Age structured populations

D. Gurarie

Discrete models (Euler-Lotka)

Total population is divided into age-bins: $Y = (y_1, y_2, \ldots, y_n)$, y_k - population of k-th bin (ages $(k-1)\Delta a < a < k\Delta a$). Time step is $\Delta t = \Delta a$ - "aging step" (transition from "k" into "k+1"). The basic processes are survival and replication:

$$\begin{aligned} &\Delta t : y_k \to s_k y_k = y_{k+1} \\ &\Delta t : y_1 \to \sum_1^n r_k s_k y_k; \text{ or } \sum_1^n r_k y_k; \end{aligned} \tag{1}$$

where $0 < s_k \le 1$ - survival factors, $0 < r_k$ - replication factors (mean # of progeny for k-th bin). We write (1) in vector-matrix form for population-state vector in discrete time-steps $t = 0, 1, 2, \ldots$

$$Y(t+1) = L \bullet Y(t); \tag{2}$$

with "Frobenius-type" Leslie matrix

$$L = \begin{bmatrix} r_1 & r_2 & \ldots & r_n \\ s_1 & 0 & \ldots & 0 \\ 0 & s_2 & 0 & \ldots \\ 0 & \ldots & s_{n-1} & 0 \end{bmatrix} \tag{3}$$

Example: Fibinacci rabbits obey 2nd order finite-difference equation (FDE) $y_{m+2} = y_{m+1} + y_m$, equivalent to system (2) for $Y_m = (y_m, y_{m-1})$ "young + old" generations, with Leslie $L = \begin{bmatrix} 1 & 1 \\ 1 & 0 \end{bmatrix}$.

Formal solution of (2) at time *m* $Y_m = L^m \bullet Y_0$, is obtained by diagonalization (eigenvalue problem) for L.

Eigenvalue method

Eigendata of L

λ_1	λ_2	...	λ_k	...
$X^1 = \left(x_k^{\ 1}\right)$	$X^{(2)}$		$X^{(k)}$	

If initial state $Y_0 = \sum c_k X^{(k)}$ is expanded in eigenvectors, then solution

$$Y_m = \sum_1^n c_k \lambda_k^{\ m} X^{(k)} \tag{4}$$

For Fibonacci example, $\lambda_{1,2} = \dfrac{1 \pm \sqrt{5}}{2}; X^{(1,2)} = \begin{pmatrix} \lambda_{1,2} \\ 1 \end{pmatrix}$; and solution of IVP $y_0 0; y_1 = 1$ is $y_m = \dfrac{\lambda_1^{\ m} - \lambda_2^{\ m}}{\sqrt{5}}$

Frobenius-**Perron** theorem applies to matrices of type (3), and more general L, to show its largest eigenvalue $\lambda_1 > 0$ ($|\lambda_k| < \lambda_1$), and vector $X^{(1)} > 0$.

We can solve eigenvalue problem $\lambda X = L \bullet X$ explicitly: coordinates of vector $X = \left(x_k\right)$ obey

$$\left\{\lambda x_k = s_{k-1} x_{k-1} : k \geq 2\right\} \Rightarrow \boxed{x_k = \frac{\sigma_k}{\lambda^{k-1}} x_1} \tag{5}$$

- all x_k - proportional to "new-born" x_1 with *survival factors*

$$\sigma_k = s_1 s_2 \ldots s_{k-1} \tag{6}$$

from "1st " trough" k-th" age). Then "replication term" for x_1 gives the characteristic equation for eigenvalue λ

$$p(\lambda) = \lambda^n - \left(r_1 \sigma_1 \lambda^{n-1} + \ldots + r_n \sigma_n\right) = 0 \tag{7}$$

Such $p(\lambda)$ has always positive real root (Fig. 1). Also note that 1st order "vector" FDE (2) is equivalent to n-th order scalar FDE for "newborn" class (like Fibonacci) $z_t = y_1(t)$

$$z_{m+n} = \sum_{k=1}^{n-1} \left(r_{n-k} \sigma_{n-k}\right) z_{m+k}; m = 0, 1, 2, \ldots \tag{8}$$

(Hint: interpret (8) as the "new-born" back history).

Stability analysis

Solution (4) at large time $Y_m \approx c_1 \lambda_1^{\ m} X^{(1)}$ depends on $\lambda_1 > 1$ (exponential growth), $\lambda_1 < 1$ (decay), or $\lambda_1 = 1$ - stationary population. That in turn depends on BRN

$$R_0 = \sum_1^n r_k \sigma_k \tag{9}$$

Namely,

$R_0 < 1$	$R_0 = 1$	$R_0 > 1$
$\lambda_1 < 1$	$\lambda_1 = 1$	$\lambda_1 > 1$

Table 2

In stationary case ($\lambda_1 = 1$) the population is distributed according to eigenvector (5) – survival factors,

$$\{x_k = \sigma_k : k = 1, 2, ..., n\}$$

If $\lambda_1 > 1$ (growing population) the leading eigenvector would favor "younger ages", $x_k = \frac{\sigma_k}{\lambda_1^k}$, and the opposite is true for "decaying" population $\lambda_1 < 1$.

Problem: Explain results of Table 2. Show (i) $p(1) = 1 - R_0$; (ii) $p'(1) = 1 - R_0 + ... > 1 - R_0$; (iii) $p'(\lambda) \geq \lambda^{n-1} p'(1)$; and deduce Table 2 from Fig.2

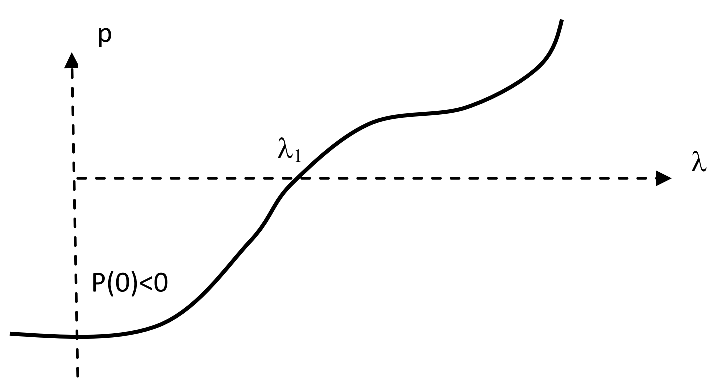

Fig.1

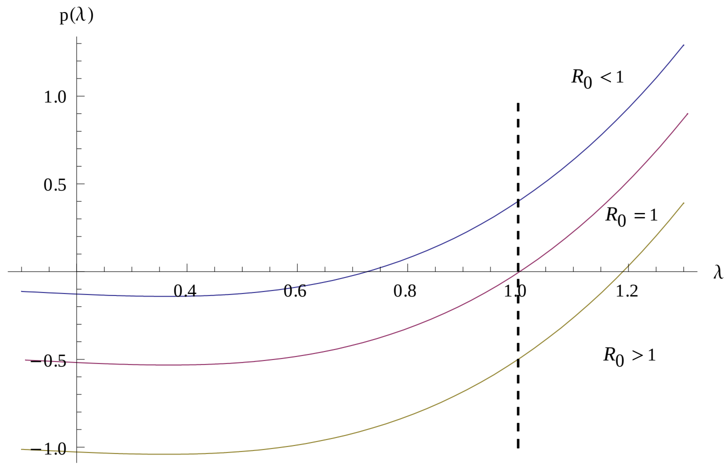

Fig.2

Continuous models: McKendrick approach

Here population $y(a,t)$ depend on two continuous variables: age $0<a<L$, and time $t>0$. Once again we consider age-dependent mortality $\mu(a)$, and fertility (birth) rate $b(a)$. The dynamic growth model is now given by a first order partial differential equation (PDE)

$$\begin{aligned} &\partial_t y + \partial_a y = -\mu(a)\, y,\ a>0 \\ &y|_{t=0} = y_0(a) \ \text{- initial condition,} \\ &y|_{a=0} = B(t) \ \text{- boundary condition (new-born)} \end{aligned} \tag{10}$$

Term $\partial_a y = \frac{y(a+da,t)-y(a,t)}{da}$ measures aging as 'transition' across infinitesimal age-bin $[a,a+da]$, the "new-born" source itself depends on population age-distribution and age-specific fertility

$$B(t) = \int_0^\infty b(a) y(a,t)\, da \tag{11}$$

First-order PDEs, like (10) are solved by the *method of characteristics*. They are often called *transport models*, and serve to describe such physical processes, as traffic or fluid flow,

$$\begin{aligned} &u_t + c u_x = 0;\ \text{or } f(u,x,t) \ \text{- source} \\ &u|_{t=0} = u_0(x) \end{aligned} \tag{12}$$

Here $u(x,t)$ represents the density of cars (or fluid) as function of space time variables x,t, and c - speed of motion. The latter $c = c(u)$ could depend on u, which makes equation (10) nonlinear (so called *quasi-linear*). In the linear case (u - constant or function of x,t), the characteristics are lines $x = ct + \xi$ (constant *c*), or more general integral curves $x(t,\xi)$ of characteristic ODE:

$$\frac{dx}{dt} = c(x,t);\ x(0) = \xi \qquad (13)$$

Here initial point ξ serves as parameter (characteristic variable). Having computed characteristics one can reduce PDE, like (12) to a family of ODEs along characteristics

$$\frac{du}{dt} = f(u,...,t);\ u|_{t=0} = u_0(\xi) \text{ - initial profile} \qquad (14)$$

Thus the method of characteristics involves two steps:

1) compute characteristics $x(t,\xi)$ via (13)
2) Solve ODE (14) for density u in terms of the initial/boundary value parameter ξ

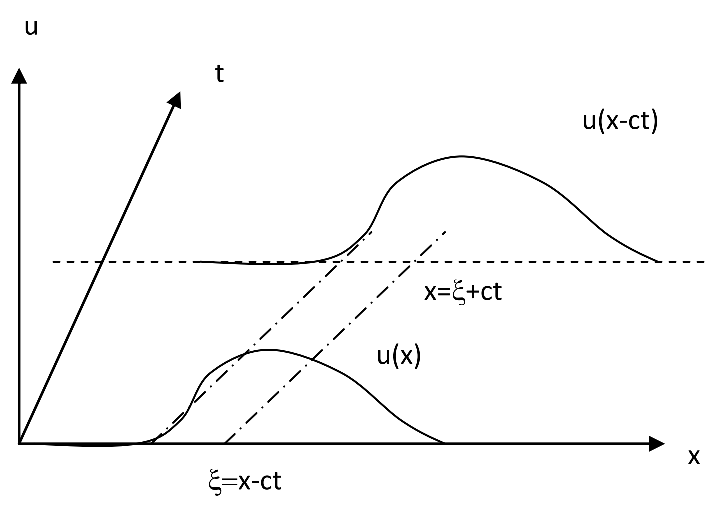

Fig.3: Traveling wave solution

We consider two special cases:

(i) constant speed *c* in transport problem (12), and $f=0$, which yields traveling wave solution $u_0(x-ct)$.

(ii) $f=-\mu u$ - mortality factor in aging problem (10), yields ODE: $\frac{du}{dt}=-\mu(a_0+t)u$, solved by multiplier,

$$\sigma(a)=e^{-\int_0^a \mu(s)ds} \tag{15}$$

It has the same meaning as σ_m of (6) in discrete case, namely *survival function*. Examples of survival function:

i) step mortality: $\mu(a)=\begin{cases}0;\ a<L \text{ - life span}\\ \infty;\ a>L\end{cases}$ (everyone lives through age L and then dies)

gives step-function $\phi(a)=\begin{cases}1;\ a<L\\ 0;\ a>L\end{cases}$

ii) constant mortality $\mu=const$, gives $\phi(a)=e^{-\mu a}$

Solution of population problem $\frac{dy}{dt}=-\mu(a(t))$ is given by multiplier $\sigma(a)$, and initial age-distribution $y_0(a)$. Thus we get population $y(a,t)$ in the upper and lower sector of the age-time quadrant (Fig.4)

$$y(a,t)=\begin{cases}y_0(a-t)\dfrac{\sigma(a)}{\sigma(a-t)};\ a>t\\ \sigma(a)\int_0^\infty b(s)y(s,t-a)ds;\ t>a\end{cases} \tag{16}$$

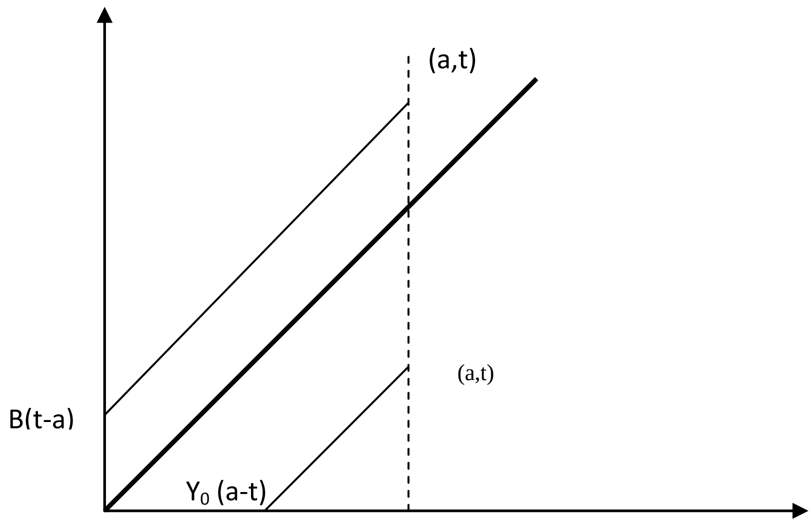

Fig.4: Characteristics of aging system (10).

While the lower sector solution (16) is written explicitly in terms of the initial age distribution $y_0(a)$, the upper one is implicit.

Still we can study equilibria and stability of solutions (10) via continuous version of BRN (9). Indeed, equilibrium of (10) gives an ODE problem

$$\partial_a y = -\mu(a)\, y(a);$$
$$\text{IC}: y(0) = \int_0^\infty b(s)\sigma(s)\,ds$$

Hence the equilibrium relation in terms of BRN

$$R_0 = \int_0^\infty b(s)\sigma(s)\,ds = 1 \tag{17}$$

like in Table 2.

More general solutions of integro-differential problem (10)-(11) depend on the "new-born" function $B(t)$, via convolution integral equation

$$B(t) = \int_0^t \underbrace{b(a)\sigma(a)}_{R(a)} B(t-a)\,da + \int_t^\infty b(a)\sigma(a)\frac{y_0(a-t)}{\sigma(a-t)}\,da = R * B + V \tag{18}$$

with kernel $R(a)=b(a)\sigma(a)$, and known "past source" $V(t)=\int_0^\infty R(a+t)B_0(a)\,da$.

In particular, looking for stationary or exponential mode solutions $y(a,t)=e^{\lambda t}x(a)$ of (10)-(11), or equivalent $B(t)=e^{\lambda t}$ of (18) we get

$$\partial_a x=-\left[\mu(a)+\lambda\right]x;a>0$$
$$x|_{a=0}=\int_0^\infty b(a)x(a)\,da$$

Hence the λ-eigenmode distribution

$$x(a)=e^{-\lambda a}\sigma(a)x_0$$

and the characteristic equation

$$F(\lambda)=\hat{R}(\lambda)=\int_0^\infty e^{-\lambda a}R(a)\,da=1 \tag{19}$$

- the Laplace transform of function $R(a)$.

For stability analysis we get similar results to discrete case (Table 2) Fig.3:

(i) stability (decay) requires $R_0<1$- low "birth over death" rate

(ii) Equilibrium: $R_0=1$ - exact balance.

(iii) instability (growth) has $R_0>1$

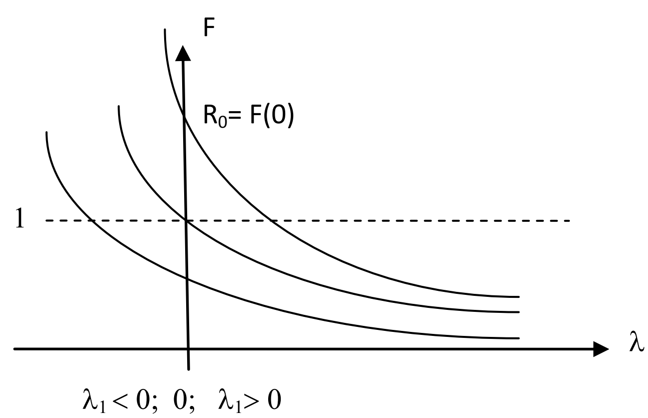

Fig.5

In general , (18) is solved by the Laplace transform method

$$\mathfrak{L}: F(t) \to \hat{F}(\lambda) = \int_0^\infty F(t) e^{-\lambda t} dt$$

Then

$$\hat{B}(\lambda) = \frac{\hat{V}}{1-\hat{R}(\lambda)} = \frac{A_1}{\lambda - \lambda_1} + \sum_k \frac{A_k}{\lambda - \lambda_k}$$

In terms of residues = roots of $\hat{R}(\lambda) - 1 = 0$. One can show all of them have $\mathrm{Re}(\lambda_k) \le \lambda_1$, so solution

$$B(t) = A_1 e^{\lambda_1 t} + \sum A_k e^{\lambda_k t}$$

Has leading exponent $\lambda_1 > 1$ or < 1 depending on BRN $R_0 = \hat{R}(0) > 1$, or < 1.

Remark: Solution (16) and stability analysis based on (19) have parallel form in the discrete (Leslie) case. Here solution $y_a(m)$ for age group $a = 0,1,2,...$, and time $m = 0,1,2,...$

$$y_a(m) = \begin{cases} y_{a-m}(0)\dfrac{\sigma_a}{\sigma_{a-m}}; & a > m \quad \text{- initial state} \\ \sigma_a \underbrace{\sum_{j=0}^{n} r_j y_j(m-a)}_{B(m-a)}; & m > a \quad \text{- survival of "new-born"} \end{cases}$$

The “new-born” source sequence B_m satisfies a discrete convolution equation

$$B_m = \sum_{j=0}^{m} (r_j \sigma_j) B_{m-j} = R * B \qquad (20)$$

solved by the z-transform (generating function) method – discrete analogue of the Laplace transform

$$\{ f_m = r_m \sigma_m \} \to F(z) = \sum_0^\infty f_m z^m \qquad (21)$$

In particular, exponential solutions of (20), $\{ B_m = \lambda^m; m = 0,1,2,... \}$, yield another form of characteristic equation for λ

$$F(\lambda)=\sum_{m=0}^{\infty}(r_m\sigma_m)\lambda^{-m}=1 \Leftrightarrow p(\lambda)=0$$

Once again we get "stability condition" in terms of BRN $R_0=\sum r_k\sigma_k$ (Fig.3 where $\lambda=0$ is shifted to $\lambda=1$). Note that "discrete" *replication* and *survival* factors are related to "continuous" *mortality* and *birth* rates as $s_k=e^{-\mu_k\Delta a}; r_k=e^{b_k\Delta a}$.

Problems:

i) Demonstrate that growing populations ($\lambda_1>0$) have larger fraction of younger ages, compared to decaying ones ($\lambda_1>0$);

ii) Use Laplace transform method to compute solutions for 2 special cases of survival function:

$$\text{(I)}\ \ \sigma(a)=\begin{cases}1; 0<a<L \text{ - life-span}\\ 0; a>L\end{cases}$$

$$\text{(II)}\ \ \sigma(a)=e^{-\mu a}; \mu \text{ - const}$$

iii) Explain why total replacement number (per adult) $B_0=\int_0^\infty b(a)\,da$ must be ≥ 1 to maintain population, (or >2 per female). Show that any survival function not-type I requires $B_0>1$. By UN estimates the replacement number to stabilize human growth is $B_0=1.07$ For additional details and data see:

http://en.wikipedia.org/wiki/Population_pyramid

http://www.census.gov/ipc/www/idb/pyramids.html

Next we outline an application of age structured population to Bernoulli analysis of smallpox inoculation.