Difference Equations Arising in Evolutionary Population Dynamics

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OUTLINE

1. The basic juvenile-adult model in structured population dynamics & the Fundamental Bifurcation Theorem at $R_0 = 1$

2. Semelparity & the Dynamic Dichotomy

3. The Darwinian semelparous model (from evolutionary game theory) & the Dynamic Dichotomy

4. Examples: trade-offs, life history strategies & evolutionary stability

5. Summary & open problems

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Density dependence

$$\left.\begin{array}{l} \varphi : \Omega \to \bar{R}^1_+ = [0, +\infty) \\ \sigma : \Omega \to (0,1) \end{array}\right\} \text{ are } C^2$$

where $(0,0) \in \Omega =$ **open** $\subseteq R^2$

$$\varphi(0,0) = \sigma(0,0) = 1$$

$b =$ **inherent (low density) adult fertility**

$s =$ **inherent (low density) juvenile survival**

$R_0 \doteq sb$

$=$ **inherent net reproductive number**

(expected offspring per individual per life time)

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

$$\left.\begin{array}{l} \varphi : \Omega \to \bar{R}^1_+ = [0, +\infty) \\ \sigma_j, \sigma_a : \Omega \to (0,1) \end{array}\right\} \text{ are } C^2$$

where $(0,0) \in \Omega =$ **open** $\subseteq R^2$

$$\varphi(0,0) = \sigma_j(0,0) = \sigma_a(0,0) = 1$$

$b =$ **inherent adult fertility**

$s_j =$ **inherent juvenile survival,** $0 < s_a =$ **inherent adult survival**

$R_0 \doteq \dfrac{s_j}{1-s_a} b =$ **inherent net reproductive number**

(expected offspring per individual per life time)

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Define :

$$a_{\pm} \doteq \left[\partial_J^0\sigma_j + \frac{s_j}{1-s_a}\partial_A^0\varphi + \frac{s_a}{1-s_a}\frac{s_j}{1-s_a}\partial_A^0\sigma_a\right] \pm \left[\partial_J^0\varphi + \frac{s_j}{1-s_a}\partial_A^0\sigma_j + \frac{s_a}{1-s_a}\partial_J^0\sigma_a\right]$$

Within-class competitive effects

Between-class competitive effects

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Fundamental Bifurcation Theorem

1. Origin is stable if $R_0 < 1$ and unstable if $R_0 > 1$.

Assume $a_+ \neq 0$.

2. Positive equilibria (transcritically) bifurcate from the origin at $R_0 = 1$.

3. Stability depends on the direction of bifurcation:

   Right (forward) bifurcating positive equilibria are stable.

   Left (backward) bifurcating positive equilibria are unstable.

4. $a_+ < 0$ => right (hence stable) bifurcation

   $a_+ > 0$ => left (hence unstable) bifurcation

Iteroparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s_j\sigma_j(J_t, A_t)J_t + s_a\sigma_a(J_t, A_t)A_t$$

Notes

- **A right (stable) bifurcation occurs if there are <u>no positive feedback effects</u> (at low density), i.e. if there are no positive derivatives**

$$\partial_J^0\sigma, \quad \partial_A^0\varphi, \quad \partial_J^0\varphi, \quad \partial_A^0\sigma \, .$$

- **Positive feedback terms (positive derivatives) are called *Allee effects.***

- **A left (unstable) bifurcation can only occur in the presence of *strong* Allee effects.**

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Lloyd & Dybas (1966, 1974)
Hoppensteadt & Keller (1976)
Bulmer (1977)
May (1979)
Ebenman (1987, 1988)
JC & Li (1989, 1992)
Wikan & (1996)
Nisbet & Onyiah (1994)

Wikan & Mjølhus (1997)
Behncke (2000)
Davydova (2004)
Davydova, Diekmann & van Gils (2003, 2005)
Mjølhus, Wikan & Solberg (2005)
JC (1991, 2003, 2006, 2010)
Kon (2005, 2007)
Diekmann & Yan (2008)
JC & Henson (2012)

Semelparity

Plants

Annuals

Monocarpic perennials

Invertebrates

Species of
Insects
Arachnids
Molluscs

Vertebrates

Species of :

Fish
Lizards
Amphibians
Marsupials

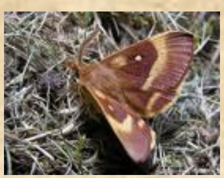
… even a mammal !

Periodical Insects

Magicicada spp.
13, 17 year cycles

"Poster-child" species

Melontha spp.
3, 4, 5 year cycles



Lasiocampa quercus var
1, 2 year cycles

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Define :

$$a_{\pm} \doteq \left[\partial_J^0\sigma + s_j\partial_A^0\varphi\right] \pm \left[\partial_J^0\varphi + s_j\partial_A^0\sigma\right]$$

Within-class competitive effects | **Between-class competitive effects**

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$

$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Fundamental bifurcation Theorem

JC & Jia Li (1989), JC (2006), JC & Henson (2012)

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Fundamental bifurcation Theorem

1. **Origin is stable if $R_0 = sb < 1$ and unstable if $R_0 > 1$.**

Assume $a_+ \neq 0$.

2. **Positive equilibria bifurcate from the origin at $R_0 = 1$.**

$a_+ < 0$ (or > 0) $\Rightarrow$ right (or left) bifurcation

3. **Synchronous 2-cycles also bifurcate from the origin at $R_0 = 1$.**

$\partial_J^0 \sigma + s\partial_A^0 \varphi < 0$ (or > 0) $\Rightarrow$ right (or left) bifurcation

4. **(a) Left bifurcations are unstable.**

   (b) A right bifurcation is stable <u>if</u> the other bifurcation is to the left.

   (c) If both bifurcations are to the right, then

Dynamic Dichotomy

$a_- > 0 \Rightarrow$ equilibria stable & 2-cycles unstable

$a_- < 0 \Rightarrow$ equilibria unstable & 2-cycles stable

Notes

- **If there are no Allee effects, that is, no positive derivatives**

$$\partial_J^0\sigma, \quad \partial_A^0\varphi, \quad \partial_J^0\varphi, \quad \partial_A^0\sigma$$

then Dynamic Dichotomy occurs.

- **Weak between-class competition gives stable equilibria**

$$a_- \doteq \left[\partial_J^0\sigma + s_j\partial_A^0\varphi\right] - \left[\partial_J^0\varphi + s_j\partial_A^0\sigma\right] > 0$$

- **Strong between-class competition gives stable synchronous 2-cycles**

$$a_- \doteq \left[\partial_J^0\sigma + s_j\partial_A^0\varphi\right] - \left[\partial_J^0\varphi + s_j\partial_A^0\sigma\right] < 0$$

- **Between-class (nymph) competition is leading hypothesis for periodical cicada dynamics**

- **Dichotomy observed in experiments with *Tribolium castaneum***

JC et al., *Chaos in Ecology,* Academic Press (2003)
King, Costantino, JC, Henson, Desharnais & Dennis, *Proc Nat Acad Sci* (2003)
Dennis, Desharnais, JC, Henson & Costantino*, Ecol Monogr* (2001)
Costantino, JC, Dennis & Desharnais, *Science* (1997)

Semelparous Juvenile-Adult Models

$$J_{t+1} = b\varphi(J_t, A_t)A_t$$
$$A_{t+1} = s\sigma(J_t, A_t)J_t$$

Typical example for which the Dynamic Dichotomy occurs:

$$\sigma(J,A) = \frac{1}{1 + c_{11}J + c_{12}A}, \quad \varphi(J,A) = \frac{1}{1 + c_{21}J + c_{22}A}$$

Leslie-Gower-type competition interaction functionals

… a natural extension of discrete logistic
(or Beverton-Holt)
equation for an unstructured population.

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u)\varphi(J_t, A_t, u)A_t \qquad \varphi(0,0,u) \equiv 1$$

$$A_{t+1} = s(u)\sigma(J_t, A_t, u)J_t \qquad \sigma(0,0,u) \equiv 1$$

$u =$ **mean of a phenotypic trait subject to Darwinian evolution**

$u \in U =$ **trait interval**

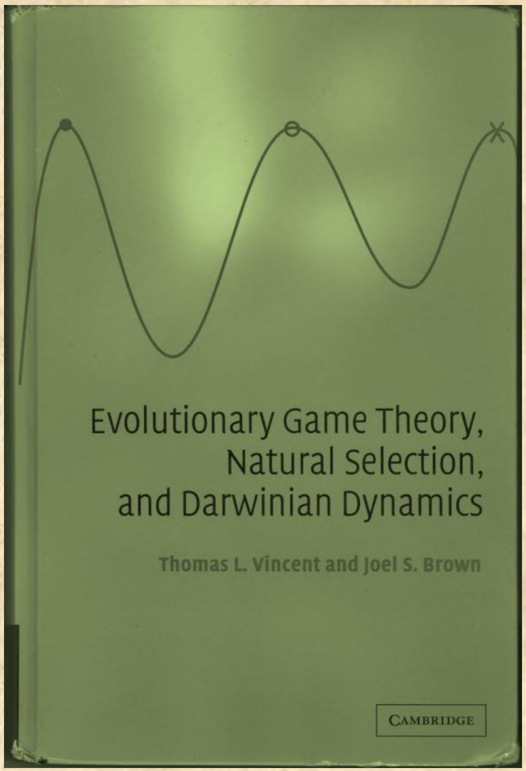
Assume $\max_U \beta(u) = 1.$

Then $b =$ **maximum adult fertility (over the trait interval** U **)**

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u_t)\varphi(J_t, A_t, u_t)A_t \qquad \varphi(0,0,u) \equiv 1$$

$$A_{t+1} = s(u_t)\sigma(J_t, A_t, u_t)J_t \qquad \sigma(0,0,u) \equiv 1$$



Vincent & Brown 2005

Using Evolutionary Game Theory Methodology

$$u_{t+1} = u_t + \frac{1}{2} v\,\partial_u \ln R_0(J, A, u)$$

$$R_0(J, A, u) \doteq b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)$$

$v =$ **trait variance (assumed constant in time)**

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u_t)\varphi(J_t, A_t, u_t)A_t \qquad \varphi(0,0,u) \equiv 1$$

$$A_{t+1} = s(u_t)\sigma(J_t, A_t, u_t)J_t \qquad \sigma(0,0,u) \equiv 1$$

$$u_{t+1} = u_t + \frac{1}{2}v\,\partial_u \ln[b\beta(u)s(u)\sigma(J,A,u)\varphi(J,A,u)]$$

- **What are the dynamics of this model ?**
- **When $v = 0$ the Fundamental Bifurcation Theorem applies and the Dynamics Dichotomy is a possibility.**
- **What happens when $v > 0$ (i.e. when evolution is present)?**

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u_t)\varphi(J_t, A_t, u_t)A_t \qquad \varphi(0,0,u) \equiv 1$$

$$A_{t+1} = s(u_t)\sigma(J_t, A_t, u_t)J_t \qquad \sigma(0,0,u) \equiv 1$$

$$u_{t+1} = u_t + \frac{1}{2}v\partial_u \ln[b\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)]$$

Extinction Equilibria & Critical Traits

An extinction equilibrium (J, A, u) is an equilibrium with $J = A = 0$.

A critical trait u satisfies $\partial_u R_0(0,0,u) = 0.$

Easy to see that …

(0, 0, u) is an extinction equilibrium if and only if u is a critical trait.

Evolutionary Semelparous Juvenile-Adult Models

$$J_{t+1} = b\beta(u_t)\varphi(J_t, A_t, u_t)A_t \qquad \varphi(0,0,u) \equiv 1$$

$$A_{t+1} = s(u_t)\sigma(J_t, A_t, u_t)J_t \qquad \sigma(0,0,u) \equiv 1$$

$$u_{t+1} = u_t + \frac{1}{2}v\partial_u \ln[b\beta(u)s(u)\sigma(J,A,u)\varphi(J,A,u)]$$

Synchronous 2-cycles

$$\begin{pmatrix} J \\ 0 \\ u_1 \end{pmatrix} \leftrightarrow \begin{pmatrix} 0 \\ A \\ u_2 \end{pmatrix}$$

Main Theorem

Assume …

1. **There exists a critical trait u^* :** $\partial_u R_0(0, 0, u^*) = 0$
2. $\partial_{uu} R_0(0, 0, u^*) \neq 0$
3. $a_+ \doteq \left[\partial_J^0 \sigma + s_j \partial_A^0 \varphi\right] + \left[\partial_J^0 \varphi + s_j \partial_A^0 \sigma\right] \neq 0$ **and** $\partial_J^0 \sigma + s \partial_A^0 \varphi \neq 0$

Then …

(a) If $\partial_{uu} R_0(0, 0, u^*) < 0$
then the Fundamental Bifurcation Theorem
and the Dynamic Dichotomy hold

… using $R_0(0, 0, u^*)$ as a bifurcation parameter.

(b) If $\partial_{uu} R_0(0, 0, u^*) > 0$
then the equilibria (extinction & positive) equilibria
and the synchronous 2-cycles
are all *unstable*.

NOTE: $R_0(0, 0, u) = b\beta(u)s(u)$

Examples

Leslie-Gower Nonlinearities

$$\sigma(J,A)=\frac{1}{1+c_{11}J+c_{12}A},\quad \varphi(J,A)=\frac{1}{1+c_{21}J+c_{22}A}$$

$c_{ij}\geq 0,$ **at least one** $c_{ii}>0$

- **No trait dependence in these density feedback terms**
- **No Allee effects**
- **Dynamic Dichotomy holds in absence of evolution**
- **Dynamic dichotomy holds occurs in the presence of evolution if**

$$\partial_{uu}R_0(0\ ,0,\ u^*) < 0$$

Examples

$$J_{t+1} = b\beta(u_t)\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = s(u_t)\frac{1}{1+c_{11}J_t + c_{12}A_t}J_t$$

$$u_{t+1} = u_t + \frac{1}{2}v\frac{\partial_u[\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0,0,u) = b\beta(u)s(u)$$

Critical trait equation:

$$\partial_u^0 R_0(0,0,u) = 0$$

$$\Leftrightarrow \beta'(u)s(u) + \beta(u)s'(u) = 0$$

Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0,0,u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

Trade-offs are of fundamental biological interest:

Survival & fertility change in opposite manner as u increases.

Mathematically:

$s(u)$ and $\beta(u)$ have opposite monotonicity

Examples

$$J_{t+1} = b\beta(u_t)\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = s(u_t)\frac{1}{1+c_{11}J_t + c_{12}A_t}J_t$$

$$u_{t+1} = u_t + \frac{1}{2}v\frac{\partial_u[\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0,0,u) = b\beta(u)s(u)$$

Critical trait equation:

$$\partial_u^0 R_0(0,0,u) = 0$$

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Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0,0,u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

Stability critieria:

$$a_- \doteq [c_{21} + s(u^*)c_{12}] - [c_{11} + s(u^*)c_{22}] < 0$$

$\Rightarrow$ **stable equilibria**

$$c \doteq \frac{c_{21} + s(u^*)c_{12}}{c_{11} + s(u^*)c_{22}}$$

competition ratio

Examples

$$J_{t+1} = b\beta(u_t)\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = s(u_t)\frac{1}{1+c_{11}J_t + c_{12}A_t}J_t$$

$$u_{t+1} = u_t + \frac{1}{2}v\frac{\partial_u[\beta(u_t)s(u_t)]}{\beta(u_t)s(u_t)}$$

Net reproductive number:

$$R_0(0,0,u) = b\beta(u)s(u)$$

Critical trait equation:

$$\partial_u^0 R_0(0,0,u) = 0$$

$$\Leftrightarrow \beta'(u)s(u) + \beta(u)s'(u) = 0$$

Dynamic Dichotomy criterion:

$$\partial_{uu}^0 R_0(0,0,u) < 0$$

$$\Leftrightarrow \beta''(u)s(u) + 2\beta'(u)s'(u) + \beta(u)s''(u) < 0$$

Stability critieria:

$c < 1 \Rightarrow$ **stable equilibria**

$c > 1 \Rightarrow$ **stable 2-cycles**

$$c \doteq \frac{c_{21} + s(u^*)c_{12}}{c_{11} + s(u^*)c_{22}}$$

competition ratio

Example 1

$$J_{t+1} = b\frac{1}{1+u_t}\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = \frac{u_t}{1+u_t}\frac{1}{1+c_{11}J_t + c_{12}A_t}J_t$$

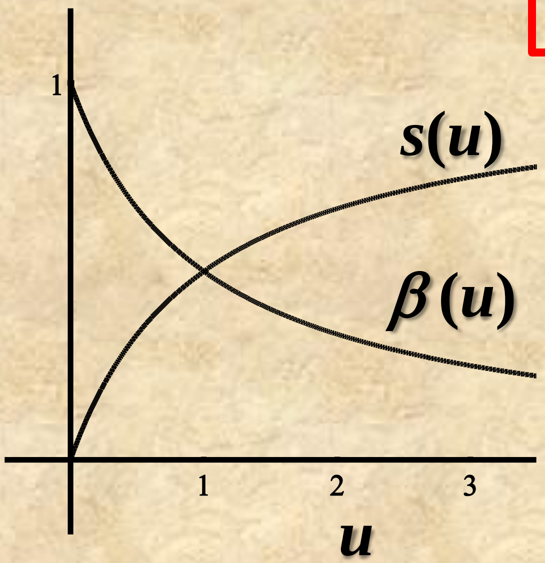
$$u_{t+1} = u_t + \frac{1}{2}v\frac{1-u_t}{(1+u_t)u_t}$$

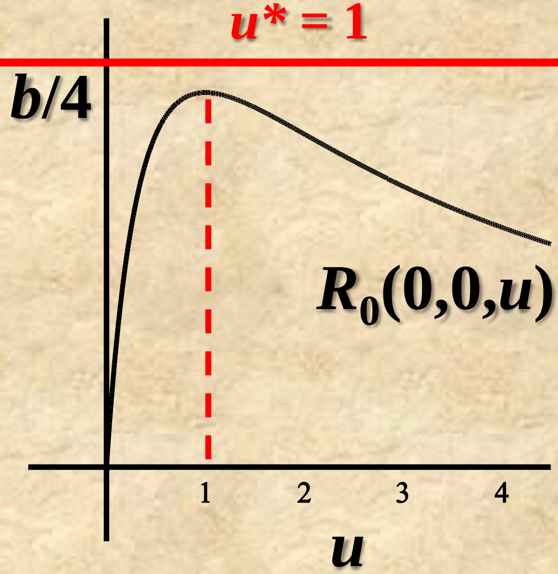
Dynamical Dichotomy holds at critical trait $u^* = 1$

$$s(u) = \frac{u}{1+u}, \quad \beta(u) = \frac{1}{1+u}$$

trait interval : $U = [0, +\infty)$

$$R_0(0,0,u) = b\frac{u}{(1+u)^2}$$





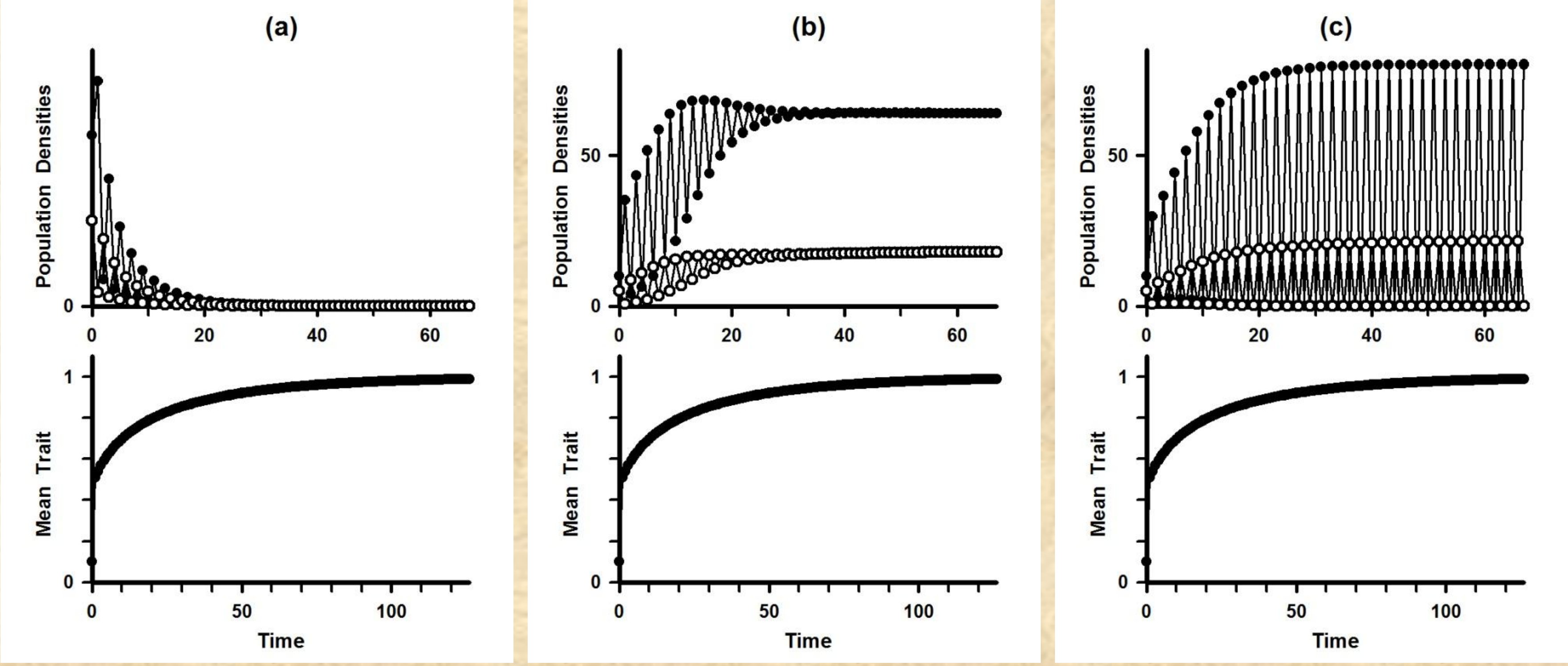
Example 1

Sample Time Series

$R_0(0,0,1) = 0.75$
Extinction

$R_0(0,0,1) = 2$
$c < 1$
Stable Equilibrium

$R_0(0,0,1) = 2$
$c > 1$
Stable 2-cycle



Example 2

$$J_{t+1} = b\frac{2\varepsilon + u_t^2}{2 + u_t^2}\frac{1}{1 + c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = \frac{2m}{1 + au_t^2}\frac{1}{1 + c_{11}J_t + c_{12}A_t}A_t$$

$$u_{t+1} = u_t - v u\frac{1 + 2\alpha + 2\alpha u_t^2}{(1 + \alpha u_t^2)(1 + u_t^2)}$$

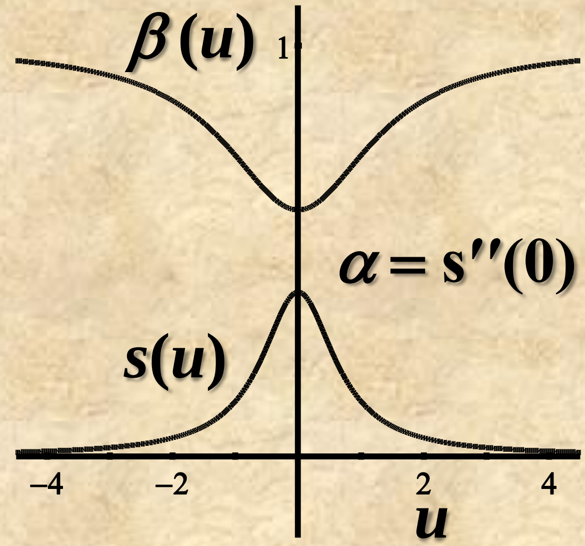
$$s(u) = \frac{2m}{1 + au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

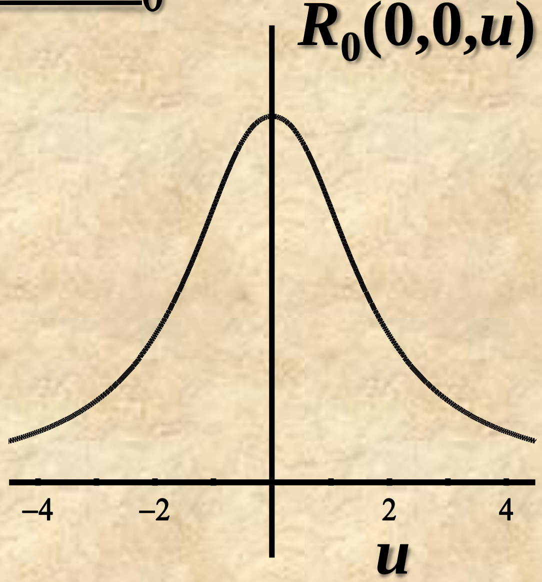
$$\alpha > 0, \quad 0 < m, \varepsilon < 1$$

trait interval : $U = R^1$

$$R_0(0,0,u) = b\frac{2m}{1 + au^2}\frac{2\varepsilon + u^2}{2 + u^2}$$

Large $\alpha > \alpha_0$





Example 2

$$J_{t+1} = b\frac{2\varepsilon + u_t^2}{2+u_t^2}\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = \frac{2m}{1+au_t^2}\frac{1}{1+c_{11}J_t + c_{12}A_t}A$$

$$u_{t+1} = u_t - \nu u\frac{1+2\alpha+2\alpha u_t^2}{(1+\alpha u_t^2)(1+u_t^2)}$$

Dynamical Dichotomy holds at critical trait $u^* = 0$

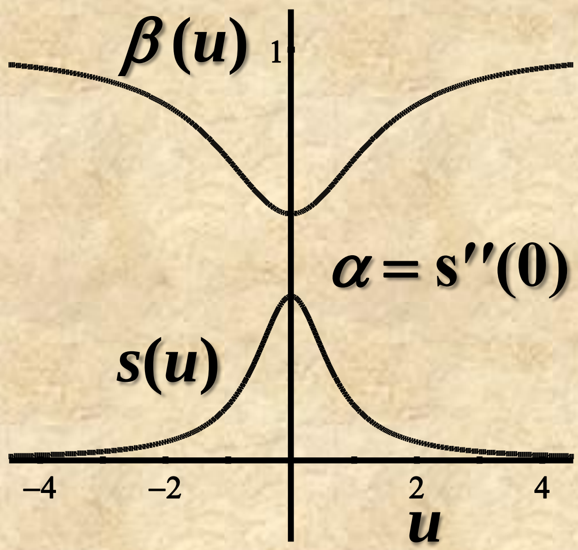
$$s(u) = \frac{2m}{1+au^2},\quad \beta(u) = \frac{2\varepsilon + u^2}{2+u^2}$$

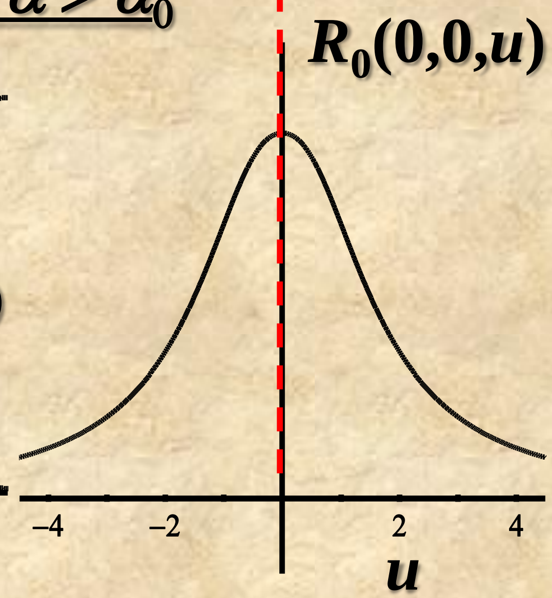
$$\alpha > 0,\quad 0 < m, \varepsilon < 1$$

trait interval : $U = R^1$

$$R_0(0,0,u) = b\frac{2m}{1+au^2}\frac{2\varepsilon+u^2}{2+u^2}$$

Large $\alpha > \alpha_0$

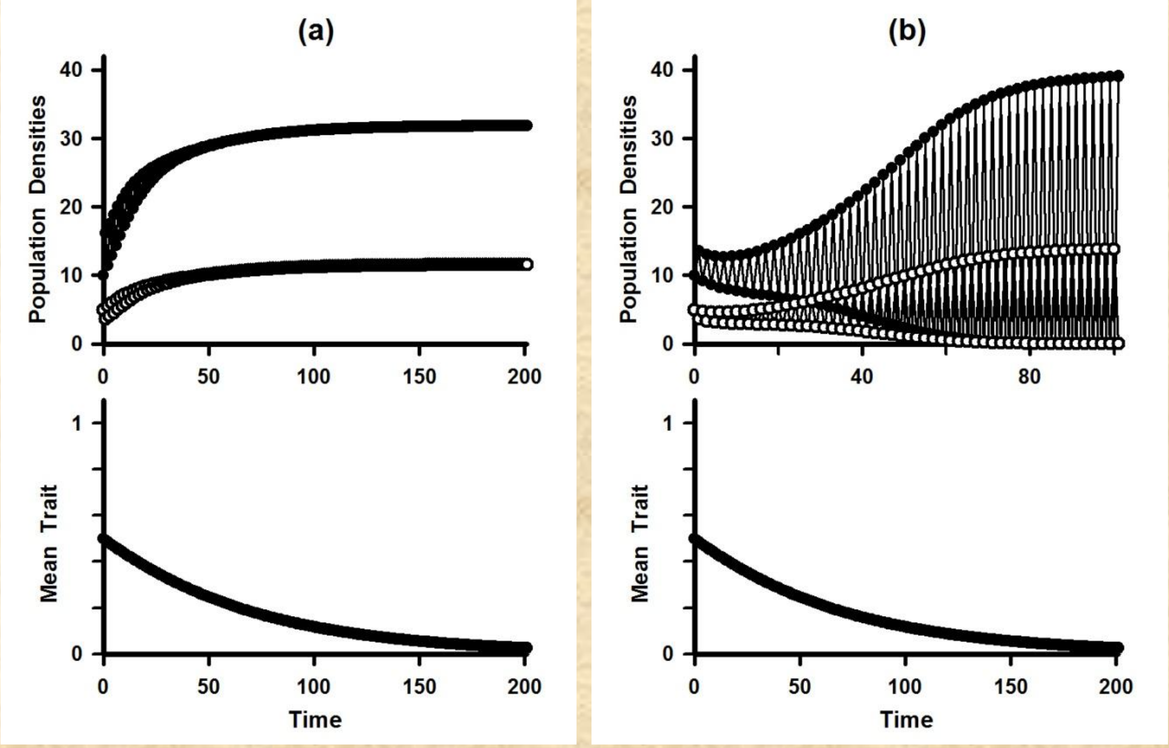




Example 1

Sample Time Series

$R_0(0,0,0) = 1.5$	$R_0(0,0,0) = 1.5$
$c < 1$	$c > 1$
Stable Equilibrium	**Stable 2-cycle**



Example 2

$$J_{t+1} = b\frac{2\varepsilon + u_t^2}{2+u_t^2}\frac{1}{1+c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = \frac{2m}{1+au_t^2}\frac{1}{1+c_{11}J_t + c_{12}A_t}A_t$$

$$u_{t+1} = u_t - vu\frac{1+2\alpha+2\alpha u_t^2}{(1+\alpha u_t^2)(1+u_t^2)}$$

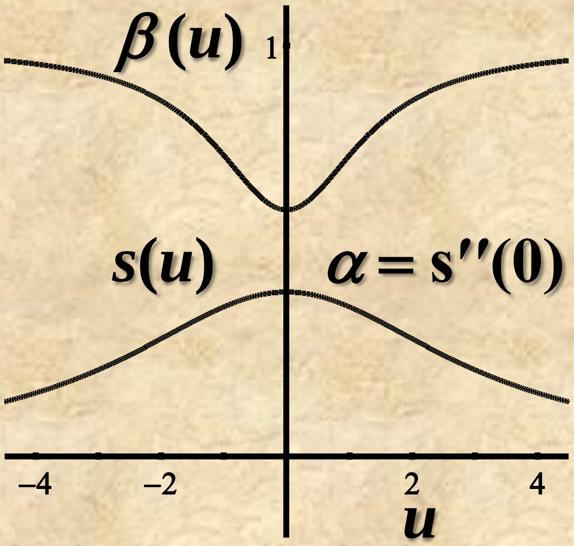
Small $\alpha < \alpha_0$

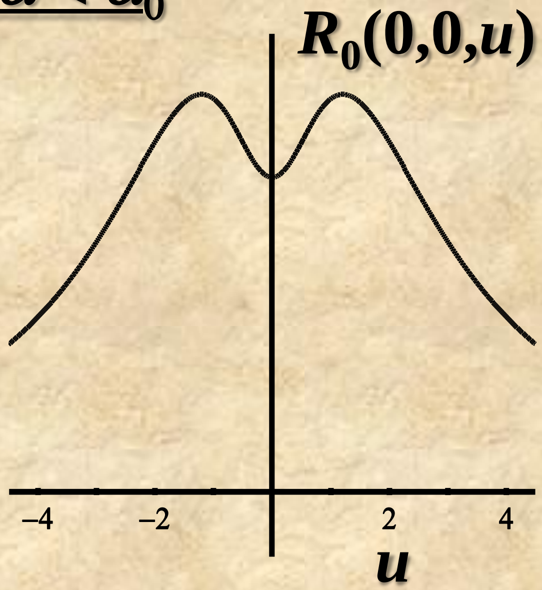
$$s(u) = \frac{2m}{1+au^2},\quad \beta(u) = \frac{2\varepsilon + u^2}{2+u^2}$$

$$\alpha > 0, \quad 0 < m, \varepsilon < 1$$

trait interval : $U = R^1$

$$R_0(0,0,u) = b\frac{2m}{1+au^2}\frac{2\varepsilon+u^2}{2+u^2}$$





Example 2

$$J_{t+1} = b\frac{2\varepsilon + u_t^2}{2 + u_t^2}\frac{1}{1 + c_{21}J_t + c_{22}A_t}A_t$$

$$A_{t+1} = \frac{2m}{1 + au_t^2}\frac{1}{1 + c_{11}J_t + c_{12}A_t}$$

$$u_{t+1} = u_t - vu\frac{1 + 2\alpha + 2\alpha u_t^2}{(1 + \alpha u_t^2)(1 + u_t^2)}$$

Dynamical Dichotomy

holds at

2 critical traits $\pm u^*$

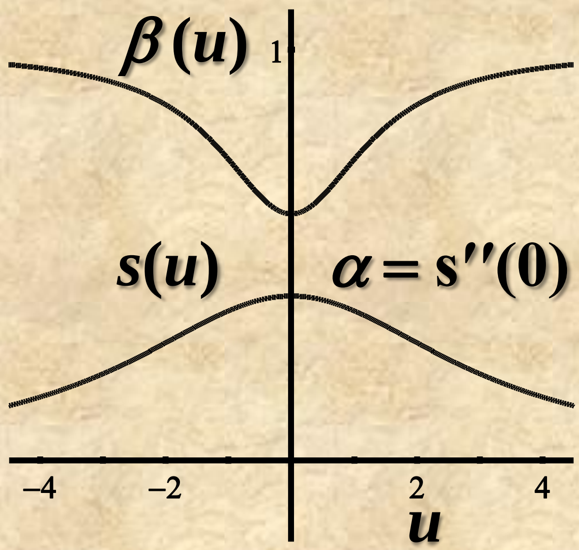
$$s(u) = \frac{2m}{1 + au^2}, \quad \beta(u) = \frac{2\varepsilon + u^2}{2 + u^2}$$

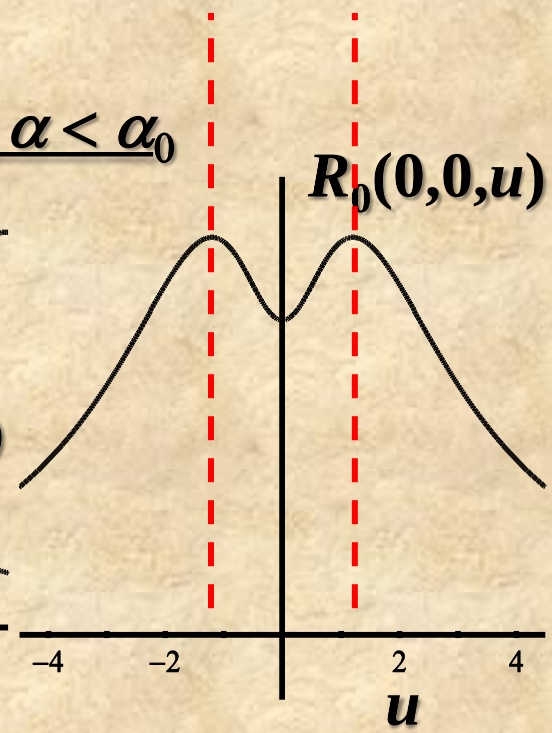
$$\alpha > 0, \quad 0 < m, \varepsilon < 1$$

trait interval : $U = R^1$

$$R_0(0,0,u) = b\frac{2m}{1 + au^2}\frac{2\varepsilon + u^2}{2 + u^2}$$

Small $\alpha < \alpha_0$





Example 2

Sample Time Series

$R_0(0,0, u^*) = 1.5$

$c < 1$

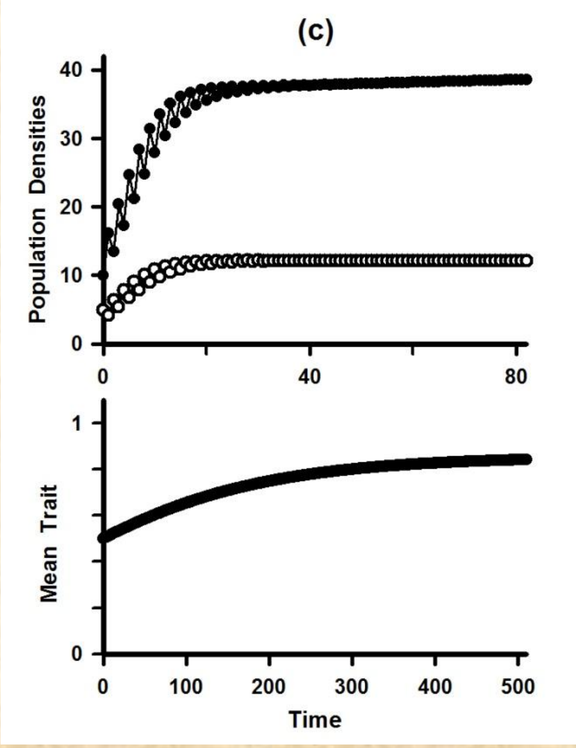
Stable Equilibrium

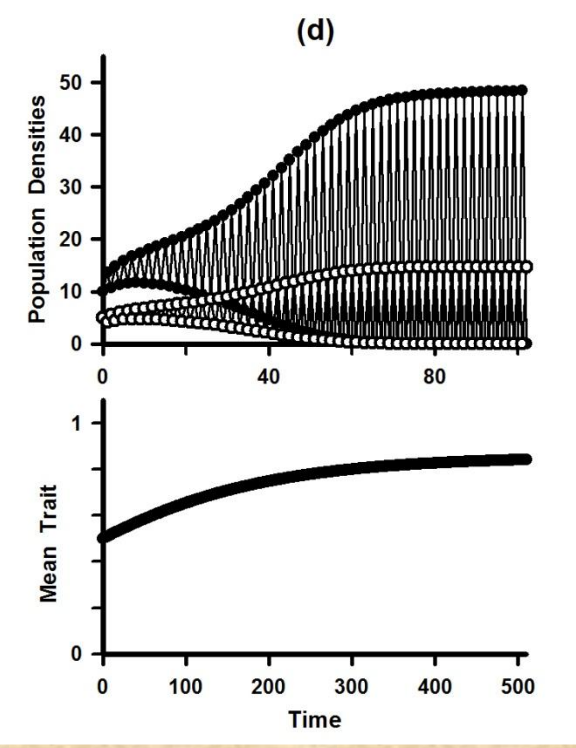
$R_0(0,0,u^*) = 1.5$

$c > 1$

Stable 2-cycle

***u* will equilibrate at negative critical trait for other initial conditions**





Summary

For the EGT semelparous juvenile-adult model :

- **The Fundamental Bifurcation Theorem holds at critical traits u^* where inherent (low density) fitness has a local maximum :**

  $$\partial_u R_0(0,0,u^*) = 0, \quad \partial_{uu} R_0(0,0,u^*) < 0$$

- **Positive equilibria & synchronous 2-cycles bifurcate at $R_0(0,0,u^*) = 1$.**

- **The Dynamic Dichotomy holds.**

  For example, when no Allee effects are present.

Open Problems

- What are the properties of the bifurcation at $R_0 = 1$ for Leslie semelparous of dimensions 3 and higher

  without evolution ? with evolution?

- Global stability results? Especially for Leslie-Gower nonlinearities.

- What happens to bifurcating branches for large $R_0 >> 1$?

- EGT Leslie semelparous models with 2 or more phenotypic traits