Difference equations in mathematical modeling: Exploring the Rosenzweig-MacArthur predator-prey model

(stability, bifurcations, permanence)

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Progress on Difference Equations, International Conference
PODE 2025
Universidad Politécnica de Cartagena, Cartagena, 28th-30th May 2025,
Spain

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Introduction

The classical Lotka-Volterra model, where we describe interactions between predators and prey:

$$\begin{aligned} \dot{x} &= rx - bxy \\ \dot{y} &= -sy + cxy,\ r, b, s, c > 0 \end{aligned} \tag{1}$$

where x denote the prey density and y denote predator density. Volterra improved the Lotka-Volterra model by adding a logistic growth function for the prey population in the absence of predators

$$\begin{aligned} \dot{x} &= rx\left(1 - \frac{x}{K}\right) - bxy \\ \dot{y} &= -sx + cxy,\ r, K, s, c > 0. \end{aligned} \tag{2}$$

The Volterra model is more stable than the Lotka-Volterra model. The coexistence equilibrium is globally stable due to prey density dependence

Rosenzweig and MacArthur suggest a hyperbolic functional response for a more realistic model (M.L. Rosenzweig, R.H. MacArthur, *Graphical representation and stability conditions of predator-prey interactions*, Am. Nat. 97 (1963), pp. 209-223.). They considered the following model

$$\begin{aligned} \dot{x} &= rx\left(1 - \frac{x}{K}\right) - \frac{bxy}{d+x} \\ \dot{y} &= -sy + \frac{cbxy}{d+x}. \end{aligned} \tag{3}$$

Model (3) has two dynamic behavior types: stable equilibrium and stable limit cycle. It is an improvement over the Lotka-Volterra model.

- M.R. Myerscough, M.J. Darwen, W.L. Hogarth, *Stability, persistence and structural stability in a classical predator-prey model*, Ecol. Modeling 89 (1980), pp. 31–42 deals with the following Rosenzweig and MacArthur model

$$\begin{aligned} \dot{x} &= rx\left(1-\frac{x}{K}\right)-byF(x) \\ \dot{y} &= -sy+cyF(x),\ r,K,b,s,c>0, \end{aligned} \tag{4}$$

  and $F(x)$ predator functional response (prey caught per predator per unit time). $F(x)$ is Holling II, Ivlev or Trigonometric.

- Gunog Seo, Gail S. K. Wolkowicz, *Sensitivity of the dynamics of the general Rosenzweig–MacArthur model to the mathematical form of the functional response: a bifurcation theory approach*, J. Math. Biol.https://doi.org/10.1007/s00285-017-1201-y 2018.

Let f be a general predator functional response in (4) with usual properties: $f(0)=0, f'(x)>0, f''(x)\leq 0$. Scaling and using a proper substitution reduced the number of parameters to three, i.e., we have

$$\begin{aligned}\dot{u} &= ru(1-u) - vf(u)\\ \dot{v} &= -sv + avf(u).\end{aligned}$$

By using the Euler forward scheme, we derive the following system.

$$\begin{aligned}u_{n+1} &= u_n + \delta[ru_n(1-u_n) - v_n f(u_n)]\\ v_{n+1} &= v_n + \delta[av_n f(u_n) - sv_n].\end{aligned} \tag{5}$$

We rescale the system (5).
Set

$$1+\delta r = \hat{r}, \quad \frac{1+\delta r}{\delta r} = \hat{\alpha}, \quad \delta a = \hat{a}, \quad \frac{s}{\hat{a}} = \hat{s}.$$

Then, system (5) becomes

$$
\begin{aligned}
u_{n+1} &= \hat{r} u_n \left(1 - \frac{u_n}{\hat{\alpha}}\right) - \delta v_n f(u_n) \\
v_{n+1} &= v_n + \hat{a} v_n (f(u_n) - \hat{s}).
\end{aligned}
\tag{6}
$$

We introduce new variables $\hat{u}_n = \frac{u_n}{\hat{\alpha}}, \quad \hat{v}_n = \frac{\delta}{\hat{\alpha}} v_n$, and define $f(\hat{u}_n \hat{\alpha}) = \hat{f}(\hat{u}_n)$. Then, system (6) takes the following form

$$
\begin{aligned}
\hat{u}_{n+1} &= \hat{r} \hat{u}_n (1 - \hat{u}_n) - \hat{v}_n \hat{f}(\hat{u}_n) \\
\hat{v}_{n+1} &= \hat{v}_n + \hat{a} \hat{v}_n (\hat{f}(\hat{u}_n) - \hat{s}).
\end{aligned}
\tag{7}
$$

By ignoring the hats, we obtain the following system with three parameters

$$
\begin{aligned}
u_{n+1} &= r u_n (1 - u_n) - v_n f(u_n) \\
v_{n+1} &= v_n + a v_n (f(u_n) - s).
\end{aligned}
\tag{8}
$$

The right-hand side of the system (8) defines the map $H : \mathbb{R}^2_+ \to \mathbb{R}^2$, where

$$
H(u, v) = (h_1(u, v), h_2(u, v)) = (ru(1 - u) - vf(u), v + av(f(u) - s)).
$$

Preservation of positivity

- Numerical simulations indicate that the first quadrant may not be positively invariant with respect to the map H.
- Define set $D = \{(u, v) \in \mathbb{R}^2_+ : H(u, v) \in \mathbb{R}^2_+\}$.
- Set $D = \{(u, v) : 0 \leq u \leq 1,\ 0 \leq v \leq g_1(u)\} \subset \mathbb{R}^2_+$, where
  $g_1(u) = \begin{cases} g_1^*(u), & 0 < u \leq 1, \\ \dfrac{r}{f'(0)}, & u = 0 \end{cases}$ and $g_1^*(u) = \frac{r(1-u)u}{f(u)}$.
  Thus, two line segments bound the domain D and a continuous curve $g_1(u)$ whose shape depends on the function f. Since the set D is a bounded and closed subset of $\mathbb{R}^2_+$, it is a compact set.

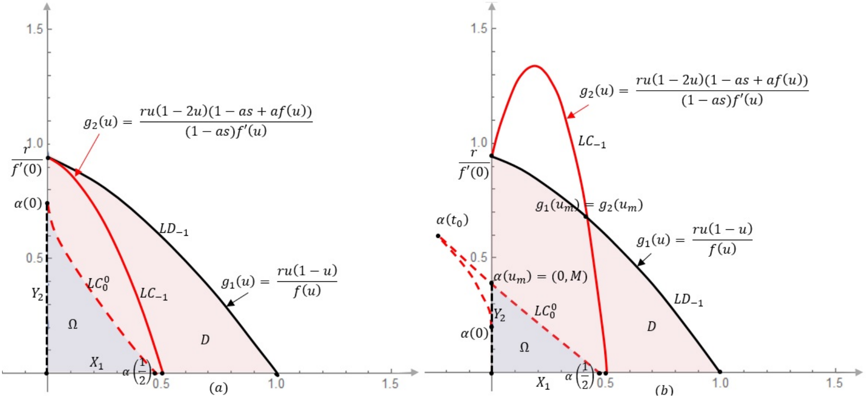

Figure: Invariant sets D and $\Omega \subset D$ where $\Omega = H(D)$, $X_1 = H([0,1/2] \times \{0\}) = [0, r/4] \times \{0\}$, $Y_1 = H(\{0\} \times [0, r/f'(0)])$, $Y_2 = H(LD_{-1})$, $\alpha(0) = (0, (1-as)r/f'(0))$, $\alpha(1/2) = (r/4, 0)$, and $LC_0^0 = \alpha([u_m, 1/2])$ (a) The case where $q(t) \neq 0$ for $0 < t < 1/2$. (b) The case where $q(t) = 0$ for exactly one t_0, $0 < t_0 < 1/2$.

- Let
$$LD_{-1} = \{(u,v) \in \mathbb{R}^2_+ : 0 \leq u \leq 1,\ v = g_1(u)\}.$$
- Function g_1 connects points $(0, r/f'(0))$ and $(1,0)$.
- The image of the curve LD_{-1} under the map H is

$$H\left(u, g_1(u)\right) = \begin{cases} \left(0, \dfrac{r(1-u)u(1-as+af(u))}{f(u)}\right), & 0 < u \leq 1, \\ \left(0, \dfrac{r(1-as)}{f'(0)}\right), & u = 0. \end{cases} \tag{9}$$

Thus, LD_{-1} is mapped into the positive v axis.

- We use the singularity theory and topology to prove the positive invariance of set D.
- For singularity theory, we refer to the classical work by H. Whitney, *On singularities of mappings of Euclidean spaces, mappings of the plane into the plane*, Annals of Mathematics 62(3) (1955), pp. 374–410.
- We also refer to paper E. C. Balreira, S. Elaydi, S., R. Luis, *Local stability implies global stability for the planar Ricker competition model*, Discrete and Continuous Dynamical Systems - Series B 19(2) (2014), pp. 323-351. http://doi.org/10.3934/dcdsb.2014.19.32.
- Using this approach, we aim to understand the map H by considering its regular and singular sets.

Definitions from Whitney [13], Balreira et al. [1], Mira et al. [2]

- Let F be a differentiable map defined on an open subset $U \subset \mathbb{R}^2$.
- The map F is considered regular at p if $detJF(p) \neq 0$; otherwise, it is singular.
- The p is a good point if either $detJ(p) \neq 0$ or $\nabla J(p) \neq 0$, where ∇ is the gradient. A map is good if every point is good.
- For a 2-dimensional continuous good map, the fundamental critical curve (Mira [2]) is defined as $LC_{-1} = \{p \in U : detJ(p) = 0 \,\text{or}\, F \,\text{is not differentiable at}\, p\}$.
- Let ϕ be parametrization of the critical curve LC_{-1} through the point p, with $\phi(0) = p$. The point p is said to be fold if $\frac{d}{dt}(F \circ \phi)(0) \neq 0$. It is cusp if $\frac{d}{dt}(F \circ \phi)(0) = 0$ and $\frac{d^2}{dt^2}(F \circ \phi)(0) \neq 0$.

Theorem (Theorem 15A,Whitney (12))

Let $F : U \to \mathbb{R}^2$ *be a differentiable map. If* $p \in U$ *is a fold point, then there are smooth coordinates* (x_1, y_1) *and* (x_2, y_2) *around* p *and* $F(p)$ *such that* F *takes the form* $x_2 = x_1$ *and* $y_2 = y_1^2$.

Theorem (Theorem 16A,Whitney (12))

$F : U \to \mathbb{R}^2$ *be a differentiable map. If* $p \in U$ *is a cusp around* p *and* $F(p)$, *then there are smooth coordinates* (x_1, y_1) *and* (x_2, y_2) *such that* F *takes the form* $x_2 = x_1$ *and* $y_2 = y_1^3 - x_1 y_1$.

- The critical curve LC_{-1} is given by the following expression

$$LC_{-1} = \left\{ (u, v) \in \mathbb{R}^2_+ : 0 \le u \le 1/2,\ v = \frac{r(1-2u)(1-as+af(u))}{(1-as)f'(u)} \right\}.$$

- The critical curve LC_{-1} is continuous and connects points $(0, r/f'(0))$ and $(1/2, 0)$.
- $LC_0 = H(LC_{-1})$
- Parametrization of LC_0

$$\begin{array}{c} (H \circ \phi_1)(u, v) = H(h_1(t, g_2(t)), h_2(t, g_2(t))) = \\ = \quad (r(1-t)t - \frac{r(1-2t)f(t)(1-as+af(t))}{(1-as)f'(t)}, \frac{r(1-2t)(af(t)-as+1)^2}{(1-as)f'(t)}) \quad . \end{array}$$

$\alpha(t) = (H \circ \phi_1)(t) = (\alpha_1(t), \alpha_2(t))$.

- All points (LC_0) are fold except one which is cusp.(Fig.(a) fold; Fig.(b) cusp).

- Let $X = [0,1] \times \{0\}$ and $Y = \{0\} \times [0, r/f'(0)]$.
- The boundary of D is $\partial D = X \cup Y \cup LD_{-1}$.
- $Y_1 = H(Y) = \{0\} \times [0, (1-as)r/f'(0)] \subset Y$.
- $X_1 = H(X) = [0, r/4] \times \{0\} \subset X$ for $0 < r < 4$.
- Define $g_3(u) = \begin{cases} g_3^*(u), & u \neq 0 \\ \dfrac{r(1-as)}{f'(0)}, & u = 0. \end{cases}$ where

  $$g_3^*(u) = \frac{r(1-u)u(1-as+af(u))}{f(u)}.$$
- $Y_2 = H(LD_{-1}) = \{(0, g_3(u)) | \text{ for } 0 \leq u \leq 1\}$.

Lemma

Consider the map H associated with system (8) and

$$LC_{-1} = \left\{ (u,v) \in \mathbb{R}^2_+ : 0 \le u \le 1/2, g_2(u) = \frac{r(1-2u)(1-as+af(u))}{(1-as)f'(u)} \right\}.$$

Then, we have $\partial H(D) \subseteq H(\partial D) \cup LC_0$, where LC_0 is the image of LC_{-1} under H, i.e., $LC_0 = H(LC_{-1})$.

- The proof is similar to the proof of Lemma 4.5. in the paper of E. C. Balreira, S. Elaydi, S., R. Luis.
- The images of regular values cannot be on the boundary and any new boundary points must be images of singular points.

Let $M = \max_{u \in [0,1]} g_3(u)$. The following lemma holds.

Lemma

There exists $0 \leq u_m < 1/2$, *such that* $M = \alpha_2(u_m) = g_3(u_m)$, *and* $g_1(u_m) = g_2(u_m)$, *where* $\alpha(t) = (H \circ \phi_1)(t) = (\alpha_1(t), \alpha_2(t))$ *is given by* (10). *Furthermore,* $Y_2 = H(LD_{-1}) = \{0\} \times [0, M]$.

- The number of common points between g_1 and g_2 is the same as the number of the intersection of the curve $\alpha(t)$ with positive $v-$axis.
- The latter points are images of the intersection points between curves g_1 and g_2.

The first theorem is proved, assuming that $LC_0^0 = LC_0 \cap \mathbb{R}_+^2$ is contained in D.

Theorem

Let $as < 1$, $0 < r < 4$, $LC_0^0 = LC_0 \cap \mathbb{R}_+^2$, *and* $M \leq r/f'(0)$, *where* $M = g_3(u_m) = \max_{u \in [0,1]} g_3(u)$. *Suppose that there is at most one* t_0, $0 < t_0 < 1/2$, *such that* $q(t_0) = 0$. *If* $q'(t_0) \neq 0$, *and* $q(t) \neq 0$ *for all* $t \neq t_0$, *and* $LC_0^0 \subseteq D$, *then, domain* D *is positive invariant under map* H, *i.e.,* $\Omega = H(D) \subseteq D \subset \mathbb{R}_+^2$.

The next theorem proves that under certain conditions, $LC_0^0 \subseteq D$, which, using the previous theorem, implies that D is positively invariant.

Theorem

Let $as < 1$, $0 < r < 4$, and $M \leq r/f'(0)$ where $M = \max_{u \in [0,1]} g_3(u)$. Suppose that there is at most one t_0, $0 < t_0 < 1/2$, such that $q(t_0) = 0$. If $q'(t_0) \neq 0$, and $q(t) \neq 0$ for all $t \neq t_0$, then $LC_0^0 \subseteq D$, and D is a positively invariant set under map H, i.e., $\Omega = H(D) \subseteq D \subset \mathbb{R}_+^2$.

Equilibrium points and linearized stability

Lemma

For system (8), the following results hold.

(a) *If* $\bar{u}$ *is solution of equation* $f(\bar{u}) = s$ *and* $\bar{u} \geq (r-1)/r$, *or* $f(\bar{u}) = s$ *has no solution, then there is no interior equilibrium, and there are only extinction equilibrium* $E_0 = (0,0)$ *and exclusion equilibrium* $E_1 = ((r-1)/r, 0)$.

(b) *If* $\bar{u}$ *is positive solution of* $f(\bar{u}) = s$ *and* $0 \leq \bar{u} < (r-1)/r$, $1 < r < 4$, *then there are three equilibrium points: extinction* $E_0 = (0,0)$, *exclusion* $E_1 = ((r-1)/r, 0)$, *and unique coexistence equilibrium*

$$\bar{E}(\bar{u}, \bar{v}) = \left(\bar{u}, \frac{\bar{u}\,(r-1-r\bar{u})}{s}\right).$$

Lemma

The equilibrium point E_0 is

(a) *locally asimptotically stable if $r < 1$;*

(b) *non-hyperbolic if $r = 1$;*

(c) *a saddle point if $r > 1$.*

Theorem

Assume that $r \in (0, 1]$. Then, E_0 is globally asymptotically stable for system (8)*.*

Lemma

Equilibrium point E_1 is

(a) *a locally asymptotically stable if* $1 < r < 3$ *and* $f\left(\frac{r-1}{r}\right) < s$.

(b) *repeller if* $3 < r < 4$ *and* $f\left(\frac{r-1}{r}\right) > s$.

(c) *non-hyperbolic if* $r = 3$ *or* $s = f\left(\frac{r-1}{r}\right)$. *Additionally, period-doubling bifurcation with a stable two-cycle occurs at* $r = 3$ *for* $s > f\left(\frac{2}{3}\right)$, *while transcritical bifurcation occurs at* $s = f\left(\frac{r-1}{r}\right)$ *when* $r \neq 3$. *Moreover, for* $r = 3$ *and* $s > f\left(\frac{2}{3}\right)$, $\bar{E}_1$ *is stable; for* $r \neq 3$ *and* $s = f\left(\frac{r-1}{r}\right)$, $\bar{E}_1$ *is unstable.*

(d) *a saddle point if*

$$\left(1 < r < 3 \text{ and } f\left(\frac{r-1}{r}\right) > s\right) \text{ or } \left(3 < r < 4 \text{ and } f\left(\frac{r-1}{r}\right) < s\right).$$

There are stable and unstable manifolds that intersect at $\bar{E}_1$. *In the first case, the local stable and unstable manifolds are*

$$\mathcal{W}_1^s = \{(u, v) : 0 < u < \infty, v = 0\},$$

$$\mathcal{W}_1^u = \{(u, v) \in \mathbb{R}^+ : u = \frac{r-1}{r} + \frac{f\left(1 - \frac{1}{r}\right)}{1 - r + as - af\left(1 - \frac{1}{r}\right)} v + \beta_1 v^2 + \beta_2 v^3 + O(|v|^4)\},$$

where $\beta_1, \ \beta_2$ *are given by* (**??**), *while in the second case,* $\mathcal{W}_2^s = \mathcal{W}_1^u$ *and* $\mathcal{W}_2^u = \mathcal{W}_1^s$.

Bifurcation diagram and Lyapunov exponents

- A dynamically interesting case in the above Lemma arises in statement (c) when period-doubling and transcritical bifurcations occur around $\bar{E}_1$.
- As r approaches the bifurcation value of 3, we show that one of the Lyapunov exponents for period-doubling bifurcation equals zero, and the other is negative.

Theorem

For $1 < r \leq 3$, and $s > f((r-1)/r)$, when r is near 3, the MLE at $(u_0, 0)$ near $\bar{E}_1$ is $\lambda_1 = \ln|2-r|$

Particularly, we have

$$\lim_{r\to 3} \lambda_1(a,r,s) = 0 \quad \text{and} \quad \lim_{r\to 3} \lambda_2(a,r,s) = \ln\left|1 - as + af\left(\frac{2}{3}\right)\right| < 0.$$

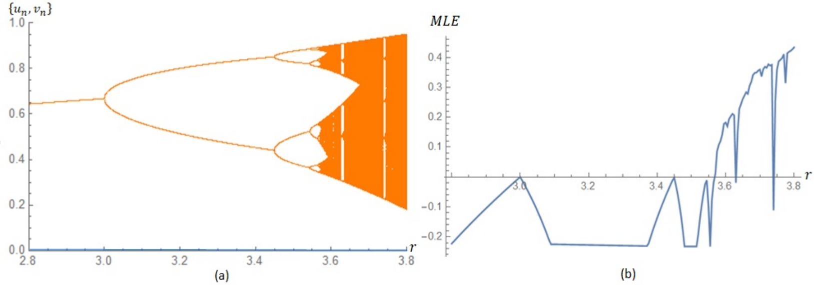

Figure: Period-doubling bifurcation and Maximum Lyapunov exponents for $r_0 = 3$, $r \in (2.8, 3.8)$, $a = 0.2$, $s = 1.8$, $a_H = 2.0$, $b_H = 1.0$, $x_0 = 0.4$, $y_0 = 0.2$ and $f(u) = \frac{2u}{u+1}$ Holling II predator functional response.

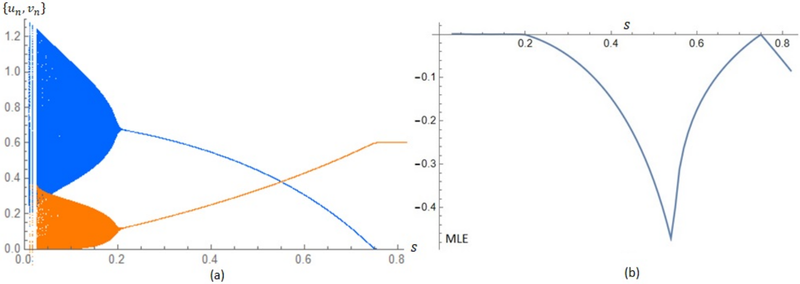

Figure: Transcritical bifurcation and Maximum Lyapunov exponents at $s_0 = 0.75$, $s \in (0.01, 0.82)$, $r = 2.5$, $a = 0.7$, $a_H = 2.0$, $b_H = 1.0$, $x_0 = 0.2$, $y_0 = 0.2$ and $f(u) = \frac{2u}{u+1}$ Holling II predator functional response.

Attractivity results at the boundary equilibrium

We prove the following lemmas that we use to obtain global asymptotic stability results for the boundary equilibrium point.

Lemma

Let (u_n, v_n) *denote the solution of the system* (8) *with the initial condition* $(u_0, v_0) \in D$. *If* $r \in (1, 2]$, *then* $\limsup_{n\to\infty} u_n \leq \dfrac{r-1}{r}$. *Moreover, if* $f\left(\dfrac{r-1}{r}\right) < s$, *then* $\lim_{n\to\infty} (u_n, v_n) = E_1$.

Lemma

Assume $2 < r < 3$, *and* $f(r/4) < s$. *Then,* $\lim_{n\to\infty} v_n = 0$, *and for all* $\varepsilon > 0$, *such that* $0 < \varepsilon < \min\{(r-2)/4, (4r^2 - r^3 - 8)/8\}$, *there exists* n_0, *such that for all* $n > n_0$, *we have* $ru_n(1-u_n) - \varepsilon \leq u_{n+1} \leq ru_n(1-u_n)$. *Furthermore, if* $0 < u_{n_0} < \dfrac{1}{2}$, *then there exists* $n_1 > n_0$, *with* $\dfrac{1}{2} < u_{n_1} < \dfrac{r + \sqrt{(r-2-2\varepsilon)\,r}}{2r}$.

Lemma

Let (u_n, v_n) *denote the solution of system* (8) *with the initial condition* $(u_0, v_0) \in D$. *If* $2 < r < 3$ *and* $f(r/4) < s$, *then* $\lim_{n\to\infty}(u_n, v_n) = E_1$.

The next result is global.

Theorem

Assume that

$$\left(1 < r \leq 2 \text{ and } f\left(\frac{r-1}{r}\right) < s\right) \text{ or } \left(2 < r < 3 \text{ and } f\left(\frac{r}{4}\right) < s\right).$$

Then, the boundary equilibrium is globally asymptotically stable.

Stability of the coexistence equilibrium point

Lemma

Assume $1 < r < 4$ *and* $0 < as < 1$. *Then, the equilibrium point* $(\bar{u}, \bar{v})$ *is*

(i) *a saddle point if* $a < \dfrac{2(1 + r - 2r\bar{u})}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \dfrac{2}{s}$.

(ii) *locally asymptotically stable if*
$$\frac{2(1 + r - 2r\bar{u})}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \frac{2}{s} < a < \frac{r - 2r\bar{u} - 1}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \frac{1}{s}.$$

(iii) *a repeller if* $a > \dfrac{2(1 + r - 2r\bar{u})}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \dfrac{2}{s}$ *and* $a > \dfrac{r - 2r\bar{u} - 1}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \dfrac{1}{s}$.

(iv) *a non-hyperbolic equilibrium if and only if* $a = \dfrac{2(1 + r - 2r\bar{u})}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \dfrac{2}{s}$ *or*

$$a = \frac{r - 2r\bar{u} - 1}{\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u})} + \frac{1}{s} \text{ and } \left|\bar{u}\,(r\bar{u} - r + 1)\,f'\,(\bar{u}) + s\,(-2r\bar{u} + r + 1)\right| < 2s$$

Period-doubling bifurcation and Neimark-Sacker bifurcation at the interior equilibrium

- We show the occurrence of the period-doubling bifurcation at the unique interior equilibrium of system (8), taking a as a bifurcation parameter. Due to the huge expressions, we skip them here.
- We use the results from S. Wiggins, *Introduction to applied nonlinear dynamical systems and chaos*. Second edition. Texts in Applied Mathematics, 2. Springer-Verlag, New York, 2003, pages 513—516.

Lemma

Assume that $Tr(\mathrm{A}) \neq 0,\ Tr(\mathrm{A}) \neq -1,\ s > 0,\ r > 0$, $0 < \bar{u} < (r-1)/r$, *where* $\bar{u}$ *is positive solution of the equation* $f(\bar{u}) = s$. *Let* $a_0 > 0$ *such that*

$$f'(\bar{u}) = \frac{s(-2r\bar{u}+r-1)}{\bar{u}(a_0 s-1)(r(\bar{u}-1)+1)} \tag{10}$$

and

$$\left|\frac{a_0 s(-2r\bar{u}+r+1)-2}{a_0 s-1}\right| < 2. \tag{11}$$

Then, $\tilde{H}$ *has fixed point at* $(0,0)$, *and conjugate complex eigenvalues* $\mu(a),\ \bar{\mu}(a)$ *of Jacobian matrix* $J_{\tilde{H}_a}(0,0)$ *for a close* a_0 *with modulus one at* $a = a_0$, *where*

$$\mu(a_0) = \frac{a_0 s(-2r\bar{u}+r+1)-2+i\Delta}{2a_0 s-2}$$

and $\Delta = \sqrt{-a_0 s(1+r(-1+2\bar{u}))(4+a_0 s(-3-r+2r\bar{u}))}$ *and* $|\mu(a_0)| = 1$. *Moreover,* μ *satisfies the following*

(a) $\mu(a_0)^k \neq 1$ *for* $k = 1,2,3,4$.

(b)

$$d(a_0) = \frac{d}{da}|\mu(a)|\Big|_{a=a_0} = \frac{s(r(2\bar{u}-1)+1)}{2(a_0 s-1)}. \tag{12}$$

Lemma (cont.)

(c) *Eigenvectors associated to the* μ *are*

$$\mathrm{q} = \mathrm{q}(a_0) = \left(\frac{a_0 s\left(-1 + r - 2r\bar{u}\right) + i\Delta}{2a_0\left(1 - r + 2r\bar{u}\right)}, 1 \right)$$

and

$$\mathrm{p} = \mathrm{p}(a_0) = \left(-\frac{ia_0\left(1 + r\left(-1 + 2\bar{u}\right)\right)}{\Delta}, \frac{1}{2} - \frac{ia_0 s\left(1 + r\left(-1 + 2\bar{u}\right)\right)}{2\Delta} \right),$$

such that $\mathrm{Aq} = \mu(a_0)\mathrm{q}$, $\mathrm{pA} = \mu(a_0)\mathrm{p}$ *and* $\mathrm{pq} = 1$.

We compute an approximation of the closed invariant curve following the procedure in K. Murakami, *The invariant curve caused by Neimark–Sacker bifurcation*. Dynamics of Continuous, Discrete and Impulsive Systems, 9(1)(2002), 121-132. We also determine the explicit form of the first Lyapunov coefficient.

Theorem

Assume that all assumptions of Lemma 17 hold. Then the following holds:

(a) *If $\alpha(a_0) < 0$ and $d(a_0) > 0$ ($d(a_0) < 0$), then there is a neighborhood $\mathcal{U}$ of the $(\bar{u}, \bar{v})$ and a $\delta > 0$ such that for $|a - a_0| < \delta$ and $(u_0, v_0) \in \mathcal{U}$, then ω-limit set of (u_0, v_0) is $(\bar{u}, \bar{v})$ if $a < a_0$ ($a > a_0$) and belongs to a closed invariant C^1 curve $\Gamma(a)$ encircling the $(\bar{u}, \bar{v})$ if $a > a_0$ ($a < a_0$). Furthermore, $\Gamma(a_0) = \{(\bar{u}, \bar{v})\}$.*

(b) *If $\alpha(a_0) > 0$ and $d(a_0) > 0$ ($d(a_0) < 0$), then there is a neighborhood $\mathcal{U}$ of the $(\bar{u}, \bar{v})$ and a $\delta > 0$ such that for $|a - a_0| < \delta$ and $(u_0, v_0) \in \mathcal{U}$, then α-limit set of (u_0, v_0) is the $(\bar{u}, \bar{v})$ if $a > a_0$ ($a < a_0$) and belongs to a closed invariant C^1 curve $\Gamma(a)$ encircling the $(\bar{u}, \bar{v})$ if $a < a_0$ ($a > a_0$). Furthermore, $\Gamma(a_0) = \{(\bar{u}, \bar{v})\}$.*

Assume $\alpha(a_0) \neq 0$ and $a = a_0 + \delta$ where δ is a sufficient small parameter. If $(\bar{u}, \bar{v})$ is fixed point of H then invariant curve $\Gamma(a)$ can be approximated by

$$\begin{pmatrix} u \\ v \end{pmatrix} \approx (\bar{u}, \bar{v}) + 2\rho_0 Re\left(\mathrm{q}e^{i\theta}\right) + \rho_0^2\left(Re\left(\mathrm{K}_{20}e^{2i\theta}\right) + \mathrm{K}_{11}\right), \quad \theta \in \mathbb{R} \tag{13}$$

where

$$\rho_0 = \sqrt{-\frac{d(a_0)}{\alpha(a_0)}\delta}.$$

Permanence of the system

- The following definition of permanence is from R. Kon and Y. Takeuchi, *Permanence of host-parasitoid system*, Nonlinear Analysis 47 (2001), pp. 1383-1393.

Definition

System (8) is permanent (for ∂X) if there is a compact set $M \subset X$ such that the minimum distance between M and ∂X is positive, and for every initial value in $intX$ the orbits enter and remain in M.

- We use the method of average Lyapunov functions developed in the V. Hutson, *A theorem on average Liapunov functions*, Monatshefte für Mathematik 98 (1984,) pp. 267–275.

Theorem (Hutson)

Consider the system

$$Z_{n+1} = F(Z_n), Z_i \in \mathbb{R}_+^n, i \geq 0.$$

Assume that X is compact and that S is a compact subset of X with an empty interior. Let S and $X \setminus S$ be forward invariant. Suppose that there is a continuous function $P : X \to \mathbb{R}_+$ which satisfies the following conditions

(a) $P(Z) = 0 \Leftrightarrow Z \in S$

(b) $\sup_{n\geq 0} \liminf_{Z_0 \to Z, Z_0 \in X\setminus S} \dfrac{P(F^n(Z_0))}{P(Z_0)} > 1 \quad (Z \in S)$

Then there is a compact forward invariant set M with $d(M, S) > 0$ which is such that every orbit in $X \setminus S$ enter and remain in M.

Corollary (Hutson)

The conclusion of the Theorem (Hutson) remains true if, instead of (b) it is assumed that $\sup_{n\geq 0} \liminf_{Z_0 \to Z, Z_0 \in X\setminus S} \dfrac{P(F^n(Z_0))}{P(Z_0)} > \begin{cases} 1, & Z \in \Omega(S), \\ 0, & Z \in S, \end{cases}$ *where* $\Omega(S)$ *is the omega limit set of* S.

For compact set $\Omega_1 \subset D$, let $S_1 = \{(u,v) \in \Omega_1 | u = 0\}$ and $S_2 = \{(u,v) \in \Omega_1 | v = 0\}$. $H(S_i) \subseteq S_i$, and $H(\Omega_1 \setminus S_i) \subseteq \Omega_1 \setminus S_i$, for $i = 1,2$. Define the following continuous functions $P_i : X \to \mathbb{R}_+ (i = 1,2)$ by $P_1((u,v)) = u$ and $P_2((u,v)) = v$. Put

$$\sigma_i(Z) = \sup_{n\geq 0} \liminf_{Z_0 \to Z, Z_0 \in Y\setminus S_i} \frac{P_i(H^n(Z_0))}{P_i(Z_0)} \quad \text{for} \quad i = 1,2$$

Theorem

Assume that $1 < r < 4$. *System* (8) *is permanent if the following condition holds:* $\sigma_2(Z) > 1 \quad$ *for any* $Z \in \Omega(S_2 \setminus \{(0,0)\})$.

Theorem

If $1 < r < 3$ *and* $f\left(\frac{r-1}{r}\right) > s$, *then system* (8) *is permanent.*

Lemma

Assume that $3 < r < 4$, $u_0 > 0$ *and* $v_0 = 0$. *Let* $\{(u_i, 0)\}_{i=0}^{\infty}$ *be a solution of the* (8). *Then, there exist* $\rho > 0$, *such that for all* $u_0 > 0$, *there is* $n_0 = n_0(u_0) > 0$ *with* $\rho < u_n < r/4$ *for all* $n > n_0$. *Furthermore, if* $\rho < u_0 < r/4$, *then* $\rho < u_n < r/4$ *for all* $n \geq 0$.

- We use Lemma 2.4

Lemma (Hofbauer et al.)

Assume that $x_i > 0 (1 \leq i \leq q)$*. Suppose that there are real numbers* $b > 0$ *and* b'*, and a sequence* $(k_j) \to \infty$ *such that* $b < (x \cdot k_j)_i < b' (1 \leq i \leq q, j \geq 1)$*. Then there are a subsequence, again denoted by* (k_j)*, and an equilibrium point* x^* *such that* $\lim_{j\to\infty} \bar{x}(k_j) = x^*$*.*

in J. Hofbauer, V. Hutson, and W. Jansen, *Coexistence for systems governed by difference equations of Lotka-Volterra type*, J. Math. Biol. (25) (1987), pp. 553-570, to prove the following result.

Lemma

Let $\{(u_i, 0)\}_{i=0}^{\infty}$ *be a solution of system* (8) *for* $u_0 > 0$ *and* $v_0 = 0$*. Suppose that there are real numbers* $\rho_1 > 0$ *and* ρ_2*, such that* $\rho_1 \leq u_i \leq \rho_2$ *for all* $i \geq 0$*. Then, there exists subsequence* $\{n_i\}$ *such that* $\lim_{n_i\to\infty} \dfrac{\sum_{j=0}^{n_i-1} \ln(1-u_j)}{n_i} = -\ln r$*.*

We prove the next lemma.

Lemma

Assume that $0 < \rho < r/4$ *and* $1 < r < 4$. *Let* ξ *and* η *are solution of the system*

$$\xi \ln(1-\rho) - \eta = \ln(1 - as + af(\rho))$$
$$\xi \ln\left(1 - \frac{r}{4}\right) - \eta = \ln\left(1 - as + af\left(\frac{r}{4}\right)\right).$$

Then if $f''(u) < 0$ *for* $u \in [\rho, r/4]$ *then* $\ln(1 - as + af(u)) \geq \xi \ln(1-u) - \eta$ *for* $\rho \leq u \leq r/4$ *where*

$$\xi = \frac{\ln(af(\rho) - as + 1) - \ln\left(af\left(\frac{r}{4}\right) - as + 1\right)}{\ln(1-\rho) - \ln\left(1 - \frac{r}{4}\right)}$$
$$\eta = \frac{\ln\left(1 - \frac{r}{4}\right)\ln(af(\rho) - as + 1) - \ln(1-\rho)\ln\left(af\left(\frac{r}{4}\right) - as + 1\right)}{\ln(1-\rho) - \ln\left(1 - \frac{r}{4}\right)}$$

We prove the following permanence result.

Theorem

Assume that $3 < r < 4$ *and* $\xi \ln r + \eta < 0$ *where* ξ *and* η *are from Lemma 28. Then, the system* (8) *is permanent.*

Numerical examples and simulations

- We consider system (8) with hyperbolic predator functional response $f(u) = a_T \tanh(b_T u)$, where $a_T, b_T > 0$.
- We choose parameters a_T, b_T, a, s, and r such that $as < 1$, and set D must be positively invariant.
- In this example, the set D is

$$D = \left\{(u, v) : 0 \leq u \leq 1,\ 0 \leq v \leq -\frac{r(u-1)u \coth\left(b_T u\right)}{a_T}\right\}.$$

- For the set D to be positively invariant, the following condition must hold
$$M \leq \frac{r}{a_T b_T}, \tag{14}$$
and there must be at most one t_0, $0 < t_0 < 1/2$, such that $q(t_0) = 0$, $q'(t_0) \neq 0$, where
$$\begin{aligned} q(t) &= 2a_T b_T \operatorname{sech}^2(tb_T)\left(a\left(-2ta_T b_T + a_T b_T + s\right) - 1\right) \\ &+ 2a_T b_T \tanh(tb_T)\operatorname{sech}^2(tb_T)\left(2t(as-1)b_T - a\left(a_T + sb_T\right) + b_T\right), \end{aligned}$$
and
$$\begin{aligned} q'(t) &= 2a_T b_T^2 \operatorname{sech}^4(tb_T)\left(4t(as-1)b_T - 2asb_T - 3aa_T + 2b_T\right) \\ &+ 2(2t-1)a_T b_T^3 \operatorname{sech}^4(tb_T)\left((1-as)\cosh(2tb_T) + aa_T \sinh(2tb_T)\right). \end{aligned}$$

- We find the interior equilibrium point in D
- Set D is positively invariant only if the following conditions hold

$$0 < s < a_T \tanh\left(\frac{(r-1)b_T}{r}\right) \quad \text{and} \quad 1 < r < 4. \tag{15}$$

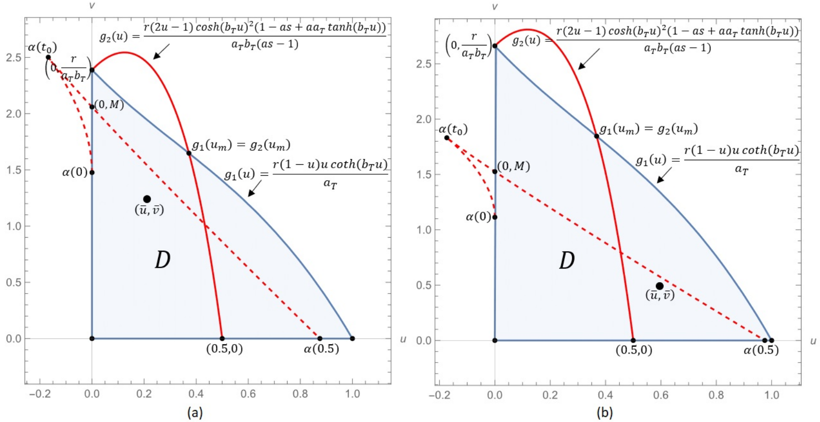

Figure: Closed invariant set D for $a_T = 0.99$, $b_T = 1.48$, and (a) $r = 3.5$, $s = 0.3$, (b) $r = 3.9$, $s = 0.7$.

- We take the values of parameters a_T, and b_T from Gregor F Fussmann, Bernd Blasius, *Community response to enrichment is highly sensitive to model structure*, Biol. Lett. 1 (2005), pp. 9-12. doi: 10.1098/rsbl.2004.0246., i.e., $a_T = 0.99, b_I = 1.48$.
- We also refer to the article Gunog Seo, Gail S. K. Wolkowicz, *Sensitivity of the dynamics of the general Rosenzweig–MacArthur model to the mathematical form of the functional response: a bifurcation theory approach*, J. Math. Biol.https://doi.org/10.1007/s00285-017-1201-y 2018. Other parameters are $r = 3.5, s = 0.3$.
- For the chosen values, the set D becomes

$$D = \{(u, v) : 0 \leq u \leq 1,\ 0 \leq v \leq -3.53535(u-1)u \coth(1.48u)\},$$

and $M = 2.05981$, $\frac{r}{f'(0)} = \frac{r}{a_T b_T} = 2.38875$, $t_0 = 0.255533$, $q'(t_0) = -13.8511 \neq 0$.

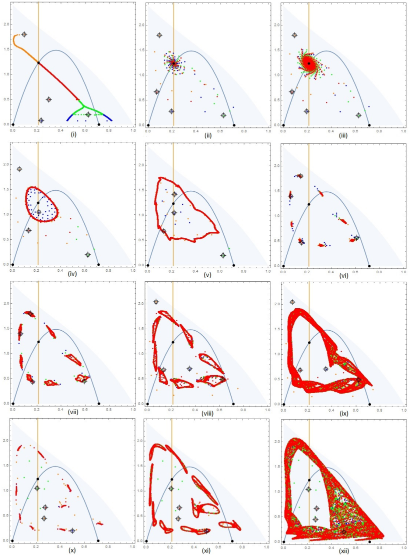

Figure: Trajectories (red, green, blue and orange) for $a_T = 0.99$, $b_T = 1.48$, $s = 0.3$, $r = 3.5$ and (i) $a = 0.01$ (ii) $a = 1.13$ (iii) $a = a_0 = 1.272554647499$ (iv) $a = 1.4$ (v) $a = 1.82$ (vi) $a = 1.90$ (vii) $a = 1.93$ (viii) $a = 1.57$ (ix) $a = 2.07$ (x) $a = 2.11$ (xi) $a = 2.17$ and (xii) $a = 2.34$.

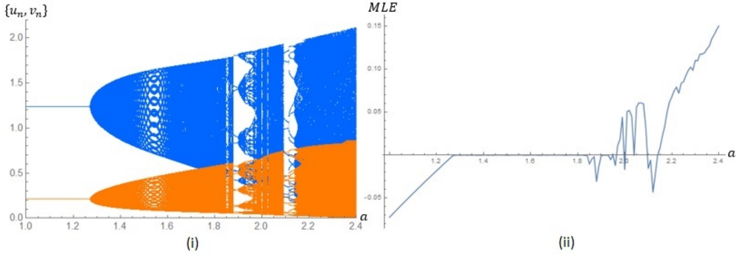

Figure: Bifurcation diagrams and Maximum Lyapunov exponents where $a_T = 0.99$, $b_T = 1.48$ and $f(u) = 0.99\tanh(1.48u)$ Hyperbolic predator functional response for $a \in (1.0, 2.4)$,and $s = 0.3$, $r = 3.5$ $x_0 = 0.3$, $y_0 = 0.2$.

- Take the values of parameters $a_T = 0.99, b_I = 1.48$, $r = 3.9$, and $s = 0.7$.
- For the chosen values, the set D becomes

$$D = \{(u, v) : 0 \leq u \leq 1,\ 0 \leq v \leq -3.93939(u-1)u \coth(1.48u)\},$$

and $M = 1.52563$, $\frac{r}{f'(0)} = \frac{r}{a_T b_T} = 2.66175$, $t_0 = 0.252524$, $q'(t_0) = -9.06119 \neq 0$.

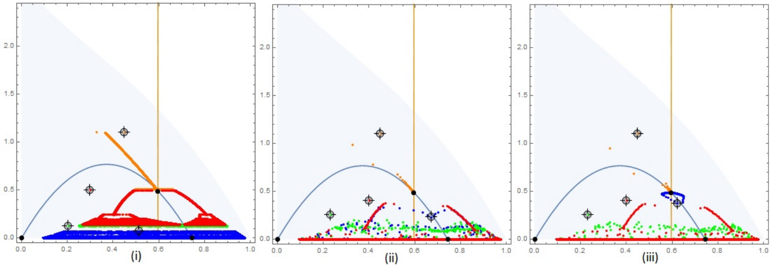

Figure: Trajectories (red, green, blue and orange) for $a_T = 0.99$, $b_T = 1.48$, $s = 0.7$, $r = 3.9$ and (a) $a = 0.01$ (b) $a = a_0 = 0.83111$ and (c) $a = 1.10$.

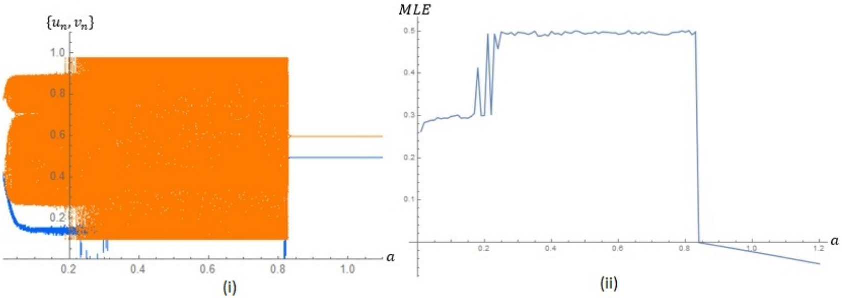

Figure: Bifurcation diagrams and Maximum Lyapunov exponents where $a_T = 0.99$, $b_T = 1.48$ and $f(u) = 0.99\tanh(1.48u)$ Hyperbolic predator functional response for $a \in (0.01, 1.1)$, and $s = 0.7$, $r = 3.9$ $x_0 = 0.60$, $y_0 = 0.49$.

GRACIAS POR SU ATENCION
THANK YOU

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