Discrete-time population growth models
II
Age, stage and size-structure

Structured models

A **structured model** is one where one (or more) variable is "split" to describe the evolution of a characteristic or trait. E.g., if $N(t)$ is population at time t, then

$$N_i(t), \quad i \in \mathcal{I}$$

represents the number of individuals in the population who have characteristic i in the (potentially infinite) set $\mathcal{I}$ at time t

Age, size and stage structure

Age: influences the capacity for reproduction, survival

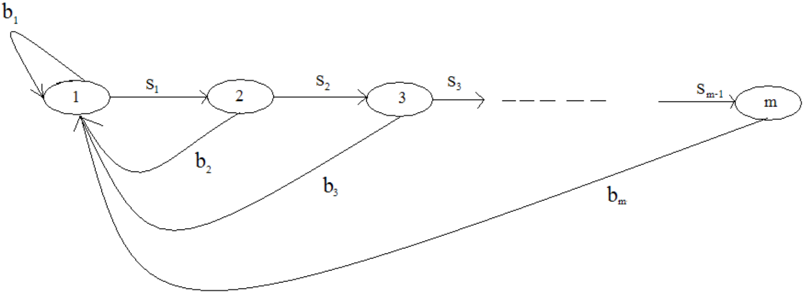
Size: influences reproductive capacity, survival, intra or interspecific competition

Stage: some species have very marked stages (larva, pupae, juveniles, ec.)

Age-structure – The Leslie matrix

m age groups, m last reproductive age. From t to $t+1$, individuals age from i to $i+1$: time interval coincides with age interval

- $x_i(t)$ number of females in i^{th} age group at time t
- b_i average number of newborn females produced by one female in i^{th} age group that survive through the time interval in which they were born, $b_i \geq 0$
- s_i fraction of i^{th} age group that lives to $(i+1)st$ age, $0 < s_i \leq 1$


b1
1
S1
2
S2
3
S3
Sm-1
m
b2
b3
bm

$$
\begin{aligned}
x_1(t+1) &= b_1 x_1(t) + b_2 x_2(t) + b_3 x_3(t) + \dots b_m x_m(t) \\
x_2(t+1) &= s_1 x_1(t) \\
x_3(t+1) &= s_2 x_2(t) \\
&\vdots \\
x_m(t+1) &= s_{m-1} x_{m-1}(t)
\end{aligned}
$$

Using matrix notation, if $X(t) = (x_1(t), \ldots, x_m(t))^T$,

$$X(t+1) = \begin{pmatrix} b_1 & b_2 & \ldots & b_{m-1} & b_m \\ s_1 & 0 & \ldots & 0 & 0 \\ 0 & s_2 & \ldots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \ldots & s_{m-1} & 0 \end{pmatrix} X(t)$$

i.e.,

$$X(t+1) = LX(t)$$

where L is a **Leslie matrix**

As before,

$$\begin{aligned} X(1) &= LX(0) \\ X(2) &= LX(1) \\ &= L\left(LX(0)\right) \\ &= L^2X(0) \end{aligned}$$

and in general

$$X(t) = L^tX(0)$$

Perron-Frobenius theorem

Theorem

If M is a nonnegative primitive matrix, then:

- *M has a positive eigenvalue λ_1 of maximum modulus.*
- *λ_1 is a simple root of the characteristic polynomial.*
- *for every other eigenvalue λ_i, $\lambda_1 > \lambda_i$ (it is strictly dominant)*
- $$\min_i \sum_j m_{ij} \leq \lambda_1 \leq \max_i \sum_j m_{ij}$$
  $$\min_j \sum_i m_{ij} \leq \lambda_1 \leq \max_j \sum_i m_{ij}$$
- *row and column eigenvectors associated with λ_1 are $\gg 0$.*
- *the sequence M^t is asymptotically one-dimensional, its columns converge to the column eigenvector associated with λ_1; and its rows converges to the row eigenvector associated with λ_1.*

- Leslie matrix is a nonnegative matrix
- Leslie matrix is irreductible if $b_m \neq 0$

If we have this, then Frobenius Theorem gives sufficient conditions that guarantee Leslie matrix has 1 positive strictly dominant eigenvalue

- If the Leslie matrix satisfies $L^p > 0$ for some positive integer p, then L is primitive

If we have this, then Frobenius Theorem $\Rightarrow$ L has a unique strictly dominant eigenvalue λ_1 satisfying $|\lambda_1| > |\lambda_i|$, for $j \neq 1$, that is positive. Associated with the strictly dominant eigenvalue λ_1 is a positive eigenvector V_1, a **stable age distribution**

Assume L irreductible and primitive and m eigenvectors form a linearly independent set; then the solution to

$$X(t+1) = LX(t)$$

can be written

$$X(t) = L^t X(0) = \sum_{i=1}^{m} c_i \lambda_i^t V_i$$

where λ_1 is the strictly dominant eigenvalue. Dividing the solution by λ_1^t gives

$$\frac{X(t)}{\lambda_1^t} = \frac{L^t X(0)}{\lambda_1^t} = c_1 V_1 + \frac{c_2 \lambda_2^t}{\lambda_1^t} V_2 + \cdots + \frac{c_m \lambda_m^t}{\lambda_1^t} V_m$$

As $|\lambda_i/\lambda_1| < 1$, $(\lambda_i/\lambda_1)^t \to 0$ as $t \to +\infty$. Thus

$$\lim_{t\to+\infty} \frac{X(t)}{\lambda_1^t} = \lim_{t\to+\infty} \frac{L^t X(0)}{\lambda_1^t} = c_1 V_1$$

So after many generations

$$X(t) = L^t X(0) = c_1 \lambda_1^t V_1$$

Population size either increases $(\lambda_1 > 1)$ or decreases $(\lambda_1 < 1)$ geometrically as t increases

Population distribution

$$\frac{X(t)}{\lambda_1^t}$$

approaches a constant multiple of the eigenvector V_1

Explicit expression for V_1 in the case of a Leslie matrix:

$$V_1 = \begin{pmatrix} 1 \\ \dfrac{s_1}{\lambda_1} \\ \vdots \\ \dfrac{s_1 s_2 \dots s_{m-2}}{\lambda_1^{m-2}} \\ \dfrac{s_1 s_2 \dots s_{m-1}}{\lambda_1^{m-1}} \end{pmatrix}$$

Characteristic equation for the Leslie matrix satisfies $\det(L - \lambda I) = 0$ or

$$\det \begin{pmatrix} b_1 - \lambda & b_2 & \dots & b_{m-1} & b_m \\ s_1 & -\lambda & \dots & 0 & 0 \\ 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1} & -\lambda \end{pmatrix} = 0$$

or

$$p(\lambda) = \lambda^m - b_1\lambda^{m-1} - b_2 s_1 \lambda^{m-2} - \dots - b_m s_1 s_2 s_3 \dots s_{m-1} = 0$$

From Descarte's Rule, since there is only one change in sign in the polynomial, $p(\lambda)$ has one positive real root, that is the dominant eigenvalue λ_1

How is the dominant eigenvalue λ_1: $\lambda_1 > 1$ or $\lambda_1 < 1$?

- $\lim_{\lambda \to \infty} p(\lambda) = \infty$
- $p(0) < 0$
- $p(\lambda)$ crosses the positive $\lambda-$axis only once at λ_1

then

- $\lambda_1 > 1 \Leftrightarrow p(1) < 0$
- $\lambda_1 < 1 \Leftrightarrow p(1) > 0$

where $p(1) = 1 - b_1 - b_2 s_1 - b_3 s_1 s_2 - \cdots - b_m s_1 s_2 s_3 \ldots s_{m-1}$, and $p(1) = 1 - R_0$. Hence

- $\lambda_1 > 1 \Leftrightarrow 1 < R_0$
- $\lambda_1 < 1 \Leftrightarrow 1 > R_0$

Definition

The reproductive number R_0 is the average number of offspring produced by an individual in its lifetime:

$$R_0 = b_1 + b_2 s_1 + b_3 s_1 s_2 + \cdots + b_m s_1 s_2 \ldots s_{m-1}$$

where each term represent the average number of offsprings produced by individuals of age i.

- $R_0 < 1$ individuals not fully replacing themselves, population shrinking
- $R_0 = 1$ individual exactly replacing themselves, population size stable
- $R_0 > 1$ individuals more than replacing themselves, population growing

Theorem

Assume the Leslie matrix L is irreducible and primitive. The characteristic polynomial of L i given by

$$p(\lambda) = \lambda^m - b_1\lambda^{m-1} - b_2 s_1 \lambda^{m-2} - \cdots - b_m s_1 s_2 s_3 \ldots s_{m-1} = 0.$$

L has a strictly dominant eigenvalue $\lambda_1 > 0$ with:

- $\lambda_1 = 1$ *if and only if* $R_0 = 1$,
- $\lambda_1 < 1$ *if and only if* $R_0 < 1$,
- $\lambda_1 > 1$ *if and only if* $R_0 > 1$,

where R_0 is the inherent reproductive number defined by

$$R_0 = b_1 + b_2 s_1 + b_3 s_1 s_2 + \cdots + b_m s_1 s_2 \ldots s_{m-1}.$$

In addition the stable age distribution V_1 satisfies

$$V_1 = \left(1, \frac{s_1}{\lambda_1}, \ldots, \frac{s_1 s_2 \ldots s_{m-2}}{\lambda_1^{m-2}}, \frac{s_1 s_2 \ldots s_{m-1}}{\lambda_1^{m-1}}\right)^T$$

What about density-dependent processes?

The matrix

$$L = \begin{pmatrix} b_1 & b_2 & \dots & b_{m-1} & b_m \\ s_1 & 0 & \dots & 0 & 0 \\ 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1} & 0 \end{pmatrix}$$

is constant. What happens if L is

$$L_t := \begin{pmatrix} b_1(X(t)) & b_2(X(t)) & \dots & b_{m-1}(X(t)) & b_m(X(t)) \\ s_1(X(t)) & 0 & \dots & 0 & 0 \\ 0 & s_2(X(t)) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1}(X(t)) & 0 \end{pmatrix}$$

???

Ergodic theory

Measure-theoretic consideration of dynamical systems: a system is *ergodic* if its behaviour is the same when averaged over time and space

Ergodic theorems in demography

Theorem (Golubitsky, Keeler & Rotschild, 1975)

Suppose that T_k is a sequence of nonnegative primitive matrices, and that $T_k \to T$ as $k \to \infty$, where T is also nonnegative and primitive. If e is the Perron-Frobenius eigenvector of T satisfying $\mathbb{1}^T e = 1$ and $\xi_{k+1} = T_k \xi_k$ is a sequence starting with $\xi_0 \geq 0$ and $\xi_0 \neq 0$, then

$$\frac{\xi_k}{\mathbb{1}^T \xi_k} \to e, \quad k \to \infty$$