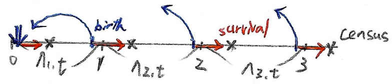
2021. 10. 26 Age-structured population models

$\vec{n}_{t+1} = L^t \vec{n}_0$

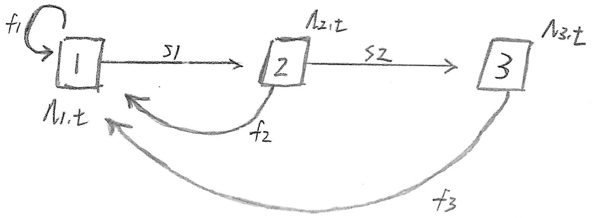
- L: Leslie matrix
- $\vec{n}$: vector of abundances at different ages

Model derivations → Dynamics (linear algebra) → stage-structure models

◎ Model derivation



Start w/ a simple age-structured diagram (birth → survive → census)



- s_i = survival probability from i to $i+1$
- f_i = fecundity of age i individuals

Assumptions:

1. Closed population
2. Age structure! Individuals identical within age class
3. Unlimited resources, growth/death density-independent, BUT age-dependent
4. Discrete growth (partitioned into "age classes")

all give birth to lowest class, no individuals stay at same age

$$\Rightarrow \begin{cases} n_{1,t+1} = f_1 \cdot n_{1,t} + f_2 \cdot n_{2,t} + f_3 \cdot n_{3,t} \\ n_{2,t+1} = s_1 \cdot n_{1,t} \\ n_{3,t+1} = s_2 \cdot n_{2,t} \end{cases} \quad \cdots ①$$

write in vector form: $\vec{n}_t = \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix}$ elements are population size of each age-class

$$\Rightarrow \vec{n}_{t+1} = \begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \end{pmatrix} = \begin{array}{c|c} & \langle from \rangle \\ \hline \langle to \rangle & \begin{pmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix} \end{array} \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix} = L \cdot \vec{n}_t \quad \cdots ②$$

L: Leslie matrix [1945]

※ Recall: Matrix multiplication

a type of transition matrix

compare to $N_t = R^t N_0$ « discrete exponential model »

$$\Rightarrow \vec{n}_t = L^t \vec{n}_0 \quad \text{... ③}$$

◎ Dynamics

What is the long-term dynamics of the Leslie matrix model?

※ Recall: eigenvalues & eigenvectors

eigenvalues

$$M\vec{u} = \lambda \vec{u} \quad \text{... ④}$$

$\lambda \vec{u} = \lambda I \vec{u}$

eigenvectors (vectors whose direction don't change after transformation)

$$\Rightarrow (M - \lambda I)\vec{u} = \vec{0}$$

characteristic equation

$$\Rightarrow \det(M - \lambda I) = 0 \quad \text{... ⑤}$$

e.g. $M = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}$, find eigenvalue & eigenvector ?

characteristic equation

$$\det\begin{pmatrix} 2-\lambda & 4 \\ 0 & 3-\lambda \end{pmatrix} = 0 \Rightarrow (2-\lambda)(3-\lambda) - 4\times 0 = 0$$

$$\Rightarrow \lambda = 2 \lor 3 \ *$$

$\begin{pmatrix} 0 & 4 \\ 0 & 1 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$

when $\lambda = 2$: $\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = 2\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} \Rightarrow \begin{cases} 2u_1 + 4u_2 = 2u_1 \Rightarrow u_2 = 0,\ u_1 = 1 \\ 3u_2 = 2u_2 \end{cases}$

$\begin{pmatrix} -1 & 4 \\ 0 & 0 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$

when $\lambda = 3$: $\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = 3\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} \Rightarrow \begin{cases} 2u_1 + 4u_2 = 3u_1 \Rightarrow u_2 = 1,\ u_1 = 4 \\ 3u_2 = 3u_2 \end{cases}$

$\Rightarrow$ eigenvector for $\lambda = 2$ is $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$, eigenvector for $\lambda = 3$ is $\begin{pmatrix} 4 \\ 1 \end{pmatrix}$ #

※ Recall: eigen decomposition

A diagonalizable matrix with eigenvalue λ & eigenvector $\vec{u}$ can be written as:

$$M = ADA^{-1}, \text{ where } D = \begin{pmatrix} \lambda_1 & 0 & \cdots & 0 \\ 0 & \lambda_2 & \cdots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & 0 & \cdots & \lambda_n \end{pmatrix},\ A = \begin{pmatrix} u_{11} & u_{12} & \cdots & u_{1n} \\ u_{21} & u_{22} & \cdots & u_{2n} \\ \vdots & \vdots & & \vdots \\ u_{n1} & u_{n2} & \cdots & u_{nn} \end{pmatrix} \quad \text{... ⑥}$$

$\vec{u}_1$ $\vec{u}_2$

matrix with eigenvectors as columns

diagonal matrix with eigenvalues as entries

inverse of A ($A \cdot A^{-1} = I$)

e.g. for $M = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}$ with $\lambda = 2, 3$, $\vec{u} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \begin{pmatrix} 4 \\ 1 \end{pmatrix}$

$A = \begin{pmatrix} 1 & 4 \\ 0 & 1 \end{pmatrix}$, $D = \begin{pmatrix} 2 & 0 \\ 0 & 3 \end{pmatrix}$, $A^{-1} = \begin{pmatrix} 1 & -4 \\ 0 & 1 \end{pmatrix}$

$$\underline{M = \begin{pmatrix} 1 & 4 \\ 0 & 1 \end{pmatrix}\begin{pmatrix} 2 & 0 \\ 0 & 3 \end{pmatrix}\begin{pmatrix} 1 & -4 \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}} \ \#$$

- This is useful because: $M^t = (ADA^{-1})^t = \overbrace{A\underbrace{DA^{-1}A}_{I}DA^{-1} \cdots ADA^{-1}}^{t \text{ times}} = AD^tA^{-1}$

$$\Rightarrow \vec{\Lambda}_t = M^t \vec{\Lambda}_0 = AD^tA^{-1}\vec{\Lambda}_0 \quad \ldots (1)$$

general solution for linear recursive equations

$$D^t = \begin{pmatrix} \lambda_1^t & 0 & \cdots & 0 \\ 0 & \lambda_2^t & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \lambda_n^t \end{pmatrix}$$

$$\Rightarrow D^t = \lambda_1^t \begin{pmatrix} 1 & 0 & \cdots & 0 \\ 0 & \left(\frac{\lambda_2}{\lambda_1}\right)^t & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \left(\frac{\lambda_n}{\lambda_1}\right)^t \end{pmatrix}$$

, with λ_1 being dominate eigenvalue, $\left(\frac{\lambda_i}{\lambda_1}\right)^t \to 0$ as t is large

largest in absolute value

$$\approx \lambda_1^t \begin{pmatrix} 1 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix}$$

$$\Rightarrow AD^t \approx \begin{pmatrix} u_{11} & u_{12} & \cdots & u_{1n} \\ u_{21} & u_{22} & \cdots & u_{2n} \\ \vdots & \vdots & & \vdots \\ u_{n1} & u_{n2} & \cdots & u_{nn} \end{pmatrix} \cdot \lambda_1^t \begin{pmatrix} 1 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix} = \lambda_1^t \begin{pmatrix} u_{11} & 0 & \cdots & 0 \\ u_{21} & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ u_{n1} & 0 & \cdots & 0 \end{pmatrix}$$

$$\Rightarrow AD^tA^{-1} \approx \lambda_1^t \begin{pmatrix} u_{11} & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ u_{n1} & 0 & \cdots & 0 \end{pmatrix}\begin{pmatrix} v_{11} & \cdots & v_{1n} \\ v_{21} & \cdots & v_{2n} \\ \vdots & & \vdots \\ v_{n1} & \cdots & v_{nn} \end{pmatrix} = \lambda_1^t \begin{pmatrix} u_{11}v_{11} & u_{11}v_{12} & \cdots & u_{11}v_{1n} \\ u_{21}v_{11} & u_{21}v_{12} & \cdots & u_{21}v_{1n} \\ \vdots & \vdots & & \vdots \\ u_{n1}v_{11} & u_{n1}v_{12} & \cdots & u_{n1}v_{1n} \end{pmatrix}_{n \times n}$$

with elements v_{ij}

$$\Rightarrow AD^tA^{-1}\vec{\Lambda}_0 \approx \lambda_1^t \begin{pmatrix} u_{11}(v_{11}\Lambda_{1,0} + v_{12}\Lambda_{2,0} + \cdots v_{1n}\Lambda_{n,0}) \\ u_{21}(v_{11}\Lambda_{1,0} + v_{12}\Lambda_{2,0} + \cdots v_{1n}\Lambda_{n,0}) \\ \vdots \\ u_{n1}\underbrace{(v_{11}\Lambda_{1,0} + v_{12}\Lambda_{2,0} + \cdots v_{1n}\Lambda_{n,0})}_{C} \end{pmatrix}$$

C, constant, some initial state

$$\Rightarrow \underline{\vec{\Lambda}_t \approx C \cdot \lambda_1^t \cdot \vec{u}_1} \quad \ldots (8)$$

with long-term, dynamics grow at a rate λ_1, which is the dominant eigenvalue, reaching age distribution $\vec{u}$

- For leslie matrix, the long-term dynamics are determined by its dominant eigenvalue & associated eigenvector
  - λ_1 → finite rate of increase (analogous to discrete exponential model)
  - $\vec{u_1}$ → stable stage distribution

total $N = \Sigma \vec{n_i}$ is growing exponentially with a fix rate, but ratio between age classes are fixed

@ Back to the Leslie matrix

$$L = \begin{pmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix}$$, its characteristic equation: $\det \begin{pmatrix} f_1-\lambda & f_2 & f_3 \\ s_1 & -\lambda & 0 \\ 0 & s_2 & -\lambda \end{pmatrix} = 0$

$$\Rightarrow (f_1-\lambda)\lambda^2 + 0 \times 0 \times f_2 + s_2 s_1 f_3 - 0(-\lambda) f_3 - 0 \cdot s_2 (f_1 - \lambda) - (-\lambda) s_1 f_2 = 0$$

$$\Rightarrow -\lambda^3 + f_1 \lambda^2 + s_1 f_2 \lambda + s_1 s_2 f_3 = 0$$

$$\Rightarrow 1 - f_1 \lambda^{-1} - s_1 f_2 \lambda^{-2} - s_1 s_2 f_3 \lambda^{-3} = 0$$

survivalship $= \frac{N_i}{N_0}$

define $l_i = s_1 \times s_2 \times \dots s_{i-1}$ = survival from birth to age i
with $l_1 = 1$

$$\Rightarrow l_3 f_3 \lambda^{-3} + l_2 f_2 \lambda^{-2} + l_1 f_1 \lambda = 1 \quad \text{...⑨ characteristic equation}$$

in fact, the general characteristic equation for n-dimension Leslie is

$$\sum_{i=1}^{n} l_i f_i \lambda^{-i} = 1 \quad \text{...⑩} \quad \text{« Euler-Lotka equation »}$$

use this function to find eigenvalue of Leslie matrix (trial-and-error)
(numerical solver)

Moreover, the stable age distribution is $\vec{u_1} = \begin{pmatrix} 1 \\ l_2 \lambda^{-1} \\ l_3 \lambda^{-2} \\ \vdots \\ l_n \lambda^{-(n-1)} \end{pmatrix}$ ...⑪

$$\because \vec{u}_{1,n-1} \times s_{n-1} = \vec{u}_{1,n} \times \lambda \Rightarrow \vec{u}_{1,n} = \frac{1}{\lambda} \cdot \vec{u}_{1,n-1} \cdot s_{n-1}$$
$$= \frac{1}{\lambda} \cdot \left[\frac{1}{\lambda} \cdot \vec{u}_{1,n-2} \cdot s_{n-2} \right] \cdot s_{n-1} = \vec{u}_{1,1} \cdot l_n \lambda^{-(n-1)}$$

for $\lambda > 1$, Always a pyramid

• Properties of the eigenvalue of Leslie matrix :

« Descartes' rule of signs »

The maximum possible number of positive real roots is determined by the number of times the polynomial coefficients change in sign

e.g. $x^3 - 2x^2 + 3x - 1 = 0$ has at max 3 positive real roots

for Leslie, $\left(\sum_{i}^{n} l_i f_i \lambda^{-i}\right) - 1 = 0 \Rightarrow$ Maximum one positive real root

« Perron - Frobenius theorem »

An irreducible non-negative matrix (almost all Leslie matrix) always has a real, positive eigenvalue. The absolute value of all other eigenvalues do not exceed that of this real-valued eigenvalue (i.e. it is the dominant eigenvalue). Moreover, there is a corresponding eigenvector with positive coordinates

$\Rightarrow$ The λ_1 & $\vec{u}_1$ of Leslie is biologically interpretable !

◎ Stage - structured models

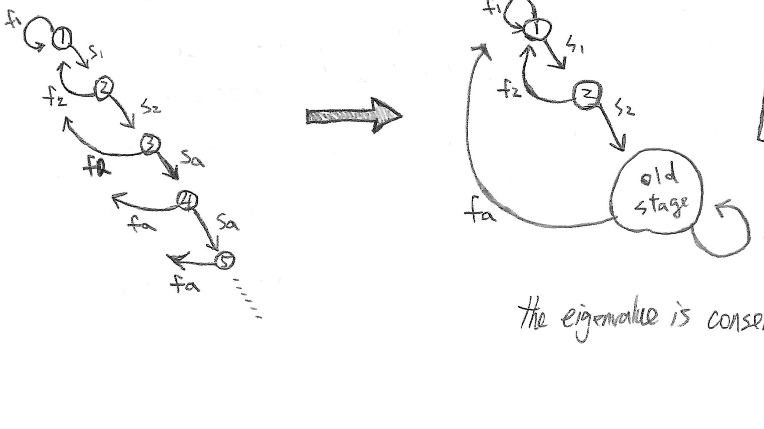
as long as CONSTANT parameters

Everything that we taught today also applies (i.e, eigenvalue & eigenvector)

1. How to deal with unknown age limit ?

① assume very large Leslie matrix

② age lumping into " Old adult stage" if old ages have identical S & f

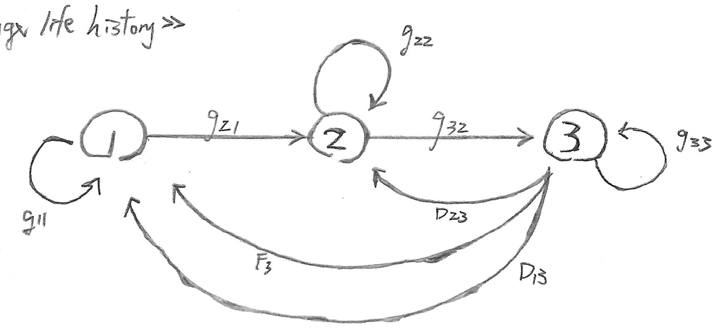


$$\begin{bmatrix} f_1 & f_2 & f_a \\ S_1 & 0 & 0 \\ 0 & S_2 & S_a \end{bmatrix}$$

the eigenvalue is conserved

2. Use size or stage as classes

« Sponge life history »



« Lefkovitch matrix »

$$\begin{array}{cc} & \langle \text{from} \rangle \\ \langle \text{to} \rangle & \begin{bmatrix} g_{11} & 0 & F_3+D_{13} \\ g_{21} & g_{22} & D_{23} \\ 0 & g_{32} & g_{33} \end{bmatrix} \end{array} \Rightarrow \begin{array}{l} \text{dominant eigenvalue} \\ \text{associated eigenvector} \end{array}$$

e.g. $M = \begin{pmatrix} 0.3 & 0.2 & 0.4 \\ 0.2 & 0 & 0.2 \\ 0.4 & 0.2 & 0.3 \end{pmatrix}$ get λ_1 & eigenvector

$\Rightarrow$ 10M's eigenvalue = 10 × M's eigenvalue

$$\downarrow \begin{pmatrix} 3-\lambda & 2 & 4 \\ 2 & -\lambda & 2 \\ 4 & 2 & 3-\lambda \end{pmatrix} \Rightarrow -\lambda(3-\lambda)^2 + 16 + 16 - (-16\lambda) - 4(3-\lambda) - 4(3-\lambda) = 0$$

$$\Rightarrow \lambda^3 - 6\lambda^2 - 15\lambda - 8 = 0$$

$$\Rightarrow (\lambda-8)(\lambda+1)(\lambda+1) = 0$$

$$\Rightarrow M\text{'s } \lambda = 0.1 \times 10M\text{'s } \lambda \rightarrow \underline{8} \vee -1 \vee -1$$

$$\downarrow \underline{\underline{0.8}}\ \#$$

$$\begin{pmatrix} 3 & 2 & 4 \\ 2 & 0 & 2 \\ 4 & 2 & 3 \end{pmatrix}\begin{pmatrix} a \\ b \\ c \end{pmatrix} = 8\begin{pmatrix} a \\ b \\ c \end{pmatrix} \Rightarrow \begin{cases} 3a + 2b + 4c = 8a \\ 2a + 2c = 8b \\ 4a + 2b + 3c = 8c \end{cases}$$

$$\Rightarrow \vec{u} = \begin{pmatrix} a \\ b \\ c \end{pmatrix} = \underline{\underline{\begin{pmatrix} 1 \\ \frac{1}{2} \\ 1 \end{pmatrix}}}\ \#$$