Two models of semelparous species.

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- usually dies afterwards,

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- beet, carrot, cabbage, onion, lettuce
- agave,
- bamboo,
- salmon,
- arachnids

and insects: magicicada

Age-structured models / Plan of the talk

Discrete-time model:

$x(t, a)$ — number of specimens at age a and at time t.
$\mathbf{x}(t) = [x(t, 1), \ldots, x(t, n)]$ — vector of subpopulation sizes.

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

Continuous-time model:

$u(t, a)$ — age-time distribution of specimens in population.
Evolution governed by an McKendrick equation

Evolution equation: $\begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu u(t, a) \\ u(t, 0) = \beta(u) \\ u(0, a) = u_0(a) \end{cases}$

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$$\text{Leslie model: } \mathbf{x}(t+1) = A\mathbf{x}(t)$$

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Approaches — Bibliography

- H. Bernardelli, *Population waves*, J. Burma Res. Soc. (1941)
- P. Cull, A. Vogt, *The periodic limit for the Leslie model*, Mathematical Biosciences (1974)
- M. G. Bulmer, *Periodical insects*, The American Naturalist (1977)
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Discrete-time model

General model:

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

$$\begin{aligned}
\mathbf{x}(t) = [x(t,1), &\quad \text{— number of specimens at age 1} \\
x(t,2), &\quad \text{— number of specimens at age 2} \\
\vdots &\qquad\qquad\qquad \vdots \\
x(t,n)\ ] &\quad \text{— number of specimens at age n}
\end{aligned}$$

Discrete-time model

One-year model:

$$x(t+1) = f(x(t))$$

where

- $x(t)$ - size of population in the year t,
- $f(x) = b(x)x, \qquad b(x)$ — birth rate,
- K — steady size, x_{max} — maximal size,
  $b(x) > 1,\ x \in (0, K); \quad b(x) < 1,\ x \in (K, x_{max})$

Example: logistic model.

$$x(t+1) = \lambda\big(1 - x(t)\big)x(t)$$

Discrete-time model

n-years model of semelparous species

- only specimens at age n reproduce
- $x(t,a)$ — number of individuals at age a at time t
- $N(t) = \sum_{a=1}^{a_{\max}} x(t,a)$ — total population size at time t
- evolution:

$$\begin{aligned} x(t+1,a+1) =& [1-\mu(a,N(t))]x(t,a), \\ x(t+1,1) =& b(N(t))x(t,n), \end{aligned}$$

- μ — mortality,
- b — birth rate — average number of offspring
  b is strictly decreasing and positive in $[0,M)$
  and $b(M)=0$, where $0 < M \leq \infty$.

Discrete-time model

Typical birth-rate functions

$$
\begin{aligned}
b(x) &= \lambda(1 - x/K) && \text{— logistic model} \\
b(x) &= \lambda e^{-cx} && \text{— Ricker's model} \\
b(x) &= \frac{\lambda}{1 + cx} && \text{— Beverton-Holt's model}
\end{aligned}
$$

Fixed point

Let $r(1) = 1$ and $r(i) = q(1) \cdot \dots \cdot q(i-1)$,

where $q(a) = 1 - \mu(a)$.

Assume that $b(0)r(n) > 1$ for $x \in (0, M)$,

1. The set

$$S = \left\{ \mathbf{x} \in \mathbb{R}^n_+ : \ \beta(\mathbf{x}) \leq \frac{b(0)N_0}{r(n)} \right\},$$

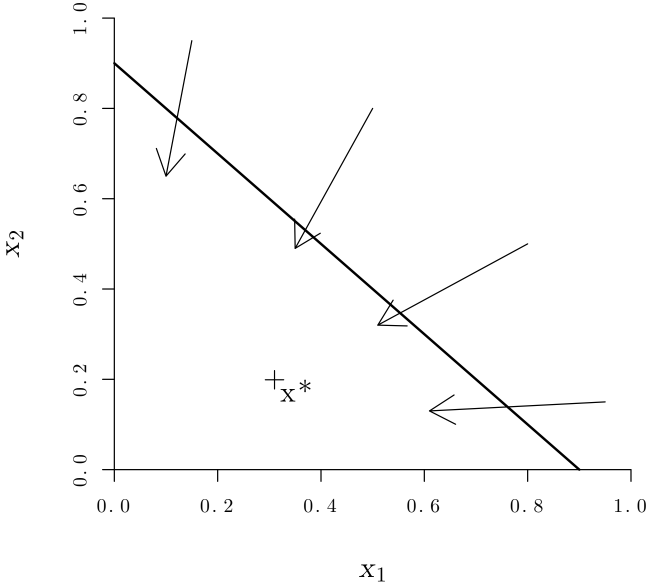
   with $\beta(\mathbf{x}) = \frac{x_1}{r(1)} + \dots + \frac{x_n}{r(n)}$, is absorbing.

2. The trivial fixed point 0 is repelling.
3. Let $N_0 \in (0, M)$ such that $r(n)b(N_0) = 1$. Then

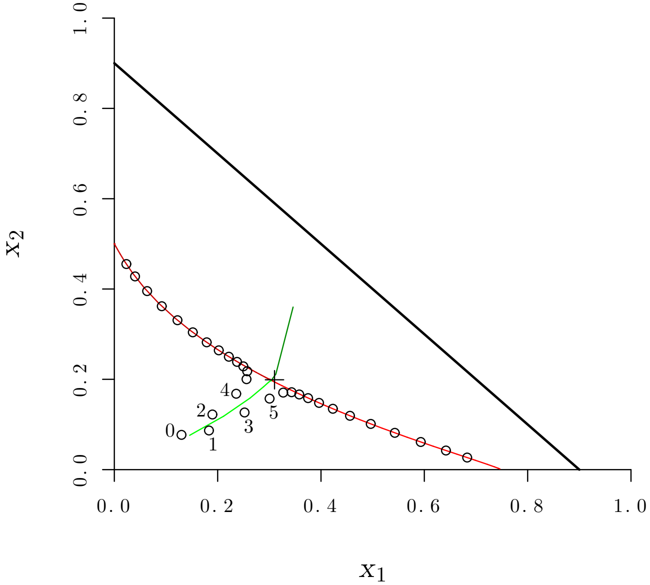
$$x_1^* = \frac{N_0}{\sum_{i=1}^n r(i)}, \quad x_2^* = r(2)x_1^*, \quad \dots, \quad x_n^* = r(n)x_1^*,$$

   is the only non-zero fixed point.

4. if n is even, then the point $\mathbf{x}^*$ is unstable.



Biennials case. x_1, x_2 — individuals at age 1, 2. x^* — fixed point.



Biennials case. x_1, x_2 — individuals at age 1, 2. x^* — fixed point.

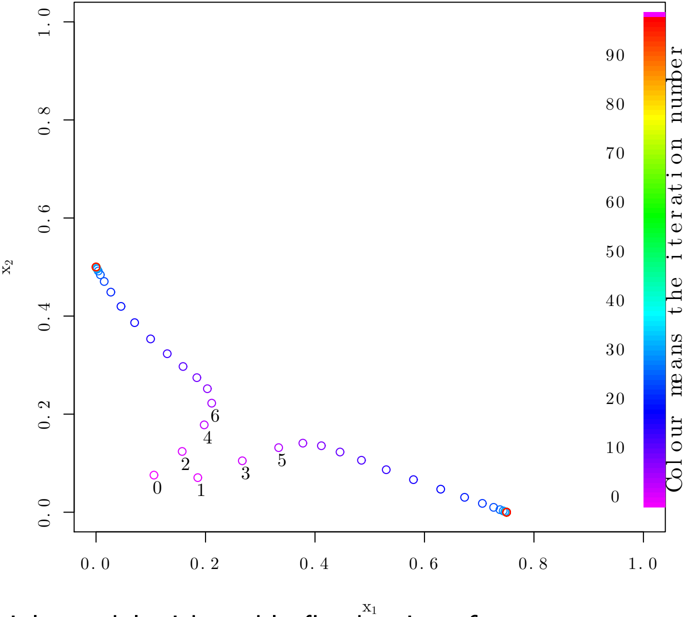
The competition between different age-classes
results in the extinction
of all but one age-classes.

(age-class = individuals at the same age)

Let $g(z) = b(r(n)z)\, r(n)\, z$ — this transformation governs the behaviour of the individuals of age one only.

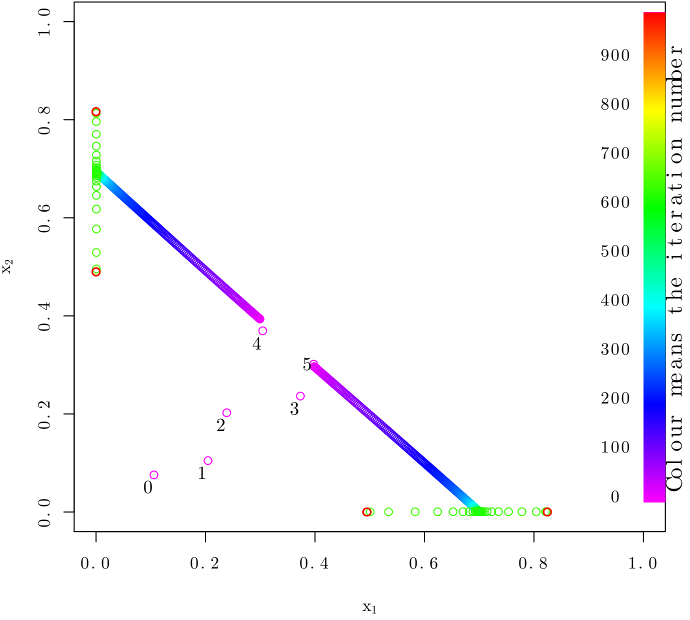
Theorem

Let $z_0 > 0$ be such a number that $z_0 = g^k(z_0)$. Then the point $\mathbf{z}_0 = [z_0, 0, \dots, 0]$ is a kn-periodic point of $\mathbf{f}$.
If z_0 is an asymptotically stable stationary point of the transformation g^k then $\mathbf{z}_0$ is an asymptotically stable stationary point of the transformation $\mathbf{f}^{kn}$.

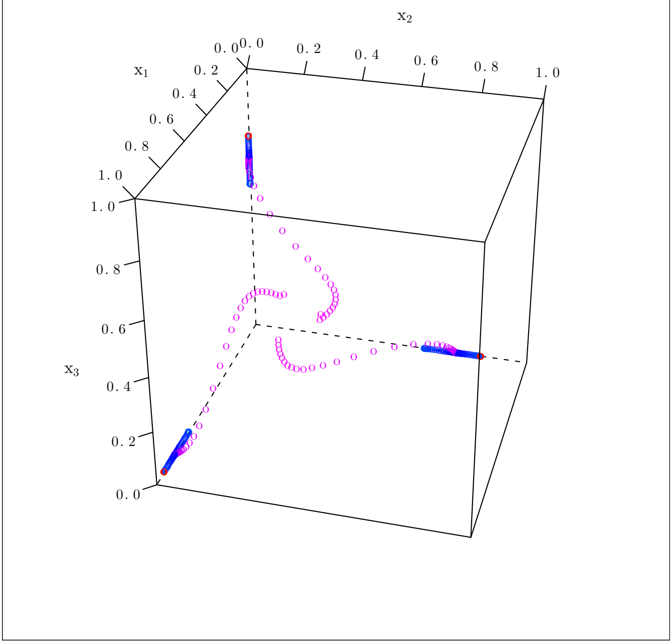


Biennials model with stable fixed point of g

$\Rightarrow$ **f** has attractive 2-periodic point



Biennials model with stable periodic point of g with period 2.



Triennials model with stable periodic point of g with period 2.

A sequence (y_k) is called ε-*pseudo-orbit* of a transformation g, if $|g(y_k) - y_{k+1}| < \varepsilon$ for all $k \geq 1$.

Definition

The transformation g is called *shadowing*,
if for every $\delta > 0$ there exists $\varepsilon > 0$ such that
for each ε-pseudo-orbit (y_k) of g
there is a point x such that $|y_k - g^k(x)| < \delta$.

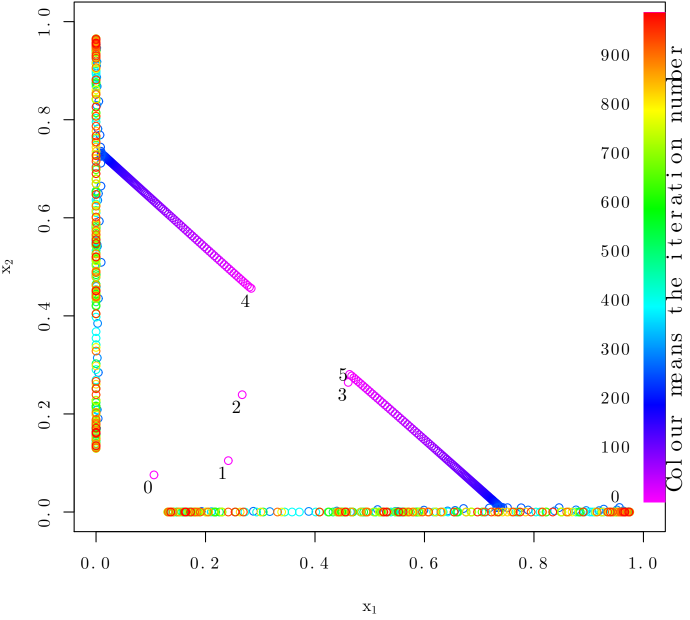
Theorem

If g is shadowing then for each $\delta > 0$ and $\rho_0 > 0$ there exists ε such that for each point

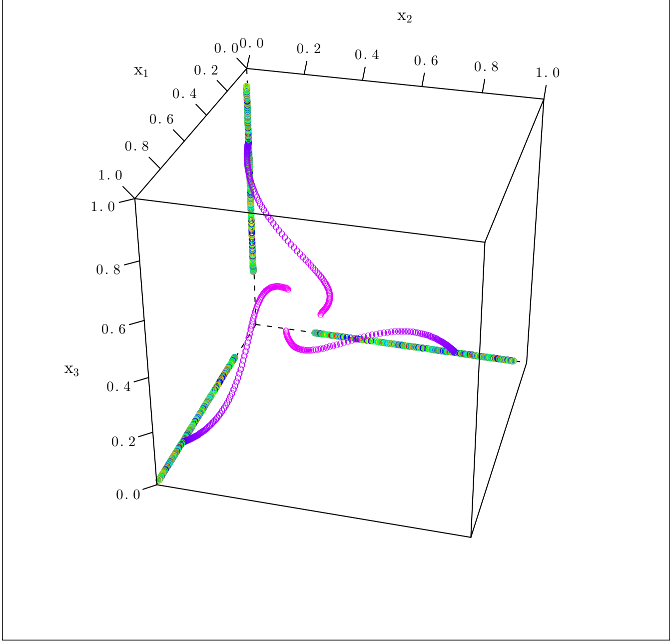
$$\mathbf{x} \in [\rho_0, M] \times [0, \varepsilon] \times \ldots \times [0, \varepsilon]$$

there exists y such that

$$\left| \left[\mathbf{f}^{kn}(\mathbf{x}) \right]_1 - g^k(y) \right| < \delta \quad \textit{for all } k \geq 1.$$



Biennials model, when g is chaotic.



Triennials model, when g is chaotic.

Going to the continuous-time model

$x(t, a)$ — number of individuals   timestep: 1

$\downarrow$ $\downarrow$

$u(t, a)$ — density of individuals   timestep: $\Delta t \ll 1$

Going to the continuous-time model

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$u(t,a)$ — density of individuals   timestep: $\Delta t \ll 1$

$$u(t+\Delta t, a+\Delta t) - u(t,a) = -\mu(a)u(t,a) + o(\Delta t)$$

$$\downarrow \qquad \downarrow$$

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u$$

Going to the continuous-time model

$x(t,a)$ — number of individuals   timestep: 1

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$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u$$

$$u(t+\Delta t, \Delta t) = \sum_a b(a, N(t))u(t,a),$$

$$\downarrow \qquad \downarrow$$

$$u(t,0) = \beta(N(t)) \int_0^m b(a)u(t,a)da$$

Continuous model

McKendrick equation:

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u,$$
$$u(t,0) = \beta(N(t)) \int_0^m b(a)u(t,a)da,$$
$$u(0,a) = u_0(a).$$

in the semelparous case $b(a) = \delta_m(a)$ an we get:

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u$$
$$u(t,0) = \beta(N(t))u(t,m)$$
$$\text{where } N(t) = \int_0^m u(t,a)da$$

We have

$$(\star) \quad u(t,a) = \Phi(a)u(t-a,0), \qquad \text{where } \Phi(a) = \exp\left\{-\int_0^a \mu(s)\,ds\right\}$$

is a survivorship function.

This gives, together with the boundary condition $u(t,0) = \beta(N(t))u(t,m)$, the renewal equation:

$$(\star\star) \quad u(t,0) = \beta\left(\int_0^m \Phi(a)u(t-a,0)\,da\right)\Phi(m)u(t-m,0).$$

Similarly to the discrete case, we assume that $\beta(0)\Phi(m) > 1$ and that β is a decreasing to zero function.

Stationary solution

$$(\star) \quad u(t,a) = \Phi(a)u(t-a,0), \qquad \text{where } \Phi(a) = \exp\Big\{ -\int_0^a \mu(s)\,ds \Big\}$$

$$(\star\star) \quad u(t,0) = \beta\bigg(\int_0^m \Phi(a)u(t-a,0)\,da \bigg)\Phi(m)u(t-m,0).$$

There exist a unique point c such that $\beta(c)\Phi(m) = 1$.

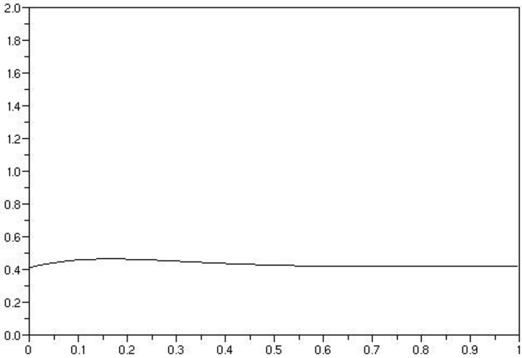
Therefore,

$$u^* = c / \int_0^m \Phi(a)da$$

is the stationary solution of $(\star\star)$,
and by $(\star)$

$$u^*(t,a) = \Phi(a)u^*$$

is the stationary solution of the McKendrick equation.



(movie)

Periodic solutions

- The function u is a periodic solution with period m, if $\int_0^m \Phi(a)u(t-a,0)\,da = c$ for $t \in \operatorname{supp} u(\cdot,0)$.
- The only classical solution with period m is the stationary solution u^*.
- However, if we consider measure solutions, we have a whole class of m-periodic solutions.

Measure periodic solutions

The measure u is a periodic solution of the renewal equation $(\star\star)$, if

$$\int_{[t-m,t)} \Phi(t-s)u(ds) = c \text{ for } t \in \operatorname{supp} u$$

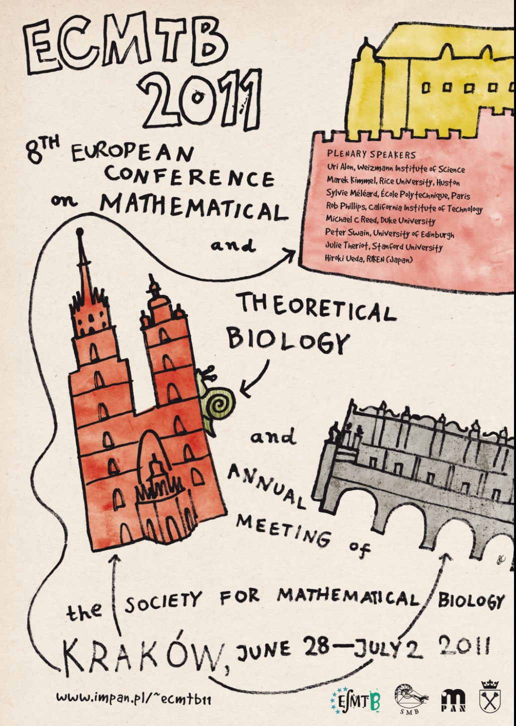
The simplest example is a measure $u = \sum_{j\in\mathbb{Z}} \frac{c}{\Phi(m)}\delta_{j*m}$. It corresponds to the initial state $u_0(da) = \frac{c}{\Phi(m)}\delta_0(da)$ of the McKendrick equation.

If we take $t_1, \ldots, t_k \in [0, m)$ then the measure

$$u = \sum_{j\in\mathbb{Z}} \sum_{i=1}^{k} \alpha_i \delta_{i+j*m}$$

is a periodic solution to the renewal equation if α_i satisfy

$$\sum^{k} \alpha_i \Phi(a_i - a_j \mod m) = c, \text{ for every } j = 1, \ldots, k.$$



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