The Discrete Dynamics of Monotonically Decomposable Maps

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Abstract

We extend results of Gouzé and Hadeler [14] concerning the dynamics generated by a map on an ordered metric space that can be decomposed into increasing and decreasing parts. Our main results provide sufficient conditions for the existence of a globally asymptotically stable fixed point for the map. Applications to discrete-time, stage-structured population models are given.

This paper is dedicated to Karl Hadeler on the occasion of his 70th Birthday

1 Introduction

The idea of decomposing a dynamical system into its increasing and decreasing parts and embedding the system into a larger symmetric monotone dynamical system is an old one. A paper of Gouzé and Hadeler [14] cites some of this history; see also Thieme [23, 24] and the references therein. Apparently it began with a 1959 paper of Schröder [20]. The early motivation was in numerical analysis where monotonically convergent iteration schemes have played an important role. See section 21.2 of the classic text of Collatz [4]. Thieme [23, 24] exploited the method to prove existence of solutions of integral equations by deriving a globally convergent iteration scheme. The first use of the idea in dynamical systems appears to be by J.-L. Gouzé in [13] who applied it to obtain global convergence to equilibrium for systems of ordinary differential equations. Later, Gouzé and Hadeler [14] extended and clarified the ideas although they did not articulate its use for global stability of equilibria. C. Cosner [3] rediscovered the idea in the context of systems of reaction diffusion systems where comparison principles allow its effective use to obtain invariant regions and convergence to equilibrium. M. Kulenović, G. Ladas, W. Sizer [18] essentially used the idea in their work on global convergence of second order difference equations. See also the monograph of M. Kulenović, G. Ladas [17]. These same ideas seem to underlie some nice results in the control theory of continuous dynamical systems obtained recently by D. Angeli and E.D. Sontag [1] and extended by various collaborators, including the present author [11, 12]. Their Small Gain Theorem can be obtained by an application of the ideas discussed here.

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Our goal in this paper is to briefly discuss the key ideas, many of which are contained in [14], although we have made certain improvements, especially regarding global convergence, and to provide examples from population biology.

2 Main Results

Let X be an ordered metric space with closed order relation $\leq$. The closedness of the order relation means that if $x_n \leq y_n$ and $x_n \to x,\ y_n \to y$, then $x \leq y$. If $x \leq y$, define the order interval $[x, y] := \{z \in X : x \leq z \leq y\}$. In most applications, $X \subset Z$, where Z is an ordered Banach space and X derives its topology and order relation from that of Z. Let $f : X \times X \to X$ be continuous.

Following Gouzé and Hadeler [14], our focus is the discrete-time dynamical system

$$x' = F(x) := f(x, x) \tag{1}$$

where x' denotes the successor to x. The following will be assumed to hold:

(H1) $\forall y \in X,\ x_1, x_2 \in X,\ x_1 \leq x_2 \Rightarrow f(x_1, y) \leq f(x_2, y)$.

(H2) $\forall x \in X,\ y_1 \leq y_2 \Rightarrow f(x, y_2) \leq f(x, y_1)$.

In short, f is nondecreasing in its first variable and nonincreasing in its second. Roughly, F is a map that combines both positive and negative feedback. We write $F^n(x)$ for the n-fold composition of F acting on x. The omega limit set of a subset $A \subset X$ is denoted by $\omega_F(A)$ and that of a single point $x \in X$, is denoted by $\omega_F(x)$.

As shown in [14], (1) can be embedded in the symmetric discrete-time dynamical system

$$\begin{aligned} x' &= f(x, y) \\ y' &= f(y, x) \end{aligned} \tag{2}$$

on $X \times X$. We use the notation $z = (x, y)$ and

$$G(z) = G(x, y) = (f(x, y), f(y, x))$$

Obviously, the diagonal

$$D = \{(x, x) : x \in X\}$$

is positively invariant under (2) and $G(x, x) = (F(x), F(x))$. The symmetry of G can be expressed by defining the reflection operator $R(x, y) = (y, x)$ and observing that $G \circ R = R \circ G$.

The "southeast" ordering on $X^2 := X \times X$ is the closed partial order relation defined by

$$(x, y) \leq_C (\bar{x}, \bar{y}) \Longleftrightarrow x \leq \bar{x} \text{ and } \bar{y} \leq y.$$

It's name derives from the fact that the bigger point lies southeast of the smaller one. Observe that $R : X^2 \to X^2$ is order reversing:

$$(x, y) \leq_C (\bar{x}, \bar{y}) \Longleftrightarrow R(\bar{x}, \bar{y}) = (\bar{y}, \bar{x}) \leq_C (y, x) = R(x, y).$$

Although the map F is not monotone, the symmetric embedding G is monotone, an idea continually rediscovered. See especially the articles of Gouzé [13] and of Gouzé and Hadeler [14] for references to earlier work. See also Cosner [3] and Kulenović and Ladas [17]. The next result is essentially known (Proposition 2.1 [14]) but we give a proof due its simplicity.

Lemma 1. *G is monotone with respect to $\leq_C$ on $X \times X$ in the sense that*

$$z \leq_C \bar{z} \Longrightarrow G(z) \leq_C G(\bar{z}).$$

Proof: $(x, y) \leq_C (\bar{x}, \bar{y}) \Longrightarrow x \leq \bar{x}$ and $\bar{y} \leq y$. Therefore,

$$\begin{aligned} x' &= f(x, y) \leq f(x, \bar{y}) \leq f(\bar{x}, \bar{y}) = \bar{x}' \\ y' &= f(y, x) \geq f(y, \bar{x}) \geq f(\bar{y}, \bar{x}) = \bar{y}' \end{aligned}$$

Thus, $G(x, y) \leq_C G(\bar{x}, \bar{y})$. ∎

Our main result is a sharpened version of Theorem 7 in [14].

Theorem 2. *Suppose that:*

$$\exists x_0, y_0,\ x_0 \leq y_0,\ \text{satisfying } f(x_0, y_0) \geq x_0,\ f(y_0, x_0) \leq y_0. \tag{3}$$

Then $F([x_0, y_0]) \subset [x_0, y_0]$ and for $z_0 = (x_0, y_0)$ and $n \geq 1$, we have:

$$z_0 \leq_C G^n(z_0) \leq_C G^{n+1}(z_0) \leq_C R z_0.$$

Assume, in addition, that

$$\{G^n(x_0, y_0)\}_{n \geq 1} \text{ converges in } X. \tag{4}$$

Then:

(i) there exist $x_*, y_* \in [x_0, y_0]$ with $x_* \leq y_*$ satisfying

$$G^n(x_0, y_0) \longrightarrow (x_*, y_*) = G(x_*, y_*),$$

implying that $f(x_*, y_*) = x_*$, $f(y_*, x_*) = y_*$.

(ii) If $x \in [x_0, y_0]$ and $\{F^n(x)\}_{n \geq 1}$ has compact closure in X, then

$$\omega_F(x) \subset [x_*, y_*]. \tag{5}$$

(iii) If $F([x_0, y_0])$ has compact closure in X, then $\omega_F([x_0, y_0]) \neq \emptyset$, and

$$\omega_F([x_0, y_0]) \subset [x_*, y_*]. \tag{6}$$

Proof: Inequality $x_0 \le y_0$ implies that $z_0 := (x_0, y_0) \le_C (y_0, x_0) = Rz_0$. Define the C-order interval

$$I = [z_0, Rz_0]_C := \{(x, y) : (x_0, y_0) \le_C (x, y) \le_C (y_0, x_0)\} = \{(x, y) : x_0 \le x, y \le y_0\}$$

and observe that

$$[z_0, Rz_0]_C \cap D = \{(x, x) : x \in [x_0, y_0]\}.$$

(3) implies that

$$(x_0, y_0) \le_C (f(x_0, y_0), f(y_0, x_0))$$

and consequently, by monotonicity of G and order reversing property of R,

$$z_0 \le_C G(z_0) \le_C RG(z_0) = G(Rz_0) \le_C Rz_0.$$

By induction, for $z \in I$ and $n \ge 0$ we have

$$z_0 \le_C G^n(z_0) \le_C G^{n+1}(z_0) \le_C G^{n+1}(z) \le_C G^{n+1}(Rz_0) \le_C G^n(Rz_0) \le_C Rz_0.$$

By our assumption (4) that the monotone sequence $\{G^n(z_0)\}$ converges, $G^n(z_0) \nearrow z_* = (x_*, y_*)$ and $G^n(Rz_0) \searrow Rz_* = (y_*, x_*)$, the monotonicity implied by the slanted arrows is relative to $\le_C$. Symmetry of G implies that if we write $G^n(z_0) = (x_n, y_n)$ then $G^n(Rz_0) = RG^n(z_0) = (y_n, x_n)$, where $x_n \nearrow x_*$ and $y_n \searrow y_*$, the monotonicity implied by the slanted arrows is relative to $\le$. Also, note that $G^n(z_0) \le_C RG^n(z_0)$ implies that $x_n \le y_n$. Putting $z = (x, x)$, where $x \in [x_0, y_0]$, into the above inequality yields

$$z_0 \le_C G^n(z_0) \le_C G^n(z) = (F^n(x), F^n(x)) \le_C G^n(Rz_0) \le_C Rz_0$$

and taking first components gives

$$x_0 \le x_n \le F^n(x) \le y_n \le y_0, \quad x \in [x_0, y_0],\ n \ge 1.$$

Obviously, $\omega_F(x) \subset [x_*, y_*]$ if the orbit of x is precompact. If $F([x_0, y_0])$ has compact closure in X, then

$$\omega_F([x_0, y_0]) = \cap_{n\ge1} \overline{F^n([x_0, y_0])} \subset [x_*, y_*]$$

∎

Global convergence was strangely ignored in [14]. The next result follows immediately from the characterization of x_* and y_* in Theorem 2.

Corollary 3. *Let the hypotheses (3) and (4) of Theorem 2 hold and suppose that*

$$a, b \in [x_0, y_0],\ a \le b,\ f(a, b) = a,\ b = f(b, a) \Rightarrow a = b \tag{7}$$

holds. Then $x_* = y_*$ and $F(x_*) = x_*$.

If $x \in [x_0, y_0]$ and $\{F^n(x)\}_{n\ge1}$ has compact closure in X, then

$$\omega_F(x) = \{x_*\}.$$

If $F([x_0, y_0])$ has compact closure in X, then

$$\omega_F([x_0, y_0]) = \{x_*\}.$$

Symmetry dictates that fixed points of (2) come in pairs (a, b) and (b, a); if $a = b$, we say the fixed point is symmetric. Since $a \leq b$ if and only if $(a, b) \leq_C (b, a)$, hypothesis (7) just says that (2) does not have a C-ordered, non-symmetric pair of equilibria in the order interval $I := [(x_0, y_0), (y_0, x_0)]_C$.

Remark 4. Hypothesis (3) of Theorem 2 implies that F maps $[x_0, y_0]$ into itself. In case that $X \subset Z$, where Z is an ordered Banach space, $[x_0, y_0]$ is convex, and $F([x_0, y_0])$ has compact closure in X, then it contains a fixed point by the Schauder Theorem. More sophisticated fixed point theorems could also be applied. By Corollary 3, (7) is sufficient for the existence and uniqueness of a fixed point of F.

Remark 5. The hypothesis (4) that the monotone, order-bounded orbit $\{G^n(x_0, y_0)\}_{n\geq 1}$ converges in X may be satisfied under a variety of assumptions concerning the space X and the map f. It is satisfied, for example, if X is a closed subset of a finite dimensional Banach space or of $L^p(\Omega)$ where monotone dominated sequences converge. It is satisfied as well if the map f has some compactness properties. If $f([x_0, y_0] \times [x_0, y_0])$ has compact closure in X, then $G([x_0, y_0] \times [x_0, y_0])$ has compact closure in $X \times X$ and the hypothesis is then satisfied.

Remark 6. If X is a convex subset of $\mathbb{R}^n$, $K = \mathbb{R}^n_+$ and F is C^1 with $|\frac{\partial F_i}{\partial x_j}(x)| \leq m_{ij}$ for all i, j and $x \in X$, then $F(x) = f(x, x)$ where

$$f(x, y) = Mx + F(y) - My$$

satisfies (H1) and (H2). Gouzé [13] gave a similar result for ordinary differential equations.

Map f is said to have a characteristic $k_x : X \to X$ if to each $y \in X$, there is a unique fixed point $x := k_x(y)$ satisfying $x' = f(x, y) = x$. It follows that x is a fixed point of F if and only if it is a fixed point of k_x.

Lemma 7. *If f has characteristic k_x and monotone orbits of the map $x \to f(x, y)$ converge for each fixed $y \in X$, then k_x is nonincreasing:*

$$y_1 \leq y_2 \Longrightarrow k_x(y_2) \leq k_x(y_1).$$

Proof: Let $x_i = k_x(y_i)$, $i = 1, 2$. Then we have $x_1 = f(x_1, y_1) \geq f(x_1, y_2)$ so, by monotonicity, $f^n(x_1, y_2) \geq f^{n+1}(x_1, y_2)$ for $n \geq 1$. If the monotone orbit $\{f^n(x_1, y_2)\}_{n\geq 1}$ converges, then it converges to $x_2 = k_x(y_2)$ by definition of the characteristic. Hence $x_2 \leq x_1$. ∎

We will not require the hypothesis of Lemma 7 but it motivates an assumption in the following result.

Corollary 8. *Suppose that $e = \inf X$ exists and belongs to X and that f has characteristic k_x satisfying $k_x(x) \leq k_x(y)$ for $y \leq x$. In addition, suppose that $f([e, k_x(e)] \times [e, k_x(e)])$ has compact closure in X. Let $X_0 := \cup_{y\geq k_x(e)}[k_x(y), k_x(e)]$. If k_x has no pair $u, v \in X$, $u < v$ such that $k_x(u) = v$, $k_x(v) = u$, then F has a fixed point $x_* \in [k_x(k_x(e)), k_x(e))]$ such that*

$$\omega_F(x) = x_*, \ x \in X_0.$$

Proof: Apply Theorem 2 and the remark following it, using $y_0 = k_x(e)$ and, for any $y \in X$ satisfying $y \geq y_0$, $x_0 = k_x(y)$. Then $x_0 \leq y_0$,

$$f(x_0, y_0) \geq f(k_x(y), y_0) \geq f(k_x(y), y) = k_x(y) = y_0,$$

and

$$f(y_0, x_0) = f(k_x(e), x_0) \leq f(k_x(e), e) = k_x(e) = y_0.$$

Then $\omega_F(x) \subset [x_*, y_*]$ for $x \in [x_0, y_0]$ where $x_* \leq y_*$, $f(x_*, y_*) = x_*$ and $f(y_*, x_*) = y_*$. Then $x_* = k_x(y_*)$ and $y_* = k_x(x_*)$ and so by hypothesis $x_* = y_*$ and Corollary 3 implies that $x_* = y_*$ is a fixed point of F and $\omega_F(x) = \{x_*\}$. As this argument applies to every $x_0 = k_x(y),\ y \geq y_0$, the result is proved. ∎

3 Higher Order Difference Equations

Motivated by the rational difference equation

$$x_{n+1} = \frac{\alpha x_n + \beta x_{n-1}}{\gamma x_n + \delta x_{n-1}},$$

where $\alpha, \beta, \gamma, \delta > 0$ and $x_0, x_{-1} > 0$, Kulenović, Ladas and Sizer [18] consider the general recursive sequence generated by

$$x_{n+1} = g(x_n, x_{n-1}) \tag{8}$$

for given $x_{-1}, x_0 > 0$ where $g : P^2 \to P := (0, \infty)$ has certain monotonicity properties. See also [17]. If (1) g is increasing in its first argument and decreasing in its second; (2) there exists $a, b > 0$ such that $a \leq g(x, y) \leq b$ for all (x, y), and (3) $g(m, M) = m$ and $g(M, m) = M$ implies $m = M$, then they show (Theorem 6.2) that (8) has a globally attracting fixed point. In case g is decreasing in x and increasing in y, then the same result holds. If g is increasing in both variables then (8) generates monotone dynamics so it can be treated using results in [21, 15, 16].

We may generalize these results by considering (8) where $g : X \times X \to X$ and X is an ordered metric space.

Theorem 9. *Let $g(x, y)$ satisfy (H1) and (H2) on $X^2 = X \times X$, and*

(i) there exists $a, b \in X$ such that $a \leq b$, $[a, b] \subset X$, $a \leq g(a, b)$ and $g(b, a) \leq b$,

(ii) $g([a, b] \times [a, b])$ has compact closure in X.

(iii) $m, M \in [a, b],\ m \leq M,\ g(m, M) = m$ and $g(M, m) = M \Rightarrow m = M$.

Then there exists $x_* \in [a, b]$ such that all orbits of (8) with $x_0, x_{-1} \in [a, b]$ converge to x_*.

If instead, $h(x, y) := g(y, x)$ satisfies (H1) and (H2) and hypotheses (i)-(iii) hold with h in place of g, then the conclusion holds.

If $g(x,y)$ is nonincreasing in both variables, the last inequalities in (i) are replaced by $a \le g(b,b)$, $g(a,a) \le b$, (ii) holds and the premise $g(m,M) = m$ and $g(M,m) = M$ of (iii) is changed to $g(m,m) = M$ and $g(M,M) = m$, then the conclusion holds.

If $g(x,y)$ is nondecreasing in both variables, the last inequalities in (i) are replaced by $a \le g(a,a)$, $g(b,b) \le b$, (ii) holds and the premise $g(m,M) = m$ and $g(M,m) = M$ of (iii) is changed to $g(m,m) = m$ and $g(M,M) = M$, then the conclusion holds.

Proof: We consider first the case that g satisfies (H1) and (H2). Converting (8) to a first order system, we have

$$\begin{aligned} x_{n+1} &= g(x_n, y_n) \\ y_{n+1} &= x_n \end{aligned}$$

or, if $z = (x,y)$ and $F(z) = (g(x,y), x)$, this becomes

$$z_{n+1} = F(z_n),\ z_0 \in X^2.$$

Define $f : X^2 \times X^2 \to X^2$ by

$$f(u,v) = (g(u_1,v_2), u_1),\ u = (u_1,u_2),\ v = (v_1,v_2).$$

Then $F(z) = f(z,z)$. Let $\le_2$ denote the usual ("northeast") partial order on X^2: $(u,v) \le_2 (\bar{u},\bar{v}) \Leftrightarrow u \le \bar{u}$ and $v \le \bar{v}$. Then f satisfies (H1) and (H2) on $X^2 \times X^2$. Let $A = (a,a)$ and $B = (b,b)$ so $A \le_2 B$,

$$A = (a,a) \le_2 (g(a,b), a) = f(A,B),$$

and

$$f(B,A) = (g(b,a), b) \le_2 (b,b) = B.$$

Furthermore, if $C, D \in [A,B] = [a,b] \times [a,b]$, $C \le_2 D$, $f(C,D) = C$, $f(D,C) = D$, then $(c_1,c_2) = (g(c_1,d_2), c_1)$ and $(d_1,d_2) = (g(d_1,c_2), d_1)$ so it follows that $C = (c,c), D = (d,d)$, $g(c,d) = c$, and $g(d,c) = d$. By hypothesis (iii), $c = d$, hence $C = D$.

The symmetric map $G : X^2 \times X^2 \to X^2 \times X^2$ given by

$$G(u,v) = (f(u,v), f(v,u)) = ((g(u_1,v_2), u_1), (g(v_1,u_2), v_1))$$

has the property that $G^2([A,B])$ is compact by hypothesis (ii). ¿From this, Theorem 2 and Corollary 3, we conclude that $\omega_F([A,B]) = \{x_*\}$ for some fixed point x_* of F.

In case that h satisfies (H1) and (H2), we define $f(u,v)$ as follows

$$f(u,v) = (g(v_1,u_2), u_1).$$

Then $F(z) = f(z,z)$ and the remainder of the argument is similar to the one above.

In case g is nonincreasing in both variables, we define $f(u,v)$ as follows

$$f(u,v) = (g(v_1,v_2), u_1).$$

Then $F(z) = f(z,z)$ and the remainder of the argument is similar to the one above.

In case g is nondecreasing in both variables, then there is no need to use Theorem 2 as F is monotone and $F^2([A,B])$ is compact so the result follows from elementary arguments.

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Remark 10. If there exist $a, b \in X$ such that $[a, b] \subset X$, $a \le g(x, y) \le b$ for all $(x, y) \in X^2$, as assumed in [17], then (1) holds. In this case, all orbits converge to x_* since $F^2(z) \in [A, B]$ for every $z \in X^2$. See [17, 18] for applications of these results to rational difference equations.

It is obvious that similar results hold for difference equations of order greater than two by this technique. For example for the third order system

$$x_{n+1} = g(x_n, x_{n-1}, x_{n-2}) \tag{9}$$

where $g : X^3 \to X$ is continuous on $X^3 = X \times X \times X$, one obtains a variant of Theorem 9 for every partition of the variables (x, y, z) into nondecreasing ones and nonincreasing ones for $g(x, y, z)$.

See Krause and Pituk [19] and El-Morshedy and Liz [10] for other approaches to such systems.

4 Stage Structured Dynamics with Stocking

4.1 No delay in density dependence

Consider the discrete, nonlinear, stage-structured demographic model with density dependent survival probabilities and fertility rates and immigration or stocking given by:

$$x_{n+1} = A(x_n)x_n + e, \ n \ge 0, \ x_0 \ge 0, \tag{10}$$

where the per-generation immigration term $e \ge 0$. See Cushing [6] for a discussion of nonlinear matrix models. The components of x_n give the populations in the various stages at census n. Here, $X = \mathbb{R}^m_+$ and $x \le y$ is the usual component-wise ordering; we write $x < y$ if $x \le y$, $x \ne y$ and $x \ll y$ when $x_i < y_i$ for all i. We make the following assumptions regarding the continuous matrix-valued mapping $x \to A(x)$:

(a) $A(y) \ge 0$ for all $y \ge 0$.

(b) $y_1 \le y_2 \Rightarrow A(y_2) \le A(y_1)$.

(c) $\rho(A(e)) < 1$ and $\exists v > 0$ such that $A(e)v = \rho v$ and $sv \ge e$ for large $s > 0$.

Here, $\rho(A)$ denotes the spectral radius of A. All inequalities involving matrices, as for vectors, are to be interpreted componentwise. Assumptions (a) and (b) are quite natural; (b) codifies the density dependent nature of survival and fertility coefficients. Note that hypothesis (c) contains a restriction on e since we require $sv \ge e$ for large $s > 0$; in case v has positive components ($v \gg 0$), then there is no restriction on e since this inequality holds for large s. Hypothesis (c) does not have a strong biological motivation; it can be viewed as assuming "large emigration". In the absence of immigration, $e = 0$, $R_0 := \rho(A(0))$ is referred to as the basic reproductive number: if $R_0 < 1$ then $x_n \to 0$, if $R_0 > 1$ then the population persists. By (b) and the Perron-Frobenius theory $\rho(A(x)) \le \rho(A(y))$ when $y \le x$ so if $R_0 \ge 1$, then

(c) requires that e be large enough. Hypothesis (c) has important mathematical implications. Observe that

$$x_n \geq e, \; n \geq 1$$

so by (b) we have

$$x_{n+1} = A(x_n)x_n + e \leq A(e)x_n + e, \; n \geq 1$$

and by iterating this inequality we get

$$x_{n+1} \leq A^{n+1}(e)x_1 + \sum_{j=0}^{n} A(e)^j e.$$

By virtue of (c), $A^{n+1}(e)x_1 \to 0$ and $\sum_{j=0}^{n} A(e)^j e \to \sum_{j=0}^{\infty} A(e)^j e = (I - A(e))^{-1}e$. Therefore, orbits are bounded. Indeed, orbits are asymptotic to $[e, x_\infty]$ where

$$x_\infty := (I - A(e))^{-1}e.$$

Defining $f : \mathbb{R}^n_+ \times \mathbb{R}^n_+ \to \mathbb{R}^n_+$ by

$$f(x, y) = A(y)x + e,$$

it is easily seen that assumptions (H1) and (H2) hold. Let $x_0 = e$, we have for all $y_0 \geq x_0$,

$$f(x_0, y_0) = A(y_0)e + e \geq e = x_0.$$

Let $y_0 = rv$ for $r > 0$ to be determined. If $\rho = \rho(A(e))$, then

$$f(y_0, x_0) = rA(e)v + e = r\rho v + e$$

so that $f(y_0, x_0) \leq y_0$ if and only if $r\rho v + e \leq rv$, or equivalently, if

$$e \leq r(1 - \rho)v.$$

Since $\rho < 1$ by (c) and $v > 0$, there exists $r_0 > 0$ such that the inequality holds for all large $r > r_0$ and consequently $y_0 \geq r_0 v > e = x_0$. Therefore, we may apply Theorem 2 to obtain the following result.

Proposition 11. *Assume that (a)-(c) hold. Then there exists a unique $x_* \geq e$ satisfying $x_* = A(x_*)x_* + e$ and every orbit of (10) converges to x_*.*

Proof: For each $r > r_0$, we may apply Theorem 2 with $x_0 = e$ and $y_0 = rv$. In order to apply Corollary 3, suppose that there exist $a \leq b$ such $a, b \in [e, rv]$, $A(b)a + e = a$, and $A(a)b + e = b$. As $e \leq a \leq b$, $A(b) \leq A(a) \leq A(e)$ implying that $\rho(A(b)) \leq \rho(A(a)) \leq \rho(A(e)) < 1$ (see [2]) and therefore

$$e = (I - A(b))^{-1}a = \sum_{j \geq 0} A(b)^j a$$

and a similar formula holds with a and b interchanged. But $A(b)^j a \leq A(a)^j b$ by (b) so we conclude that $a = b$. The existence of $x_* \in [e, rv]$ and the global convergence to x_* of orbits initiating in $[e, rv]$ follows. Since $x_n \geq e$ for $n \geq 1$ and $rv > x_\infty$ for large r, the global convergence claim holds. ∎

Remark 12. The map $F(x) = A(x)x + e$ is sublinear in the sense that $0 < \lambda < 1 \Rightarrow \lambda F(x) \leq F(\lambda x)$. However, it is not monotone so the usual sublinearity type results do not generally apply. See e.g. [16].

4.2 The LPA model for the flour beetle *Tribolium*

The LPA model of Costantino et al. [5] is greatly celebrated in population biology due to the close correspondence between its predictions and observed features in controlled laboratory experiments. It accounts for larvae, pupae, and adult insect densities at 14-day time (census) units. A remarkable aspect of the population dynamics of the flour beetle *Tribolium castaneum* is cannibalism of adults on pupae and adults and pupae on eggs which result in strong nonlinearities in the mathematical model. Originally formulated with no artificial addition (stocking) of insects at each census, the model takes the form of (10) with $e = 0$,

$$x = (x_1, x_2, x_3) = (L, P, A) \in \mathbb{R}^3_+,$$

and

$$A(x) = \begin{pmatrix} 0 & 0 & d\exp(-ax_1 - bx_3) \\ p & 0 & 0 \\ 0 & q\exp(-cx_3) & r \end{pmatrix} \tag{11}$$

where $p, q, r \in (0, 1]$ are survival probabilities, a, b, c are coefficients related to cannibalism and $d > 0$ to fecundity. See [5, 7, 8] for details of the modeling; we have renamed their parameters for mathematical convenience.

As the experimental protocol reported in [5, 7, 8] allows interventions at each census, it is in principle possible to add larvae, pupae, or adults at each census, thus yielding (10) with stocking $e \geq 0$ where e_1 denotes the number of added larvae, e_2 pupae, and e_3 adults at each census. We note that artificial removal of organisms at each census was carried out in experiments described in [5] in order to corroborate bifurcation studies with different survival rates.

Obviously, hypotheses (a) and (b) are satisfied. As $A(e)$ is irreducible, its Perron-Frobenius eigenvector v corresponding to $\rho = \rho(A(e))$ satisfies $v \gg 0$ so (c) holds provided $\rho < 1$. An easy calculation gives the characteristic equation associated with $A(e)$

$$-\lambda^3 + r\lambda^2 + Q = 0$$

where

$$Q = pqd\exp(-ae_1 - (b + c)e_3)$$

The spectral radius is the positive root. Therefore, we have

$$\rho(A(e)) < 1 \Leftrightarrow ae_1 + (b + c)e_3 > \log(R_0)$$

where

$$R_0 = \frac{pqd}{1 - r}$$

is the basic reproductive ratio [8] in the absence of stocking.

Corollary 13. *Global convergence to a fixed point $x_*(e) \geq e$ occurs for the LPA model with stocking vector e provided that*

$$ae_1 + (b + c)e_3 > \log(R_0) \tag{12}$$

The right side of (12) is negative, and therefore there is no restriction on $e \geq 0$ (it could be zero corresponding to no stocking), if $R_0 < 1$. Of course, if $e = 0$, then $x_* = 0$.

Corollary 13 is rather striking in view of the complicated dynamics that is possible without stocking $e = 0$ [7, 8]. Constant stocking can stabilize the population dynamics of the flour beetle *Tribolium.*

4.3 One generation delay in density dependence

It is plausible that density dependence in (10) is delayed one generation resulting in

$$x_{n+1} = A(x_{n-1})x_n + e, \ n \geq 0, \ x_{-1}, x_0 \geq 0. \tag{13}$$

The same arguments used in Proposition 11, but using Theorem 9 with $g(x, y) = A(y)x + e$ instead of Theorem 2 and Corollary 3, establish the following result.

Proposition 14. *Assume that (a)-(c) hold. Then there exists a unique $x_* \geq e$ satisfying $x_* = A(x_*)x_* + e$ and every orbit of (13) converges to x_*.*

It is instructive to see why our results are not expected to work well for the stage structured model (10) when $e = 0$ and $R_0 > 1$ and we would like to use our result to show convergence of iterates to a positive equilibrium x_*. If $A(x_*)$ is strongly positive, then $\rho(A(x_*)) = 1$ and we might seek $0 < x_0 < x_* < y_0$ to apply Theorem 2. Monotonicity of A and the spectral radius imply that $\rho(A(y_0)) \leq \rho(A(x_*)) = 1 \leq \rho(A(x_0))$ and mild additional assumptions imply that these inequalities are strict. Hypothesis (3) requires that

$$A(y_0)x_0 \geq x_0, \ A(x_0)y_0 \leq y_0$$

but here is the problem since the inequality $A(y_0)x_0 \geq x_0$ implies that (Theorem 1.11, [2]) $\rho(A(y_0)) \geq 1$ and the second inequality implies that $\rho(A(x_0)) \leq 1$. Provided one of the inequalities above is strict, these latter inequalities give a contradiction. This failure of the method emphasizes the point made by Gouzé and Hadeler [14] that it is not sufficient to find f satisfying (H1) and (H2) such that $F(x) = f(x, x)$, but one must find f **and** x_0 and y_0 such that (3) holds.

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