$$v^T x_{t+1} \geq v^T (A + pbc^T) x_t = v^T x_t > 0.$$

Thus, induction on t shows that

$$v^T x_t \geq \min\{v^T x_0, v^T b\eta\} > 0, \quad t \geq 0.$$

Finally, since $v^T x_t \leq \|v\|_\infty \|x_t\|$, setting

$$M := \frac{\min\{v^T x_0, v^T b\eta\}}{\|v\|_\infty} > 0,$$

we conclude that $\|x_t\| \geq M > 0$ for all $t \geq 0$, proving the claim. □

The next lemma (the second part of which is a corollary of a result in [8]) gives sufficient conditions for the dynamics of a n-th order difference equation to be dominated by the dynamics of a first order difference equation.

Lemma 4. *Let $G\colon \mathbb{R}_+^n \to \mathbb{R}_+$ be continuous and assume that there exists a continuous map $d\colon \mathbb{R}_+ \to \mathbb{R}_+$ such that, for each $(u_1,\dots,u_n)^T \in \mathbb{R}_+^n$ with $G(u_1,\dots,u_n) \geq \max\{u_1,\dots,u_n\}$, there exists z in the convex hull of $\{u_1,\dots,u_n\}$ satisfying $d(z) \geq G(u_1,\dots,u_n)$. Furthermore, assume that $y^* > 0$ is a global stable attractor of the first-order difference equation $y_{t+1} = d(y_t)$. Then the following statements hold.*

(i) *Every solution of the nth-order difference equation* (9) *is bounded.*

(ii) *Under the additional assumptions that*

- *for each $(u_1,\dots,u_n)^T \in \mathbb{R}_+^n$ with $G(u_1,\dots,u_n) \leq \min\{u_1,\dots,u_n\}$, there exists z in the convex hull of $\{u_1,\dots,u_n\}$ satisfying $d(z) \leq G(u_1,\dots,u_n)$,*
- *every non-zero solution $(y_t)_{t\geq 0}$ of the nth-order difference equation* (9) *satisfies*

$$\liminf_{t\to\infty} y_t > 0, \tag{12}$$

y^* is a global stable attractor of (9).

Proof. (i) Since $y^* > 0$ is a global stable attractor of the difference equation defined by d, we have

$$(d(y) - y)(y - y^*) < 0, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\}. \tag{13}$$

Let $(y_t)_{t\geq 0}$ be a non-zero solution of (9) and define

$$M := \max\{M_0, y_{1-n}, \dots, y_0\},$$

where $M_0 := \max\{d(x) : x \in [0, y^*]\}$. Assume that $\max\{y_t, y_{t-1}, \dots, y_{t-n+1}\} \leq M$. The claim will follow by strong induction, provided we can show that $y_{t+1} \leq M$. Seeking a contradiction, suppose that

$$y_{t+1} = G(y_t, y_{t-1}, \dots, y_{t-n+1}) > M. \tag{14}$$

By hypothesis, there exist numbers $\gamma_{t,0},\dots,\gamma_{t,n-1} \in \mathbb{R}_+$ with $\sum_{k=0}^{n-1}\gamma_{t,k} = 1$ and such that $z = \sum_{k=0}^{n-1}\gamma_{t,k}y_{t-k}$ satisfies

$$y_{t+1} = G(y_t, y_{t-1}, \dots, y_{t-n+1}) \leq d(z).$$

By the definition of M and M_0,

$$z \leq y^* \;\Rightarrow\; y_{t+1} \leq d(z) \leq M_0 \leq M,$$

and, moreover, by (13),

$$z > y^* \;\Rightarrow\; y_{t+1} \leq d(z) \leq z = \sum_{k=0}^{n-1}\gamma_{t,k}y_{t-k} \leq M.$$

Combining this with (14), we arrive at the contradiction $M < y_{t+1} \leq M$.

(ii) Set $I := (0, \infty), g := G|_{I^n}$ and $h := d|_I$. Statement (i), together with the hypothesis (12), guarantees that the n-th order equation

$$y_{t+1} = g(y_t, y_{t-1}, \ldots, y_{t-n+1}) \tag{15}$$

is persistent (in the sense of [8]). By hypothesis, $y^* > 0$ is global stable attractor of the difference equation $z_{t+1} = h(z_t)$ and therefore, an application of Proposition 3.4 in [8] shows that y^* is a global stable attractor of (15). Finally, let $(y_t)_{t\geq 0}$ be a non-zero solution of (9). It remains to show that $\lim_{t\to\infty} y_t = y^*$. By (12), there exists $k \geq 0$ such that $y_t > 0$ for all $t \geq k$ and consequently, the positive sequence $(\tilde{y}_t)_{t\geq 0}$ given by $\tilde{y}_t := y_{t+k+n-1}$ is a solution of (15). Thus,

$$\lim_{t\to\infty} y_t = \lim_{t\to\infty} \tilde{y}_t = y^*,$$

completing the proof. □

3. Existence of a global stable attractor - main result

Our main result shows that, in the case under consideration, the sector condition (C) can be weakened.

Theorem 1. *Let A and b be of the form (4), $c \in \mathbb{R}^n_+ \setminus \{0\}$ and assume that (A3) is satisfied. Let $f\colon \mathbb{R}_+ \to \mathbb{R}_+$ be a continuous map such that $f(0) = 0$, $f(y) > 0$ for $y > 0$ and the following condition holds.*

(H) *The difference equation $z_{t+1} = f_p(z_t)$ has a global stable attractor $y^* > 0$.*

Then, $x^* = y^* p(I - A)^{-1} b$ is a positive global stable attractor of (2). The components x^*_i of x^* are given by $x^*_1 = y^* p b_1/\delta$ and $x^*_i = y^* p b_1 \prod_{j=1}^{i-1} a_j/\delta$ for $i = 2, \ldots, n$.

Proof. Let $x_0 \in \mathbb{R}^n_+ \setminus \{0\}$ and let $(x_t)_{t\geq 0}$ be the corresponding solution of (2). We denote the i-th component of x_t by $x_{t,i}$. First, we note that the system (2) can be reduced to the following n-th order scalar difference equation for $x_{t,1}$:

$$\begin{aligned} x_{t+1,1} \quad = \quad & (1-\delta)x_{t,1} + b_1 f\big(c_1 x_{t,1} + c_2 a_1 x_{t-1,1} + \cdots \\ & + [c_n \prod_{k=1}^{n-1} a_k] x_{t-(n-1),1}\big), \quad t \geq 0 \end{aligned} \tag{16}$$

with initial conditions,

$$x_{0,1} = x_{0,1},\ x_{-1,1} = \frac{x_{0,2}}{a_1}, \ldots,\ x_{-(n-1),1} = \frac{x_{0,n}}{\prod_{k=1}^{n-1} a_k},$$

belonging to $\mathbb{R}_+$ and not all zero.

With the aim of using Lemma 4, we define the continuous maps $G\colon \mathbb{R}_+^n \to \mathbb{R}_+^n$ and $d\colon \mathbb{R}_+ \to \mathbb{R}_+$ by

$$G(u_1,\dots,u_n) = (1-\delta)u_1 + b_1 f\big(c_1u_1 + c_2a_1u_2 + \cdots \quad + [c_n \prod_{k=1}^{n-1} a_k]u_n\big)$$

and

$$d(y) = \frac{b_1}{\delta} f\big(\frac{\delta}{b_1p}y\big) = \frac{b_1p}{\delta} f_p\big(\frac{\delta}{b_1p}y\big),$$

respectively.

By (H), b_1py^*/δ is a global stable attractor for the first order equation $y_{t+1} = d(y_t)$. Furthermore, we have

$$\begin{aligned} G(u_1,\dots,u_n) &= (1-\delta)u_1 + \delta\frac{b_1}{\delta} f\big(\frac{\delta}{b_1p}(\gamma_1u_1 + \cdots + \gamma_nu_n)\big) \\ &= (1-\delta)u_1 + \delta d(\gamma_1u_1 + \cdots + \gamma_nu_n) \end{aligned}$$

with

$$\gamma_1 = \frac{b_1pc_1}{\delta} \quad \text{and} \quad \gamma_i = \frac{b_1pc_i\prod_{k=1}^{i-1} a_k}{\delta}, \quad i = 2,\dots,n.$$

Invoking (10), we see that $0 \le \gamma_i \le 1$ and $\sum_{i=1}^n \gamma_i = 1$. Furthermore, if $G(u_1,\dots,u_n) \ge \max\{u_1,\dots,u_n\}$, then

$$G(u_1,\dots,u_n) \le (1-\delta)G(u_1,\dots,u_n) + \delta d(\gamma_1u_1 + \cdots + \gamma_nu_n),$$

which implies $G(u_1,\dots,u_n) \le d(z)$ with z in the convex hull of $\{u_1,\dots,u_n\}$. Similarly, if $G(u_1,\dots,u_n) \le \min\{u_1,\dots,u_n\}$, then

$$G(u_1,\dots,u_n) \ge (1-\delta)G(u_1,\dots,u_n) + \delta d(\gamma_1u_1 + \cdots + \gamma_nu_n),$$

which implies $G(u_1,\dots,u_n) \ge d(z)$ with z in the convex hull of $\{u_1,\dots,u_n\}$.

We claim that it is sufficient to show that

$$\liminf_{t\to\infty} x_{t,1} > 0. \tag{17}$$

Indeed, if (17) holds, then statement (ii) of Lemma 4 guarantees that b_1py^*/δ is a global stable attractor for the n-th order difference equation (16) to which we have reduced system (2). It then follows that $x_{t,1} \to b_1py^*/\delta$ as $t \to \infty$, and, moreover, using the special structure of A and b, we conclude that, for $i = 2,\dots,n$, $x_{t,i} \to y^*pb_1\prod_{j=1}^{i-1} a_j/\delta$ as $t \to \infty$.

We proceed to establish (17). Noting that, by statement (i) of Lemma 4, $(x_{t,1})_{t\ge0}$ is bounded, it follows from the structure of A and b that the sequence $(x_t)_{t\ge0}$ is also bounded. Furthermore, condition (H) guarantees that (11) holds and thus there exists $\kappa > 0$ such that $f(c^Tx_t) \ge \kappa c^Tx_t$ for every $t \ge 0$. Consequently,

$$x_{t+1} = Ax_t + bf(c^Tx_t) \ge (A + \kappa bc^T)x_t, \quad t \ge 0.$$

Now, by (A3), there exists an integer k such that the matrix $(A + \kappa bc^T)^k$ is positive. Denoting by e_i the i-th element of the canonical basis of $\mathbb{R}^n$, we have, for every $i = 1, \ldots, n$,

$$x_{t,i} = e_i^T x_t \geq e_i^T (A + \kappa bc^T)^k x_{t-k}, \quad t \geq k.$$

Denoting the minimum of the positive n components of the row $e_i^T (A + \kappa bc^T)^k$ by $\varepsilon_i > 0$, it follows that

$$x_{t,i} \geq \varepsilon_i \|x_{t-k}\|_1, \quad t \geq k.$$

Invoking Lemma 3 yields that $\inf_{t \geq k} x_{t,i} > 0$, and (17) follows, completing the proof. □

As has been mentioned in the Introduction, stability results for systems of the form (2) with f satisfying a sector condition, are known in systems & control theory as absolute stability results. Not surprisingly, whilst absolute stability criteria guarantee stability for all nonlinearities in the given sector, they can be conservative in the sense that there may exist nonlinearities (or indeed, large classes of nonlinearities) which do not satisfy the relevant sector condition, but for which system (2) is nevertheless (globally asymptotically) stable. This is illustrated by Theorem 1 which shows that, for systems of the form (2) with A and b given by (4), the equilibrium x^* is a stable global attractor for any nonlinearity f satisfying (H), an assumption considerably less restrictive than the sector condition (C).

4. Consequences of the main result

Theorem 1 shows that (2) (with A and b given by (4)) has a global stable attractor, provided the one-dimensional difference equation $z_{t+1} = f_p(z_t)$ has a global stable attractor. Results on the existence of global attractors in one-dimensional dynamics go back, at least, to the paper [11] by Coppel, where it is proved that the absence of orbits of period two is necessary and sufficient for the existence of a positive global attractor. Coppel's result is not easily applicable, but there are other results which are. Some of these will now be used to formulate conditions which are easier to verify and which are sufficient for hypothesis (H) to hold.

Many density dependencies considered in ecology are ultimately decreasing, thereby taking into account the intra-species competition in the presence of limited resources. It has been proved that if f is a density dependence, then usually local stability implies global stability [12]. The first such result was proved by Singer [13]. It is based on properties of functions with negative Schwarzian derivative. Combining [13] (see also [14, 15]) with Theorem 1, leads to the following corollary.

Corollary 1. *Assume A and b are as in* (4)*, $c \in \mathbb{R}^n_+ \setminus \{0\}$ and* (A3) *holds. Let $f \in C^3(\mathbb{R}_+, \mathbb{R}_+)$ be such that $f(0) = 0$, $f(y) > 0$ for all $y > 0$ and*

(S) *f has a unique critical point $c \in (0, \infty)$ with $f'(y) > 0$, $y \in (0, c)$, $f'(y) < 0$, $y \in (c, \infty)$; f is concave in $(0, c)$; and its Schwarzian derivative Sf satisfies*

$$Sf(y) := \frac{f'''(y)}{f'(y)} - \frac{3}{2}\left(\frac{f''(y)}{f'(y)}\right)^2 < 0, \quad y \in \mathbb{R}_+ \setminus \{0, c\}.$$

If f_p has a positive fixed point y^* with $|f_p'(y^*)| < 1$, then system (2) *has a positive global stable attractor.*

As we will see soon, Corollary 1 is a useful tool in the stability analysis of systems of the form (2) with A and b given by (4). Evidently, condition (S) is difficult to compare with the sector condition (C). The next result, which follows from Theorem 1 combined with the enveloping technique developed by Cull [7, Corollary 5], provides a generalization of (C).

Corollary 2. *Assume A and b are as in* (4)*, $c \in \mathbb{R}^n_+ \setminus \{0\}$ and* (A3) *holds. Let $f \colon \mathbb{R}_+ \to \mathbb{R}_+$ be a continuous map satisfying the following condition.*

(E) *There exists $y^* > 0$ such that f_p satisfies condition* (11) *and*

$$(f_p(y) - \psi_\eta(y))(y - y^*) > 0, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\}, \tag{18}$$

where ψ_η is the linear fractional function

$$\psi_\eta(y) = \frac{y^*(y^* - \eta y)}{\eta y^* - (2\eta - 1)y}, \quad \text{with } \eta \in [0, 1/2]. \tag{19}$$

Then, system (2) *has a positive global stable attractor.*

We say that f_p is *enveloped* by the linear fractional function (19) if condition (18) holds. With the particular choice of $\eta = \frac{1}{2}$, condition (E) is equivalent to condition (C).

Example 1. We illustrate our results by analyzing a population model for *Chinook Salmon* (*Oncorhynchus tshawytscha*) [16]. Consider system (2) with A, b and c as in (4) and $n = 5$. Following Example 4.1 in [1], we adopt the parameter values of A and b as

$$\delta = 1,\ a_1 = 0.0131,\ a_2 = 0.8,\ a_3 = 0.7896,\ a_4 = 0.6728,\ b_1 = 1$$

and $c = rc_0$ with

$$c_0^T = (0, 0, 0.3262, 5.0157, 39.6647), \quad r \in (0, \infty). \tag{20}$$

We have $p = p_0/r$, with $p_0 := 1/(c_0^T(I - A)^{-1}b) \approx 3.7628$, where 3.7628 is sightly smaller than p_0.

We consider two cases: generalized Beverton-Holt function and Hassel map.

Case (i). Let f be the generalized Beverton-Holt function given by

$$f(y) = \frac{8y/5}{1 + 3y^5/5}. \tag{21}$$

In the introduction, we have graphically seen that f does not satisfy the sector condition (C) for $p = 1$, and numerically we have observed that f does not satisfy this condition for $p < 1.1162$. Thus, the results in [1] do not apply if $p < 1.1162$. However, the generalized Beverton-Holt function (21) satisfies condition (S) (see [17]). Moreover, the fixed points of f_p are 0 and

$$y^* = \sqrt[5]{\frac{5p - 8}{3p}}.$$

Additionally, $f_p'(y^*) = (25p - 32)/8$. Thus, if $p = p_0/r \in (24/25, 8/5)$, then $|f_p'(y^*)| < 1$, and Corollary 1 guarantees the existence of a positive global stable attractor.

Note that $p = p_0/r \in (24/25, 8/5)$ is guaranteed if $2.3519 < r < 3.9195$. Figure 2 illustrates that the result is quite sharp. There, we have plotted the asymptotic population size as a function of the parameter r. We observe that the population goes to extinction for $r < 2.3519$, at which point a positive attractor appears in a saddle-node bifurcation and it is present for $2.3519 < r < 3.9195$. As r increases beyond 3.9195, the attractor seems to persist for a while (see

detail graph in the middle of the figure). The population size is always positive, but as r increases further, the range of fluctuations also increases. The panels at the bottom of Figure 2 show the evolution of the population size in the first 300 generations to illustrate the three described behaviours.

Case (ii). Let f be the Hassel map given by

$$f(y) = \frac{125y}{(1+24y)^{3/2}}. \tag{22}$$

Again, we have seen in the introduction that f does not satisfy the sector bounded condition (C) for $p = 1$. Indeed, it can be seen numerically that condition (C) fails outside the range $1.1999 < p < 125$. On the other hand, its Schwarzian derivative,

$$Sf(y) = \frac{31104y^2 - 10368y - 1296}{82944y^4 - 6912y^3 - 432y^2 + 24y + 1},$$

is not negative as its graph illustrates, see Figure 3.

Therefore, it is not possible to use Corollary 1 and the result in [1] guarantees the existence of an attractor in a bounded interval of the parameter r only. However, we will see that an application of Corollary 2 leads to a substantial improvement of the result.

The fixed points of f_p are 0 and

$$y^* = \frac{25 - p^{2/3}}{25p^{2/3}}.$$

For $p < 125$, the map f_p satisfies condition (11) and is enveloped by the linear fractional function $\psi_0(y) = (y^*)^2/y$. The latter follows from a change of variables $y = zy^*$, allowing us to apply the results for Model VI in [7]. Therefore, Corollary 2 guarantees the existence of a positive global stable attractor for all $r \in (p_0/125, \infty)$ with $p_0/125 \approx 0.0301$.

Example 2. In this example we consider a recent result published in [18], where it was analyzed how harvesting influences the dynamics of the following stage-structure model with two age classes (juveniles and adults):

$$\begin{aligned} x_{t+1,1} &= g((1-h_2)x_{t,2}), \\ x_{t+1,2} &= (1-h_1)s_1x_{t,1} + (1-h_2)s_2x_{t,2}, \end{aligned} \tag{23}$$

where $x_{t,1}$ and $x_{t,2}$ denote the numbers of juveniles and adults at time step t, respectively, $h_1, h_2 \in [0,1)$ and $s_1, s_2 \in (0,1]$ are the corresponding harvest and survivorship rates, and $g(y) = \alpha y e^{-\beta y}$ is the Ricker map with $\alpha > 1$, $\beta > 0$.

Changing variables, $y_t := (\beta/r)x_{t,2}$, where $r := \ln \alpha > 0$, (23) can be reduced to the following second-order scalar difference equation

$$y_{t+1} = (1-h_2)s_2 y_t + (1-h_1)s_1(1-h_2)y_{t-1}e^{r(1-(1-h_2)y_{t-1})}. \tag{24}$$

By using a result in [19], it is proved in [18] (see [18, Proposition 2.1]) that (24) has a positive global attractor for

$$r \in (r_0, r_0+1], \quad \text{where } r_0 := \ln\big(\frac{1-(1-h_2)s_2}{(1-h_1)(1-h_2)s_1}\big). \tag{25}$$

We will use Corollary 1 to show that the existence of a positive global attractor for (24) is guaranteed for a range of parameter values r larger than that given in (25). To this end, we note that equation (24) can be rewritten as a system of the form (2) with $\delta = 1-(1-h_2)s_2$, $a_1 = 1$, $b_1 = 1$, $c_1 = 0$, $c_2 = 1-h_2$ in (4), and $f(y) := (1-h_1)s_1 y e^{r(1-y)}$. This function f satisfies condition (S), see e.g. [14]. Moreover,

$$p = \frac{1-(1-h_2)s_2}{1-h_2}.$$

Routine calculations show that f_p has a unique positive fixed point $y^* = 1 - r_0/r$ if, and only if, $r > r_0$ and that this fixed point satisfies $f'(y^*) = p(1+r_0-r)$. Consequently, $|f'(y^*)| < p$ if, and only if, $r \in (r_0, r_0+2)$, and thus, Corollary 1 guarantees that system (23) has a positive global attractor for $r \in (r_0, r_0+2)$, thereby increasing the range of parameter values r as compared to (25).

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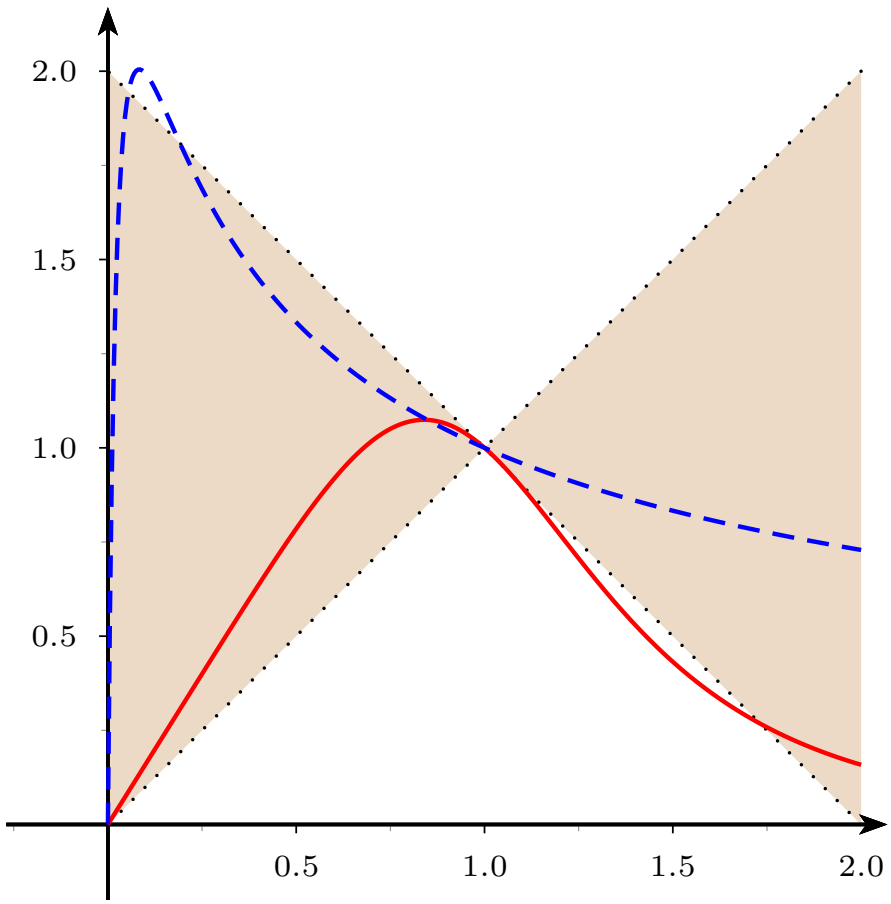

Figure 1: The sector region, in the case $p = 1$, appears in light brown colour. Observe that condition (C) is not satisfied: neither by the generalized Beverton-Holt map with $K = \sqrt[5]{5/3}$, $\lambda = 8/5$, $\beta = 5$ (solid red curve) nor by the Hassel map with $K = 1/24$, $\lambda = 125$, $\beta = 3/2$ (dashed blue curve). For the chosen parameters $y^* = 1$ is the unique positive solution of the equation $f(y) = y$ and $|f'(1)| < 1$ for both maps.

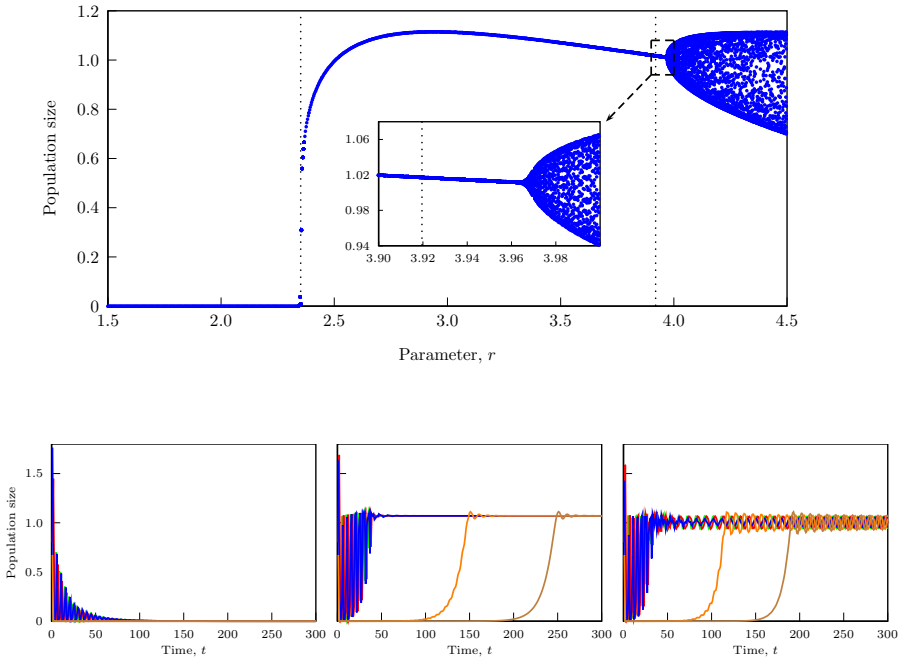

Figure 2: Asymptotic population size as a function of the parameter in Example 1 (the top panel). We have calculated 6020 generations to remove the initial transients and the plot shows the sizes of the last 20 generations. The initial population size is chosen as a pseudo-random vector for each of the 1000 different values of r considered. Simulations of the global dynamics with increasing r (bottom panels): for $r \in (0, 2.3518)$ the population goes towards extinction (left); for $r \in (2.3519, 3.9195)$ there is a positive stable equilibrium; and for $r > 3.9195$ the equilibrium becomes unstable but solutions remain bounded. In each of the three cases we have chosen the following five different initial conditions biased totally to each of the five stage classes, $x_0 = e_i$ for $i = 1, \ldots, 5$.

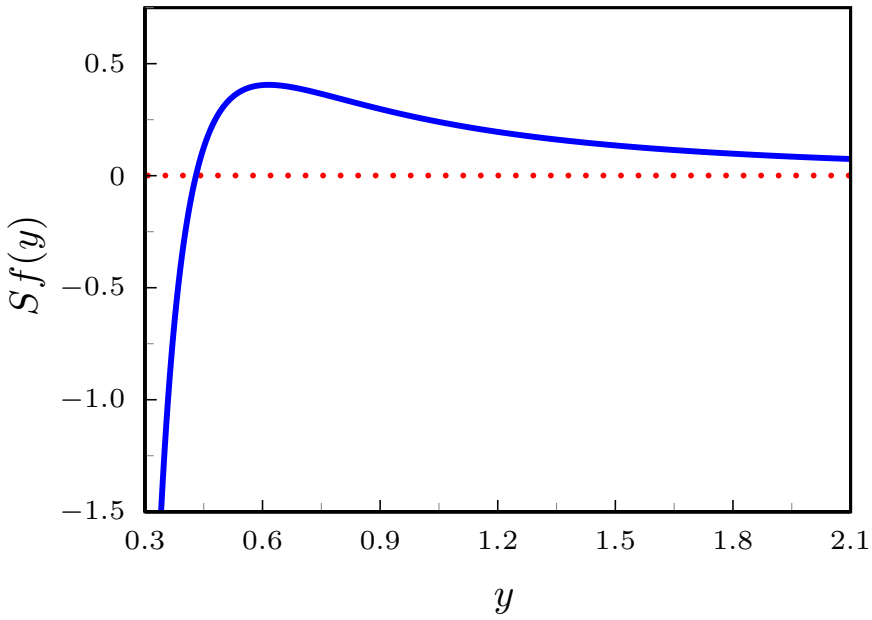

Figure 3: Schwarzian derivative of the Hassel map (22).