Continuous age-structured models

Leslie model

Let $N(t) = (n_1(t), \dots, n_m(t))^T$,

$$N(t+1) = \begin{pmatrix} \beta_1 & \beta_2 & \dots & \beta_{m-1} & \beta_m \\ s_1 & 0 & \dots & 0 & 0 \\ 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1} & 0 \end{pmatrix} N(t)$$

i.e.,

$$N(t+1) = LN(t)$$

where L is a **Leslie matrix**

Write

- time as t_i ($i \in \mathbb{N}$)
- age as a_i ($i \in \mathbb{N}$)
- birth as $\beta_i = \beta(a_i)$
- survival as $s_i = s(a_i)$ with $s(a_i) = 0$ for $i > m$
- population numbers/density as $n_i(t) = n(t_i, a_i)$

Then Leslie model is

$$n(t_i, a_i) = s(a_{i-1})n(t_{i-1}, a_{i-1})$$

and

$$n(t_{i+1}, 0) := n(t_{i+1}, a_0) = \sum_{i=0}^{\infty} \beta(a_i)n(t_i, a_i)$$

Time and age go hand in hand

Assume age and time evolve similarly, i.e.,

$$\Delta t = t_{i+1} - t_i = a_{i+1} - a_i = \Delta a$$

Exponential survival time

Suppose population decreases exponentially in time

For small Δa,

$$s(a_{i-1}) = e^{-\mu(a_{i-1})\Delta a} \simeq 1 - \mu(a_{i-1})\Delta a$$

where $\mu(a_i)$ is mortality at age a_i

Density for age a_i at time t_{i+1} as function of density for age a_{i-1} at time t_i:

$$n(t_{i+1}, a_i) = s(a_{i-1})n(t_i, a_{i-1})$$

So, assuming exponential decrease of population in time,

$$n(t_{i+1}, a_i) \simeq [1 - \mu(a_{i-1})\Delta a]n(t_i, a_{i-1})$$

i.e.,

$$s(a_{i-1}) \simeq [1 - \mu(a_{i-1})\Delta a]$$

We have

$$n(t_{i+1}, a_i) \simeq [1 - \mu(a_{i-1})\Delta a] n(t_i, a_{i-1})$$

so

$$\begin{aligned} n(t_{i+1}, a_i) - n(t_i, a_{i-1}) &\simeq [1 - \mu(a_{i-1})\Delta a] n(t_i, a_{i-1}) - n(t_i, a_{i-1}) \\ &\simeq -\mu(a_{i-1}) n(t_i, a_{i-1}) \Delta a \end{aligned}$$

Do the usual trick:

$$n(t_{i+1}, a_i) - n(t_i, a_{i-1}) = n(t_{i+1}, a_i) - n(t_i, a_i) + n(t_i, a_i) - n(t_i, a_{i-1})$$

So

$$n(t_{i+1}, a_i) - n(t_i, a_{i-1}) \simeq -\mu(a_{i-1}) n(t_i, a_{i-1}) \Delta a$$

takes the form

$$n(t_{i+1}, a_i) - n(t_i, a_i) + n(t_i, a_i) - n(t_i, a_{i-1}) \simeq - \mu(a_{i-1}) n(t_i, a_{i-1}) \Delta a$$

i.e.,

$$\frac{n(t_{i+1}, a_i) - n(t_i, a_i)}{\Delta a} + \frac{n(t_i, a_i) - n(t_i, a_{i-1})}{\Delta a} \simeq - \mu(a_{i-1}) n(t_i, a_{i-1})$$

We have

$$\frac{n(t_{i+1}, a_i) - n(t_i, a_i)}{\Delta a} + \frac{n(t_i, a_i) - n(t_i, a_{i-1})}{\Delta a} \simeq - \mu(a_{i-1}) n(t_i, a_{i-1})$$

But recall that $\Delta a = \Delta t$, so

$$\frac{n(t_{i+1}, a_i) - n(t_i, a_i)}{\Delta t} + \frac{n(t_i, a_i) - n(t_i, a_{i-1})}{\Delta a} \simeq - \mu(a_{i-1}) n(t_i, a_{i-1})$$

Take limit as $\Delta t = \Delta a \to 0$:

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

Describing births

Let $b(a)$ be reproduction rate at age a, then

$$\begin{aligned}
B &= \text{births from } t_j \text{ to } t_{j+1} \\
&= \int_0^\infty \int_{t_j}^{t_{j+1}} b(a) n(x,a)\, dx\, da \\
&\simeq \int_0^\infty b(a) \frac{n(t_{j+1},a) + n(t_j,a)}{2} \Delta t\, da
\end{aligned}$$

(assuming we track females and sex-ratio 1)

$$\begin{aligned}
&\simeq \frac{1}{2} \sum_{i=0}^{\infty} b(a_i)[n(t_{j+1},a_i) + n(t_j,a_i)]\Delta t \Delta a \\
&= \frac{1}{2} \sum_{i=0}^{\infty} b(a_i) n(t_j,a_i) \Delta t \Delta a + \frac{1}{2} \sum_{i=0}^{\infty} b(a_i) s(a_{i-1}) n(t_j,a_{i-1}) \Delta t \Delta a \\
&= \frac{1}{2} \sum_{i=0}^{\infty} [b(a_i)\Delta t \Delta a + b(a_i) s(a_{i-1}) \Delta t \Delta a] n(t_j,a_i)
\end{aligned}$$

Let ℓ be probability that newborns survive for period of $\Delta t/2 = \Delta a/2$, then

$$n(t_{j+1}, 0) \simeq \ell B = \frac{\ell}{2} \sum_{i=0}^{\infty} [b(a_i)\Delta t \Delta a + b(a_i)s(a_{i-1})\Delta t \Delta a] n(t_j, a_i)$$

So

$$\beta(a_i) \simeq \frac{\ell}{2}[b(a_i)\Delta t \Delta a + b(a_{i+1})s(a_i)\Delta t \Delta a]$$

McKendrick–Von Foerster equation

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

with boundary condition (BC)

$$n(t,0) = \int_0^\infty b(a) n(t,a) da$$

and initial condition (IC)

$$n(0,a) = f(a)$$

Linear first-order hyperbolic PDE

Suppose $u(t,x)$ satisfies

$$a(t,x)\frac{\partial u}{\partial t} + b(t,x)\frac{\partial u}{\partial x} + c(t,x)u = 0$$

with $x \in \mathbb{R}$, $t \in \mathbb{R}_+$ and IC:

$$u(0,x) = \phi(x)$$

(BC not required as $x \in \mathbb{R}$)

Method of characteristics

Express PDE as an ODE (or DDE) along *characteristic curves*, the latter expressed in terms of auxiliary variables s and τ. Along characteristics, τ constant

Assume

$$u(t,x) \equiv u(t(s,\tau), x(s,\tau)) \equiv u(s,\tau)$$

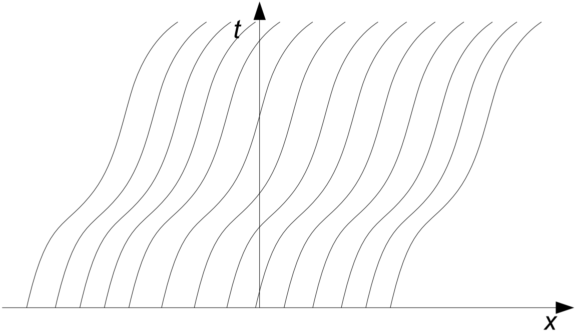
Find characteric curves by solving

$$\frac{dt}{ds} = a(t,x) \qquad \frac{dx}{ds} = b(t,x)$$

with IC

$$t(0,\tau) = 0, \quad x(0,\tau) = \tau, \qquad u(0,\tau) = \phi(\tau)$$

$$t(0,\tau)=0, \quad x(0,\tau)=\tau, \qquad u(0,\tau)=\phi(\tau)$$



Using the chain rule,

$$\begin{aligned}\frac{du}{ds} &= \frac{\partial u}{\partial t}\frac{dt}{ds} + \frac{\partial u}{\partial x}\frac{dx}{ds} \\ &= a(t,x)\frac{\partial u}{\partial t} + b(t,x)\frac{\partial u}{\partial x}\end{aligned}$$

So, along characteristic curves (where τ constant),

$$a(t,x)\frac{\partial u}{\partial t} + b(t,x)\frac{\partial u}{\partial x} + c(t,x)u = 0$$

and its IC $u(0,x) = \phi(x)$ is replaced by

$$\frac{du}{ds} + c(t,x)u = 0, \quad s \in \mathbb{R}_+$$

with IC

$$u(0,\tau) = \phi(\tau)$$

McKendrick–Von Foerster equation

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

with boundary condition (BC)

$$n(t,0) = \int_0^\infty b(a)n(t,a)da$$

and initial condition (IC)

$$n(0,a) = f(a)$$

Using characteristics

Here, PDE has a BC, so instead of an IVP, we will get a BVP. First,

$$a(t,x) = b(t,x) = 1$$

so characteristic curves are found by integrating

$$\frac{dt}{ds} = \frac{dx}{ds} = 1$$

with IC

$$a > t : \quad t(0,\tau) = 0 \text{ and } x(0,\tau) = \tau$$

and

$$a < t : \quad t(0,\tau) = \tau \text{ and } x(0,\tau) = 0$$

So we find

$$a > t: \quad t = s \text{ and } a = s + \tau, \text{ so } \tau = a - t$$

and

$$a < t: \quad t = s + \tau \text{ and } a = s, \text{ so } \tau = t - a$$

So K–VF reduces to

$$\frac{dn}{ds} = -\mu(a)n$$

with IC

$$\begin{aligned} a > t: &\quad n(0,\tau) = f(\tau) \\ a < t: &\quad n(\tau,0) = \int_0^\infty b(a)n(\tau,a)da \end{aligned}$$

Case $a > t$

$$\frac{dn}{ds} = -\mu(a)n, \quad n(0,\tau) = f(\tau)$$

Integrated form of the solution:

$$n(s,\tau) = n(0,\tau)\exp\left[-\int_0^s \mu(x+\tau)dx\right]$$

So

$$\begin{aligned} n(s,\tau) &= f(\tau)\exp\left[-\int_0^s \mu(x+\tau)dx\right] \\ &= f(a-t)\exp\left[-\int_0^s \mu(x+a-t)dx\right], \quad y = x+a-t \\ n(t,a) &= f(a-t)\exp\left[-\int_{a-t}^a \mu(y)dy\right] \end{aligned}$$

Case $a < t$

$$\frac{dn}{ds} = -\mu(a)n, \quad n(0,\tau) = f(\tau)$$

Integrated form of the solution:

$$n(s,\tau) = n(0,\tau)\exp\left[-\int_0^s \mu(x)dx\right], \quad \tau = t - a$$

So

$$n(t,a) = n(t-a,0)\exp\left[-\int_0^a \mu(y)dy\right]$$

Since RHS involves $n(t-a,0)$, no explicit solution. Can solve this iteratively (Picard) as an integral equation

Asymptotic behaviour

If no age dependence, model reduces to a classic exponential growth model. So, by analogy, we seek solutions of the following form

$$n(t, a) = e^{\lambda t} r(a)$$

with $r(a) \in \mathbb{R}_+$, called *similarity* or *seperable* solutions

If $\lambda < 0$, then $\lim_{t\to\infty} n(t, a) = 0$, if $\lambda > 0$, then $\lim_{t\to\infty} n(t, a) = \infty$ provided $r(a) > 0$. If $\lambda = 0$, then $n(t, a) = r(a)$ is an equilibrium

Substitute $n(t,a) = e^{\lambda t} r(a)$ into

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

giving

$$\lambda e^{\lambda t} r(a) + e^{\lambda t} r'(a) = -\mu(a) e^{\lambda t} r(a)$$

or

$$r'(a) = -[\mu(a) + \lambda] r(a)$$

$$r'(a) = -[\mu(a) + \lambda] r(a)$$

Separate, integrate, giving

$$r(a) = r(0) \exp\left[-\lambda a - \int_0^a \mu(s)\, ds\right] > 0$$

for $r(0) > 0$. Substitute $n(t, a) = e^{\lambda t} r(a)$ into integral birth equation:

$$\begin{aligned} n(t, 0) &= e^{\lambda t} r(0) \\ &= \int_0^\infty b(a) n(t, a)\, da \\ &= \int_0^\infty b(a) e^{\lambda t} r(0) \exp\left[-\lambda a - \int_0^a \mu(s)\, ds\right] da \end{aligned}$$

We have

$$e^{\lambda t} r(0) = \int_0^\infty b(a) e^{\lambda t} r(0) \exp\left[-\lambda a - \int_0^a \mu(s)\ ds\right] da$$

Eliminate $e^{\lambda t} r(0)$, giving

$$1 = \int_0^\infty b(a) \exp\left[-\lambda a - \int_0^a \mu(s)\ ds\right] da$$

which is the *characteristic equation* associated to the PDE

Let

$$\phi(\lambda) = \int_0^\infty b(a) \exp\left[-\lambda a - \int_0^a \mu(s)ds\right]$$

Then

$$\mathcal{R}_0 = \phi(0) = \int_0^\infty b(a) \exp\left[-\int_0^a \mu(s)ds\right]$$

is the *inherent net reproductive number*

$\phi(\lambda) \searrow$ on $\mathbb{R}$, $\lim_{\lambda\to-\infty} \phi(\lambda) = +\infty$ and $\lim_{\lambda\to\infty} \phi(\lambda) = -\infty$

$\mathcal{R}_0 < 1$ iff the solution λ_0 to $\phi(\lambda) = 1$ satisfies $\lambda_0 < 0$. Also, $\mathcal{R}_0 > 1$ iff $\lambda_0 > 0$

Theorem

Assume sols to M–VF PDE are of the form $n(t,a) = e^{\lambda t} r(a)$. *If* $\mathcal{R}_0 < 1$, *then* $\lim_{t\to\infty} n(t,a) = 0$ *and if* $\mathcal{R}_0 > 1$, *then* $\lim_{t\to\infty} n(t,a) = \infty$