Evolutionary Discrete-Time Models in Ecology and Epidemiology

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Outline

- Introduction
- Skew-Product dynamical systems
- Periodic Systems
- One-Point Compactification
- Applications to Epidemic Models
- Applications to population dynamics
- Open Problems

Introduction

The theory of non-autonomous discrete dynamical systems has been developed by many authors including the main contributors Bernd Aulbach and his students and Peter Kloeden and his collaborators investigated the limit sets of non-autonomous discrete systems that are asymptotically autonomous. The special case of non-autonomous periodic discrete systems was, thoroughly, investigated by Elaydi and Sacker , and the references there in, by Kloeden , Silva and Franco, Silva, and Sim, Franke and Yakubu. D'Aniello and Steele investigated the limit sets of 2- periodic (alternating) systems, and D'Aniello and Oliveira investigated attracting periodic orbits of these systems.

One of our objectives here is to extend this result to non-autonomous discrete systems that are asymptotic to autonomous systems in which the phase space is a locally compact metric space. We extend the metric space to its one point compactification of the phase space. Then we extend the dynamical system to the compactified space. The final step is to embed the non-autonomous system into an autonomous skew-product discrete dynamical system . The theoretical results are then applied to evolutionary population models,

Discrete dynamical systems

Let (X, d) be a metric space, T a topological group, and let $\pi : X \times T \to X$. Then the triple (X, T, π) is called a *dynamical system* if

(i) (identity axiom) $\pi(x, 0) = x$ for all $x \in X$, where 0 is the identity of T.

(ii) (homomorphism axiom) $\pi(\pi(x, s), t) = \pi(x, s + t)$.

(iii) (continuity axiom) π is continuous.

If T is a topological semigroup, then (X, T, π) is called a *semi-dynamical system*.
If $T = \mathbb{Z}_+$, the set of non-negative integers, then the *(forward) orbit* of a point x with respect to π, is defined as $O(x, \pi) = \{\pi(x, t) : t \in \mathbb{Z}_+\}$, and the *$\omega$-limit set* of π at $x \in X$ is

$$\omega(x, \pi) = \{z : \exists\{n_k\} \subseteq \mathbb{Z}_+ \text{ with } \pi(x, n_k) \to z, n_k \to \infty \text{ as } k \to \infty\}.$$

Non-autonomous difference equations

Let $X = (X, d)$ be a compact metric space and let $\mathcal{F} = \{f_0, f_1, \ldots, f_n, \ldots\}$, with $f_i : X \to X$, $i \in \mathbb{Z}_+$, continuous maps. We examine the semi-dynamical system

$$\pi : (X \times \mathcal{F}) \times \mathbb{Z}_+ \to X \times \mathcal{F}$$

with $\pi((x, f_i), 0) = (x, f_i)$, for any $x \in X$ and $i \in \mathbb{Z}_+$ and, for each $n \geq 1$, $\pi((x, f_i), n) = (\Phi_{n,i}(x), f_{n+i})$, where $\Phi_{n,i} = f_{i+n-1} \circ f_{i+n-2} \circ \ldots \circ f_{i+1} \circ f_i$. Note that $\Phi_{1,i} = f_i$.

$$\begin{tikzcd}
X \times \mathcal{F} \times \mathbb{Z}_+ \arrow[r, "\pi"] \arrow[d, "\mathcal{P}\times id"'] & X \times \mathcal{F} \arrow[d, "\mathcal{P}"] \\
\mathcal{F} \times \mathbb{Z}^+ \arrow[r, "\alpha"'] & \mathcal{F}
\end{tikzcd}$$

Non-autonomous Systems

Define, for $x \in X$, $x_0 = x$, $x_1 = f_0(x)$, $x_2 = (f_1 \circ f_0)(x_0)$, ..., and for each $n \in \mathbb{N}$, $x_{n+1} = (f_n \circ f_{n-1} \circ \ldots \circ f_1 \circ f_0)(x_0)$, so to obtain the difference equation

$$x_{n+1} = f_n(x_n)$$

which we treat in the setting of skew-product dynamical systems by considering the mappings

$$f_i : \mathcal{X}_i \to \mathcal{X}_{i+1},$$

where $\mathcal{X}_i$, the *fiber* over f_i, is just a copy of X residing over f_i and consisting of those x on which f_i acts. The product space we consider is $X \times \mathcal{F}$ where $\mathcal{F} = \{f_0, f_1, \ldots, f_n, \ldots\} \subseteq C(X, X)$.

Non-autonomous Systems

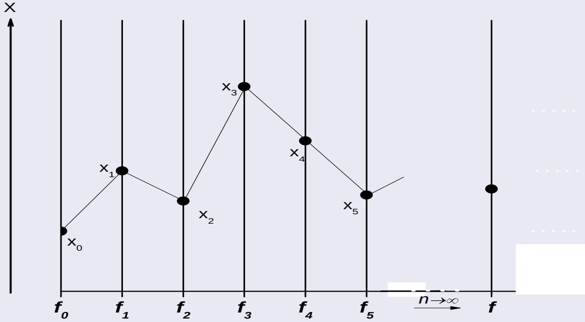


Figure 1: The space $\hat{\mathcal{F}} = \{f_n : n = 0, 1, 2, \ldots\} \cup \{f\}$, where $f_n \to f$, uniformly, as $n \to \infty$. If x_0 is on the fiber $\mathcal{X}_0$, then $f_0(x_0) = x_1$ is in the fiber $\mathcal{X}_1$, and $f_1(x_1) = x_2$ is on the fiber $\mathcal{X}_2$, etc.

Non-autonomous Periodic Systems

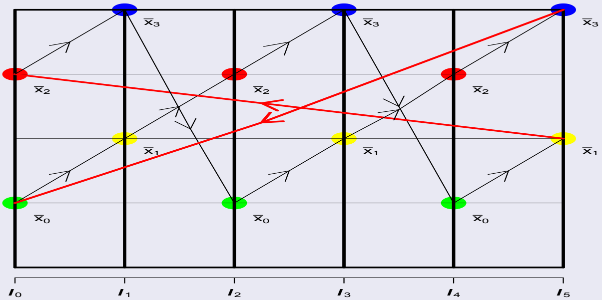


Figure 2: A nonautonomous periodic difference equation with period 4 with the set of maps $\{f_0, f_1, f_2, f_3, f_4, f_5\}$. But of period 8 in the skew-product dynamical system

Ascoli-Arzela's Theorem

Theorem

Let $X = (X, d)$ be a compact metric space and let $f_n : X \to X$, $n = 0, 1, \ldots$ be a sequence of continuous maps uniformly convergent to a function f. Then $\overline{\mathcal{F}} = \mathcal{F} \cup \{f\}$ is compact in the compact open topology.

Proof.

It is straightforward to show that the set $\overline{\mathcal{F}}$ is closed, bounded and equicontinuous in the space of compact open topology (for the compact open topology, Recall that, in metric spaces, the convergence in this topology can be characterized by the uniform convergence on every compact subset of X. Hence, by Ascoli-Arzela's theorem, it follows that $\overline{\mathcal{F}}$ is compact in the space of continuous functions $C(X, X)$. $\square$

Definition

Let $X = (X, d)$ be a compact metric space and let $f_n : X \to X$, $n = 0, 1, \dots$ be a sequence of continuous maps uniformly convergent to a function f. We can extend π to $\tilde{\pi} : X \times \overline{\mathcal{F}} \times \mathbb{Z}_+ \to X \times \overline{\mathcal{F}}$ in the following way

$$\tilde{\pi}((x, f), j) = (f^j(x), f),$$

for each $x \in X$ and $j \in \mathbb{Z}_+$.

Theorem

The map $\tilde{\pi} : X \times \overline{\mathcal{F}} \times \mathbb{Z}_+ \to X \times \overline{\mathcal{F}}$ is a dynamical system.

Assumption A_1 and Forward Invariance

Let $\mathbb{R}^n_+$ denote the cone of nonnegative vectors, with interior $\mathrm{int}(\mathbb{R}^n_+)$ and boundary $\partial(\mathbb{R}^n_+)$. Assume:

A_1

$f, f_t : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ are continuous for all $t \in \mathbb{Z}_+$, and $f_t \to f$ uniformly as $t \to \infty$.

A_2

For each t, $f_t : \mathrm{int}(\mathbb{R}^n_+) \to \mathrm{int}(\mathbb{R}^n_+)$.

Under assumptions A_1, A_2, if $\mathbf{x}(0) \in \mathrm{int}(\mathbb{R}^n_+)$ then every solution of

$$\mathbf{x}(t+1) = f_t(\mathbf{x}(t))$$

and

$$\mathbf{x}(t+1) = f(\mathbf{x}(t))$$

stays in the interior $\mathrm{int}(\mathbb{R}^n_+)$ for all $t \in \mathbb{Z}_+$.

Main Theorem 1

Theorem (D'Aniello and Elaydi)

Assume A_1, A_2, and that the limiting equation has a fixed point $\mathbf{x}^* \in \mathbb{R}^n_+$. Then:

1. *If $\mathbf{x}^* \in \mathrm{int}(\mathbb{R}^n_+)$ and is globally asymptotically stable on $\mathrm{int}(\mathbb{R}^n_+)$ for the limiting system, then every solution of the nonautonomous system with $\mathbf{x}(0) \in \mathrm{int}(\mathbb{R}^n_+)$ satisfies $\mathbf{x}(t) \to \mathbf{x}^*$.*
2. *If $\mathbf{x}^* \in \partial(\mathbb{R}^n_+)$ and is globally asymptotically stable on $\mathrm{int}(\mathbb{R}^n_+)$, then every solution of the nonautonomous system with $\mathbf{x}(0) \in \mathrm{int}(\mathbb{R}^n_+)$ satisfies $\mathbf{x}(t) \to \mathbf{x}^*$.*

Main Theorem 2

Theorem (D'Aniello and Elaydi)

Assume A_1, A_2, and that the limiting equation has a periodic cycle $\mathbf{c_p}^* \in \mathbb{R}^n_+$ of period p. Then:

1. *If $\mathbf{c_p}^* \in \mathrm{int}(\mathbb{R}^n_+)$ and is globally asymptotically stable on $\mathrm{int}(\mathbb{R}^n_+)$ for the limiting system, then every solution of the nonautonomous system with $\mathbf{x}(0) \in \mathrm{int}(\mathbb{R}^n_+)$ satisfies $\mathbf{x}(t) \to \mathbf{c_p}^*$.*
2. *If $\mathbf{c_p}^* \in \partial(\mathbb{R}^n_+)$ and is globally asymptotically stable on $\mathrm{int}(\mathbb{R}^n_+)$, then every solution of the nonautonomous system with $\mathbf{x}(0) \in \mathrm{int}(\mathbb{R}^n_+)$ satisfies $\mathbf{x}(t) \to \mathbf{c_p}^*$.*

Discrete-Time SIS Epidemic Model

The SIS model is given by

$$\begin{cases} S(t+1) = f\big(N(t)\big) + \gamma\,\varphi\big(\frac{I(t)}{N(t)}\big)\,S(t) + \gamma\,\alpha\,I(t), \\ I(t+1) = \gamma\big[1 - \varphi\big(\frac{I(t)}{N(t)}\big)\big]\,S(t) + \gamma\,(1-\alpha)\,I(t). \end{cases}$$

- Recruitment: $f(N) = \dfrac{aN}{1+bN}$, $a, b > 0$.
- Survival probability: γ.
- Recovery rate: $1 - \alpha$.
- $\varphi\big(\frac{I}{N}\big) \in [0,1]$, $\mathcal{C}^2$, $\varphi' < 0$, $\varphi'' > 0$.
- $\varphi(0) = 1$, $\lim_{x\to\infty} \varphi(x) = 0$.
- Example: $\varphi\big(\frac{I}{N}\big) = e^{-\beta\, I/N}$, $\beta > 0$.

Total Population Dynamics

Let $N(t) = S(t) + I(t)$. Then

$$N(t+1) = S(t+1) + I(t+1) = \frac{a\,N(t)}{1 + b\,N(t)} + \gamma\,N(t) =: h\big(N(t)\big).$$

Equilibrium (fixed point) N^* is given by

$$N^* = \frac{a - (1-\gamma)}{b\,(1-\gamma)}$$

Compute

$$h'(N) = \frac{a}{(1+bN)^2} + \gamma.$$

- $h'(0) = a + \gamma$.
- $h'(N^*) = \dfrac{(1-\gamma)^2}{a} + \gamma$.

Cases:

1. If $a+\gamma > 1$, then $N^* > 0$ and $h'(0) > 1$.
2. If $a+\gamma \leq 1$, then only $N^* = 0$, with $0 < h'(0) \leq 1$.

Lemma

$h(N) = \frac{aN}{1+bN} + \gamma N$ *is strictly increasing on* $[0, \infty)$.

Sketch.

If $0 \leq N_1 < N_2$, then both $\frac{aN}{1+bN}$ and γN increase, so $h(N_1) < h(N_2)$. $\square$

Theorem

- label=() *If* $a + \gamma \leq 1$, *then* $N(t) \to 0$ *as* $t \to \infty$.
- label=() *If* $a + \gamma > 1$, *then* $N(t) \to N^*$ *as* $t \to \infty$.

As $t \to \infty$, $N(t) \to N^*$. Define the limiting equation of the infected I

$$g(I) = I(t+1) = \gamma\left(1 - e^{-\beta I/N^*}\right)(N^* - I) + \gamma(1-\alpha)\, I.$$

Then

$$g'(I) = \gamma\left[e^{-\beta I/N^*}\left(\beta(1 - \tfrac{I}{N^*}) + 1\right) - \alpha\right], \quad g'(0) = \gamma(\beta + 1 - \alpha).$$

Basic (Net) Reproduction Number

In general, the basic reproduction number R_0 of an epidemiological model can be defined as "The expected number of secondary cases produced, in a completely susceptible population, by a typical infective individual". Consequently, the value of R_0 allows to forecast if the disease will persist or vanish. We have

$$I(t+1) = \gamma(1-\varphi(I/N))S(t) + \gamma(1-\alpha)I(t) = \mathfrak{F}(t) + \mathfrak{T}(t)$$

$$F = \frac{\partial \mathfrak{F}(t)}{\partial I}\Big|_{(S^*,0)} = \frac{\partial}{\partial I}\left(\gamma(1-\varphi(I/N))\,S\right|_{(S^*,0)} = \beta\gamma$$

$$T = \frac{\partial \mathfrak{T}(t)}{\partial I}\Big|_{(S^*,0)} = \frac{\partial}{\partial I}\left(\gamma(1-\alpha)i\right)\Big|_{(S^*,0)} = \gamma(1-\alpha)$$

We can write:

$$R_0 = F(1-T)^{-1} = F\cdot\frac{1}{1-T} = \frac{\beta\gamma}{1-\gamma(1-\alpha)}$$

Global Stability of DFE

Theorem

If $R_0 \leq 1$, then $\lim_{t\to\infty} I(t) = 0$ and the disease-free equilibrium $(S^*, 0)$ is globally asymptotically stable, i.e. $(S(t), I(t)) \to (S^*, 0)$.

Idea.

$0 < g'(0) \leq 1$, $g'' < 0 \Rightarrow g(I) < I$ for all $I > 0$. $\square$

Endemic Equilibrium ($R_0 > 1$)

If $R_0 > 1$, then $g'(0) > 1$ and $g''(I) < 0$. Moreover

$$g(N^*) = \gamma(1-\alpha)\, N^* < N^*,$$

so by concavity there is a unique $I^* > 0$ with $g(I^*) = I^*$.

Theorem

If $R_0 > 1$, then $I(t) \to I^*$ and $(S(t), I(t)) \to (S^*, I^*)$ globally. In other words, the endemic equilibrium is globally asymptotically stable.

Nonautonomous periodic SIS Model

The non-autonomous p-periodic SIS epidemic model under Beverton–Holt demography is given by:

$$\begin{cases} S(t+1) = \dfrac{a(t)N(t)}{1+b(t)N(t)} + \gamma(t)\,\varphi\Big(\frac{I(t)}{N(t)}\Big)\,S(t) + \gamma(t)\,\sigma(t)\,I(t), \\ I(t+1) = \gamma(t)\Big(1-\varphi\big(\frac{I(t)}{N(t)}\big)\Big)S(t) + \gamma(t)\big(1-\sigma(t)\big)I(t). \end{cases} \tag{2.1}$$

where $a(t), b(t), \gamma(t), \sigma(t), \beta(t)$ are p-periodic functions.

The escape function $\varphi : [0,\infty) \to [0,1]$ is concave, C^2, and satisfies:

- $\varphi(0) = 1$, $\varphi' > 0$ and $\varphi'' > 0$;
- We take

$$\varphi\big(\tfrac{I}{N}\big) = e^{-\beta(t)\,I/N}.$$

Total Population Equation

Summing yields $N(t) = S(t) + I(t)$ and

$$N(t+1) = \frac{a(t)N(t)}{1+b(t)N(t)} + \gamma(t)\,N(t) =: G_t\big(N(t)\big), \qquad (2.2)$$

with $G_{t+p} = G_t$. Define the composition

$$\phi_t \;=\; G_{t-1} \circ G_{t-2} \circ \cdots \circ G_0.$$

Lemma

The composition of monotone maps is monotone.

Corollary

The map $\phi_p = G_{p-1} \circ \cdots \circ G_0$ is monotone.

Dynamics of Total Population

Theorem

Let $M := \prod_{i=0}^{p-1}(a_i + \gamma_i)$. *Then:*

1. *If* $M < 1$, *then* $N(t) \to 0$ *as* $t \to \infty$.
2. *If* $M > 1$, *all orbits converge to a unique positive p-periodic cycle* $\{\overline{N}_0, \overline{N}_1, \ldots, \overline{N}_{p-1}\} = N_p^*$.

Proof Sketch

Case i) $M < 1$:

- $G_i'(0) = a_i + \gamma_i \leq 1$, G_i concave down, so $\phi_p'(0) = P < 1$.
- Monotonicity + concavity imply $\phi_p(N) < N$ for all $N > 0$.
- Hence $N(t) \to 0$.

Case ii) $M > 1$:

- $\phi_p'(0) = M > 1$, ϕ_p increasing and concave down, bounded above.
- Existence and uniqueness of fixed point $\overline{N}_0$ yields globally stable cycle.

Global Stability of Disease-Free Equilibrium

For $M > 1$, let $N_p^*(t)$ be the positive p-periodic cycle. Substitute $S = N_p^* - I$ into (2.1) to get

$$I(t+1) = \gamma(t)\left(1 - e^{-\beta(t)I/N_p^*}\right)(N_p^* - I(t)) + \gamma(t)(1-\sigma(t))I(t) =: H_t(I(t)). \quad (3)$$

Define $\psi_p = H_{p-1} \circ \cdots \circ H_0$, then

$$\psi_p'(0) = \prod_{i=0}^{p-1} \gamma_i(\beta_i + 1 - \sigma_i).$$

The net reproduction number is

$$R_0 = \prod_{i=0}^{p-1} \frac{\beta_i \gamma_i}{1 - \gamma_i(1 - \sigma_i)}.$$

Theorem

If $R_0 \leq 1$, then $I(t) \to 0$ as $t \to \infty$, and the DFE $(S^*, 0)$ is globally asymptotically stable. If $R_0 > 1$, the DFE is unstable.

Theorem

If $R_0 > 1$, then $I(t) \to I_p^*$ as $t \to \infty$, and the endemic p-periodic cycle (S_p^*, I_p^*) is globally asymptotically stable.

Evolutionary Game Theory Framework

The base Darwinian model is

$$\begin{cases} x(t+1) = r\big(x(t),\ v,\ u(t)\big)\big|_{v=u(t)}\, x(t), \\ u(t+1) = u(t) + \sigma^2\, \frac{\partial}{\partial v} \ln r\big(x(t), v, u(t)\big)\big|_{v=u(t)}. \end{cases}$$

- $x(t)$: population density, $v(t)$: individual trait, $u(t)$: mean trait, σ^2: evolutionary speed.
- $\ln r$ is the *fitness function*.

Choice of Growth-Rate Function

We choose the evolutionary Beverton-Holt equation $x(t+1) = r(x, v, u)x(t)$ where

$$r(x, v, u) = \frac{b(v)}{1 + c(v-u)\,x},$$

with

$$b(v) = b_0\, e^{-\frac{v^2}{2}}, \quad c(\xi) \text{ smooth}, \ c_0 = c(0) > 0, \ c_1 = c'(0).$$

No scaling on $v \implies \mathrm{Var}(b(v)) = 1$, maximum at $v = 0$.

Compute the fitness gradient:

$$\frac{\partial}{\partial v} \ln\Big(b(v)\, \tfrac{1}{1+c(v-u)x} \Big)\Big|_{v=u} = -\,u \;-\; \frac{c_1\, x}{1 + c_0\, x}.$$

Hence the two-dimensional model :

$$\begin{cases} x(t+1) = b_0\, e^{-\frac{u(t)^2}{2}}\, \dfrac{x(t)}{1 + c_0\, x(t)}, \\ u(t+1) = (1-\sigma^2)\, u(t) \;-\; \sigma^2\, \dfrac{c_1\, x(t)}{1 + c_0\, x(t)}. \end{cases}$$

Model Mapping and Goals

Define

$$F(x, u) = \big(f(x, u), g(x, u)\big)$$

Objectives:

- Find and classify fixed points,
- Local and global stability,
- Bifurcation (Neimark–Sacker for $b_0 > 1$).

Let $\sigma \neq 0$. Then:

1. If $b_0 \leq 1$, the only fixed point is $O = (0,0)$.
2. If $b_0 > 1$, there is a unique interior fixed point $E^* = (x^*, u^*)$ with $x^* > 0$.

$$\begin{cases} b_0 \leq 1,\ 0 < \sigma^2 < 2 \implies O \text{ is GAS}, \\ b_0 > 1,\ \sigma^2 > 2 \implies O \text{ is unstable}, \\ \text{otherwise, } O \text{ is a saddle.} \end{cases}$$

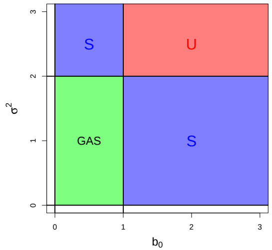


Figure 3: Stability regions for O in (b_0, σ^2)-space.

Bifurcation Overview

Let us recall that for planar smooth mappings varying with a critical parameter, there are three types of bifurcations at a fixed point, depending on how the fixed point loses stability as the parameter changes.

- Saddle-node bifurcation: eigenvalue passes through $+1$
- Period-doubling bifurcation: eigenvalue passes through -1
- Neimark–Sacker bifurcation: a pair of complex conjugate eigenvalues cross the unit circle ($|\lambda| = 1$)

Neimark–Sacker Bifurcation

It is important to recall that a Neimark–Sacker bifurcation is characterized by the appearance of closed invariant curves. There are two types:

- Supercritical: stable invariant curves emerge
- Subcritical: unstable invariant curves appear and vanish

Whether the bifurcation is supercritical or subcritical can be determined by transforming the map into its normal form, subject to nondegeneracy conditions.

Generic Neimark–Sacker Theorem I

Theorem

Suppose a two-dimensional discrete-time system $\mathbf{x} \mapsto F(\mathbf{x}, \beta)$ *has a fixed point* $\mathbf{x}^*(\beta)$ *with Jacobian eigenvalues* $\lambda_\pm = r(\beta)e^{\pm i\theta(\beta)}$, *where* $r(\beta^*) = 1$ *and* $\theta(\beta^*) = \theta_0$. *If*

1. $r'(\beta^*) \neq 0$ *(transversality)*
2. $e^{ik\theta_0} \neq 1$ *for* $k = 1, 2, 3, 4$ *(nonresonance)*

then, in appropriate coordinates, the map becomes

$$z \mapsto e^{i\theta(\gamma)}(1 + \gamma + (d(\gamma) + ib(\gamma))|z|^2)z + O(|z|^4),$$

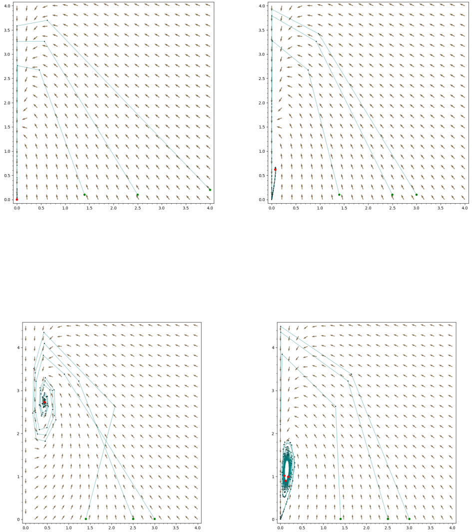
and $d(0) < 0$ *(resp.* > 0*) yields supercritical (resp. subcritical) bifurcation.*

Generic Neimark–Sacker Theorem II

Theorem

Under certain conditions, $d(0) < 0$, and the fixed point (x^*, u^*) undergoes a supercritical Neimark-Sacker bifurcation at a critical value $b_0 = b_0^*$.

Phase Portraits



Mixed Monotone Mapping

Definition

Let $(X, \leq)$ be an ordered metric space. A continuous map $F : X \to X$ is *mixed monotone* if there exists (not necessarily continuous)

$$f : X \times X \longrightarrow X$$

such that for all $\mathbf{x}, \mathbf{y} \in X$:

1. $F(\mathbf{x}) = f(\mathbf{x}, \mathbf{x})$,
2. if $\mathbf{x}_1 \leq \mathbf{x}_2$ then $f(\mathbf{x}_1, \mathbf{y}) \leq f(\mathbf{x}_2, \mathbf{y})$,
3. if $\mathbf{y}_1 \leq \mathbf{y}_2$ then $f(\mathbf{x}, \mathbf{y}_2) \leq f(\mathbf{x}, \mathbf{y}_1)$.

Model and Ordering

$$F(x,u) = \begin{pmatrix} \dfrac{b_0\, x}{1 + c_0 x}\, e^{-u^2/2} \\ (1-\sigma^2)\, u - \dfrac{\sigma^2\ c_1\ x}{1 + c_0 x} \end{pmatrix},$$

defined on the *fourth quadrant* $x \geq 0,\ u \leq 0$.

We use the *southeast* order:

$$(x_1, u_1) \leq_{se} (x_2, u_2) \quad \Longleftrightarrow \quad x_1 \leq x_2,\ u_2 \leq u_1.$$

Lemma (Mixed Monotonicity)

If $c_1 > 0$ and $1 < \sigma^2 < 2$, then F is mixed monotone w.r.t. $\leq_{se}$.

Proof outline:

- Define
$$f((x_1, u_1), (x_2, u_2)) \;=\; F(x_1, u_2).$$
- Check:
  1. $f((x, u), (x, u)) = F(x, u)$.
  2. Monotonicity in first slot: if $(x_1, u_1) \leq_{se} (x_2, u_2)$ then $F(x_1, u) \leq_{se} F(x_2, u)$.
  3. Antitonicity in second slot: if $(x_1, u_1) \leq_{se} (x_2, u_2)$ then $F(x, u_2) \leq_{se} F(x, u_1)$.

Theorem: Global Stability (Fourth Quadrant)

Theorem

Let

$$0 < \ c_1 < \frac{c_0}{\sigma^2}, \quad 1 < \sigma^2 < 2 - b_0 e^{-1/2}, \quad b_0 > 1.$$

If the interior equilibrium (x^*, u^*) is locally asymptotically stable, then it is globally asymptotically stable in the fourth quadrant.

A simple change of variable $u \mapsto -u$ (using symmetry of $e^{-u^2/2}$) handles the case $-\frac{c_0}{\sigma^2} < c_1 < 0$ and yields global stability of the interior equilibrium.

Future Work

We studied local/global stability and bifurcation of the autonomous evolutionary Beverton–Holt model.

We plan to extend our study in two main directions:

1. Effects of the Allee effect on model dynamics.
2. Dynamics under seasonal (periodic) environments.
3. Dynamics under multi-traits

Direction 1: Allee Effect

- **Allee effect:** positive correlation between population growth rate and size at low densities.
- We focus on the *strong* Allee effect.
- Expectation: two attractors
  - Extinction state ($x = 0$)
  - Survival state ($x > 0$)

Direction 2: Seasonal Environments

- Introduce periodic fluctuations in key parameters.
- Model becomes *non-autonomous* and p-periodic.
- Goal: analyze how regular environmental changes affect long-term dynamics.

Attenuation & Resonance

- How do seasonal fluctuations affect evolutionary dynamics?
- Compare:
  - Average equilibrium of constant environments.
  - Average state of the p-periodic cycle.
- This phenomenon — *attenuation* vs. *resonance* — has been studied for 1D periodic Beverton–Holt models..