Discrete Planar Systems that Model Stage-Structured Populations

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The planar stage-structured model

We consider the planar system of difference equations

$$x_{n+1} = \sigma_{1,n}(x_n, y_n)y_n + \sigma_{2,n}(x_n, y_n)x_n$$
$$y_{n+1} = \phi_n(x_n, y_n)x_n$$

- For each $n \geq 0$ the functions $\sigma_{1,n}, \sigma_{2,n}, \phi_n : [0, \infty)^2 \to [0, \infty)$ are bounded on the compact sets in $[0, \infty)^2$ – for example, if $\sigma_{1,n}, \sigma_{2,n}, \phi_n$ are continuous functions for every n

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- The possibility of discontinuity allows for such things as random fluctuations in the parameter functions
- (0,0) is a fixed point of the system so the possibility of extinction is preserved
- This system generalizes the lowest dimensional stage-structured models that are used to explore the dynamics of single-species populations in discrete time.

Adult-juvenile models

Green tree frogs

The tadpole-adult model for the green tree frog *Hyla cinerea* population by Ackleh and Jang (*JDEA, v.13, 2007*) can be written as

$$\begin{aligned} x_n &= \frac{y_n}{a + k_1 y_n} + \frac{x_n}{c + k_2 x_n} \\ y_n &= b_n x_n \end{aligned}$$

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- The sequence b_n maybe constant or have period 2.
- Effects of periodicity on survival and extinction are examined.

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A model with harvesting

A general model that includes harvesting by Zipkin, et al (*Ecol. Appl. v.19, 2009*) can be written as

$$x_{n+1} = (1 - h_j)s_j y_n + (1 - h_a)s_a x_n$$
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- The functions σ_i in this case do not depend on densities (x_n, y_n) while ϕ partially depends on density (adult only)
- The system is autonomous (fully time-independent).

Adult-juvenile models

A harvesting model with the Ricker function

The fertility function f in the Zipkin, et al model maybe of different types, including Beverton-Holt (rational) or Ricker (exponential) as in

$$x_{n+1} = (1 - h_j)s_j y_n + (1 - h_a)s_a x_n$$
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- This model is analyzed by Liz and Pilarczyk (*J. Theor. Biol. v.297, 2012*).
- Simple and complex behavior are shown to occur in this model for different harvesting rates.

Adult-juvenile models

A general non-autonomous model

A general formulation of these models is given by Cushing *(J. Math. Biol. v.53, 2006)* as follows

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\begin{aligned}
x_{n+1} &= s_{1,n}\sigma_1(c_{1,1,n}y_n, c_{1,2,n}x_n)y_n + s_{2,n}\sigma_2(c_{2,1,n}y_n, c_{2,2,n}x_n)x_n \\
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- This model is both density- and time-dependent
- b_n is assumed to be periodic and results on extinction, survival and occurrence of cycles are obtained in terms of a threshold for the mean value of b_n
- A number of biologically motivated restrictions are assumed on the parameters

Convergence to the origin, extinction

In the general model

$$x_{n+1} = \sigma_{1,n}(x_n, y_n)y_n + \sigma_{2,n}(x_n, y_n)x_n$$
$$y_{n+1} = \phi_n(x_n, y_n)x_n$$

let $\sigma_{i,n}, \phi_n$ be all bounded functions for $i = 1, 2$ and every $n = 0, 1, 2, \ldots$ and define

$$\bar{\sigma}_{i,n} = \sup_{u,v \geq 0} \sigma_{i,n}(u, v), \quad \bar{\phi}_n = \sup_{u,v \geq 0} \phi_n(u, v).$$

Theorem (extinction)

If the following inequality holds

$$\limsup_{n \to \infty} (\bar{\sigma}_{1,n}\bar{\phi}_{n-1} + \bar{\sigma}_{2,n}) < 1$$

then $\lim_{n \to \infty} x_n = 0$ for every orbit $\{(x_n, y_n)\}$ of the planar system in the positive quadrant $[0, \infty)^2$. If also either the sequence $\{\bar{\phi}_n\}$ is bounded, or the following inequality holds

$$\liminf_{n \to \infty} \bar{\sigma}_{1,n} > 0,$$

then every orbit of the system converges to (0,0).

Convergence to the origin, extinction

- Aside from being bounded, the functions $\sigma_{1,n}, \sigma_{2,n}, \phi_n$ are not otherwise restricted in the above Theorem. This allows for arbitrary fluctuations in parameter values. In particular, the Theorem yields a general extinction result for stage-structured models that include a noise term or other fluctuations of sufficiently low-amplitude.

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- The extinction theorem is valid even if the separate sequences $\{\sigma_{1,n}\}$ or $\{\bar{\phi}_n\}$ are not bounded by 1 as long as $\bar{\sigma}_{1,n}\bar{\phi}_{n-1} \leq \delta - \bar{\sigma}_{2,n}$ for (large) n.

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- More specific statements can be made for periodic coefficients but we will not discuss these.

The autonomous system

$$x_{n+1} = \sigma_1(x_n, y_n)y_n + \sigma_2(x_n, y_n)x_n$$
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The inequality in the above corollary is the same as what we get for the local asymptotic stability of the origin if the functions σ_1, σ_2, ϕ are smooth and take their maximum values at (0,0), as assumed in Cushing's paper.

Special cases with interspecies competition

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Important special cases of the autonomous system have not yet been thoroughly investigated.

- They include the Beverton-Holt type model

$$x_{n+1} = \sigma_1 y_n + \sigma_2 x_n$$
$$y_{n+1} = \frac{\beta x_n}{1 + c_1 x_n + c_2 y_n}$$

  and the Ricker type model

$$x_{n+1} = \sigma_1 y_n + \sigma_2 x_n$$
$$y_{n+1} = \beta x_n e^{\alpha - c_1 x_n - c_2 y_n}$$

  with constants $\sigma_1, \beta, c_2 > 0$ and $\sigma_2, c_1 \geq 0$.

  The assumption $c_2 > 0$, which adds inter-species competition leads to theoretical issues that are not yet well-understood.

Special cases

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- For the Ricker version a wide variety of orbits may occur, including chaotic behavior. Liz and Pilarczyk study the case where $c_2 = 0$. We take a quick look at a case with $c_2 > 0$.

Boundedness and extinction in the Ricker system

For the autonomous Ricker system

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corollary

Assume that $\sigma_2 < 1$ and $c_1 > 0$. Then:
(a) Every orbit of the above Ricker system in $[0, \infty)^2$ is uniformly bounded.
(b) All orbits in $[0, \infty)^2$ converge to (0,0) if the following holds

$$\sigma_1 \beta e^{\alpha} + \sigma_2 < 1.$$

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Since $y_n = (x_{n+1} - \sigma_2 x_n)/\sigma_1$ a further substitution yields

$$x_{n+2} = \sigma_2 x_{n+1} + \sigma_1 \beta x_n e^{\alpha - (c_1 - c_2 \sigma_2/\sigma_1) x_n - (c_2/\sigma_1) x_{n+1}}$$

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This can also be written as

$$x_{n+1} = \sigma_2 x_n + x_{n-1} e^{a - (c_1 - c_2 \sigma_2/\sigma_1) x_{n-1} - (c_2/\sigma_1) x_n}, \quad a = \alpha + \ln(\sigma_1 \beta)$$

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When $c_2 = 0$ Liz and Pilarczyk apply a result of Gyori and Turfimchuk (*JDEA, v.6, 2000*) to obtain conditions for the global attractivity of the positive fixed point.

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- If $\sigma_2 = 0$ then the second-order folding equation reduces to

$$x_{n+1} = x_{n-1} e^{a - c_1 x_{n-1} - (c_2/\sigma_1) x_n}$$

  which can be written more succinctly by a change of variable $r_n = c_1 x_n$ as

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- We consider the case $c_2 = \sigma_1 c_1$ $(b = 1)$ but $a > 1$.

Semiconjugate factorization

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- This equation admits a semiconjugate factorization. We make the following change of variables:

$$t_n = \frac{r_n}{r_{n-1} e^{-r_{n-1}}}$$

  that is known as an order-reducing form symmetry.

Semiconjugate factorization

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- The pair of first-order equations

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constitutes a semiconjugate factorization of the second-order equation above.

Orbits in the state-space

- All solutions of the first-order equation

$$t_{n+1} = \frac{e^a}{t_n}$$

with $t_0 \neq e^{a/2}$ are periodic with period 2:

$$\left\{ t_0, \frac{e^a}{t_0} \right\} = \left\{ \frac{r_0}{r_{-1} e^{-r_{-1}}}, \frac{r_{-1} e^{a - r_{-1}}}{r_0} \right\}.$$

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- The orbit of each nontrivial solution $\{r_n\}$ of the second-order equation

$$r_{n+1} = r_{n-1}e^{a-r_{n-1}-r_n}$$

in its state-space, namely, the (r_n, r_{n+1})-plane, is restricted to the class of curve-pairs

$$\xi_1(r, t_0) = \frac{e^a}{t_0} r e^{-r} \quad \text{and} \quad \xi_2(r, t_0) = t_0 r e^{-r}$$

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- If $t_0 = e^{a/2}$ then the above two curves coincide

$$\xi_1(r, t_0) = \xi_2(r, t_0) = e^{a/2} re^{-r} = re^{a/2-r}$$

A multitude of multi-stable solutions

- If r_{-1} is fixed and r_0 changes, then t_0 changes proportionately to r_0. These changes in initial values are reflected as changes in the *parameters* of the curve pairs.

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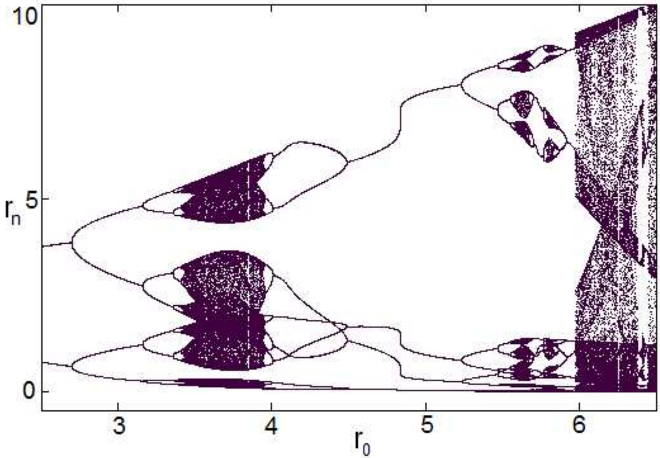
- These qualitatively different types of behavior are split over the pair of curves ξ_1 and ξ_2.

Solutions that bifurcate with changing initial values

In this figure $\alpha = 4.5$ and $r_{-1} = a/2 = 2.25$. The changing values of r_0 are shown on the horizontal axis in the range 2.5 to 6.5. For every grid value of r_0 in the indicated range the last 200 (of 300) points of the solution $\{r_n\}$ are plotted vertically.



Multi-stable periodic and non-periodic solutions

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Theorem

(a) Except possibly for solutions $\{r_n\}$ whose initial values satisfy $r_0 = r_{-1} e^{a/2 - r_{-1}}$ (i.e. $t_0 = e^{a/2}$) there are no positive solutions that are periodic with an odd period.

(b) For all sufficiently large values of a the second-order equation has periodic solutions of all possible periods as well as chaotic solutions in the sense of Li and Yorke.

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