Structured Population Dynamics in ecology and epidemiology

Intensive Programme - Mathematical Models in Life and Social Sciences - September 7-19 2009 - Alba Adriatica, Italy.

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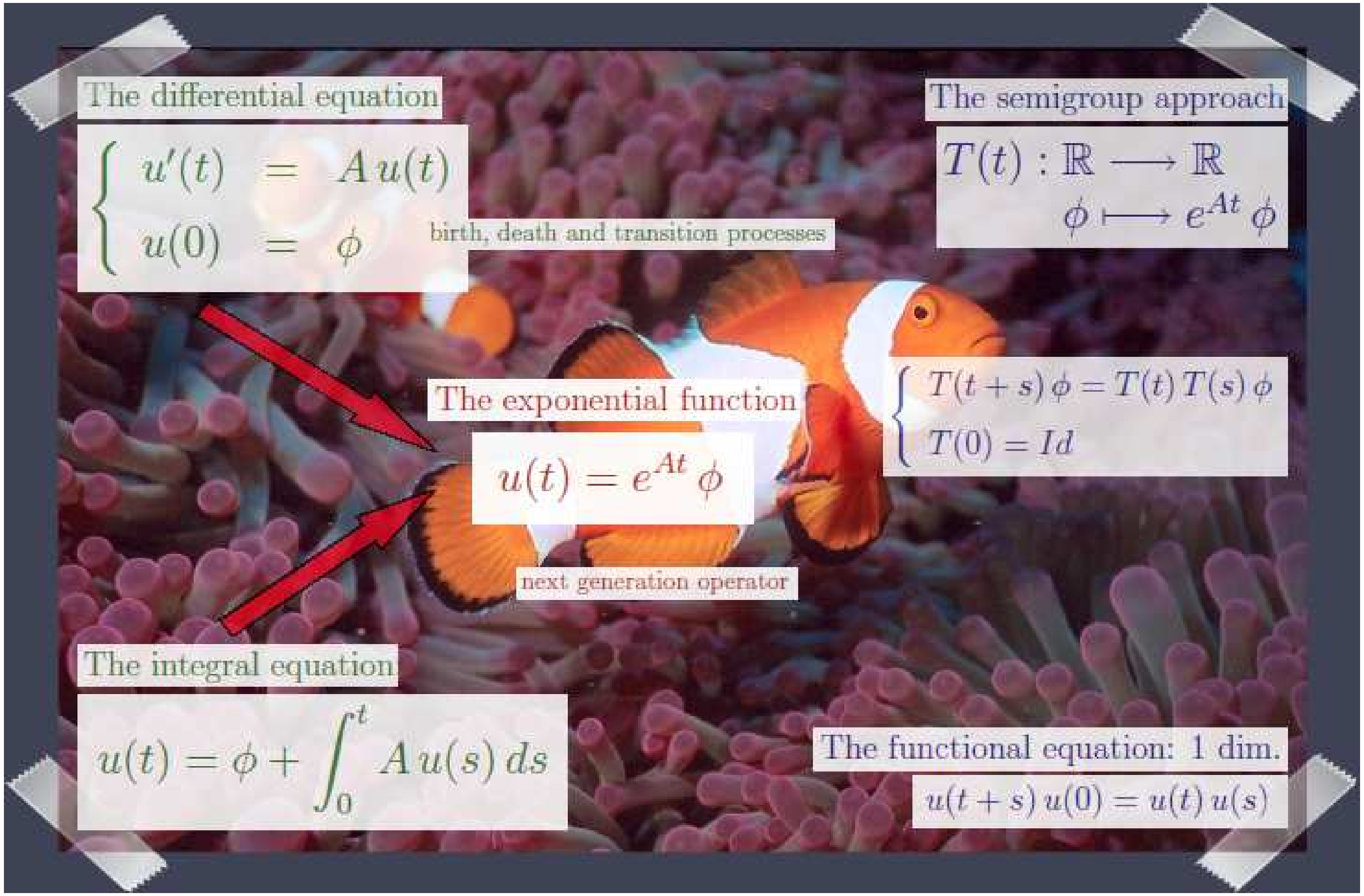
Education and Culture DG
Lifelong Learning Programme

Outline of the course

- ★ Introduction: time-continuous linear population dynamics. Semigroup approach.
- ★ Early ecological models and epidemiological models. Exponential/logistic population growth. SIS and SIR models.
- ★ Continuously age-structured population models. Linear Lotka-Mckendrick equation. Non-linear Gurtin-MacCamy equation. Kermack-Mckendrick equation. Size-dependent problems. Numerical Simulations.
- ★ Matrix models. Leslie/Usher/*Tridiagonal* models.

Introduction



The differential equation

$$\begin{cases} u'(t) = A\,u(t) \\ u(0) = \phi \end{cases}$$

birth, death and transition processes

The semigroup approach

$$T(t) : \mathbb{R} \longrightarrow \mathbb{R}$$
$$\phi \longmapsto e^{At}\,\phi$$

$$\begin{cases} T(t+s)\,\phi = T(t)\,T(s)\,\phi \\ T(0) = Id \end{cases}$$

The exponential function

$$u(t) = e^{At}\,\phi$$

next generation operator

The integral equation

$$u(t) = \phi + \int_0^t A\,u(s)\,ds$$

The functional equation: 1 dim.

$$u(t+s)\,u(0) = u(t)\,u(s)$$

Time-continuous Linear Population Dynamics.

Introduction (cont’)

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- ★ Semigroup approach: the evolution is described by a family of operators that map an initial state of the system to all subsequent states.

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- ★ Both "equivalent" forms of the equation lead to an explicit evolution given by the exponential function.
- ★ Linear models can be improved by non-linear ones where usually it is not possible to find exact solutions.
- ★ Semigroup approach: the evolution is described by a family of operators that map an initial state of the system to all subsequent states.
- ★ The diagram is general, i.e. we can change $\mathbb{R}$ (scalar case) by $\mathbb{C}$, or $\mathbb{R}^n$, or a Banach space like $\mathcal{L}^1$, $\mathcal{C}^0$.

Introduction (cont')

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- ⋆ In the infinite dim. case, A is a linear operator. If it is bounded then the formula of the series applies.
- ⋆ In many applications, the operators are unbounded and one has problems with the choice of the domain.
- ⋆ However, for a large class of unbounded operators (Hille-Yosida), the operator exponential can be computed as $e^{At}\,\phi = \lim_{n\to\infty} \left(Id - A\frac{t}{n}\right)^{-n} \phi$. For the rest, e^{At} is just a notation.

Early ecological models

Unstructured models for a single-species. Closed population. Intrinsic growth rate $r = \beta - \mu$. Basic reproduction num. $R_0 = \frac{\beta}{\mu}$. Birth and death processes.

- ⋆ Malthus: $x(t{+}1){=}x(t){+}r\,x(t)$, $x(t{+}\Delta t){=}x(t){+}r\,x(t)\Delta t$ and taking the limit $x'(t) = rx$. Exponential population growth/decay $x(t) = e^{rt}x(0)$.

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- ★ Competition for resources: $x'(t) = \mathrm{r}(x)\,x$. Verhulst (Logistic equation): $x'(t) = r\,(1 - \frac{x}{K})x$, $r > 0$. Logistic population growth $x(t) = \frac{Kx(0)}{x(0)+(K-x(0))e^{-rt}}$. $x^* = K$.

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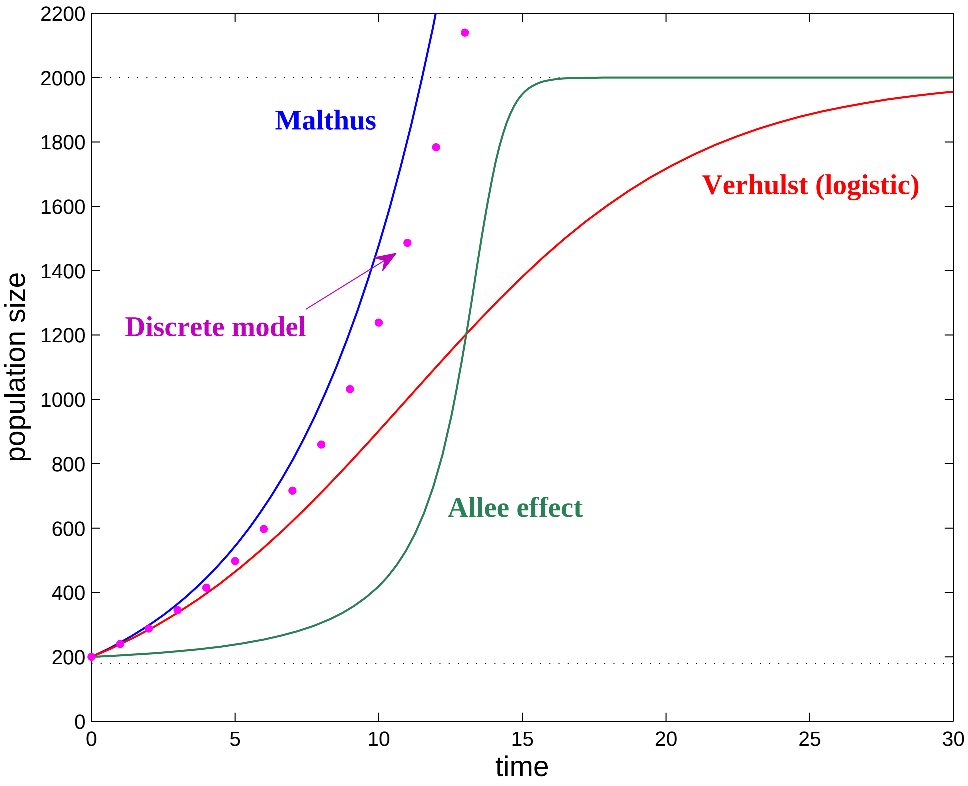
- ★ Allee effect: competition and (implicit) sexual reproduction. $x'(t) = r\,(1 - \frac{x}{K})(\frac{x}{K_0} - 1)x$, $K_0 < K$.

Early ecological models (cont’)



Evolution in time ($r > 0$ or $R_0 > 1$) of the population size for the discrete ($x(t) = (1 + r)^t x_0$) and continuous (Malthus, Verhulst, Allee) models. If r small $e^{rt} \approx (1 + r)^t$.

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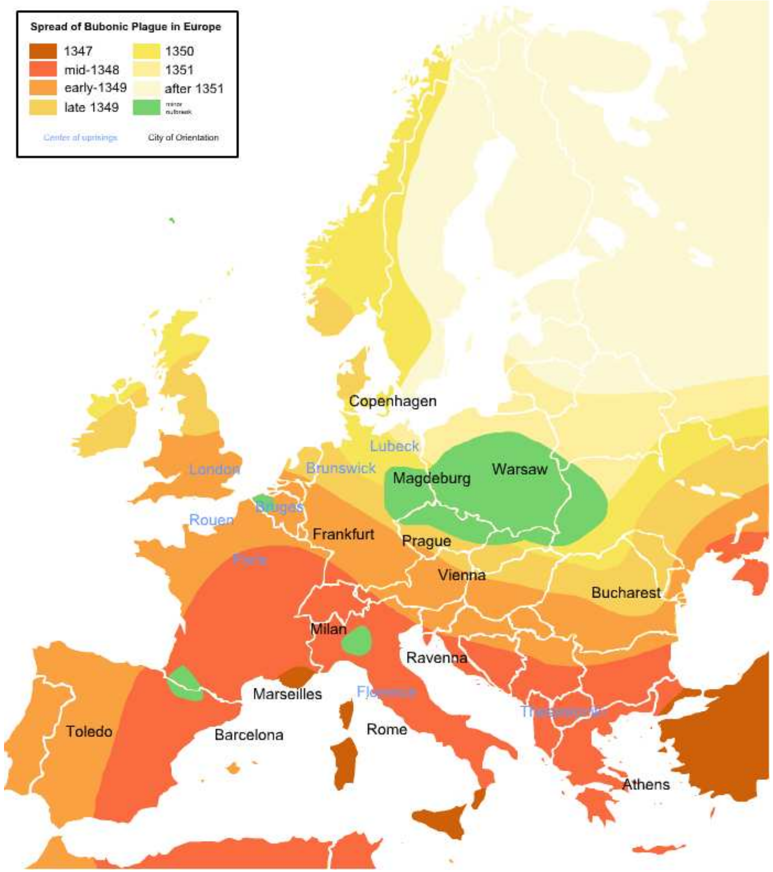
- ★ R_0 average number of newborns produced by one individual during its lifetime. $r >=< 0 \Leftrightarrow R_0 >=< 1$.
- ★ Probabilistic interpretation: death process $x'(t) = -\mu x$. $\frac{x(t)}{x(0)} = e^{-\mu t}$, proportion between the actual and the initial population, or probability of an individual being alive at $t \geq 0$ given that he was alive at $t = 0$. So, the probability of dying is exponentially distributed: $P(X \leq t) = F(t) = 1 - e^{-\mu t}$, life expectancy $E[X] = \frac{1}{\mu}$. Per capita instantaneous death rate:

$$\lim_{dt \to 0} \frac{P(X \leq t+dt \,|\, X > t)}{dt} = \frac{F'(t)}{1 - F(t)} = \mu \,.$$

Early epidemiological models

The “Black Death”(in a picture of the 14th century), the plague that spread across Europe from 1347 to 1352 and made 25 millions of victims.

Early epidemiological models



The Black Death rapidly spread along the major European sea and land trade routes [from Wikipedia]. 2009 new pandemia (influenza A virus subtype H1N1)? ...

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- ★ Structure of the population according to the disease stage: *Susceptible, Infected, Removed*, ...
- ★ Basic distinction between those diseases that impart lifelong immunity and those which do not: SIR and SIS models.

$$S \xrightarrow{\beta} I \xrightarrow{\gamma} R$$

$$S \underset{\gamma}{\overset{\beta}{\rightleftarrows}} I$$

Early epidemiological models (cont')

- ★ Homogeneous mixing assumption. Force of infection, rate at which susceptible become infected (proportional to the number of infective contacts):

$$\text{infectiveness} \times \text{contact rate} \times \frac{\text{Infected}}{\text{Total}} = \phi \, c \, \frac{I}{N} \, .$$

Limited or non-limited transmission if c fixed or proportional to the population size. Duration of the infection exponentially distributed with mean $\frac{1}{\gamma}$.

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  Limited or non-limited transmission if c fixed or proportional to the population size. Duration of the infection exponentially distributed with mean $\frac{1}{\gamma}$.

- ★ Focus on the (short) epidemic period so that births and disease-unrelated deaths can be neglected and therefore the total population is conserved.

SIR model

The SIR model for diseases imparting immunity

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Total population is constant $N(t) = S(t) + I(t) + R(t) = N(0)$.
Implicit solutions: $\frac{dI}{dS} = \frac{\gamma}{\beta S} - 1$,

$$S + I - \frac{\gamma}{\beta} \ln S = \text{ct.} \qquad R(t) = N(0) - (S(t) + I(t)) \ .$$

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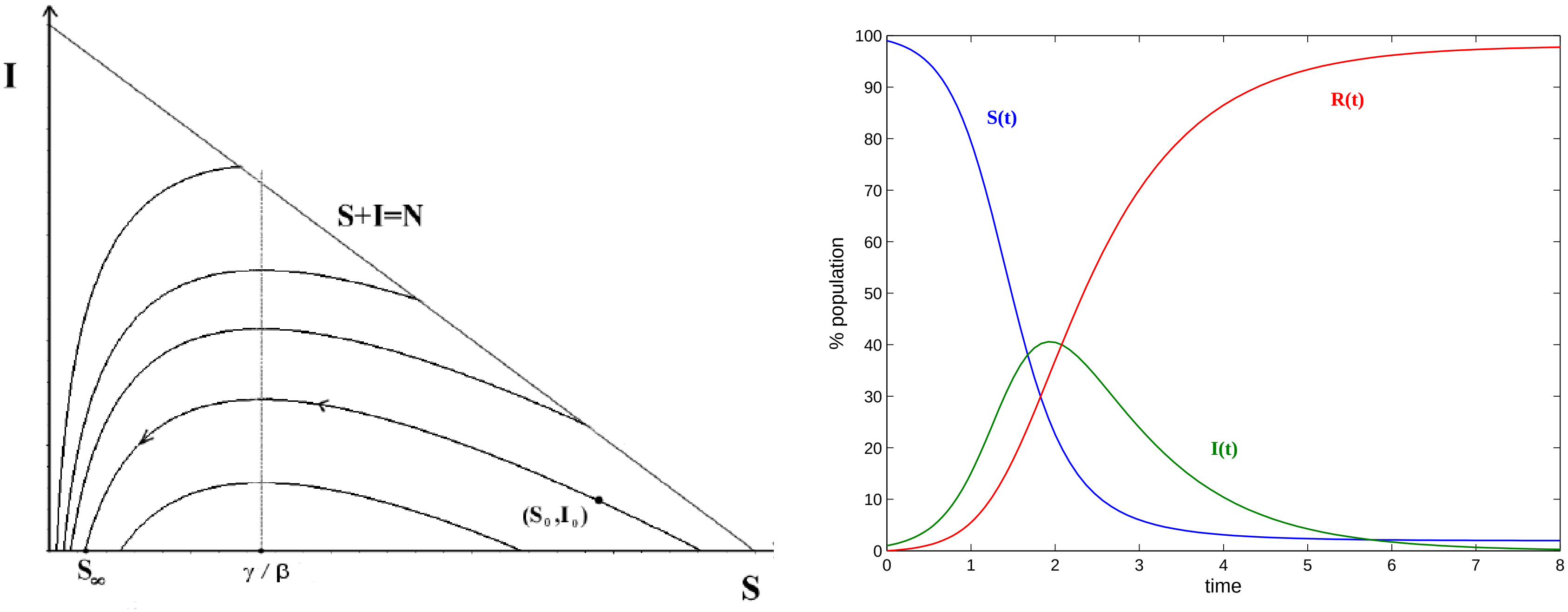
Final size of the epidemic $S_\infty > 0$ is given by the solution of

$$S_\infty - \tfrac{\gamma}{\beta} \ln S_\infty = S(0) + I(0) - \tfrac{\gamma}{\beta} \ln S(0)\ .\ I_\infty = 0\, , R_\infty = N(0) - S_\infty .$$

SIR model (cont’)

R_0 average number of infections produced by an infective individual in a wholly $(S(0) \approx N, I(0) \approx 0, R(0) = 0)$ susceptible population.



Phase portrait and evolution in time ($R_0 = \frac{\beta}{\gamma} N > 1$).

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Reduction to a single equation for the fraction of infected indiv. $i(t) = \frac{I(t)}{N}$: (a particular logistic equation)

$$\frac{di}{dt} = (\beta N(1-i) - \gamma)i\,, \quad 0 \le i(0) \le 1$$

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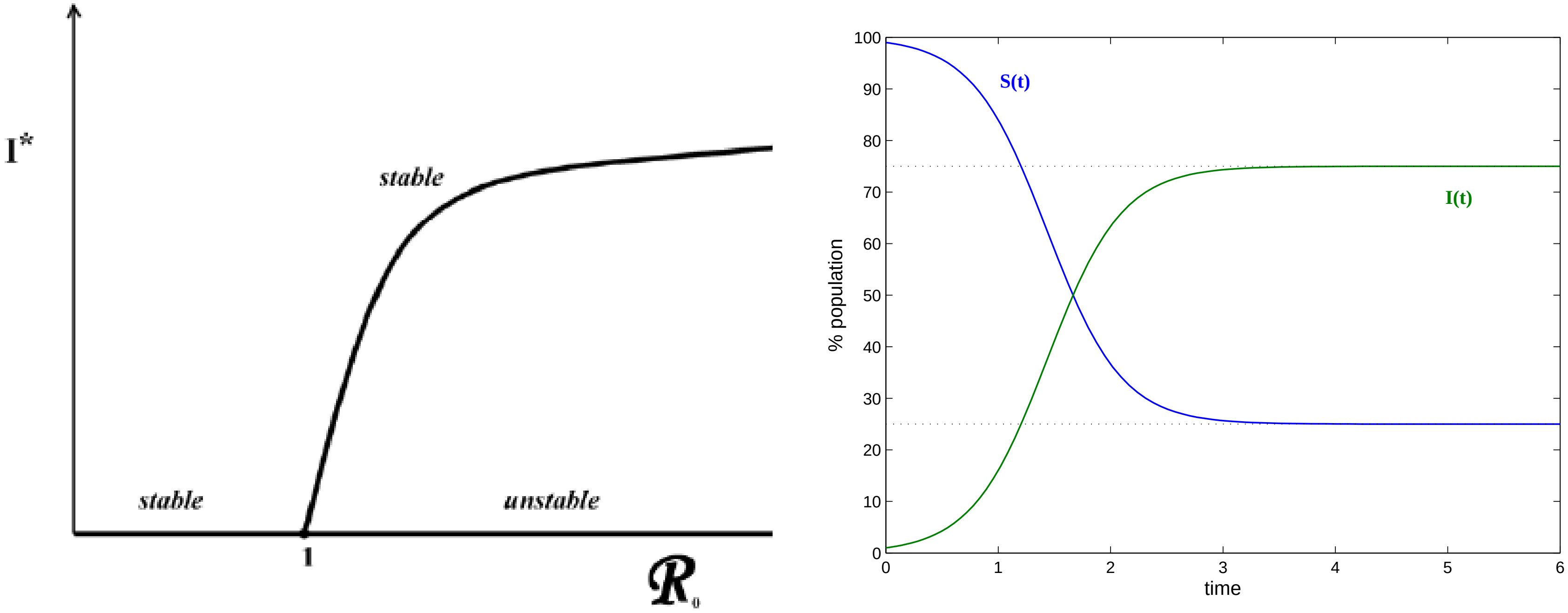
Disease-free equilibrium $i^* = 0$.

Endemic equilibrium $i^* = 1 - \frac{\gamma}{\beta N}$ which exists if $R_0 > 1$.

SIS model (cont’)

Exchange of stability. The Endemic equilibrium is stable (for each N) whenever it exists.



Bifurcation diagram and evolution in time ($R_0 = \frac{\beta}{\gamma} N > 1$).

Age structure

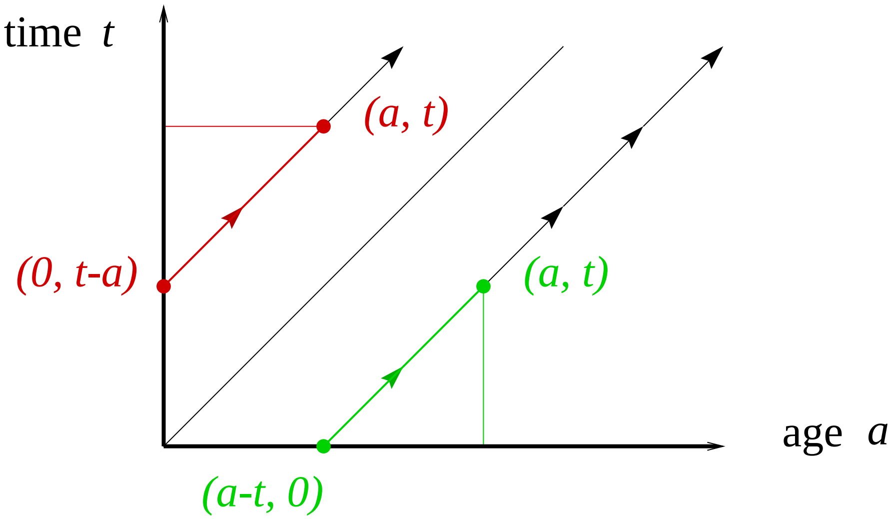
General continuously age-structured population models.

n types of individuals:

$u(\cdot, t)$ in $\mathrm{X} = L^1(0, \infty; \mathbb{R}^n)$,

G : $\mathrm{X} \to \mathrm{X}$, B : $\mathrm{X} \to \mathbb{R}^n$.

$$\frac{da}{dt} = 1\,.$$



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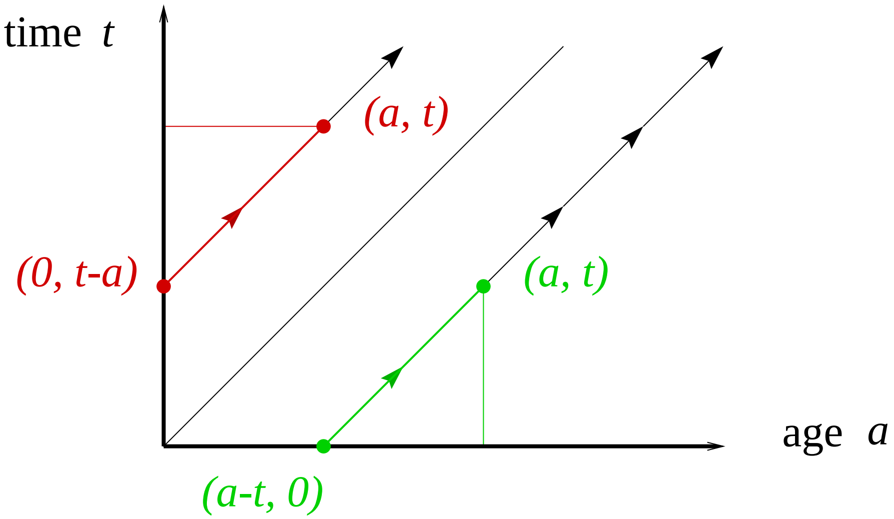

Nonlocal nonlinear 1st hyperbolic partial differential equations:

$$\frac{\partial}{\partial t}u(a,t)+\frac{\partial}{\partial a}u(a,t) = \mathsf{G}(u(\cdot,t))(a),\ u(0,t) = \mathsf{B}(u(\cdot,t)),\ u(\cdot,0) = u^0$$

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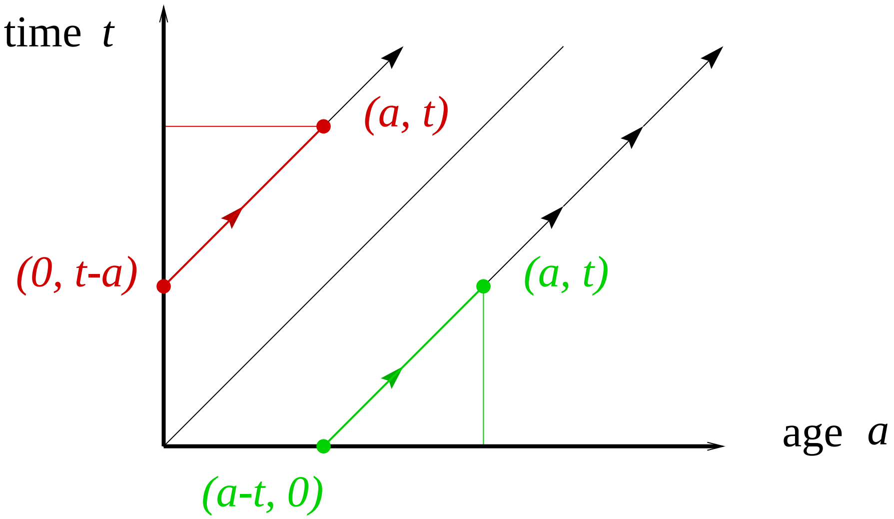

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$$u(a,t) = \begin{cases} u^0(a-t) + \int_0^t \mathsf{G}(u(\cdot,s))(s+a-t)\,ds & a \geq t \\ \mathsf{B}(u(\cdot,t-a)) + \int_{t-a}^t \mathsf{G}(u(\cdot,s))(s+a-t)\,ds & a < t \end{cases}$$

Lotka-Mckendrick equation

Linear system as a first order linear pde and a nonlocal boundary condition for the age-density of individuals

$$\begin{cases} u_t(a,t) + u_a(a,t) + \mu(a)\, u(a,t) = 0 \\[2ex] u(0,t) = \displaystyle\int_0^{a_\dagger} \beta(a)\, u(a,t)\, da\,. \end{cases} \tag{1}$$

where β and μ are the age-specific fertility and mortality rates. Maximum age $a_\dagger = \infty$ or finite.

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Basic reproduction number R_0: the average number of newborns produced by one individual during its lifetime.

Lotka-Mckendrick equation (cont')

Integration of (1) along the characteristic lines:

$$u(a,t) = \begin{cases} u^0(a-t)\,\frac{\Pi(a)}{\Pi(a-t)} & a \geq t \\ u(0,t-a)\,\Pi(a) & a < t\,. \end{cases} \tag{2}$$

Survival probability $\Pi(a) = e^{-\int_0^a \mu(\sigma)\,d\sigma}$, $\Pi(a_\dagger) = 0$. Population size $P(t) = \int_0^{a_\dagger} u(a,t)\,da$, $P'(t) = \int_0^{a_\dagger} (\beta(a) - \mu(a))\,u(a,t)\,da$.

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Solutions with separate variables: $u(a,t) = c\,e^{\lambda(t-a)}\,\Pi(a)$, with $\lambda \in \mathbb{C}$ solution of $1 = \int_0^{a_\dagger} \beta(a) e^{-\lambda a}\,\Pi(a)\,da$. Unique real root α^* such that $\mathrm{Re}(\lambda) < \alpha^*$.

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$R_0 = \int_0^{a_\dagger} \beta(a)\,\Pi(a)\,da$. $\alpha^* >=< 0 \Leftrightarrow R_0 >=< 1$. Age-profile independent of time here.

Renewal equation

Linear integral convolution eq. for birth rate $B(t) = u(0,t)$:

$$B(t) = \int_0^t K(t-x)B(x)\,dx + F(t)\ , \qquad (3)$$

where $K(a) := \beta(a)\Pi(a)$ and $F(t) := \int_0^\infty K(a+t)\,\frac{u^0(a)}{\Pi(a)}\,da$.
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Solution of (3) using Laplace transforms:
$\hat{B}(\lambda) = \hat{K}(\lambda)\hat{B}(\lambda) + \hat{F}(\lambda)$, and isolating $\hat{B}(\lambda) = \frac{\hat{F}(\lambda)}{1-\hat{K}(\lambda)}$.

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$\hat{B}(\lambda) = \hat{K}(\lambda)\hat{B}(\lambda) + \hat{F}(\lambda)$, and isolating $\hat{B}(\lambda) = \frac{\hat{F}(\lambda)}{1-\hat{K}(\lambda)}$.
Therefore, $B(t)$ is given by the inverse Laplace transform of the rhs. Asymptotic behaviour $B(t) \sim b_0 e^{\alpha^* t}$, $b_0 \geq 0$.
Once we know $B(t)$, $u(a,t)$ is recovered by (2).

Asynchronous exponential growth

Non-trivial initial conditions ($c>0$). Asymptotic behaviour:

$$u(a,t) \sim c\, e^{\alpha^*(t-a)}\, \Pi(a) \qquad \text{with } c = \frac{\int_0^\infty e^{-\alpha^* t} F(t)\, dt}{\int_0^\infty a\, e^{-\alpha^* a} \beta(a) \Pi(a)\, da}\, .$$

Convergence in L^1 and pointwise.

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Convergence in L^1 and pointwise.

Adjoint operator: Mortality term can be removed.

$$\begin{cases} u_t(a,t) = -u_a(a,t)\,,\ u(0,t) = \int_0^\infty \beta(a)\, u(a,t)\, da & \text{original (i)} \\ v_t(a,t) = v_a(a,t) + \beta(a)\ v(0,t) & \text{adjoint (i')} \end{cases}$$

Rhs of (i) is the original linear operator ($\phi \mapsto -\phi'$, with domain b.c.) and the rhs of (i') is its adjoint operator ($\phi \mapsto \phi' + \beta\, \phi(0)$).

Asynchronous exponential growth (cont')

Normalized eigenfunctions of (i): $\tilde{u}(a) = \lambda e^{-\lambda a}$.

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$\tilde{v}(a)$ with $\int_0^\infty \tilde{v}(a)\,\tilde{u}(a)\,da = 1$.

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$$-\tilde{v}'(a) + \lambda\, \tilde{v}(a) = \beta(a)\; \tilde{v}(0)\,.$$

Solution: $\tilde{v}(a) = \tilde{v}(0)\, e^{\lambda a}\, \int_a^\infty \beta(t) e^{-\lambda t}\, dt$ with $\tilde{v}(0)$ given by the normalization condition above.

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Solution: $\tilde{v}(a) = \tilde{v}(0)\, e^{\lambda a} \int_a^\infty \beta(t) e^{-\lambda t}\, dt$ with $\tilde{v}(0)$ given by the normalization condition above.

Finally, the constant c in the asynchronous exponential growth is given by

$$c = \int_0^\infty \tilde{v}(a)\, u^0(a)\, da \qquad \text{with } \lambda = \alpha^*\,.$$

“Stable” age distribution

Age-profile: normalized eigenfunction.

$$\lim_{t\to\infty}\frac{u(a,t)}{P(t)}=\frac{e^{-\alpha^* a}\,\Pi(a)}{\int_0^{a_\dagger} e^{-\alpha^* a}\,\Pi(a)\,da}\,.$$

Convergence in L^1. Independent of the value of R_0 and the (*non-trivial*) initial condition.

“Stable” age distribution

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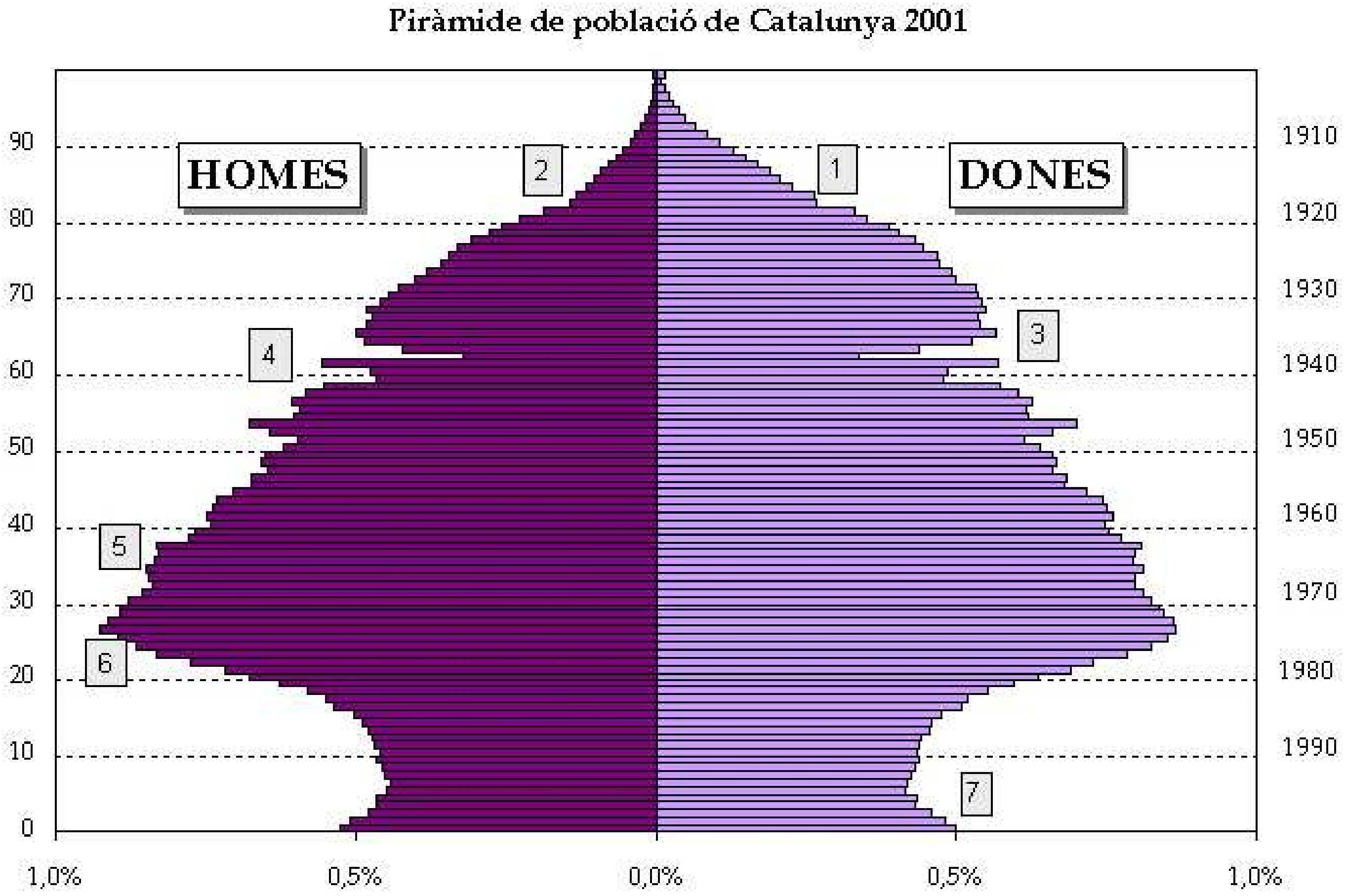
Comparison with transport equations: $x \in \mathbb{R}$, $t \geq 0$.

$$\begin{cases} u_t(x,t) + \nu\, u_x(x,t) = 0\,, \\ u(x,0) = u^0(x)\,. \end{cases}$$

Characteristic lines: $x - \nu\, t =$ ct. General solution: $u(x,t) = u^0(x - \nu\, t)$.

Demography



An age distribution coming from the demography (Catalonia).

Gurtin-MacCamy equation

Nonlinear system as an extension of (1)

$$\begin{cases} u_t(a,t) + u_a(a,t) + \mu(a, S_1(t), \ldots, S_n(t))\, u(a,t) = 0 \\ u(0,t) = \displaystyle\int_0^{a_\dagger} \beta(a, S_1(t), \ldots, S_n(t))\, u(a,t)\, da \\ S_i(t) = \int_0^{a_\dagger} \sigma_i(a)\, u(a,t)\, da \qquad i = 1, \ldots, n\,. \end{cases} \tag{4}$$

where β and μ are the age-specific and density-dependent fertility and mortality rates. $S_i(t)$ are weighted population sizes.

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Analogous integration along characteristics using a density-dependent survival probability $\Pi(a, \mathbf{S})$.

Gurtin-MacCamy equation (cont')

- ★ Existence and uniqueness of (4) via a nonlinear integral system for the birth rate and the weighted population sizes.

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- ★ Extinction equilibrium $u^* \equiv 0$. Stability: either using the total population as a Lyapunov functional or by a linearization (L-M with $\mu(a,\mathbf{0})$ and $\beta(a,\mathbf{0})$).

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- ⋆ Non-trivial steady states $u^*(a) = u^*(0)\, \Pi(a, \mathbf{S}^*)$. The vector $\mathbf{S}^*$ is given by system of n nonlinear equations:

$$1 = \int_0^{a_\dagger} \beta(a, \mathbf{S}^*)\, \Pi(a, \mathbf{S}^*)\, da\,, \qquad \frac{S_1^*}{\int_0^{a_\dagger} \sigma_1(a)\, \Pi(a, \mathbf{S}^*)\, da} = \cdots = \frac{S_n^*}{\int_0^{a_\dagger} \sigma_n(a)\, \Pi(a, \mathbf{S}^*)\, da}$$

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- Principle of linearized stability for a general nonlinear multi-state age-dependent problem [N. Kato].

Kermack-Mckendrick equation

Extension of the SIR model. Demographic changes neglected. Structuring variable: τ age of infection.

$$\begin{cases} S'(t) = -\displaystyle\int_0^{\tau_\dagger} \beta(\tau)\, i(\tau,t)\, d\tau\, S(t) \\ i_t(\tau,t) + i_\tau(\tau,t) + \gamma(\tau)\, i(\tau,t) = 0 \\ i(0,t) = \displaystyle\int_0^{\tau_\dagger} \beta(\tau)\, i(\tau,t)\, d\tau\, S(t) \\ R'(t) = \displaystyle\int_0^{\tau_\dagger} \gamma(\tau)\, i(\tau,t)\, d\tau \end{cases}$$

where γ is the age-specific removal/recovery rate and β is the age-specific transition rate. Maximum age of infection $\tau_\dagger$.

Kermack-Mckendrick equation (cont')

$$S(t) \xrightarrow{\beta(\tau)} i(\tau,t) \xrightarrow{\gamma(\tau)} R(t)$$

Total population is constant:

$N(t) = S(t) + \int_0^{\tau_\dagger} i(\tau,t)\, d\tau + R(t) = N(0)$.

Kermack-Mckendrick equation (cont')

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Similar description of the epidemics. Final size of the epidemic $S_\infty > 0$ is given by an equation of the same type as in SIR. The total number of infected individuals tends to zero and $R_\infty = N(0) - S_\infty$.

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Basic reproductive number:
$R_0 = \int_0^{\tau_\dagger} \beta(\tau)\ \exp(-\int_0^{\tau} \gamma(\sigma) d\sigma) d\tau\, N$.

Miscellaneous

Reducible size-dependent problems. Structuring variable: x size (e.g. body length).

$$\begin{cases} u_t(x,t) + (\gamma(x)\,u(x,t))_x + \mu(x,P)\,u(x,t) = 0 \\ \gamma(x_0)\,u(x_0,t) = \displaystyle\int_{x_0}^{x_\infty} \beta(x,P)\,u(x,t)\,dx\,. \end{cases}$$

Individuals are born at the same size x_0 and the individual growth rate is a function of size: $\frac{dx}{dt} = \gamma(x)$, $x(0) = x_0$.

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Individuals are born at the same size x_0 and the individual growth rate is a function of size: $\frac{dx}{dt} = \gamma(x)$, $x(0) = x_0$. Change of variables $a = \int_{x_0}^{x} \frac{d\bar{x}}{\gamma(\bar{x})}$. So, $a = a(x)$ and $x = x(a)$. The size-dependent problem can be reduced to an age-dependent problem for the density $v(a,t) := \gamma(x(a))\,u(x(a),t)$.

Miscellaneous II

Linear chain trick. Lotka-Mckendrick equation (1) with constant mortality μ, a fertility rate of the form $\beta(a) = \beta_0 + \beta_1 e^{-\alpha a} + \beta_2 a e^{-\alpha a} \geq 0$, and $a_\dagger = \infty$.

Miscellaneous II

Linear chain trick. Lotka-Mckendrick equation (1) with constant mortality μ, a fertility rate of the form $\beta(a) = \beta_0 + \beta_1 e^{-\alpha a} + \beta_2 a e^{-\alpha a} \geq 0$, and $a_\dagger = \infty$.

Defining $U(t) = \int_0^{a_\dagger} u(a,t)\,da$, $V(t) = \int_0^{a_\dagger} e^{-\alpha a} u(a,t)\,da$ and $W(t) = \int_0^{a_\dagger} a e^{-\alpha a} u(a,t)\,da$ the system reduces to an ode

$$\begin{pmatrix} U'(t) \\ V'(t) \\ W'(t) \end{pmatrix} = \begin{pmatrix} \beta_0 - \mu & \beta_1 & \beta_2 \\ \beta_0 & \beta_1 - \mu - \alpha & \beta_2 \\ 0 & 1 & -\mu - \alpha \end{pmatrix} \begin{pmatrix} U \\ V \\ W \end{pmatrix}.$$

The system preserves positivity. Moreover, if ct. μ and β_i above are density-dependent then we get a similar (nonlinear) system.

Numerical simulations

An example of a simple discretization. System (4) with mortality rate $\mu(a)$. Change of variables $u(a,t) = v(a,t)\,\Pi(a)$:

$$\begin{cases} v_t(a,t) + v_a(a,t) = 0\,, \quad v(0,t) = \int_0^{a_\dagger} \hat\beta(a,\mathbf{S})\,v(a,t)\,da \\ S_i(t) = \int_0^{a_\dagger} \hat\sigma_i(a)\,v(a,t)\,da \qquad i = 1,\ldots,k\,. \end{cases}$$

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A simple implicit numerical scheme, e.g. square mesh ($\Delta a = \Delta t$), and Simpson's rule combined with Newton's method for the boundary condition:

$$\begin{aligned} v_j^{n+1} &= v_{j-1}^n \qquad j = 1,\ldots,J \\ v_0^{n+1} &= \Phi(\Delta a, v_0^{n+1}, v_1^{n+1}, \cdots, v_J^{n+1})\,. \end{aligned}$$

Numerical simulations (cont')

Monogonont rotifera. State variables in the sexual phase: mictic females and haploid males [Calsina & R.]

$$\left\{\begin{array}{rcll} v_t(a,t)+v_a(a,t) & = & -\big(C_0+EH(t)\big)v(a,t)-EH(t)v^*(a) & a\in(0,T) \\ v_t(a,t)+v_a(a,t) & = & -\mu v(a,t) & a\in(T,1) \\ \frac{dV_1}{dt}(t) & = & v(1,t)-\mu V_1(t) & \\ \frac{dH}{dt}(t) & = & V_1(t)-\delta H(t) & \end{array}\right.$$

$$v(0,t)=0,\, v(T^+,t)=v(T^-,t). \qquad v(a,0)=v^0(a),\, V_1(0)=V_1^0,\, H(0)=H^0\,.$$

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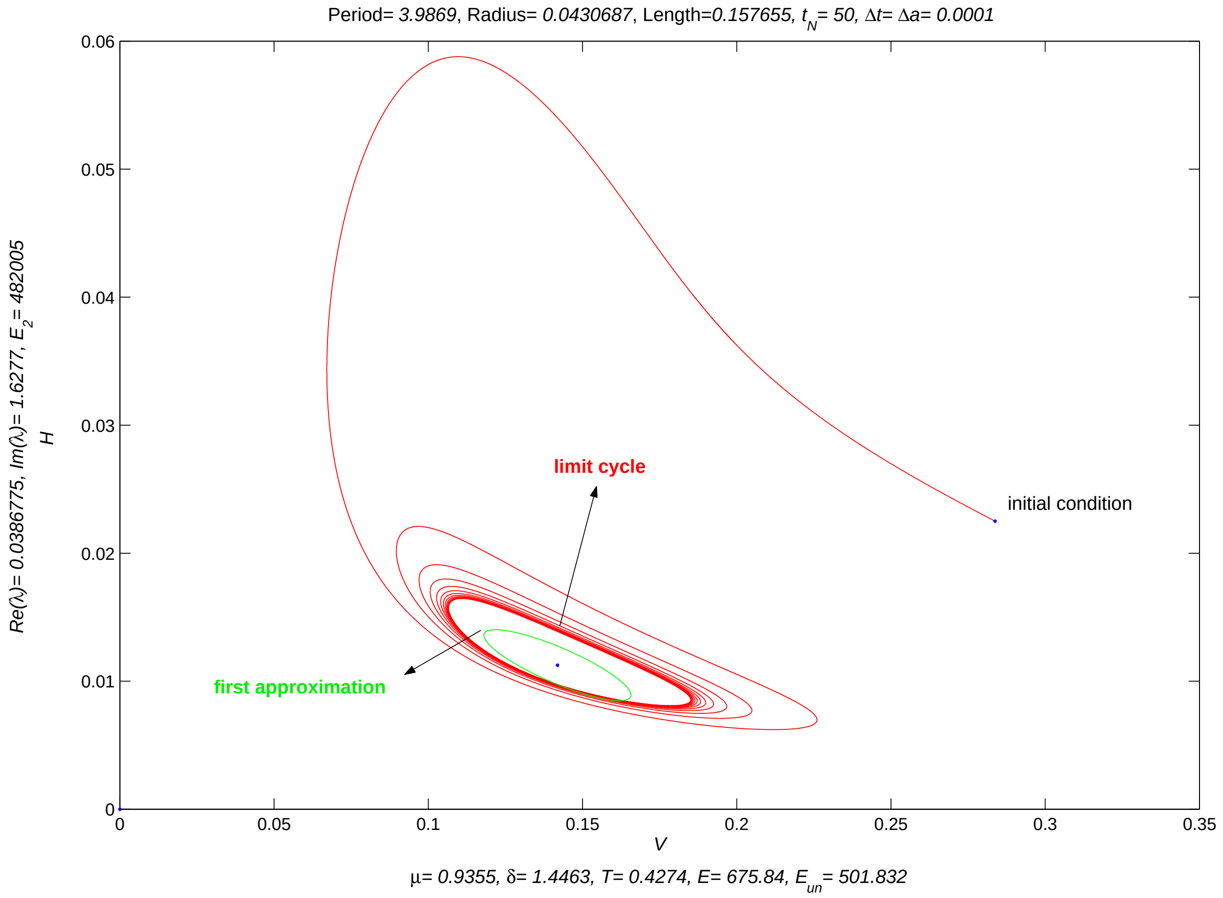
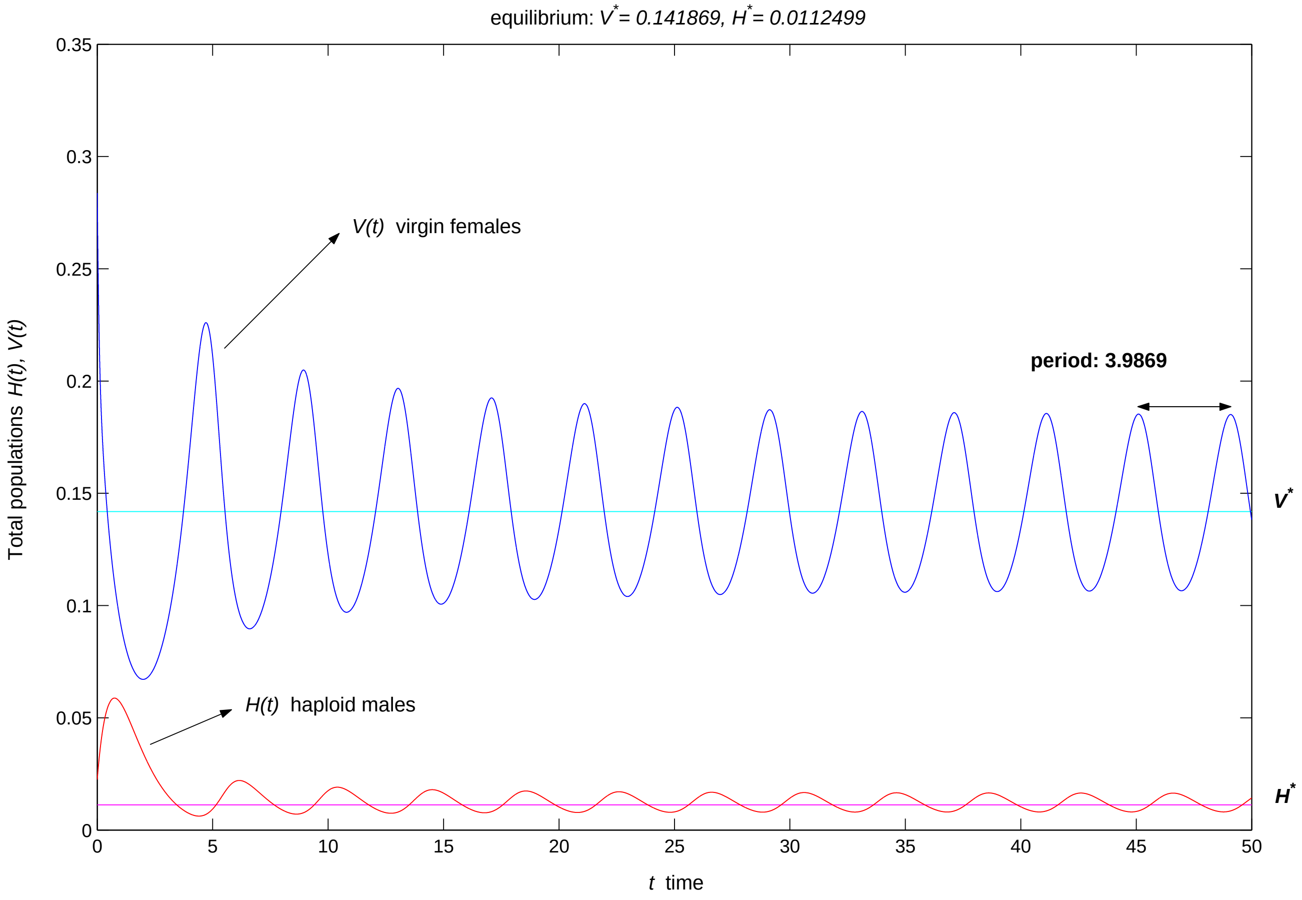
Integration along characteristic lines and variation of the constants formula.

Numerical simulations (cont')



Periodic orbit in population size (*Virgin females*, *Haploid males*).

Numerical simulations (cont')



Population sizes as functions of time.

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- ★ t_{ij} fraction of individuals in the jth class that will survive and move to the ith class in a unit of time, and f_{ij} the number of newborns in the ith class that descend from one individual in the jth class in a unit of time. Notice $\sum_i t_{ij} \leq 1$.

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Matrix Population Models (cont')

Birth, death (survival) and transition processes:

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} t_{11}+f_{11} & \cdots & t_{1n}+f_{1n} \\ t_{21} & \cdots & t_{2n} \\ \vdots & & \vdots \\ t_{n1} & \cdots & t_{nn} \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix} .$$

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If $P = W \cdot \Lambda \cdot V^{\mathrm{T}}$, Λ diagonal matrix of the eigenvalues and the matrices W , V^{T} the right and left eigenvectors, then $\mathbf{x}(t) = W \cdot \Lambda^t \cdot V^{\mathrm{T}}\,\mathbf{x}(0)$, $t = 0, 1, 2\ldots$. Equivalently, $\mathbf{x}(t) = \sum_{i=1}^{n} c_i\,\lambda_i^t\,\mathbf{w}_i$ with c_i suitable cts related to i.c.

Perron-Frobenious theory

Non-negative matrices A. Eigenvalues $|\lambda_1| \geq |\lambda_2| \geq \cdots \geq |\lambda_n|$ with right and left eigenvectors $\mathbf{w}_i$ and $\mathbf{v}_i$.
Irreducible: $(Id + A)^{n-1} > 0$. Primitive: $A^k > 0$, $k \leq (n-1)^2+1$.
Primitive $\Rightarrow$ Irreducible.

- ★ Reducible: $\lambda_1 \geq 0$, $\mathbf{w}_1 \geq 0$ and $\mathbf{v}_1 \geq 0$, $\lambda_1 \geq |\lambda_i|$, $i > 1$.

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  λ_1 is the unique eigenvalue with a non-negative eigenvector.
- ★ Irreducible and imprimitive:
  $\lambda_1 > 0$ simple root, $\mathbf{w}_1 > 0$ and $\mathbf{v}_1 > 0$, $\lambda_1 = |\lambda_i|$, $i = 2, \cdots, d$ and $\lambda_1 > |\lambda_i|$, $i > d$. λ_1 is unique as above.

Fundamental theorem of demography

P primitive, $\lambda_1 > 0$ dominant eigenvalue with right and left eigenvectors $\mathbf{w} > 0, \mathbf{v} > 0$ normalized so that $\mathbf{v}^{\mathrm{T}}\mathbf{w} = 1$.

$$\begin{pmatrix} p_{11} & \cdots & p_{1n} \\ \vdots & & \vdots \\ p_{n1} & \cdots & p_{nn} \end{pmatrix}^t \sim \lambda_1^t \begin{pmatrix} w_1 \\ \vdots \\ w_n \end{pmatrix} \begin{pmatrix} v_1 & \cdots & v_n \end{pmatrix}.$$

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$$\begin{pmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{pmatrix} \sim c\,\lambda_1^t \begin{pmatrix} w_1 \\ \vdots \\ w_n \end{pmatrix}, \quad c := \begin{pmatrix} v_1 & \cdots & v_n \end{pmatrix} \begin{pmatrix} x_1(0) \\ \vdots \\ x_n(0) \end{pmatrix}.$$

Fundamental theorem of demography (cont')

Total population $N(t) = |\mathbf{x}(t)| := \sum_i |x_i(t)|$. ($c > 0$).

$$\lim_{t\to\infty} N(t) = \begin{cases} 0 & \text{if } \lambda_1 < 1\,, \\ c|\mathbf{w}| & \text{if } \lambda_1 = 1\,, \\ \infty & \text{if } \lambda_1 > 1\,. \end{cases} \quad , \qquad \lim_{t\to\infty} \frac{N(t+1)}{N(t)} = \lambda_1\,.$$

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"Stable" distribution: normalized left eigenvector.

$$\lim_{t\to\infty} \frac{1}{N(t)} \begin{pmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{pmatrix} = \frac{1}{|\mathbf{w}|} \begin{pmatrix} w_1 \\ \vdots \\ w_n \end{pmatrix}\,.$$

Independent of the value of λ_1 and the (non-trivial) i.c.

Basic reproduction number

No immortal individuals: $\lim_{t\to\infty} T^t = 0$.

$$R := F\,(Id - T)^{-1} = F\,(Id + T + T^2 + T^3 + \cdots\,)\,.$$

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R_0 spectral radius of the matrix R. r_{ij} number of i class offspring that an individual born into class j will produce over its lifetime.

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Examples with newborns belonging to the 1st class.
Eigenvalues of R: $R_0 = r_{11}$ (*average number of newborns produced by one individual during its lifetime*) and the other $(n-1)$ being equal to zero.

Basic reproduction number (cont')

- ★ Age-structure (Leslie matrix): T has the 1st subdiagonal.

  $R_0 = \sum_{i=1}^{n} f_{1i} \prod_{j=1}^{i} t_{j,j-1}$, with $t_{10} := 1$.

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- ★ Size-structure (Usher matrix): T has the diagonal and the 1st subdiagonal. $R_0 = \sum_{i=1}^{n} f_{1i} \prod_{j=1}^{i} \frac{t_{j,j-1}}{1 - t_{jj}}$.

Basic reproduction number (cont’)

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- ★ Class-structure [R., Saldaña & Senar]: T is tridiagonal (main, sub and super), so only transitions to adjacent classes. $R_0 = \sum_{i=1}^{n} f_{1i} \prod_{j=1}^{i} \frac{t_{j,j-1}}{(1 - t_{jj})(1 - p_j)}$, with $0 \leq p_j < 1$ suitable values computed recursively.

Fibonacci’s rabbits

Leonardo Pisano, also known as Fibonacci, was born in Italy in about 1170 but educated in North Africa, where his father was a diplomat, and died in 1250. His famous book, *Liber abaci*, was published in 1202 and brought decimal or Hindu-Arabic numerals into general use in Europe. In the third section of this book he posed the following question:

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> *A certain man put a pair of rabbits in a place surrounded on all sides by a wall. How many pairs of rabbits can be produced from that pair in a year if it is supposed that every month each pair begets a new pair which from the second month on becomes productive?*

Fibonacci's rabbits (cont')

- ⋆ $u_{j,n}$ the number of j-month-old pairs of rabbits at time n in months, and $u_n = \sum_{j=0}^{\infty} u_{j,n}$ the total number of pairs of rabbits at time n.

Fibonacci's rabbits (cont')

- ★ $u_{j,\,n}$ the number of j-month-old pairs of rabbits at time n in months, and $u_n = \sum_{j=0}^{\infty} u_{j,\,n}$ the total number of pairs of rabbits at time n.
- ★ No rabbits ever die, so the number of j-old pairs at time n equals to the number of $(j+1)$-old pairs at time $n+1$: $u_{j+1,\,n+1} - u_{j,\,n} = 0\,,\;\; u_{0,\,n} = \sum_{j=2}^{\infty} u_{j,\,n}$, where the number of newborn pairs equals to the number of adult pairs.

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- ★ Homogeneous linear recurrence equation: $u_{n+2} = u_{n+1} + u_n$, $n \geq 0$.

Fibonacci's rabbits (cont')

- ★ Starting by a single newborn pair of rabbits, the answer to the question of the book is the famous Fibonacci sequence:
  1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, ***233****,* . . .

Fibonacci's rabbits (cont')

- ★ Starting by a single newborn pair of rabbits, the answer to the question of the book is the famous Fibonacci sequence:
  1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, ***233****,* $\ldots$
- ★ General solution: a linear combination of λ^n, where λ are the solutions of $\lambda^2 = \lambda + 1$.

$$u_n = c_1\,(\frac{1+\sqrt{5}}{2})^n + c_2\,(\frac{1-\sqrt{5}}{2})^n\,,\ n \geq 0\,.$$

Fibonacci's rabbits (cont')

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- ★ Asymptotic behaviour: ($c_1 > 0$).
  $\lim\limits_{n\to\infty} \dfrac{u_{n+1}}{u_n} = \dfrac{1+\sqrt{5}}{2} \simeq 1.618 > 1$, the golden ratio.

Final exercise:

Consider the following linear problem of the Fibonacci's rabbits in continuous age and time:

$$u_t(a,t) + u_a(a,t) = 0\,, \quad u(0,t) = \int_2^\infty u(a,t)\,da \ , \qquad (5)$$

where $u(a,t)$ is the age-density of pairs of rabbits.

1. Find the eigenvalues and the eigenfunctions of the linear system (5). Hint: compute the solutions with separate variables.
2. Compute the "stable" age distribution of the pairs of rabbits and $\lim_{t\to\infty} \frac{P(t+1)}{P(t)}$, where $P(t)$ is the total population.

References

[1] F. Brauer and C. Castillo-Chávez. Mathematical models in population biology and epidemiology. 2001.

[2] R. Rudnicki, editor. Mathematical modelling of population dynamics. 2002.

[3] H.R. Thieme. Mathematics in population biology. 2003.

[4] M. Iannelli. Mathematical theory of age-structured population dynamics. 1995.

[5] M. Iannelli, M. Martcheva and F.A. Milner. Gender-structured population modeling. 2005.

[6] G.F. Webb. Theory of nonlinear age-dependent population dynamics. 1985.

References

[7] N.F. Britton. Essential mathematical biology. 2003.

[8] J.A.J. Metz and O. Diekmann. The Dynamics of Physiologically Structured Populations. 1986.

[9] J.M. Cushing. An introduction to structured population dynamics. 1998.

[10] H. Caswell. Matrix population models. 2001.

[11] B. Perthame. Transport Equations in Biology. 2007.

[12] O. Diekmann and J.A.P. Heesterbeek. Mathematical epidemiology of infectious diseases. 2000.